

## Primate Evolution: Evidence From the Fossil Record, Comparative Morphology, and Molecular Biology

PHILIP D. GINGERICH  
*Museum of Paleontology, The University of Michigan, Ann Arbor,  
Michigan 48109*

**KEY WORDS** Primate evolution, Phylogeny, Stratophenetics, Cladistics, Molecular clocks

**ABSTRACT** Our understanding of primate evolution is ultimately based on patterns of phyletic relationship and morphological change documented in the fossil record. Stratophenetic interpretation of living and fossil primates yields an objective alternative to the arbitrary *scala naturae* assumed implicitly in traditional comparative biology. Fossils provide an outline of primate history constraining comparative analyses incorporating taxa and morphological characteristics not represented in the fossil record. Extant taxa without known prehistoric relatives may be interpolated into this outline using deductive cladistic analysis of morphological characteristics and overall molecular similarity. Cladistic analysis provides a method for evaluating the relative strength of stratophenetic links between taxa. The phyletic node connecting Anthroproidea-Adapoidea-Lemuroidea is analyzed here as an example: the link between Eocene Adapoidea and primitive Anthroproidea appears stronger than that between Adapoidea and Lemuroidea because it is based on shared-derived rather than shared-primitive characteristics. Full integration of molecular results with morphological information requires a better understanding of rates of molecular change over geological time. Rates of molecular evolution can be studied using paleontologically documented divergence times for Prosimii-Anthroproidea (ca. 55 m.y.B.P.), Platyrrhini-Catarrhini (ca. 40 m.y.B.P.), and Hominoidea-Cercopithecoidea (ca. 25 m.y. B.P.). Immunological distances combined with these divergence times indicate that primate albumin, widely used as a molecular clock in primatology, has evolved nonlinearly over geological time. A nonlinear albumin clock yields divergence times of about 9 million years before present for humans and chimpanzees, and about 13 million years before present for humans and orangutans (compared with 4 m.y.B.P. and 7 m.y.B.P., respectively, based on a linear albumin clock). Apparent slowing of albumin evolution over time remains to be fully explained. Other proteins and nucleic acids may provide better clocks. Cladistic analysis of morphological characteristics and comparative study of molecular structure, interpreted in the context of the fossil record, promise to contribute to a more complete understanding of primate evolution.

Evolution is a complex subject encompassing the history of life and its governing processes. Our understanding of evolution is based on interpretation of patterns of diversity, ecology, behavior, visible morphology, and invisible molecular structure that have changed and continue to change through time. The widely varying organic forms that surround us are a product of diversification over hundreds of millions of years of geological time. Evolutionary time, on a geological scale, is the

domain of paleontology, and calibration of rates for numerous important processes depends on evidence in the fossil record. The fossil record is necessarily the ultimate test of many systematic and evolutionary hypotheses. It is less complete for some groups of organisms than one would hope, and hypotheses about their evolution are consequently untested and untestable. Primates, and mammals in general, have a relatively dense and continuous fossil record permitting hypotheses of relationships and rates to be explored in more depth than would otherwise be possible.

Different approaches to evolution and different scales of inquiry yield patterns appropriate for understanding different processes. Some approaches answer specific questions, while others are more general. Some approaches ultimately fail to answer any questions. There is a disturbing tendency in modern evolutionary studies for advocates of one narrow viewpoint to see their approach as the only possible source of information bearing on a question, but this is usually related to limited understanding of the question itself. Here I shall attempt to relate diverse patterns from paleontology, comparative anatomy, and molecular biology to the study of primate evolution, concluding that paleontologists, cladists, and molecular systematists can learn much more working together than any one group can learn working alone.

This essay is not an exhaustive review. It is intended rather to illustrate the interdependence of paleontology, comparative morphology, and molecular systematics. The fossil record provides an outline of primate phylogeny that can be augmented and refined using deductive cladistic methods. Recent taxa can be interpolated into this augmented phylogeny on the basis of their molecular distance from taxa of known phylogenetic relationship. The final result should be a comprehensive phylogeny based on all evidence of relationship. Such a phylogeny can be used to interpret the evolutionary history and comparative biology of all morphological or behavioral characteristics of the organisms being studied. A particular group of special interest, our own order Primates, is used to illustrate these points.

#### FOSSIL RECORD AND PRIMATE PHYLOGENY: STRATOPHENETICS

The concept of evolution as organic transmutation is a product of 18th- and 19th-century paleontology and biostratigraphy. Evolution was first used in this modern sense by Charles Lyell in 1832. Patterns of organic diversity and morphology preserved in the geological record are the proof of evolution. It is an established fact that life has a history, yet we have much to learn about phylogeny—the course of evolution through time, and we have much to learn about evolutionary processes—how evolution works.

Fossils were necessary for development of the modern concept of evolution, but clearly they were not sufficient. Darwin's *Origin of Species*, first published in 1859, builds on paleontological evidence, but it is not a treatise on fossils nor on the fossil record. Rather, Darwin combined observations on variation and inheritance in living populations with an awareness of finite resources and artificial selection to explain present organic diversity as a product of natural selection over long intervals of time. In recent years, the inquiry has broadened, with evolutionary biologists now exploring structure and diversity on a molecular level as well as organismal, species, and higher levels.

In the century and a half since Cuvier first described a fossil primate, the fossil record has improved dramatically. What does this tell us about primate phylogeny—about the diversification and genealogical relationships of primates in the past? A holistic approach to primate history must consider the distribution of species in time, space, and form. Reductionists sometimes claim that morphology is the only "biological" attribute of organisms, but existence in time and space are also intrinsic attributes of life. Primates, like other organisms, are appropriately considered in terms of their age and geographical distribution as well as their form (Fig. 1).

We live in the present, and the diversity of primates is best known (although probably not greatest) in the present. Hence, the present is a logical starting point for reconstructing primate history. Primatologists generally agree in recognizing six major groups of living primates: Hominoidea (apes and humans), Cercopithecoidea

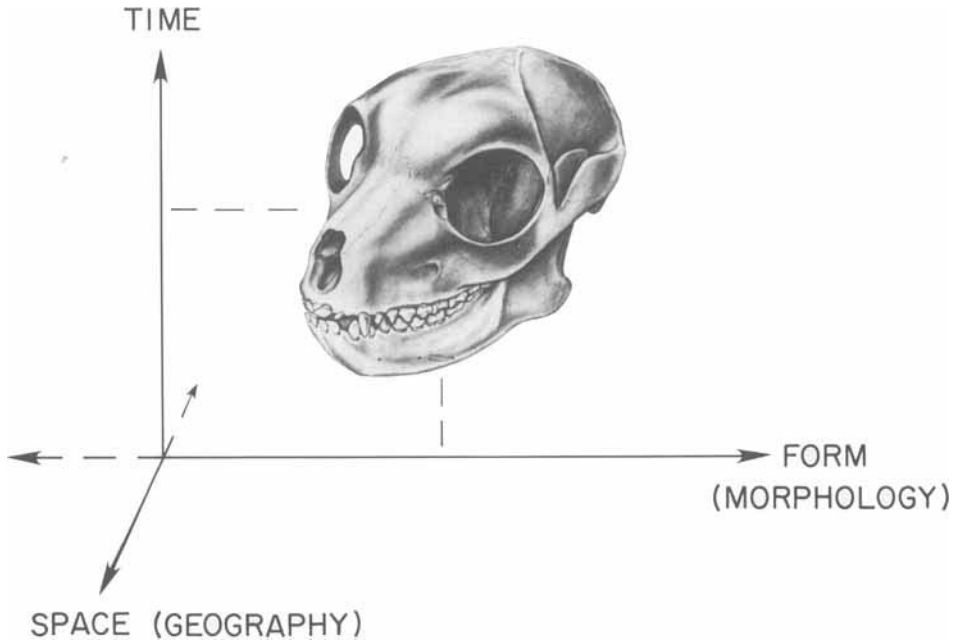


Fig. 1. Skull of middle Eocene adapoid *Smilodectes gracilis* from western North America. Geological age and geographic location are intrinsic properties of fossils, coordinate in importance with their morphology. Time, space, and form are essential attributes of all organisms, living and fossil. Neontological studies necessarily restrict comparisons to Recent animals, while paleontological studies incorporate time as well as space and form. Evolution, as a process and as an historical phenomenon, is necessarily studied in the context of time.

(Old World monkeys), Ceboidea (New World monkeys), Lorisioidea (lorises, bush babies, etc.), Lemuroidea (lemurs, sifakas, etc.), and Tarsioidea (tarsiers). A seventh group, Tupaioida (tree shrews), is sometimes included as well.

To speak or write about primates, it is necessary to adopt some classification of overall diversity within the order. While most authors (e.g., Napier and Napier, 1967; Simons, 1972; Szalay and Delson, 1979) would agree in recognizing the six (or seven) superfamilies of extant primates listed above, there is less agreement about how these superfamilies should be grouped and extinct forms incorporated in a general classification. The conservative classification employed here is listed in Table 1 (it is conservative both in being traditional and familiar, and in employing a limited number of hierarchical levels). I emphasize that groups recognized in Table 1 are often paraphyletic in a cladistic sense. While a classification should be consistent with phylogeny in a general way, there are a number of practical reasons why classifications are not explicit verbal expressions of phylogeny (Gingerich, 1979b): phylogeny is sometimes poorly known, even moderately complex phylogenies cannot be expressed in words, asymmetrical phylogenies lead to an excessively complex hierarchy of levels, and familiar groupings are based on adaptive grades as well as phylogeny.

Classification is different from phylogeny. The order Primates dates from publication of the definitive 10th edition of Linnaeus's *Systema Naturae* in 1758. Fossil primates were unknown to Linnaeus, and it is clear that fossils and evolutionary relationships are not required for establishment of successful classifications of primates or other organisms. It is important in reading the following discussion (and much of the literature on primate evolution) to remember that classifications are abstractions that incorporate some evolutionary relationships, but never reflect all that is known about underlying evolutionary patterns. The primary objective of classification is communication, which always requires some organization and sim-

TABLE 1. Traditional classification of the order Primates<sup>1</sup>

Classification		Known temporal distribution	Geographic range
Order Primates			
Suborder Anthropoidea (Simii)			
Infraorder Catarrhini			
Superfamily Hominoidea	(1)	Oligocene–Recent	Africa, Europe, Asia (worldwide today)
Superfamily Cercopithecoidea	(2)	Early Miocene–Recent	Africa, Europe, Asia
Infraorder Platyrrhini			
Superfamily Ceboidea	(3)	Early Oligocene–Recent	South America
Suborder Prosimii			
Infraorder Lemuriformes			
Superfamily Adapoidea		Early Eocene–late Miocene	Africa, Europe, Asia, North America
Superfamily Lorisoidea	(4)	Early Miocene–Recent	Africa, Asia
Superfamily Lemuroidea	(5)	Pleistocene–Recent	Africa (Madagascar)
Infraorder Tarsiiformes			
Superfamily Tarsiioidea	(6)	Early Eocene–Recent	Europe, Asia
Suborder Praesimii			
Infraorder Tupaiiformes			
Superfamily Tupaiioidea	(7)	Late Miocene–Recent	Asia
Infraorder Plesiadapiformes <sup>2</sup>			
Superfamily Plesiadapoidea <sup>2</sup>		Middle Paleocene–late Eocene	North America, Europe
Superfamily Microsypoidea <sup>2</sup>		Early Paleocene–late Eocene	North America, Europe

<sup>1</sup>Living superfamilies are numbered in parentheses for emphasis. Known temporal distribution and geographic ranges are listed at right. Subordinal grouping corresponds to primate grades 1–3 of MacPhee et al. (1983).

<sup>2</sup>Taxonomic group without living representatives.

plification to be effective. Phylogeny and evolution, not classification, are the subjects of this paper, but classification necessarily enters the discussion and one must be careful to distinguish organization of the names we give to groups of animals from relationships of the groups themselves.

Given the six (or seven) superfamilial groups of modern primates, we can ask what happens as each of these is traced backward through successively earlier epochs of the Cenozoic. Convergence of morphology as groups are traced back in time is evidence of common ancestry, and we can use this evidence to infer how primate superfamilies are related to each other. This approach to the study of phylogeny is as old as evolution itself, and it is often labeled the "evolutionary" or "electric" approach to systematics. I coined the term *stratophenetics* (Gingerich, 1976) for this approach principally to distinguish it from *cladistics*, a narrower comparative method that is also evolutionary in principle, but is sometimes based purely on morphology with little regard for time (see below).

Stratophenetics recognizes that modern organisms can be rationally grouped on the basis of overall similarity (i.e., "phenetic" resemblance in form; geographical distribution may be included as well). Fossils in the geological record can be treated in the same way, combining species within stratigraphic intervals into groups based on overall similarity in morphology (and geographical distribution). Stratigraphic superposition provides evidence of temporal ordering crucial for interpreting strata and contained fossils in light of what came before and after. Stratophenetics is empirical and, where the fossil record is reasonably dense, at the scale of a given study (here the superfamilial level), similar taxa in one time interval may be linked phenetically to those in adjacent or nearby intervals to provide a minimum spanning tree of living and fossil primates, taking into account their ages, geographical distributions, and morphology (Gingerich, 1979a,b). At the same time, the empirical nature of stratophenetics, with emphasis on the distribution of evidence, is useful in identifying where evidence is lacking (see below).

An outline of primate phylogeny is sketched in Figure 2, based on phenetic grouping of fossil and living primates within intervals from the Paleocene to the Recent. These groups are linked in turn to other similar forms in adjacent or nearby

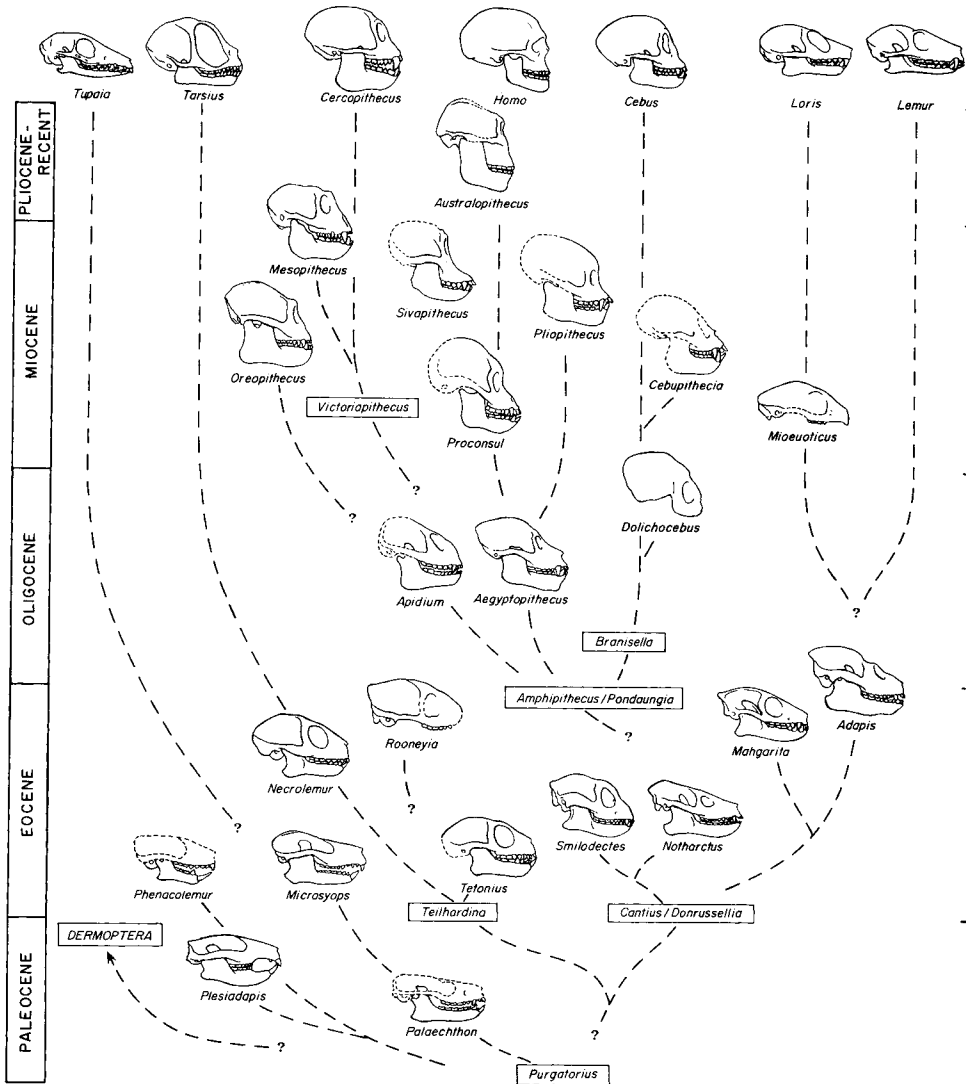


Fig. 2. Stratophenetically constructed outline of primate phylogeny. Form is arrayed on the abscissa, and the ordinate encompasses Cenozoic time. Superfamilies of living primates (Tupaioidea, Tarsiioidea, Cercopithecoidea, Hominoidea, Ceboidea, Lorisioidea, and Lemuroidea) are grouped at the top of the chart. Representative fossil primates known from partial or complete skulls are ordered in time and form relative to other known fossils. Abundant but less complete dental remains support the pattern of linking shown here, but little is known of the evolutionary history of Tupaioidea or Lorisioidea before the Miocene, Tarsiioidea from the Oligocene to Recent, or Lemuroidea before the Pleistocene. Relationships of Eocene Adapoidea (including *Cantius*, *Smilodectes*, *Notharctus*, *Mahgarita*, and *Adapis* shown here) to Anthropoidea and Lemuroidea are discussed in the text; deductive cladistic analysis indicates that characteristics shared by Anthropoidea and Adapoidea are predominantly derived, whereas characteristics shared by Lemuroidea and Adapoidea are largely primitive. Lemuroidea and Lorisioidea may have diverged from a *Cantius*- or *Donrussellia*-like ancestor as early as the late Paleocene or earliest Eocene, and *Adapis* may or may not be a part of this clade. Note that Cercopithecoidea and Hominoidea converge near the Oligocene-Miocene boundary (ca. 25 million years before present [m.y.B.P.], these groups together converge with Ceboidea near the Eocene-Oligocene boundary (ca. 40 m.y.B.P.), and all three anthropoid superfamilies together converge with Tarsiioidea and hypothesized ancestral Lorisioidea and Lemuroidea near the Paleocene-Eocene boundary (ca. 55 m.y.B.P.). Tupaioidea, if correctly included in Primates, probably diverged from primitive plesiadapiform primates near the beginning of the Paleocene.

intervals. The ordinate in the bivariate diagram is time, considered at the scale of epochs, and the abscissa is form, expressed taxonomically at a superfamilial level. A third dimension, representing geographical distribution, could be added by lifting groups of primates from each epoch out of the page by a distance corresponding, say, to positions of the continents on the earth's surface. Any fully representative quantitative study would require multivariate treatment, and the present version is purposely simplified.

The stratophenetic outline of primate phylogeny shown in Figure 2 indicates that primates have undergone a number of successive radiations through the course of Cenozoic time. The first radiation, beginning in the early Paleocene with *Purgatorius*, or a *Purgatorius*-like structural ancestor, gave rise to a diversity of specialized rodentlike forms (*Plesiadapis*, *Phenacolemur*, *Microsypops*, etc.). Tree shrews (Tupaioidea) may be living representatives of the *Purgatorius*-like stem giving rise to all later primates. Plesiadapiformes, like Tupaiiformes, lack diagnostic specializations of more advanced primates of modern aspect, and there is some reasonable doubt about whether they belong in Primates at all. Nevertheless, Plesiadapiformes are most similar to Tarsiiformes and Lemuriformes among Eocene mammals, supporting their inclusion in this order, broadly defined.

A second radiation of primates, beginning in the early Eocene, features two dentally similar stem genera, *Teilhardina* and *Cantius*. *Teilhardina* apparently gave rise to a large radiation of tarsierlike Omomyidae (including *Tetonius*, *Necrolemur*, etc.) in the Eocene, and *Teilhardina* or a similar form ultimately probably gave rise to living *Tarsius*. *Cantius*, on the other hand, gave rise to a large radiation of lemurlike Adapidae in the Eocene (including *Notharctus*, *Adapis*, etc.). Adapids combine a suite of dental characteristics seen in later ceboid, cercopithecoid, and hominoid primates with other features of the dentition, basicranium, and postcranial skeleton shared by lemuroids and lorisooids. Omomyids and adapids differ in the form of their incisor and canine teeth, and also in basicranial structure and postcranial skeletal anatomy.

Omomyidae resemble more primitive plesiadapiform primates dentally and in some basicranial structures, and I originally thought this might be an indication of close relationship (Gingerich, 1976; Gingerich and Schoeninger, 1977). Recent fieldwork in Wyoming bearing on the origin of early Eocene primates of modern aspect indicates that there is a substantial faunal turnover at the Paleocene-Eocene boundary, with primates of modern aspect appearing as immigrants (Rose, 1981). Consequently, there is now less reason to expect faunal continuity across this boundary and less reason to expect the ancestors of Eocene Omomyidae to be preserved in Paleocene faunas sampled to date. In addition, newly discovered specimens of early *Cantius*, *Donrussellia*, and *Teilhardina* indicate that it is difficult to distinguish the most primitive Adapidae and Omomyidae. Thus Omomyidae probably represent a distinct tarsiiform radicle within the prosimian radiation rather than part of the praesimian plesiadapiform radiation (Gingerich, 1981).

The oldest certain representatives of higher primates (Anthropoidea) are Oligocene *Apidium* and *Aegyptopithecus*, known from partial skulls and extensive postcranial remains found in the Fayum Province of Egypt. *Amphipithecus* and *Pondaungia* from the late Eocene of South Asia (and *Oligopithecus* from the Oligocene of Egypt) are known only from partial dentitions, but these show features of both Adapidae and primitive Anthropoidea (Szalay, 1970; Simons, 1971; Ba Maw et al., 1979), linking the earliest anthropoids to a probable adapid origin (see Gingerich, 1980, for full discussion). Another primitive anthropoid, *Branisella*, is known from the early Oligocene of Bolivia (Hoffstetter, 1969), indicating that Ceboidea have inhabited South America since at least early Oligocene times.

The relationship of Cercopithecoidea and Hominoidea to earlier anthropoids is uncertain, but Old World monkeys can be traced back in the fossil record to early Miocene *Victoriapithecus* and *Prohylobates* in Africa (Szalay and Delson, 1979). Hominoidea can be traced back in time to early Miocene *Proconsul* in Africa, which is so similar to *Aegyptopithecus* that there is little question that the Egyptian genus

belongs in Hominoidea as well. *Aegyptopithecus* is simultaneously a suitable structural ancestor for Cercopithecoidea, although it lacks the bilophodont cheek teeth characteristic of Old World monkeys. *Aegyptopithecus* differs from Cercopithecoidea in cranial and postcranial features that can only be regarded as primitive or generalized for Catarrhini (Delson, 1975; Fleagle and Kay, 1982; Fleagle and Simons, 1982).

Modern Lorisoidea can be traced to early Miocene *Mioeoticus* and allied forms (Walker, 1974), but little is known of the origin and radiation of this group. Lemuroidea are confined geographically to Madagascar today, and nothing is known of their evolutionary history before the late Pleistocene. Lorisoidea and Lemuroidea may be derived from Eocene Adapidae, but this link is based on shared primitive characteristics (discussed below), and there is little direct evidence bearing on the question in the fossil record.

One advantage of organizing information about fossil primates stratophenetically (as in Fig. 2) is in permitting a realistic appraisal of what we know and do not know about primate history. This approach identifies important gaps in the fossil record. Hominoidea and Cercopithecoidea have a reasonably dense fossil record, and they can be traced back through the Miocene to an *Aegyptopithecus*-like structural ancestor in the late Oligocene or earliest Miocene. Primitive anthropoids like *Apidium* and *Aegyptopithecus* are most similar to Adapidae among Eocene primates. Adapids appear to converge structurally with primitive tarsioid Omomyidae at the beginning of the Eocene. Paleocene primates are almost all highly specialized *Plesiadapis*-like forms filling niches occupied today by rodents. The remainder of the chart in Figure 2 indicates that Tupaioidea have a possible (and questionable) relationship to primates through primitive Plesiadapiformes, while Tarsioidea can be traced with some confidence to Eocene Omomyidae. These links are based almost entirely on structural similarity of preserved parts of the anterior dentition, cheek teeth, and basi-cranium, and there is little evidence of connecting intermediates in the fossil record from the Eocene to the Recent. Similarly, Lorisoidea and Lemuroidea are linked to each other and to Adapidae on the basis of dental, cranial, and postcranial similarities, but there is little direct evidence for this connection in the Oligocene, Miocene, or Pliocene-Recent fossil record.

Hypotheses based on stratophenetic linking are robust in the sense that they attempt to incorporate all evidence in the fossil record—temporal, geographical, and morphological—bearing on the evolutionary history of a given group. New evidences about fossils and/or new fossils are required to test stratophenetic hypotheses of phylogeny, and fortunately new fossils are found frequently in many parts of the world.

It should be emphasized that the importance of a paleontologically based stratophenetic outline of phylogeny, like that presented in Figure 2, extends beyond primate paleontology. It provides a reference framework for comparative study of primates at all levels. Soft-anatomical characteristics, molecular traits, and even behaviors known only in living primates are properly compared and interpreted in light of this framework. Cladistics and molecular studies permit augmentation and refinement (see below), but the fossil record is the basis of what we know about primate evolution. This is not to say that the fossil record provides all (or even most) evidence about primate relationships. The fossil record provides little more than an outline, but this outline necessarily constrains interpretation of all evidence from other sources. An outline of primate phylogeny based on the fossil record is objective in a way that the alternative, an arbitrary *scala naturae* based on philosophical preconceptions, is not.

#### COMPARATIVE ANATOMY AND PRIMATE PHYLOGENY: CLADISTICS

Cladistics is a comparative approach to study of the structure and relationships of clades, groups of organisms sharing common ancestry. Cladistics is practiced in two forms, which are distinguished by different modes of assigning primitive or derived polarities to morphological characters. What I shall here call deductive cladistics

proceeds from knowledge of the generalized common ancestor of a given group of organisms, using the form of the common ancestor to assign primitive-to-derived polarities to morphological characters. Taxa are ordered and grouped at successively lower levels on the basis of their shared derived features. Inductive cladistics begins with hypothesized character polarities of terminal members of an evolutionary radiation, inferring the structure of successively more generalized common ancestors from characteristics of the terminal members themselves.

Deductive cladistic analysis, constrained by the fossil record, is an approach to phylogeny widely used in systematic biology for many years. Deductive cladistics is similar to phenetics in grouping organisms on the basis of similarity, but here the similarity is of a restricted kind: similarity of shared, evolutionarily advanced ("derived") characteristics. In a purely phenetic study, no account is taken of which characters are primitive and which are derived. In a deductive cladistic study, the primitive states of all characters are given by the common ancestor of the group under study. Similarities inherited from a common ancestor (shared primitive features) do not influence subsequent groupings. The second step in cladistic analysis is to evaluate all possible tree diagrams or abstracted "cladograms" consistent with given polarities to see which are most parsimonious; that is, which diagrams of relationship require the smallest number of parallel evolutionary changes and the smallest number of reversals. Given the common ancestor and character polarities determined from this, all such analyses have solutions (sometimes multiple solutions). And, one drawback to cladistic algorithms is that they always give answers at all scales of inquiry. Rarely is an attempt made to identify gaps in knowledge or to compare the relative magnitudes of gaps with those inherent in other studies.

In a cladistic analysis, taxa of each pair being compared, say *B* and *C*, are separated by a gap equal to the morphological and temporal distance from one taxon (*B*) to the pair's hypothetical common ancestor (*A*) and back to the other taxon (*C*). In other words, the gap is the distance *B*-to-*A* plus *A*-to-*C*. The minimum possible gap occurs when *B* is in fact the ancestor of *C* (i.e., *B* corresponds exactly to *A*, *B*-to-*A* = 0), and the total gap is the distance *B*-to-*C*. A gap of *B*-to-*C* is equivalent to the gap one would see in comparing *B* and *C* stratophenetically. In other words, gaps in cladistic analyses are never smaller than those inherent in a corresponding stratophenetic analysis.

Inductive cladistics is a more recent development in systematics, initiated by an entomologist (Hennig, 1950, 1966; see also Gaffney, 1979), and most actively pursued by entomologists, ichthyologists, and ornithologists, all of whom study enormously diverse and complex groups of organisms with fossil records inadequate to document the origin of much of their modern diversity. Inductive cladistics has influenced some paleontologists to deny fossils any special role in reconstructing phylogeny (Schaeffer et al., 1972).

A central problem in applying inductive cladistic methods is determination of initial primitive-to-derived character polarities. There are three standard approaches to this problem: (1) outgroup comparison, in which closely related taxa outside the group being studied are assumed to retain states primitive for all characters in the groups under consideration; (2) commonality, in which the relative frequency of expression of characteristics within a group is assumed to identify primitive characteristics; and (3) ontogeny, in which the transformation of characters during growth is presumed to recapitulate and reflect the sequence of appearance of characteristics during phylogeny. Outgroup comparison requires that the appropriate outgroup be known in advance (a given in deductive cladistics; one could reasonably argue that knowledge of the appropriate outgroup makes an inductive problem deductive). This outgroup must retain all character states that the last common ancestor shared with the group under study. Commonality assumes that evolutionary advancement never involves acquisition of new characteristics permitting broad adaptive radiations, an assumption contrary to much evidence for teleosts among fishes, passerines among birds, rodents among mammals, and cercopithecoids among primates, to cite some common examples. Ontogeny, unfortunately, yields a



most imperfect record of evolutionary history; i.e., many steps are not represented, and those that remain are difficult to relate to adaptations in adult animals. An additional problem arises when outgroups, commonality, and ontogeny yield conflicting results.

If one knows the structure of a phylogenetic tree, at least in outline (as in deductive cladistics), it is usually possible to derive a most parsimonious interpretation of the polarities of morphological characters distributed on the tree. Conversely, if one knows the polarities of all morphological characters in advance, it is often possible to construct a parsimonious cladogram representing one or more plausible phylogenetic trees. In purely comparative studies, one is given neither the phylogenetic tree nor the polarity of morphological characters, and there is consequently insufficient information to begin any kind of cladistic analysis. The only objective way out of this dilemma is to constrain cladistic problems stratophenetically (Cartmill, 1981), making them deductive. This is the approach used, explicitly or implicitly, by many evolutionary systematists. It requires that some initial outline of the phylogeny of a group be determined empirically from the fossil record. Subsequent deductive cladistic analysis is guided by this stratophenetic outline.

The following example illustrates a problem that can profitably be studied using deductive cladistic reasoning within the context of a stratophenetic outline of phylogeny. Adapidae (placed in a distinct superfamily Adapoidea in Table 1) are one of two dominant groups of Eocene primates (the other being tarsiid Omomyidae). Adapids have traditionally been regarded as Eocene "lemurs" because they share important morphological resemblances with extant lemurs. These characteristics include small brain size, lack of postorbital closure, relatively broad, simple, lemur-like upper molars, presence of a free ringlike ectotympanic bone in the middle ear, and a lemur- or lorislake postcranial skeleton. However, adapids share other important morphological resemblances with primitive anthropoid primates. These characteristics include the vertical, spatulate form of upper and lower incisors, possession of a fused mandibular symphysis, and presence of robust, projecting, sexually dimorphic canine teeth.

Adapids first appeared in the fossil record in the early Eocene, some 15–20 million years before the first anthropoids, and 50 million years before the first lemuroidea are known in the fossil record. Given the much earlier appearance of Adapoidea in the fossil record and the phenetic resemblances cited, it is plausible that Adapoidea are related to Anthroidea and Lemuroidea in one of the three ways shown diagrammatically in Figure 3. Adapoidea may be broadly ancestral to Anthroidea but not Lemuroidea (option A); Adapoidea may be broadly ancestral to both Anthroidea and Lemuroidea (option B); or Adapoidea may be broadly ancestral to Lemuroidea but not Anthroidea (option C). The pattern of stratophenetic linking discussed above and shown in Figure 2 would suggest initially that options A, B, and C are all equally likely. All are variations of the idea that an adapoidlike ancestor gave rise to Anthroidea and Lemuroidea.

Deductive cladistic analysis provides a method of evaluating the three possible phylogenetic hypotheses relating Adapoidea, Anthroidea, and Lemuroidea in the context of established trends of morphological evolution in primates. Hypothesis A implies that the superfamily Adapoidea is more closely related phyletically to Anthroidea than either group is to Lemuroidea. This relationship is shown diagrammatically in cladogram A of Figure 3. Hypothesis B implies that the superfamily Lemuroidea is more closely related to Anthroidea than either is to Adapoidea. This relationship is shown diagrammatically in cladogram B of Figure 3. Hypothesis C implies that superfamilies Lemuroidea and Adapoidea are more closely related to each other than either is to Anthroidea. This relationship is shown diagrammatically in cladogram C of Figure 3.

Cladograms A, B, and C can be evaluated by comparing the distribution of character states in each case. Five characters representative of the cranial morphology of adapoids, anthropoids, and lemuroidea are shown, as listed here:

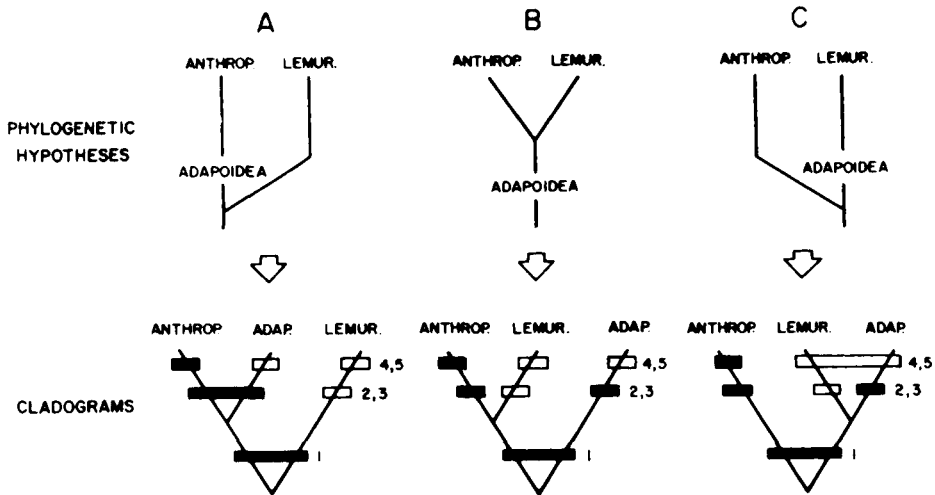


Fig. 3. Cladistic analysis of the Adapoidea-Anthropoidea-Lemuroidea node shown in Figure 2. All three possible arrangements of taxa are shown in phylogenetic hypotheses A, B, and C. Each phylogenetic tree can be redrawn as a cladogram (lower figures), and the distribution of characters and character states evaluated in the context of these cladograms. Primitive-derived character polarities are most reliably determined from the stratophenetic outline of phylogeny of the entire order shown in Figure 2 (see text). Primitive character states are drawn as open rectangles, and derived states are shaded. Note that Anthropoidea and Adapoidea grouped together (cladogram A) are the only clade that shares derived character states. Anthropoidea-Lemuroidea (cladogram B) do not share any character states, and Lemuroidea-Adapoidea (cladogram C) share primitive states. Consequently, phylogenetic hypothesis A carries more weight than B or C, and Lemuroidea may have diverged from a broad Adapoidea-Anthropoidea radicle at or near the time this radicle diverged from Tarsioida. Interpreted in context of the known fossil record, deductive cladistic analysis permits more refined hypotheses of relationship than would otherwise be possible.

Character	Primitive state	Derived state
1. Postorbital bar	Absent	Present
2. Mandibular symphysis	Unfused	Fused
3. Canine teeth	Projecting, nondimorphic	Projecting, dimorphic
4. Ectotympanic	Free	Fused
5. Postorbital closure	Absent	Present

Primitive or derived polarities are assigned to each character on the basis of the distribution of character states near the adapoid-lemuroid-anthropoid node shown in Figure 2. Derived character states are shaded and primitive states are unshaded in Figure 3. Presence of a postorbital bar (character 1) is a derived state shared by all of the taxa being compared. Characters 2 and 3, conformation of the mandibular symphysis and form of the canine teeth, are derived states in Anthropoidea and Adapoidea but primitive in Lemuroidea. Characters 4 and 5, conformation of the ectotympanic and condition of postorbital closure, are derived in Anthropoidea and primitive in Adapoidea and Lemuroidea.

By deductive cladistic criteria, the cladogram grouping Adapoidea and Anthropoidea (cladogram A) carries more weight than either of the other possibilities because it is supported by shared derived character states (for characters 2 and 3). Grouping Anthropoidea and Lemuroidea as sister taxa relative to Adapoidea (cladogram B) is not supported by any shared character states, and grouping Lemuroidea and Adapoidea as sister taxa relative to Anthropoidea is supported only by shared-primitive character states (for characters 4 and 5).

This example illustrates how deductive cladistic analysis can be used to evaluate competing hypotheses considered to be equally likely on stratophenetic grounds. Preference for phylogenetic hypothesis A over hypotheses B and C is supported by the shared-derived states of characters 2 and 3 in cladogram A. Thus the link between Anthroidea and Adapoidea shown in Figure 2 is stronger than that between Lemuroidea and Adapoidea. Lemuroidea could as well be derived from forms ancestral to known Adapoidea, whereas Anthroidea are more likely to be derived from a structural ancestor within Adapoidea. While the analysis presented here is not exhaustive by any means, it is worth noting that Cartmill and Kay (1978) too found all links between adapoids and lemuroids to be based on primitive characteristics, concluding that adapoids may be persistently primitive "Haplorhini" (an hypothesized clade including Anthroidea and Tarsiidea but excluding Lemuroidea and Lorisioidea). This is equivalent to extending the lineage leading to *Loris* (Lorisioidea) and *Lemur* (Lemuroidea) in Figure 2 from a question mark in the Oligocene, as shown, back to common ancestry with *Teilhardina* and *Cantius/Donrussellia* in the late Paleocene or early Eocene.

#### MOLECULAR BIOLOGY AND PRIMATE PHYLOGENY; CALIBRATION OF MOLECULAR CLOCKS

In the past 20 years, precise methods have been developed for measuring differences between living animals at a molecular level. The most widely used methods are indirect, involving immunological or electrophoretic comparison of selected proteins and hybridization of nucleic acids. Direct sequencing of amino acids in proteins and nitrogenous bases in nucleic acids is too time consuming to be applicable in broad systematic studies. The topology of branching of primate lineages derived from molecular studies is generally consistent with that shown in Figure 2 (see, for example, Dene et al., 1976; Sarich and Cronin, 1976). Prosimii diverged first from Anthroidea, then Platyrrhini and Catarrhini diverged within Anthroidea, and finally Hominoidea and Cercopithecoidea diverged within Catarrhini. (It is important to remember that phylogenies and divergence times are not necessarily congruent with classifications, and comparison here should be made with Fig. 2 rather than Table 1).

Another interesting problem concerns rates of molecular evolution and the possible clocklike behavior of evolution at this level. Molecular clocks are calibrated by comparison with one or more divergence times documented in the fossil record. In the order Primates, three divergence times are sufficiently well established on the basis of fossils (Fig. 2) to be of importance:

- (1) Prosimii-Anthroidea, divergence in the late Paleocene to middle Eocene, average of estimated divergence times ca. 55 million years before present (m.y.B.P.).
- (2) Platyrrhini-Catarrhini, divergence in the late Eocene to early Oligocene, average of estimated divergence times ca. 40 m.y.B.P.
- (3) Cercopithecoidea-Hominoidea, divergence in the late Oligocene to early Miocene, average of estimated divergence times ca. 25 m.y.B.P.

These divergence times are consistent with times published by Radinsky (1978) with two exceptions. It seems very unlikely that platyrrhines and catarrhines diverged as long ago as 55 m.y.B.P. or that prosimians and anthropoids diverged as recently as 45 m.y.B.P. I would suggest 45 m.y.B.P. to be a more realistic upper limit, and 40 m.y.B.P. to be a more reasonable average for divergence of Platyrrhini-Catarrhini. In addition, 50 m.y.B.P. is a more realistic lower limit, and 55 m.y.B.P. is a more reasonable average for the estimated time of divergence of Prosimii-Anthroidea. Younger limits given for divergence times are generally based on the documented appearance of both taxa being compared in the fossil record. Older limits are based on reasonably good worldwide coverage of mammalian faunas lacking primates of the grade in question. Mammals are sufficiently mobile geographically, mammalian faunas are sufficiently well known, and there is sufficient

progressive evolution throughout primate history to make it reasonable to date divergence times to within about  $\pm 15\%$ .

It is generally assumed that underlying rates of molecular evolution fluctuate about some uniform average rate over time, and it is further assumed that observed rates of molecular evolution should be constant when measured over different intervals of time. While the former assumption is reasonable, the latter assumption is not. Fluctuations in evolutionary rates play a larger and larger role over longer intervals of time, systematically damping rates calculated over longer and longer intervals. Functional limits to the range of possible variations (and our inability to measure extremes) also depress rates measured over longer and longer intervals (Gingerich, 1983). In molecular terms, the number of reversals and multiple substitutions at the same loci will be proportional to degree of divergence, yet these reversals and multiple substitutions cannot be detected. Existence of a functional component in DNA and protein sequences means that molecular variation is channeled. Thus, even if actual underlying rates of mutation are constant over time, perceived rates should decrease with time (as they appear to do, for example, in sequence divergence of mitochondrial DNA, Brown, 1983; and probably DNA-DNA hybridization, Sibley and Ahlquist, 1981; but see Sibley and Ahlquist, 1984). One important consequence of this is the expectation that molecular differences should not scale linearly with time: molecular clocks should be nonlinear. Many of these and following points have been made in one way or another by Goodman (1963, 1976), Read and Lestrel (1970), Uzzell and Pilbeam (1971), Kohne (1975), Read (1975), Benveniste and Todaro (1976), and Corruccini et al. (1980). Important points contradicting prevailing views of molecular evolution and its relationship to geological time can be illustrated with reference to Sarich's (1968, 1970) original data on albumin evolution in primates.

To illustrate the nonlinearity of change on a molecular level, Sarich's (1968, 1970) immunological distances (ID) for Prosimii-Anthroidea, Platyrrhini-Catarrhini, and Cercopithecoidea-Hominoidea are plotted against divergence time (DT) in Figure 4, using the divergence times (DT) of 55, 40, and 25 million years discussed above. Sarich (1968, 1970) indicates that a linear model relating his immunological distances and divergence times has the form

$$ID = 1.67 DT \quad (1)$$

and this equation is plotted as a dashed line in Figure 4. Linearity can be tested by fitting a simple power function to the distribution, noting the value of the exponent (linearity requires an exponent of 1.0). Using Sarich's (1968, 1970) immunological distances with divergence times given here, the best-fit power function is

$$ID = 0.27 DT^{1.49} \quad (2)$$

and this equation is plotted as a solid line in Figure 4. Regression of log ID on log DT is appropriate for calculation of scaling coefficients because a range of ID values is known for each DT. Furthermore, regression of log ID on log DT, used here to predict divergence times within Hominoidea, yields more conservative scaling coefficients and younger divergence times than would regression of log DT on log ID or computation of principal axes. The empirically derived exponent of 1.49 for albumin ID scaling in primates has a 95% confidence interval of 1.31–1.67. It is clearly significantly different from 1.00, indicating that albumin immunological distance scales nonlinearly with divergence time in primates. (It may be noted parenthetically that the "relative rate test" often used as evidence of linearity works equally well whether rates scale linearly with geological time or not; thus, it is not a test of linearity on this time scale.)

The molecular clock that best conforms to the empirical relationship of albumin immunological distance and divergence time in primates is that given in Equation 2. This clock can be used in conjunction with Sarich's (1970) immunological distances for hominoid primates to estimate divergence times that cannot be established paleontologically. Table 2 provides a comparison of divergence times estimated using

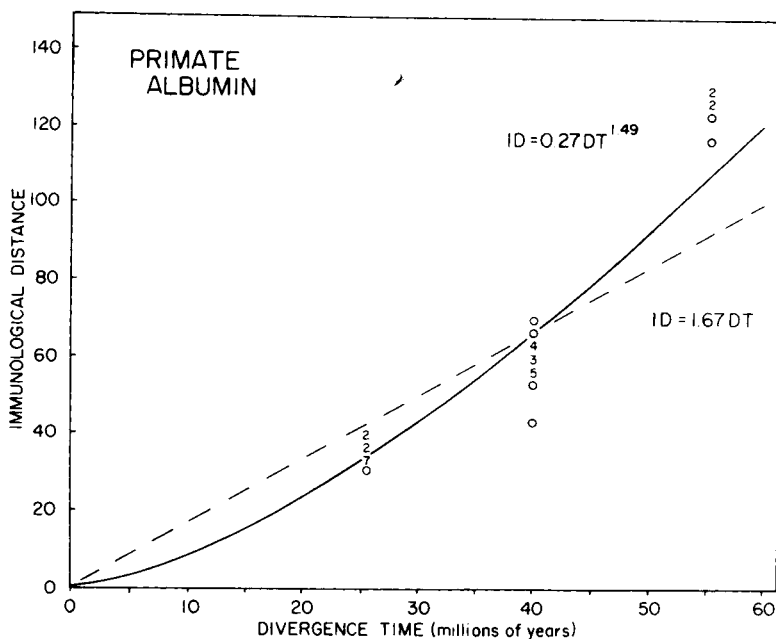


Fig. 4. Nonlinear scaling of albumin evolution in primates. Immunological distance (ID) values are plotted against divergence times (DT) for the Cercopithecoidea-Hominoidea divergence (25 m.y.B.P.), Catarrhini-Platyrrhini divergence (40 m.y.B.P.), and Anthropoidea-Prosimii divergence (55 m.y.B.P.). Immunological distances are taken from Sarich (1968, 1970) and divergence times are based on stratopheletic interpretation of the fossil record (Fig. 2). Sarich's model for a linear albumin clock ( $ID = 1.67 DT$ ) is plotted as a dashed line. The nonlinear model proposed here for the same data ( $ID = 0.27 DT^{1.49}$ ) is plotted as a solid line (see text for discussion). Divergence times for apes and humans derived from the two models are compared in Table 2. If the mutation rate underlying molecular evolution is constant (linear, with an exponent of 1.0), time averaging of neutral mutations and multiple mutations at the same loci will cause perceived rates to be nonlinear, with exponents less than 1.0. The resulting curve should be concave-downward rather than upward as observed here (solid line). This anomalous behavior is common in published molecular studies; it remains to be adequately explained.

TABLE 2. Comparison of divergence times (DT) for apes and humans calculated from albumin immunological distances (ID) using the linear model of Sarich (1968, 1970; Equation 1 in text) and nonlinear model proposed here (Equation 2 in text)<sup>1</sup>

Genera compared	Albumin ID (Sarich, 1970)	Divergence time (millions of years)	
		Linear clock	Nonlinear clock
<i>Homo-Pan</i>	7	4.2	8.9
<i>Homo-Gorilla</i>	9	5.4	10.5
<i>Homo-Pongo</i>	12	7.2	12.8
<i>Homo-Hylobates</i>	15	9.0	14.8
<i>Homo-Symphalangus</i>	15	9.0	14.8

<sup>1</sup>These models are compared graphically in Figure 4.

Equation 1 from Sarich and divergence times estimated using Equation 2 derived here. The principal differences of note are in Sarich's divergence times of 4.2 and 7.2 million years for human-chimpanzee (*Homo-Pan*) and human-orangutan (*Homo-Pongo*), respectively, based on a linear model, compared with much older divergence times of 8.9 and 12.8 million years, respectively, estimated here using the same data and a nonlinear scaling model.

Divergence times calculated here based on nonlinear scaling conform to divergence times estimated from the fossil record of hominoid evolution much better than divergence times based on linear scaling. However, divergence times based on nonlinear scaling of albumins still sample differences in a single protein. It is highly desirable that other approaches like DNA-DNA hybridization (Sibley and Ahlquist, 1984), based on a much broader sample of the genome, be calibrated paleontologically, because once this is done, DNA-DNA hybridization promises to contribute a more refined chronology of human evolution.

The scaling of immunological distances illustrated in Figure 4 raises another serious question. As discussed above, measures of molecular difference (like ID) should increase less rapidly over longer and longer measurement intervals (DT). One would expect the solid curve in Figure 4 to be concave downward rather than concave upward. The exponent of DT should be less, not greater, than 1.0. Goodman (1976; see also Goodman et al., 1983) has noted, in other contexts, the apparent slowdown or deceleration of molecular evolution over time implied by the concave-upward shape of the solid curve in Figure 4, explaining this as a result of decreasing mutation rates and intensification of stabilizing selection in the course of primate evolution. If mutation rates are decreasing and stabilizing selection intensifying, the underlying rate of change in primate albumins might really be scaling with an exponent of 1.5 or more (the exponent of 1.49 that we perceive empirically is necessarily lower than the actual underlying rate of change because of the effects of time averaging). Explanation of observed deceleration of molecular evolution in primates in terms of decreasing mutation rates and stabilizing selection may be correct, but other explanations are also possible. We would do well to examine molecular data that do not show expected effects of time averaging in a very critical light.

#### CONCLUSIONS

Paleontology plays a fundamental role in documenting the major features of primate evolution. Fossils will never tell the whole story, but they have unique importance in relating visible morphology and molecular structure to geological time, a dimension of primary importance for evolutionary studies. The fossil record, interpreted stratophenetically, provides an outline of primate phylogeny, and this outline can be refined and amplified using deductive cladistic principles and methods, increasing our understanding of systematic relationships and character evolution beyond what can be learned from fossils alone.

The fossil record provides divergence times essential for measurement of rates of evolution on a molecular scale. Clocklike regularities in molecular evolution, interpreted in light of temporal scaling, can be used in turn to estimate divergence times not well constrained by fossils. Clearly paleontologists, comparative anatomists, and molecular biologists have much to learn from each other, and integration of discoveries from all three fields will lead to a more complete understanding of our evolutionary past.

#### ACKNOWLEDGMENTS

This essay reflects the influence of far too many colleagues to acknowledge each individually. I thank Drs. Daniel Fisher and David Pilbeam for discussion, and Drs. Catherine Badgley, Matt Cartmill, Charles Sibley, B. Holly Smith, and an anonymous reviewer for reading and improving earlier drafts of the manuscript. Figures were drawn by Karen Klitz. This research was supported by National Science Foundation grant BNS 80-16742.

## LITERATURE CITED

- Ba Maw, Ciochon, RL, and Savage DE (1979) Late Eocene of Burma yields earliest anthropoid primate *Pondaungia cotteri*. *Nature* 282:65-67.
- Benveniste, RE, and Todaro, GJ (1976) Evolution of Type C viral genes: Evidence for an Asian origin of man. *Nature* 261:101-108.
- Brown, W (1983) Evolution of animal mitochondrial DNA. In M Nei and RK Koehn (eds): *Evolution of Genes and Proteins*. Sunderland: Sinauer Associates Inc., pp. 62-88.
- Cartmill, M (1981) Hypothesis testing and phylogenetic reconstruction. *Z. Zool. Systematik Evol. Forsch.* 19:73-96.
- Cartmill, M, and Kay, RF (1978) Cranio-dental morphology, tarsier affinities, and primate suborders. In DJ Chivers and KA Joysey (eds): *Recent Advances in Primatology*. London: Academic Press, pp. 205-214.
- Corruccini, RS, Baba, M, Goodman, M, Ciochon, RL, and Cronin, JE (1980) Non-linear macromolecular evolution and the molecular clock. *Evolution* 34:1216-1219.
- Delson, E (1975) Toward the origin of Old World monkeys. In: *Evolution des Vertébrés—Problèmes actuels de Paléontologie*. Coll. Int. C.N.R.S. 218:839-850.
- Dene, HT, Goodman, M, and Prychodko, W (1976) Immunodiffusion evidence on the phylogeny of the primates. In M Goodman, RE Tashian, and JH Tashian (eds): *Molecular Anthropology*. New York: Plenum Press, pp. 171-195.
- Fleagle, JG, and Kay RF (1982) New interpretations of the phyletic position of Oligocene hominoids. In RL Ciochon and R Corruccini (eds): *New Interpretations of Ape and Human Ancestry*. New York: Plenum Press, pp. 181-210.
- Fleagle, JG, and Simons, EL (1982) The humerus of *Aegyptopithecus zeuxis*: A primitive anthropoid. *Am. J. Phys. Anthropol.* 59:175-193.
- Gaffney, ES (1979) An introduction to the logic of phylogeny reconstruction. In J Cracraft and N Eldredge (eds): *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, pp. 79-111.
- Gingerich, PD (1976) Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Univ. Mich. Pap. Paleontol.* 15:1-140.
- Gingerich, PD (1979a) Stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In J Cracraft and N Eldredge (eds): *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, pp. 41-77.
- Gingerich, PD (1979b) Paleontology, phylogeny, and classification: An example from the mammalian fossil record. *Syst. Zool.* 28:451-464.
- Gingerich, PD (1980) Eocene Adapidae, paleobiogeography, and the origin of South American Platyrrhini. In RL Ciochon and AB Chiarelli (eds): *Evolutionary Biology of the New World Monkeys and Continental Drift*. New York: Plenum Press, pp. 123-138.
- Gingerich, PD (1981) Early Cenozoic Omomyidae and the evolutionary history of tarsiform primates. *J. Hum. Evol.* 10:345-374.
- Gingerich, PD (1983) Rates of evolution: effects of time and temporal scaling. *Science* 222:159-161.
- Gingerich, PD, and Schoeninger, MJ (1977) The fossil record and primate phylogeny. *J. Hum. Evol.* 6:483-505.
- Goodman, M (1963) Man's place in the phylogeny of the primates as reflected in serum proteins. In SL Washburn (ed): *Classification and Human Evolution*. Chicago: Aldine, pp. 204-234.
- Goodman, M (1976) Toward a genealogical description of the primates. In: M Goodman, RE Tashian, and JH Tashian (eds): *Molecular Anthropology*. New York: Columbia University Press, pp. 321-353.
- Goodman, M, Baba, ML, and Darga, LL (1983) The bearing of molecular data on the cladogenesis and times of divergence of hominoid lineages. In RL Ciochon and RS Corruccini (eds): *New Interpretations of Ape and Human Ancestry*. New York: Plenum Press, pp. 67-86.
- Hennig, W (1950) *Grundzüge einer Theorie der Phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.
- Hennig, W (1966) *Phylogenetic Systematics*. Urbana: University of Illinois Press.
- Hoffstetter, R (1969) Un primate de l'Oligocène inférieur sud-américain: *Branisella boliviana* gen. et sp. nov. *C.R. Acad. Sci. [D] (Paris)* 269:434-437.
- Kohne, D (1975) DNA evolution data and its relevance to mammalian phylogeny. In WP Luckett and FS Szalay (eds): *Phylogeny of the Primates*. New York: Plenum Press, pp. 249-264.
- MacPhee, RDE, Cartmill, M, and Gingerich, PD (1983) New Paleocene primate basicrania and definition of the order Primates. *Nature* 301:509-511.
- Napier, JR, and Napier, PH (1967) *A Handbook of Living Primates*. New York: Academic Press.
- Radinsky, L (1978) Do albumin clocks run on time? *Science* 200:1182-1183.
- Read, DW (1975) Primate phylogeny, neutral mutations and molecular clocks. *Syst. Zool.* 24:209-221.
- Read, DW, and Lestrel, PE (1970) Hominid phylogeny and immunology: a critical appraisal. *Science* 168:578-580.
- Rose, KD (1981) The Clarkforkian Land-Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. *Univ. Mich. Pap. Paleontol.* 26:1-196.
- Sarich, VM (1968) The origin of the hominids: an immunological approach. In: SL Washburn and PC Jay (eds): *Perspectives on Human Evolution*. New York: Holt, Reinhart, and Winston, pp. 94-121.
- Sarich, VM (1970) Primate systematics with special reference to Old World monkeys: A protein perspective. In: JR Napier and PH Napier (eds): *Old World monkeys*. New York: Academic Press, pp. 175-226.

- Sarich, VM, and Cronin, JE (1976) Molecular systematics of the primates. In M Goodman, RE Tashian, and JH Tashian (eds): *Molecular Anthropology*. New York: Plenum Press, pp. 141-170.
- Schaeffer, B, Hecht, MK, and Eldredge, N (1972) Phylogeny and paleontology. *Evol. Biol.* 6:31-46.
- Sibley, CG, and Ahlquist, JE (1981) The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. In GGE Scudder and RL Reveal (eds): *Evolution Today, Proc. Second Int. Congr. Syst. Evol. Biol.* Pittsburgh: Hunt Inst. Botanic Document., pp. 301-335.
- Sibley, CG, and Ahlquist, JE (1984) The phylogeny of the hominoid primates as indicated by DNA-DNA hybridization. *J. Mol. Evol.* (in press).
- Simons, EL (1971) Relationships of *Amphipithecus* and *Oligopithecus*. *Nature* 232:489-491.
- Simons, EL (1972) *Primate Evolution: An Introduction to Man's Place in Nature*. New York: Macmillan.
- Szalay, FS (1970) Late Eocene *Amphipithecus* and the origins of catarrhine primates. *Nature* 227:355-357.
- Szalay, FS, and Delson, E (1979) *Evolutionary History of the Primates*. New York: Academic Press.
- Uzzell, T, and Pilbeam, D (1971) Phyletic divergence dates of hominoid primates: A comparison of fossil and molecular data. *Evolution* 25:615-635.
- Walker, A (1974) A review of the Miocene Lorisidae of East Africa. In RD Martin, GA Doyle, and A Walker (eds): *Prosimian Biology*. London: Duckworth, pp. 435-447.