

Philip D. Gingerich

*Museum of Paleontology,
The University of Michigan,
Ann Arbor, Michigan 48109,
U.S.A.*

Margaret Schoeninger

*Department of Anthropology,
The University of Michigan,
Ann Arbor, Michigan 48109,
U.S.A.*

The Fossil Record and Primate Phylogeny

Fossils provide the only direct evidence of the evolutionary history of primates. A method of phylogeny reconstruction is outlined which is based on an evaluation of phenetic resemblances of fossils interpreted in their stratigraphic context. This *stratophenetic* approach to phylogeny involves three successive steps: (1) organization of fossils stratigraphically, (2) phenetic linking of similar forms from adjacent stratigraphic intervals, (3) critical testing—Is the density and continuity of the fossil record sufficient to support the proposed linkings?—Does the proposed phylogeny make sense cladistically?—Does it make sense paleogeographically?

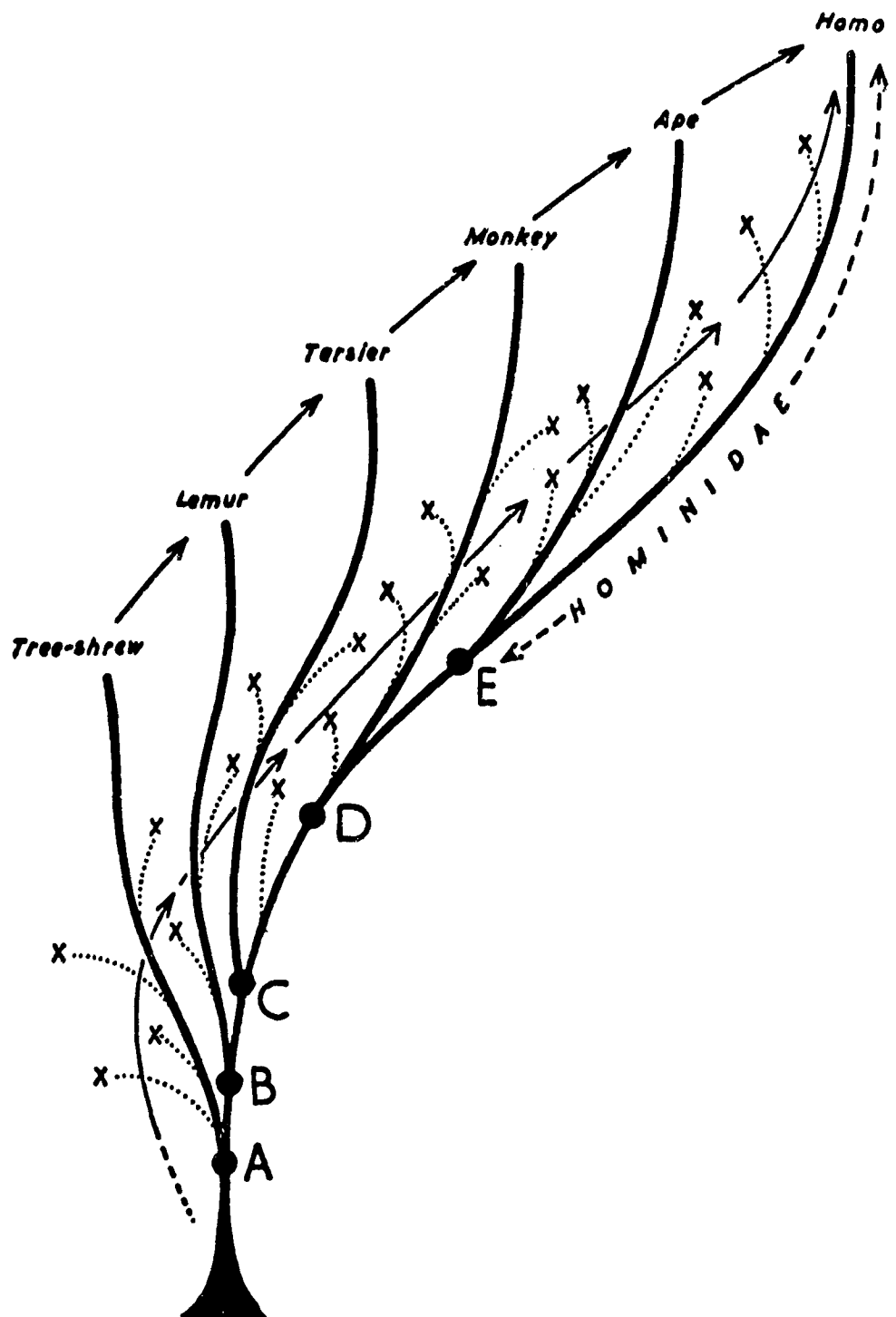
Evaluation of the known fossil record of primates, following the stratophenetic approach outlined here, has suggested that microsyopoids are primitive primates and that fossil tarsiods and plesiadapoids form a closely linked group. Early anthropoids link most closely with Eocene adapoids, supporting an adapoid origin of Anthropoidea. Large gaps remain in the fossil record of lemuroid and lorisoid primates: they may have been derived from an *Adapis*-like Eocene genus, or they may possibly have evolved independently of other primates since the late Cretaceous or the Paleocene. This question is closely related to the problem of whether living *Tarsius* or modern lemurs and lorises are more closely related to the living higher primates. The fossil record and the paleogeography of Central America suggest that platyrrhines evolved from an early anthropoid stock and may have entered South America from Asia via North America at about the end of the Eocene.

Dental remains are the only evidence of Plio-Pleistocene hominids known in sufficient quantities from successive stratigraphic intervals to permit stratophenetic analysis. Studying the stratigraphic distribution of measurements of tooth size in the East Rudolf sample of fossil hominids and comparing this with dental variation in a modern human population suggests the probable presence of two hominid lineages in East Africa throughout much of the Plio-Pleistocene. Study of all dental and skeletal remains in an explicitly stratigraphic and temporal context should help to clarify the course and complexity of early hominid evolution.

1. Introduction

A phylogeny is an attempted reconstruction of the evolutionary history of a group of organisms. As such, a phylogeny can only be expected to reflect history to the extent that actual historical records (fossils) are available to document successive stages of evolutionary change. Since fossils are generally relatively rare and preserve only a small part of the anatomy of the organism represented, the fossil record often does not provide sufficient information to permit very complete historical reconstruction. The only alternative is to make a detailed comparative study of the living representatives of the group of interest and then arrange the living animals in a sequence or pattern that is, in some sense, the simplest or most parsimonious arrangement. In the absence of historical documentation such a pattern cannot, however, be regarded as more than a somewhat arbitrary arrangement.

Figure 1. *Scala naturae* of living primates illustrating the basic pattern of phylogenetic relationships advocated by most primatologists in this century. From Le Gros Clark (1962).



The evolutionary history of the Primates is of considerable interest because humans are members of this mammalian order, and numerous phylogenies of the primates have been published in recent years. While each new phylogeny usually differs in minor detail from previous ones, the basic pattern of the various primate phylogenies proposed in recent years differs little from one to another. This basic pattern is illustrated here in Figure 1, reproduced from Le Gros Clark (1962). The phylogenies of Simons (1964), Goodman (1973), Martin (1973), Minkoff (1974), and Hoffstetter (1974*b*), to list a few of the recent ones, show basically the same relationships of the major groups of primates. Both Goodman (1973) and Martin (1973) reproduce Elliot Smith's (1924) phylogenetic tree of the primates, which shows how little our understanding of relationships of the major groups of primates has changed in the past fifty years.

The general method of reconstructing evolutionary history from the evidence of comparative anatomy involves estimating and evaluating similarities and differences between the organisms of interest, in this case different primates. Similarities and differences are usually evaluated by one or the other of two methods. The method

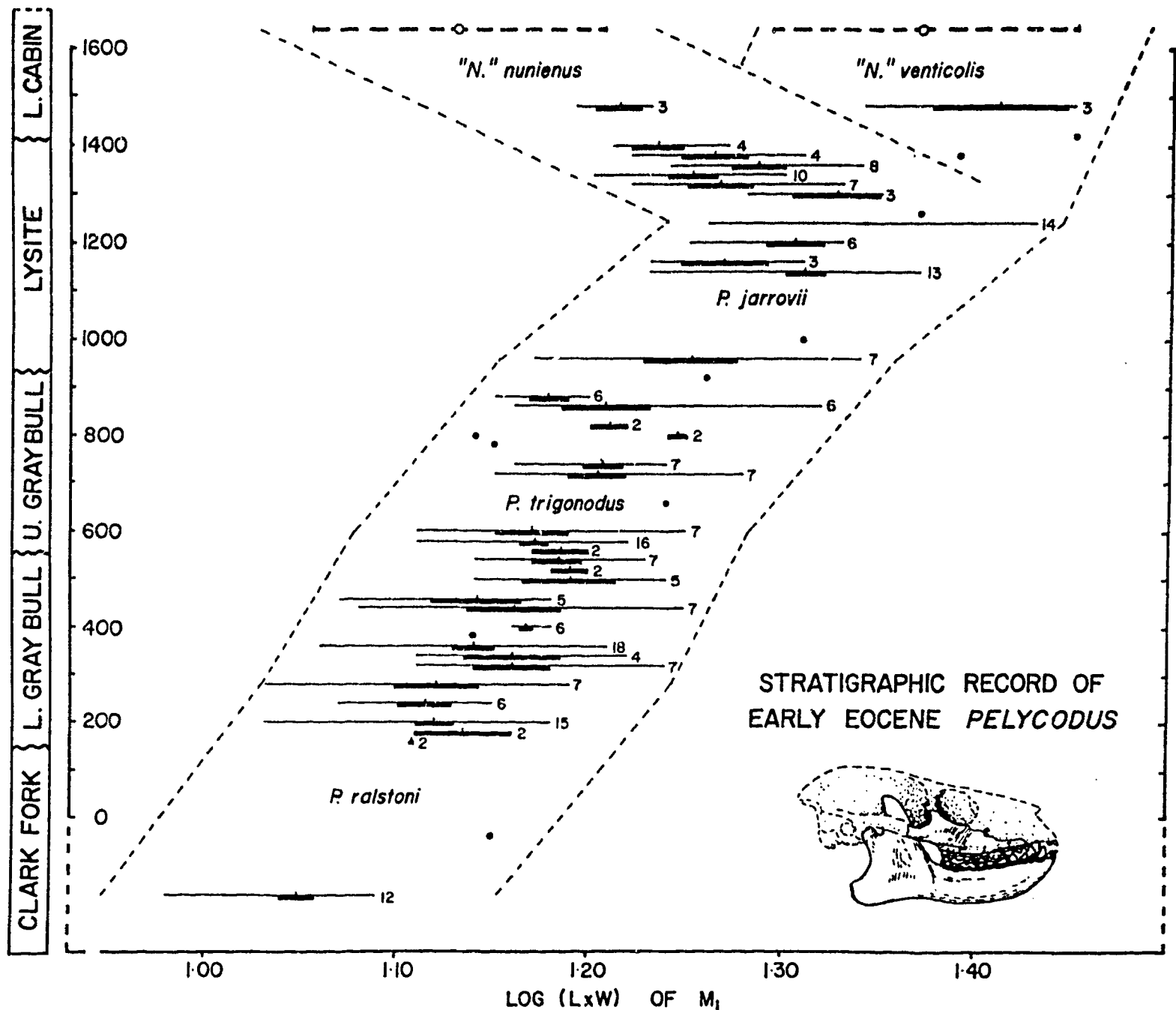
applied in most of the early studies is the least presumptuous, as it groups taxa on the basis of their overall similarity, or "phenetic" resemblance. Referring to the groups represented in Figure 1, humans and apes are most similar to each other and they are thus grouped together. Monkeys are most similar to the human-ape group, and are joined to it next, then the tarsiers, the lemurs, and finally the tree shrews.

In recent years a more sophisticated variation of the phenetic method has been applied in arranging primate taxa into related groups. This "cladistic" method attempts to group taxa only on the basis of the number of advanced or "derived" characteristics they share, rather than considering the total number of characteristics shared. Given a sufficient number of characters for study, one might expect both the phenetic and cladistic methods to yield similar arrangements of taxa. However it is rarely possible to obtain a large number of independent morphological characters and the two methods sometimes yield conclusions differing significantly. The most serious problem with the cladistic method lies in the virtual impossibility of identifying which characteristics are derived and which are primitive for each particular local comparison of two or three taxa. For example, among the evolutionary rules available for designating a given characteristic as a derived state are both recapitulation (Haeckel's law) and its converse neoteny (or paedomorphism), giving the investigator some freedom of choice in the matter. Similarly, an investigator is free to designate a widely distributed character state as primitive by "communality" or, conversely, to designate a relatively rare state with a restricted distribution as primitive by suggesting that its bearers are relicts of an archaic radiation. Thus, in practice, the identification of a given character state as primitive or derived is often highly arbitrary.

A fundamental criticism of both the phenetic and cladistic methods of phylogeny reconstruction involves the way these methods treat fossils, the only actual historical records of the evolutionary events one wishes to reconstruct. Neither method utilizes the geological age of fossils in establishing the relationships of the taxa being studied. Fossils are either treated as if they were just additional living forms, albeit poorly known ones anatomically (e.g. Delson & Andrews, 1975), or they are inserted, where possible, into a phylogenetic tree constructed from assumptions about living primates alone (e.g. Martin, 1973). No political historian would ignore the dates of documents bearing on political history, or attempt to fit the documents into a scheme of "history" derived from a study of modern political systems alone—and this seems a curious approach to reconstructing primate history as well. A method is needed which takes explicit account of the age of available primate fossils.

Our purpose here is to review a particular paleontological approach derived from the study of certain early Tertiary mammals. The available comparative anatomical information for these groups of mammals is very limited, and reconstruction of their evolutionary history is dependent on detailed stratigraphic information. One of the groups, the Plesiadapidae, is an archaic family of Middle Paleocene through Early Eocene primates known from North America and Europe. While not contributing to the later evolution of primates, this family is nevertheless important in being one of the best known groups of primates stratigraphically—large samples of most of the species of Plesiadapidae are known from eight stratigraphic intervals positioned one above the other in western North America. Virtually all of the fossil specimens bearing on the evolution of this family have recently been restudied in a carefully documented stratigraphic context (Gingerich, 1974*b*, 1976*b*). The method of phylogeny reconstruction

Figure 2. Phylogeny of early Eocene *Pelycodus* in the Big Horn Basin of Wyoming. Abscissa is log of length \times width of the first lower molar, ordinate is height of sample in a measured stratigraphic section. Horizontal line is sample range, number at right is sample size, vertical slash is mean, and heavy bar is standard error of mean. Solid circles are individual specimens. All samples are arranged in proper stratigraphic order, and linkings (dashed lines) give a direct reading of the phylogeny of *Pelycodus* in the area and time period sampled. Customary placement of the two Lost Cabin species *nunienus* and *venticolis* in "*Notharctus*" is completely arbitrary—both are very closely linked to *Pelycodus*. From Gingerich (1976a).



advocated here has grown out of that study and similar studies of abundant Eocene mammals in stratigraphic context (Gingerich, 1974a, 1976a).

Since stratigraphic and phenetic information forms the basis for phylogenies constructed according to the method outlined here, the method may be termed "*stratophenetic*" to distinguish it clearly from other "evolutionary" methods like cladistics which are based on different initial assumptions. The stratophenetic method, although derived independently, appears to be in large part just a rather more explicit statement of the evolutionary systematics advocated previously by Simpson (1961), and others.

We shall first outline the method of phylogeny reconstruction based on the strati-

graphic distribution and phenetic affinity of fossils, and then illustrate this method by applying it to the fossil record bearing on the origin of anthropoid primates and to a portion of the fossil record of human evolution.

2. Stratigraphy and Phylogeny Reconstruction

A basic attribute of a fossil is its geological age, whether dated radiometrically or simply dated stratigraphically relative to other fossils. One of the fundamental principles of stratigraphy is the law of superposition, whereby it is recognized that in a normal sequence of sediments, strata at the top of the sequence are younger than the underlying strata. As a result, fossils found in strata at the top of a sequence will be younger than fossils found in strata lower in the sequence. Thus it is possible, in many cases, to determine the relative temporal relationships of a number of fossil species from their stratigraphic distributions. Figure 2 illustrates diagrammatically the stratigraphic and temporal distribution of samples of the Early Eocene primate *Pelycodus* from the Big Horn Basin in western North America.

The relative temporal relationships of fossil species are important for two reasons. (1) Only through an understanding of temporal relationships of species can the minimum number of evolutionary lineages present in any area be determined. As Figure 2 illustrates, two species of "*Notharctus*" ("*N.* *nuniensis*" and "*N.* *venticolis*") are known to have coexisted in the Big Horn Basin of Wyoming during Lost Cabin time because a large and a small species of "*Notharctus*" are found together in the very same deposits. During Lysite time and earlier, there is evidence for only a single lineage of *Pelycodus*—the variability of tooth size in any given sample is no greater than that found in one species. (2) The temporal relationships of fossil species are important for a second reason: a younger species cannot be the ancestor of an older one. Thus, referring to Figure 2 again, *P. jarrovii* could not be the ancestor of *P. ralstoni* or of *P. trigonodus*. Whether an older species can be inferred to be the ancestor of a younger one depends on the temporal and geographic proximity of the two species, on the continuity of the fossil record connecting the two, and to some degree on parsimony—to postulate that *P. trigonodus* did not evolve from *P. ralstoni* would require the existence of an additional, completely hypothetical lineage of *Pelycodus*. Unless evidence of such a lineage is found, the most parsimonious interpretation is certainly that *P. trigonodus* is a direct descendent of *P. ralstoni*.

A single evolving lineage of *Pelycodus* was present in the Big Horn Basin during Clark Fork, Gray Bull, and most of Lysite time, however by Lost Cabin time there is clear evidence of two evolving lineages. As this example illustrates, the most parsimonious phylogenetic hypothesis is the one that requires the smallest number of evolutionary lineages to account for the available stratigraphical and anatomical evidence.

Phylogeny reconstruction

Reconstructing a phylogeny from fossil data involves three consecutive steps: (1) data organization, (2) linking, and (3) testing. The first step, *data organization*, is best illustrated graphically, as in Figure 2, where statistical parameters of measurements of tooth size of samples of *Pelycodus* are plotted against the stratigraphic position of the locality from which each sample was collected. Each sample is thus organized temporally

relative to the other available samples. Body size is plotted here because it is one of the most important aspects of a species' adaptation, but any other anatomical parameter of interest, such as mesostyle development, etc., could be plotted on the abscissa as well (the size of M_1 is used as an estimate of body size because this tooth is generally the least variable of the cheek teeth and it is thus presumably the tooth most highly correlated with average body size for a given population of mammals; Gingerich, 1974c). Tooth size is plotted on a logarithmic scale to make the variability of samples of specimens of large body size comparable to that of samples of specimens of smaller body size.

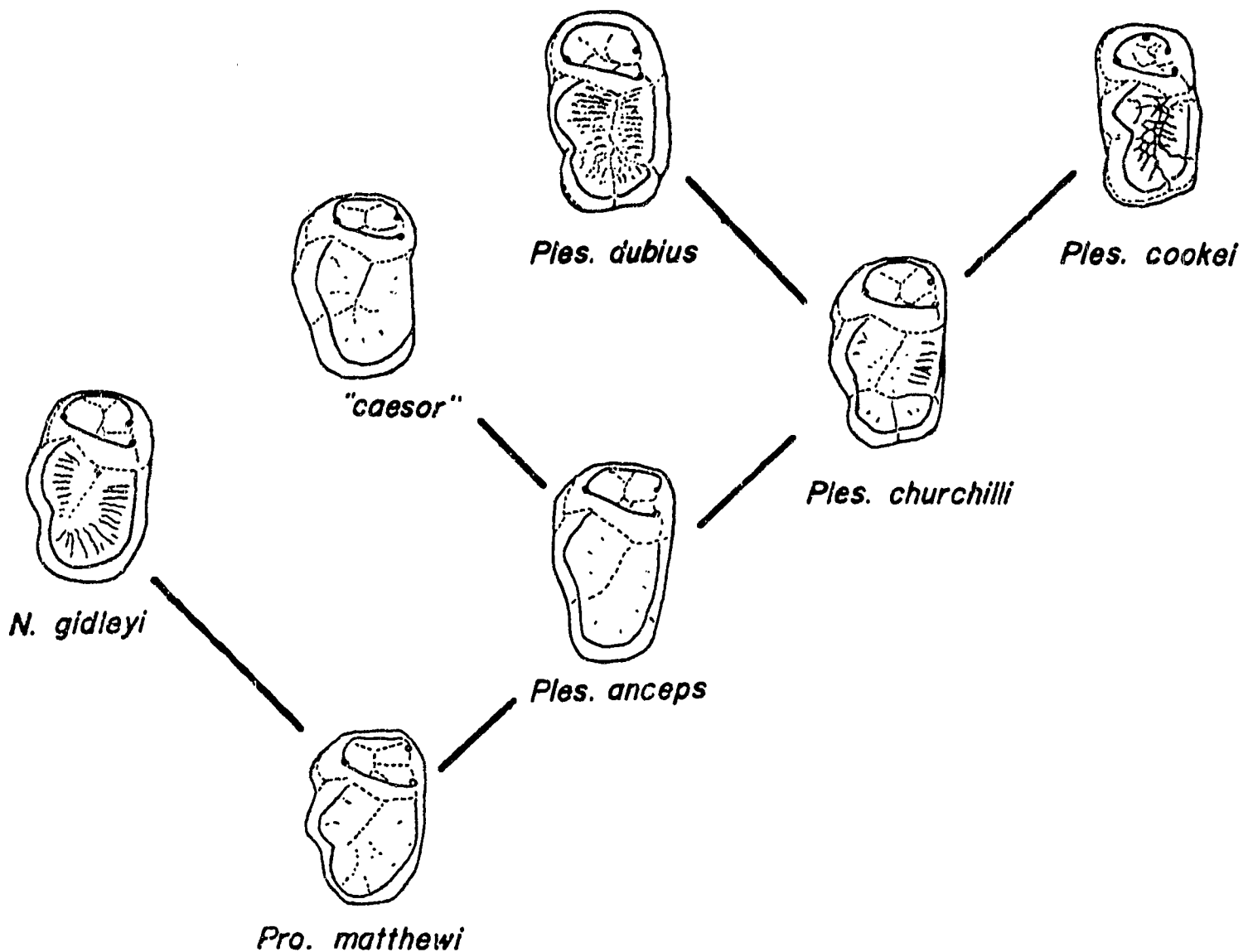
Once the data are organized in their stratigraphic context, one can begin *linking* samples that are similar in morphology and closely approximated in time. This procedure is iterative—beginning at the bottom of Figure 2, for example, the sample of 12 specimens there is closest stratigraphically and phenetically to the single specimen just above, which is in turn closest to the overlying sample of 2, which is in turn closest to the overlying sample of 15, etc. This method yields a more or less direct reading of the phylogenetic relationships of successive samples preserved in the geological record. How credible such a direct reading actually is depends on the density and continuity of the available fossil record. The dashed lines bounding lineages in Figure 2 illustrate the most parsimonious interpretation of the phylogeny of *Pelycodus* in the Big Horn Basin, given the available information.

It should be noted explicitly that this most parsimonious interpretation requires no *a priori* assumptions about phylogenetic size increase (Cope's rule—note that "*N.*" *nunienus* gets smaller with time), about evolutionary irreversibility (Dollo's law—note that "*N.*" *nunienus* reverses to the size of *P. trigonodus*), or about the unique acquisition of distinctive morphological characters (a distinctive "*Notharctus*"-type mesostyle evolved independently in "*N.*" *nunienus* and "*N.*" *venticolis* from a rudimentary mesostyle in *P. jarrovi*, for example). These basic ideas about phyletic evolution, like the basic principles of mechanics, could not be predicted from theory alone—they are essentially empirical, and it is only with an adequate fossil record that any real understanding can be gained of the importance of size increase, irreversibility, or parallelism in primate evolution.

Recognition of the artificiality of applying *a priori* rules to interpretations of phylogeny is of particular importance in that *a priori* concepts of character evolution pervade the modern use of cladistic methods to reconstruct phylogenies. There is, in the absence of an adequate fossil record, no way to be certain which characteristics of an organism are primitive and which are derived, or which evolved independently in different lineages. Knowledge of both is essential to reconstruct a phylogeny on the basis of living forms alone.

To take one example for which stratigraphic documentation is now available, two characteristics of the last lower molar in species of the Plesiadapidae show significant differences in different species: the enamel in some species is highly crenulated, and the talonid or "heel" in some species is squared and fissured rather than round and unfissured (see Figure 3). In making a comparative analysis before stratigraphic information was available, it was assumed that enamel crenulation was an important derived characteristic, and differences in heel shape were thought to be unimportant. Thus it appeared initially that *N. gidleyi*, *Ples. dubius*, and *Ples. cookei* constituted a derived, monophyletic group of species because they shared crenulated enamel. However, considering all of the species in their stratigraphic context and reconstructing the phy-

Figure 3. Phylogenetic relationships of seven species of Plesiadapidae, showing the morphology of M_3 characteristic of each. Note particularly the independent evolution of highly crenulated enamel in *N. gidleyi*, *Ples. dubius* and *Ples. cookei*. Note also the squared, fissured hypoconulid heel in *Ples. churchilli*, *Ples. dubius* and *Ples. cookei*. Data from Gingerich (1976b).



logeny of the Plesiadapidae as outlined above, it is clear that highly crenulated enamel evolved independently in three out of four North American lineages of Plesiadapidae. Furthermore, heel shape and fissuring appear in retrospect to be important characteristics by which *Ples. dubius*, *Ples. cookei* and *Ples. churchilli* can be diagnosed from the other North American plesiadapids (see Figure 3). Neither of these conclusions could have been anticipated before the stratigraphic analysis was completed, yet the untested erroneous initial postulates would have formed the basis of an important part of any cladistic analysis of the phylogenetic relationships of the species of Plesiadapidae. This is not to say that cladistic analysis is not an important aspect of the study of phylogeny, but the importance of cladistics lies in testing phylogenies rather than in the actual construction of them.

Critical *testing* is the third step in considering a phylogeny reconstructed from stratigraphic and phenetic linking. Are the stratigraphic and the phenetic links sufficiently close that other possible arrangements can safely be ruled out? Does the proposed phylogeny make sense cladistically? That is, are the evolutionary reversals and parallel acquisitions of similar character states, if any, plausible in terms of our understanding of the animals' adaptations? Judging from the stratigraphic distribution of character

states, are the states linking given groups primitive or derived states—this has some bearing on the relative importance to be attached to linkings when the density and continuity of the stratigraphic record is inadequate. As a final question, does the proposed phylogeny make sense in terms of paleogeography? Ultimately, of course, future discoveries provide the best test of the adequacy of a given stratophenetic hypothesis.

Figure 2 illustrates a phylogeny derived from a relatively continuous stratigraphic record. It meets the above tests in having close phenetic and stratigraphic links between samples and in showing a cladistically parsimonious pattern of character evolution (the independent acquisition of large mesostyles in "*N.*" *nunierus* and "*N.*" *venticolis* can be explained by the occlusal function of these structures (Schoeninger, in prep.). The phylogeny is plausible geographically since all of the fossil evidence comes from a single depositional basin.

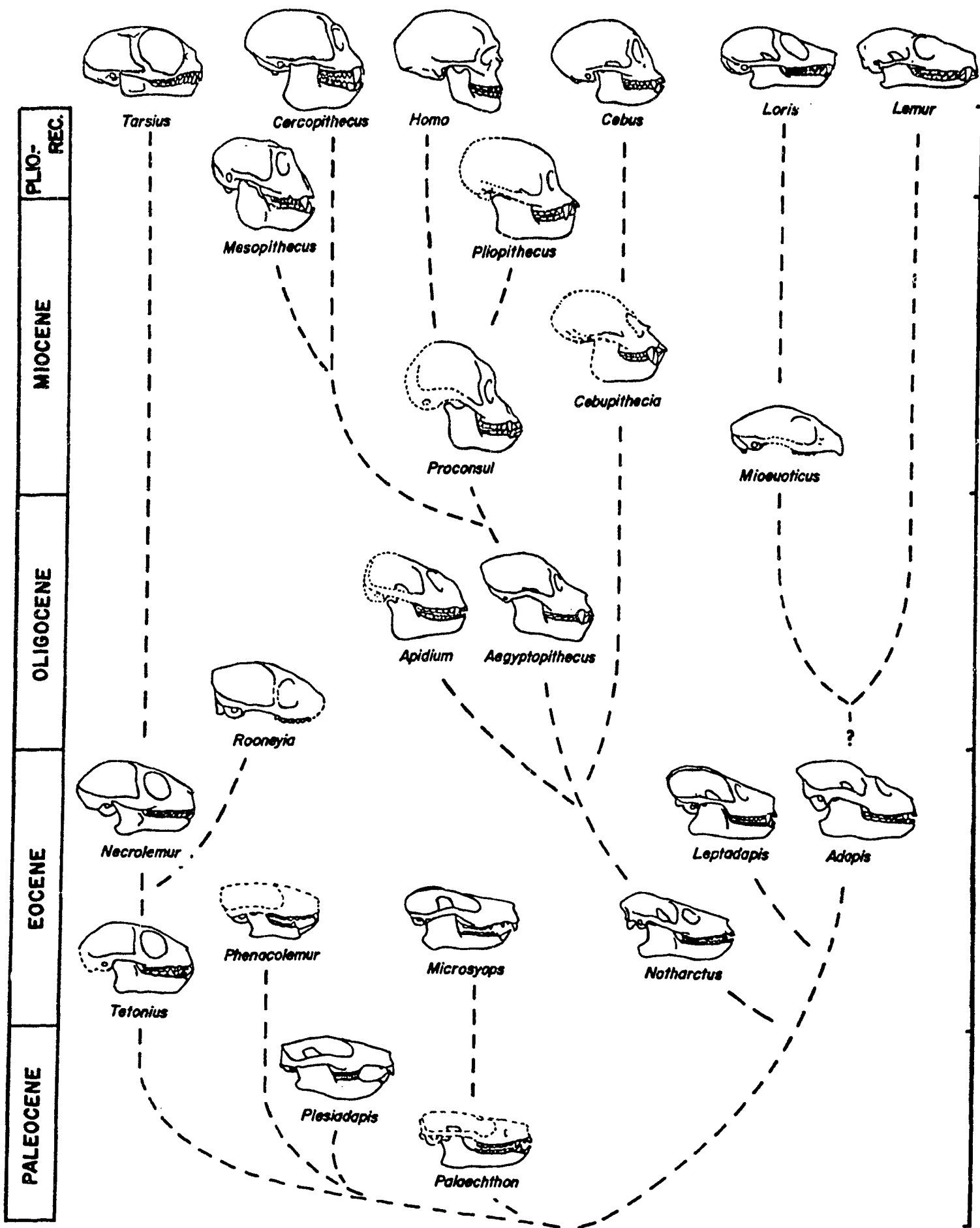
In the following discussion, two phylogenetic problems which have a less dense and less continuous fossil record are outlined. The fossil evidence bearing on the origin of higher primates will be discussed first, followed by a discussion of the Plio-Pleistocene record of human evolution. Although the fossil evidence is in both cases less complete than that documenting the evolution of Early Eocene *Pelycodus*, the method of analysis employed here is the same as that applied in Figure 2.

3. The Fossil Record and the Origin of Anthroidea

The standard interpretation of primate phylogeny places the tarsier, among living prosimians, closest to the origin of the Anthroidea (cf. Figure 1). The idea that the tarsier is different from lemuriform primates and more closely related to the anthropoid primates dates back to the studies of Hubrecht (e.g. 1897) on the placenta, Gadow's (1898) classification of the primates, Pocock's (1918) study of the rhinarium, Woollard's (1925) study of the gross anatomy of *Tarsius*, and other anatomical studies as well. The idea also derived much support from Schlosser's (1911) misinterpretation of the anterior dentition of the Oligocene catarrhine *Parapithecus* (cf. Elliot Smith, 1919, p. 474). Subsequently, the phylogenetic hypothesis that the tarsier is the living prosimian most closely related to the Anthroidea has rarely been seriously questioned, and the arrangement is now commonly formalized in classifications by uniting the tarsier with higher primates in the suborder Haplorhini.

Convincing fossil evidence supporting the derivation of higher primates from a tarsioid ancestral stock has never been offered. The evidence sometimes put forward in support of a tarsioid origin of Anthroidea has proven in some cases erroneous, and in other cases non-diagnostic. (a) As Simons has discussed in a series of papers (the most recent being 1974), Schlosser misinterpreted the anterior dentition of *Parapithecus* due to a break through the symphyseal region of the mandible. (b) The external auditory tube of *Necrolemur* and other fossil tarsioids resembles that of modern Catarrhini, but it is unlike the ring-shaped ectotympanic of all early fossil anthropoids yet known. (c) Supposed molar resemblances of fossil Omomyidae to early anthropoids simply reflect a basic primate pattern—there is nothing about the molar morphology of omomyids that favors them as anthropoid ancestors over Eocene adapids. Furthermore, two of the few "omomyids" known from the Eocene of Eurasia which might be considered to be related to the origin of higher primates (*Periconodon* and *Hoanghoni*) are not omomyids but adapids (Szalay, 1974: 53; Gingerich, 1977).

Figure 4. Skulls of representative living and fossil primates arranged in relative stratigraphic order. Dashed lines show the proposed pattern of phenetic linking in a very general way. Note particularly the close linking of tarsioids with plesiadapiform primates, and of anthropoids with adapid primates. *Notharctus* is representative of primitive adapids only—anthropoid primates were almost certainly derived from an Old World adapid, not *Notharctus* itself. *Leptadapis* is now regarded as a synonym of *Adapis* (Gingerich, 1977).



The fossil evidence

In recent years much new fossil evidence has been discovered which bears on the problem of anthropoid origins. The most important of this new evidence was discovered and collected from Oligocene sediments in Egypt by Yale expeditions directed by E. L. Simons. This evidence includes a nearly complete cranium of the early ape *Aegyptopithecus*, portions of several skulls of *Apidium*, and the more complete dentitions of *Parapithecus* alluded to above (Simons, 1974). A new skull of *Rooneyia* (Wilson, 1966), and additional study of the skulls of *Phenacolemur* (Szalay, 1972), *Plesiadapis* (Russell, 1959; Gingerich, 1975a); *Microsyops* (McKenna, 1966; Gingerich, 1976b), and *Palaechthon* (Kay & Cartmill, 1974) have also contributed to our understanding of the early evolution of primates. Representative fossil skulls contributing significant information on the phylogenetic history of primates are illustrated in Figure 4.

The skulls in Figure 4 are organized by their stratigraphic position. Following the methodology outlined above, the skulls can then be linked on the basis of close stratigraphic proximity and close anatomical similarity. The dashed lines in Figure 4 show, in a very general way, the pattern of stratophenetic linking connecting the major groups of fossil primates known from skulls. In some instances additional dental evidence is available supporting the linking. Thus, for example, *Palaechthon* and *Microsyops* appear on the basis of close dental resemblances to be very closely related, *Palaechthon* probably being ancestral to *Microsyops* (Bown & Gingerich, 1973). *Tetonius*, *Plesiadapis*, *Phenacolemur*, etc., appear to form a fairly closely linked group of Paleocene and Eocene tarsier-like primates (Gingerich, 1975a). *Notharctus*, "*Leptadapis*" and *Adapis* also form a closely linked group of "lemuroid" primates.

The cercopithecoid, hominoid and ceboid primates link together to form an anthropoid group apparently radiating initially in the Late Eocene. Of particular interest is the question of where this group of Anthropoidea links with earlier and possibly ancestral Eocene primates. As is apparent in Figure 4, there are two possibilities: the anthropoids may have been derived from the Eocene tarsier-like group of primates (*Tetonius*, etc.), or from the Eocene "lemuroid" group (*Notharctus*, etc.). Comparing Oligocene anthropoids (especially *Apidium* and *Aegyptopithecus*) with Eocene tarsioids and "lemuroids", the early anthropoids show much greater similarity to primitive adapoids such as *Notharctus* than to any known living or fossil tarsioid. This resemblance includes such features as the following.

1. *General skull shape*—primitive anthropoids and Eocene adapoids both have a relatively long snout with approximately parallel tooth rows, whereas Eocene tarsioids are characterized by a shorter snout and more divergent mandibular rami.
2. *Symphyseal fusion*—primitive anthropoids and several Eocene adapoids have solidly coossified mandibular rami, whereas all Eocene tarsioids have a mobile mandibular symphysis.
3. *Incisor morphology*—primitive anthropoids and all Eocene adapoids have short, nearly vertical incisors with spatulate crowns and I_1 relatively smaller than I_2 , whereas Eocene tarsioids have more procumbent incisors with moderately to sharply pointed crowns and I_1 equal in size to or sometimes much larger than I_2 .
4. *Canine morphology and sexual dimorphism*—primitive anthropoids and Eocene adapoids have strong, interlocking upper and lower canine teeth with a caninc honing faet

on the most anterior lower premolar, whereas the canine teeth of Eocene tarsioids are usually small, premolariform, and often do not occlude at all. The canines of *Aegyptopithecus* appear to have been sexually dimorphic as in most modern anthropoids—this dimorphism is apparently present in some Eocene adapids (a quantitative study is in progress), but has never been suggested for an Eocene tarsioid.

5. *Cheek tooth morphology*—primitive anthropoids and many Eocene adapoids have quadritubercular lower molars with the paraconid cusp being greatly reduced or lost entirely, whereas a paraconid is retained on the lower molars of most Eocene tarsioids.
6. *Ectotympanic morphology*—primitive anthropoids and Eocene adapoids have a ring-shaped ectotympanic which is either partially free within the auditory bulla (adapoids, ?*Apidium*) or fused to the lateral wall of the bulla (*Aegyptopithecus*, platyrrhines), whereas the two Eocene tarsioids for which the auditory region is known (*Necrolemur* and *Rooneyia*) have a tarsier-like tubular ectotympanic.

The latter feature, ectotympanic morphology, was first emphasized by Gingerich (1973), and several reviews critical of the interpretation proposed in that paper have appeared subsequently (Hoffstetter, 1974a,b; Hershkovitz, 1974; Cartmill, 1975). While not wishing to overstate the meagre evidence in this case, two important points should be emphasized. First, *Apidium* (and *Aegyptopithecus*) clearly did not have an extended external auditory tube like later catarrhines or like all known tarsioid primates. Both had basically a platyrrhine ectotympanic configuration. The ectotympanic of *Apidium* apparently differed from that of living and fossil platyrrhines (where known) in having the distal end of the annulus resting in a cup-shaped depression in the squamosal, rather than fused to it over a broad flat area. This latter feature suggests that the ectotympanic ring itself may have been partially free of the auditory bulla—a condition seen in Eocene “lemuroids” and modern lemurs, but completely unlike the anatomy of any living or fossil tarsioid.

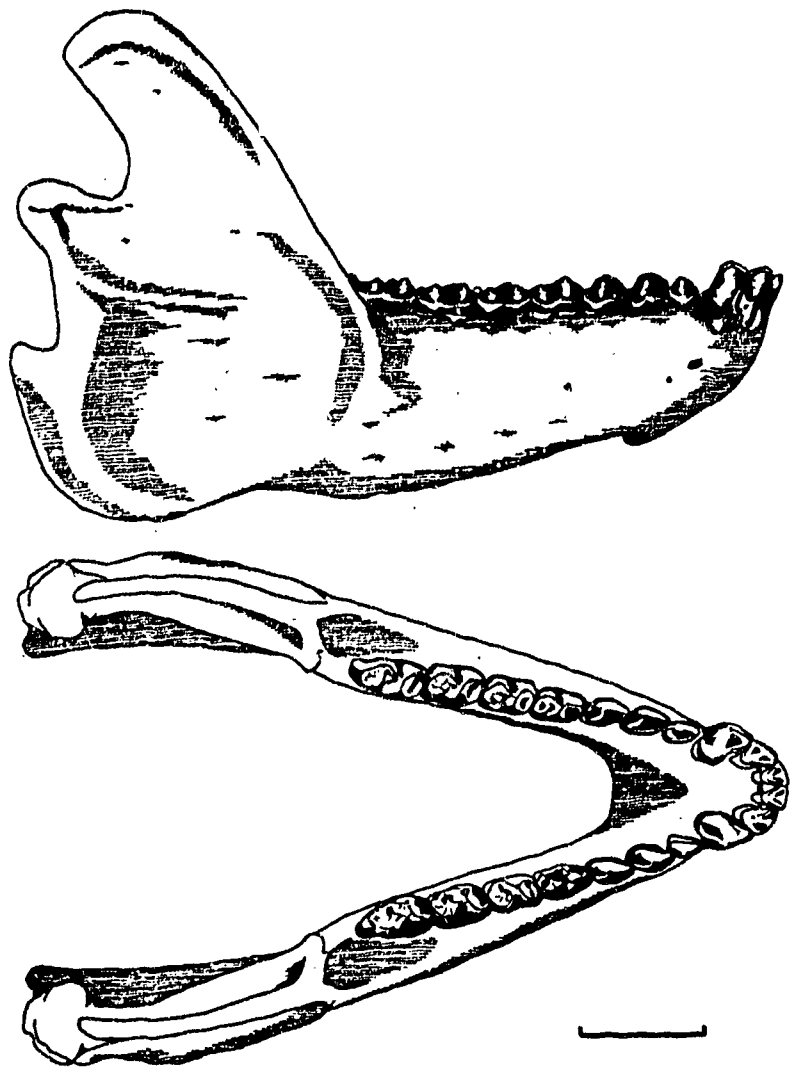
Adapoids and “lemuroids”

As a result of further study, it is now clear that considerable caution must be used when comparing Eocene “lemuroids” (i.e. adapoids) with modern lemurs, and the term adapoids will henceforth be used to refer to the known Eocene “lemuroids”.

Among the Eocene adapoids, *Adapis* appears to be the most likely ancestor of the living lemuroids and lorisoids. *Adapis* has a unique anterior dentition consisting of two lower canines and four lower incisors which together form a single sectorial functional unit (Figure 5). Such a six-tooth anterior dental unit would appear to be possibly preadapted to form the six tooth dental comb or scraper seen in lemuroids and lorisoids. *Adapis* also shares a number of unique cheek tooth features with *Hapalemur* and *Lepilemur* (Gingerich, 1975b). However, a major problem with linking the living lemuroids to *Adapis* or a similar ancestor arises because of the virtually complete gap in the fossil record of some 40 million years between known *Adapis* fossils and the modern lemurs. The density and continuity of the fossil record is simply not sufficient to indicate anything very certain about the origin of modern lemurs.

Furthermore, in testing this particular linking of adapoids and lemuroids cladistically, it is clear that some important features (such as the free ectotympanic ring) are probably

Figure 5. Reconstruction of the mandible of an adapoid *Adapis parisiensis*, based on Princeton University specimen 11499 and on specimens in the Muséum National d'Histoire Naturelle in Paris. Note particularly the anthropoid sectorial incisors and fused mandibular symphysis. Note also the incisiform canines in this species. Scale = 1 cm.



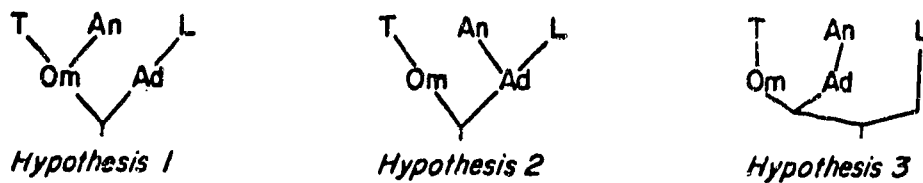
shared retentions of the primitive condition and thus cannot be weighted very heavily as phylogenetic evidence. The possibility remains that lemuroids and lorisooids are derived from some distinctive Late Cretaceous or Paleocene stock of early primates for which no fossil record is presently known (a possibility we consider unlikely).

Adapoids and anthropoids

The linking between early Anthropoidea and Eocene adapoids is much closer than that between modern lemuroids and adapoids, being supported by a fairly dense and continuous series of anatomically and temporally intermediate forms. In fact, it is sometimes difficult to distinguish advanced adapoid primates from primitive anthropoids: *Oligopithecus*, *Amphipithecus* and *Cercamonius* (Gingerich, 1975c) are three such intermediate forms of considerable importance in this regard.

The most commonly advanced phylogeny of primates is outlined below as Hypothesis 1 (where T = Tarsiidae, An = Anthropoidea, L = living Lemuroidea, Om = Omomyidae, Ad = Adapidae). Under this hypothesis both Tarsiidae and Anthropoidea are derived from omomyids, and lemurs are derived from adapids. On the basis of the paleontological record and the linkings discussed above, an alternative phylogeny is advanced here, labelled Hypothesis 2—here tarsiids are derived from omomyids, but both anthropoids and lemurs are derived from adapids. Taking into account the relatively weak linking of lemurs and lorises with adapids due to the very poorly known fossil record of these forms after the Eocene (Figure 4), a third phylogenetic hypothesis cannot be ruled out. Hypothesis 3 differs from Hypothesis 2 only in showing a derivation

of lemurs and lorises from the ancestral primate stock rather than directly from known adapids. The three hypotheses can be diagrammed as follows:



These appear to be the three most likely hypotheses of primate relationships, and none of the three can be completely eliminated from consideration. Each has certain comparative anatomical or paleontological evidence in its favor, but each also requires a significant amount of parallel evolution. Hypothesis 1 is consistent with the conclusions of Pocock (1918) with regard to the rhinarium in primates, and Lockett (1974) with regard to placental evolution in primates, in that the Tarsiidae and Anthropoidea (and presumably the Omomyidae) share a haplorhine rhinarium and a hemochorial placenta. However, Hypothesis 1 also requires a considerable amount of parallel evolution for all of the characters listed above which are found in primitive Anthropoidea and Adapidae but are unknown in Omomyidae.

Hypothesis 2 is consistent with the paleontological evidence in that the connection between Anthropoidea and Adapidae is supported by a fairly dense and continuous fossil record. Similarly, Tarsiidae and living lemuroids are plausibly derived from Omomyidae and Adapidae, respectively. However, this hypothesis contradicts the evidence just cited regarding the distribution of a haplorhine rhinarium and hemochorial placenta in primates—these soft anatomical characters would have to be interpreted as resulting from parallel evolution or possibly as retentions of the primitive primate condition.

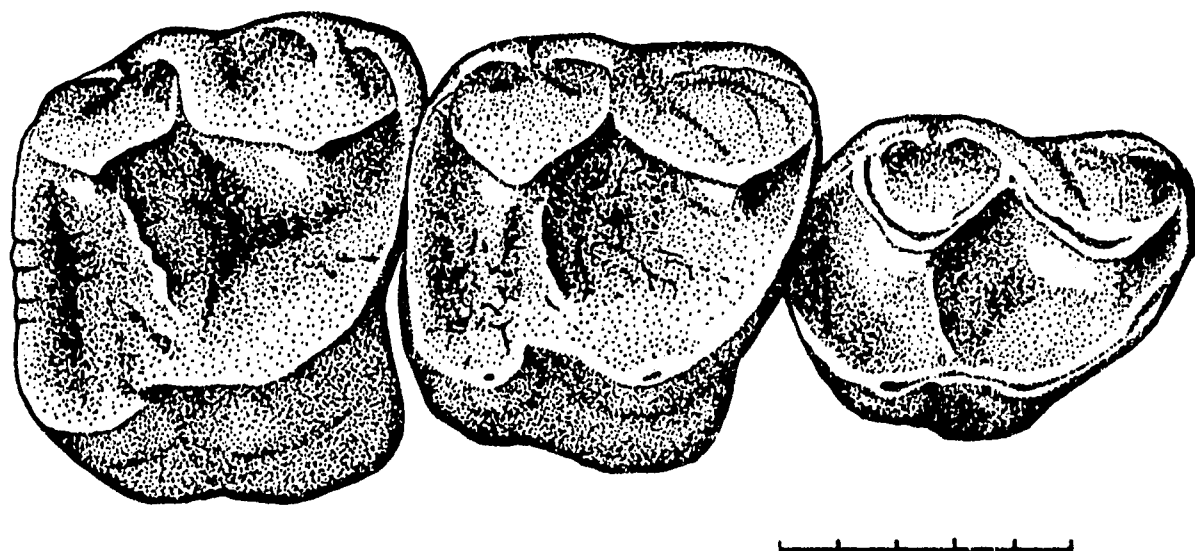
In some ways Hypothesis 3 is the most attractive. It is consistent with evidence for deriving Tarsiidae from Omomyidae, and Anthropoidea from Adapidae. Hypothesis 3 is also consistent with the distribution of nasal form and hemochorial placentation in Tarsiidae and Anthropoidea (and presumably in Omomyidae and Adapidae as well). The dental resemblances of some adapids to some living lemuroids would have to be interpreted as results of parallel evolution under Hypothesis 3.

Considering the continuity of the fossil record illustrated in Figure 4 and the existence of some apparently derived dental resemblances shared by adapids and living lemuroids (Gingerich, 1975b), Hypothesis 2 appears to be the strongest—although Hypothesis 3 cannot be ruled out. Unless considerable new fossil evidence is found bridging the broad morphological gap between omomyids and primitive anthropoids, Hypothesis 1 appears the least likely of the three hypotheses.

Hypocones, biogeography and the origin of South American monkeys

Two additional points might be added here which have a bearing on the origin of South American platyrrhines and the early evolution of Anthropoidea. The earliest South American primate, *Branisella*, comes from lower Oligocene strata of Bolivia. It is known only from one fragmentary maxilla, but it appears to represent an early platyrrhine monkey (Hoffstetter, 1969). Thus it is clear that anthropoid primates entered South America sometime before the Early Oligocene. From what stock of earlier primates are they derived, and how did they reach South America?

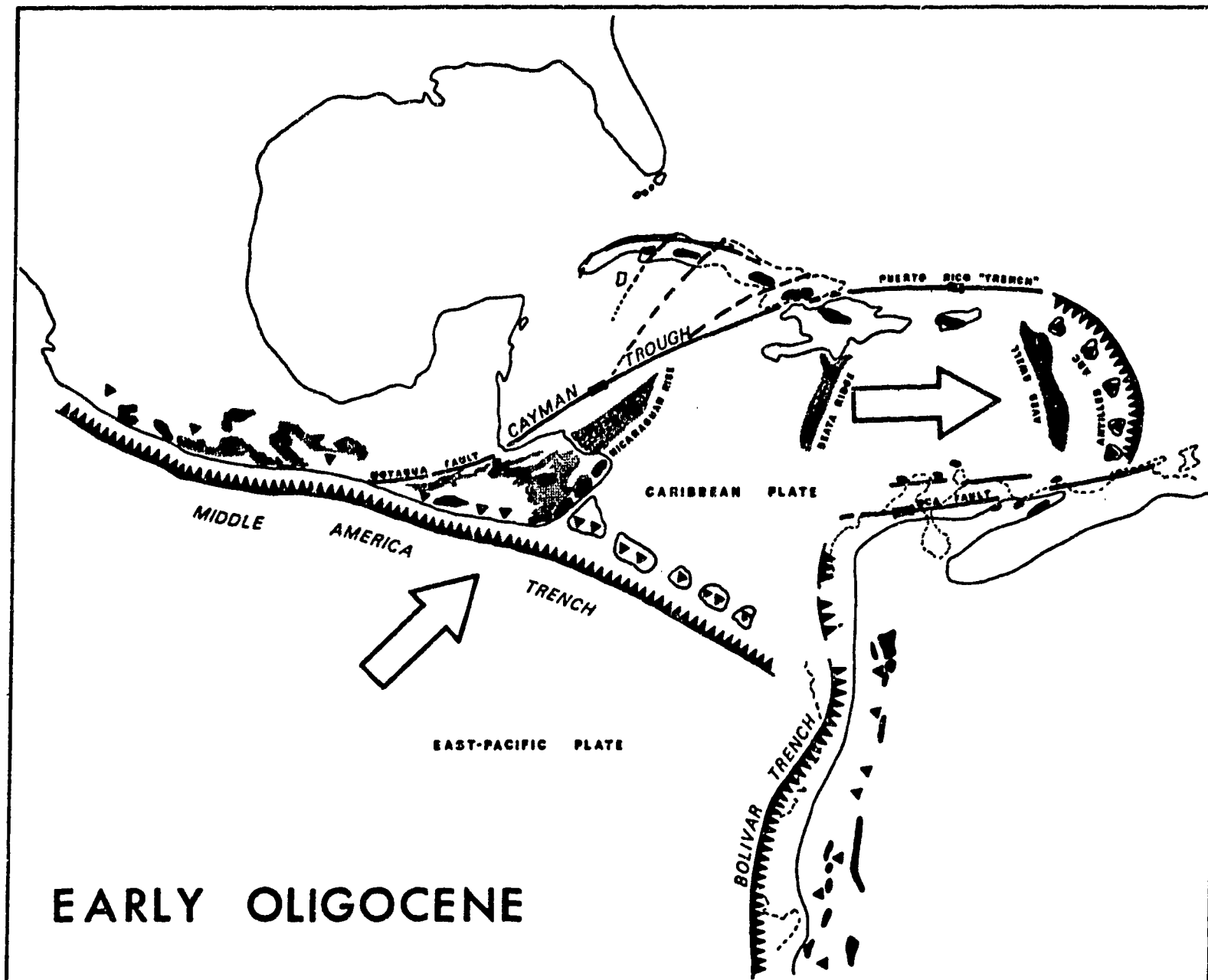
Figure 6. Right dP^4M^{1-2} of *Alouatta palliata* showing "pseudohypocones" developed on the postprotocingulum rather than on the internal cingulum. This is especially clear on dP^4 . Miocene *Cebupithecia* and recent *Callicebus* also have pseudohypocones. Specimen illustrated is University of Michigan Museum of Zoology no. 76692. Scale = 5 mm.



The adapid *Notharctus* and its relatives from the Eocene of North America are sometimes considered as possible ancestors of South American monkeys, but they are generally ruled out of such an ancestral position because of their different mode of development of the hypocone cusp on the upper molars. In notharctines (European *Pelycodus* excepted) the hypocone is formed from the postprotocingulum or "nannopithec-fold" behind the protocone (a so-called "pseudohypocone"). Most anthropoid primates, on the other hand, have a "true" hypocone formed from the posterolingual basal cingulum of the upper molars. As Figure 6 shows, some South American anthropoids do have a *Notharctus*-like "pseudohypocone", so this is clearly not an absolute character ruling out a notharctine origin of platyrrhine monkeys. However, the fact that the earliest platyrrhine *Branisella* has a "true" hypocone suggests that this condition is probably primitive within platyrrhines, and for reasons of morphological continuity it seems likely that Old World adapids rather than North American notharctines gave rise to the Anthropoidea. The paleogeographic distribution of early anthropoids in Asia and Africa during the Late Eocene and Early Oligocene lends further support to this hypothesis.

The second question to be discussed here concerns the nature of the seaway separating North and South America in the Eocene and Oligocene, and the time and route of colonization of South America by primates. Frakes & Kemp (1972), Hoffstetter (1974b), and others have stated or implied that North and South America were distantly separated in the early Tertiary, and that deep open ocean with a strong east-west equatorial current lay between. Hoffstetter (1974b, p. 347) further implies that rafting of primates from Africa to South America would be easier than rafting from North America to South America. Several points argue against the geographic reconstruction described by Hoffstetter and others. Our 1975 University of Michigan expedition, collecting in early Eocene strata in Wyoming, discovered the third specimen of a notoungulate mammal to be found in North America. Notoungulates underwent a broad radiation in South America beginning in the Paleocene, and the presence of a notoungulate in North America in the early Eocene would be difficult to explain if North and South America

Figure 7. Paleogeography of the Central American region in the Early Oligocene. Solid triangles represent volcanoes. Note two possible migration routes via present Central America and via the West Indies. From Malfait & Dinkelman (1972).



were separated by the barriers of distance and ocean currents implied by Frakes and Kemp, and by Hoffstetter.

The geology of Central America is very difficult to study, since this region has been tectonically active and continuously evolving throughout the course of the Tertiary, and its geology is nowhere very well exposed today. Nevertheless, a coherent picture of the geological history of this critical region is slowly beginning to emerge from geological and geophysical studies. In a recent summary, Malfait & Dinkelman (1972, see also Barr, 1974) present a series of paleogeographic maps showing the development of the Caribbean lithospheric plate. Their reconstruction of this region in the Early Oligocene is of considerable interest to the present discussion (Figure 7). The distances between North and South America are not portrayed as being nearly as great as those given by Frakes & Kemp (1972), nor does the seaway separating the two continental masses appear to be the open ocean implied by Hoffstetter. Not one but two volcanic chains connected the two continents, one in the position of the present Central America, the other following the course of the present West Indies.

While much additional detailed work remains to be done on the mammalian faunas of the northern and southern hemispheres and on their migrations, an earlier study by Simpson should be noted in the context of the above discussion. Comparing the North American and Eurasian mammalian faunas of the Tertiary, Simpson (1947) found that the Late Eocene and Early Oligocene were times of great faunal interchange, particularly between North America and Asia. The Late Eocene was the time of first appearance of ambiguous adapoid-anthropoid primates, it was a time of significant holarctic faunal migration of mammalian faunas and, given the paleogeographic reconstruction of Figure 7, it is not unreasonable that this is the time primates first entered South America. Where these early anthropoids originated remains a problem (?Africa, ?Asia), but the fossil record suggests that they were derived from an adapoid rather than tarsoid ancestral stock, and it seems most likely that platyrrhines entered South America after migrating through North America.

4. Phylogeny of East African Hominidae

In the preceding sections a method of phylogeny reconstruction has been outlined that emphasizes the importance of stratigraphy in organizing fossils into limited time intervals for study. Within each temporal interval it is necessary to determine the number of biological species sampled. The samples of species from each stratigraphic interval are then linked to similar samples from adjacent stratigraphic intervals which, given a sufficiently dense and continuous fossil record, yield a pattern reflecting the phylogenetic history of the group under study. This stratophenetic approach is fundamentally different from others commonly employed in paleontology and paleoanthropology in both method and results.

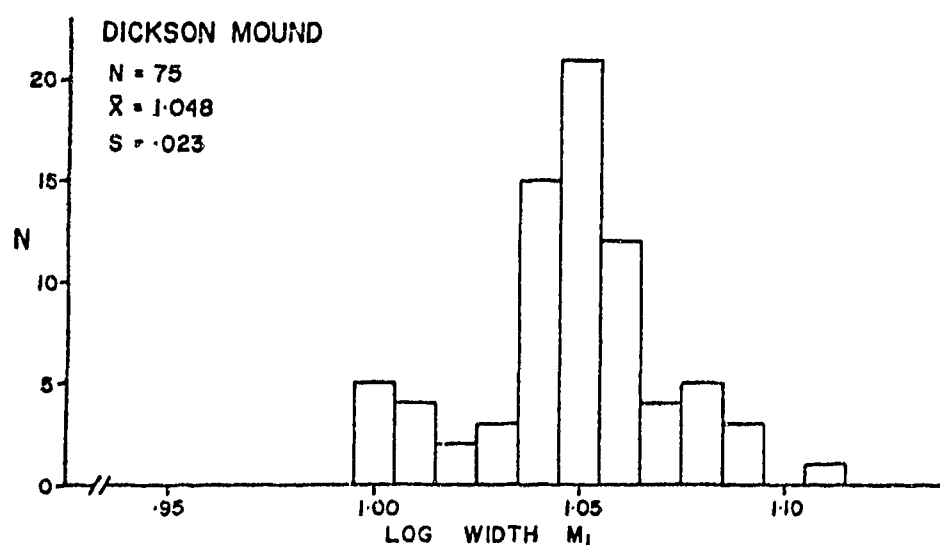
The stratophenetic approach differs from other methods in three important ways that strongly affect resulting interpretations, as follows.

(1) Fossils are sought from stratigraphically related localities. Isolated fossil localities which cannot be reliably dated relative to each other can contribute very little toward understanding the direction or rate of evolution of a taxon. For example, the South African *Australopithecus* sites have greatly increased our knowledge of the anatomy of *Australopithecus* but they have contributed relatively little to understanding *evolution* within this genus. The East Rudolf fossil hominid localities in Kenya, on the other hand, are of unique importance because the relative temporal relationships of fossils there can be determined stratigraphically.

(2) A given sequence of strata is broken into as many successive stratigraphic intervals as possible in order to resolve as much detailed evolutionary change as possible. Here again the East Rudolf sequence of sediments, being divisible into four successive stratigraphic intervals spanning some 1.5–2 m.y., potentially preserves a sufficiently detailed fossil record to reveal continuous evolutionary change.

(3) The stratophenetic approach is explicitly non-typological. Only after a pattern of change through time is discovered and interpreted are names applied to segments or intervals of the pattern. The alternative approach, common practice in paleoanthropology, seeks first to group and name fossils according to arbitrary morphological characteristics. The relationships between these "types" or "species" are then analyzed, often with no attention being paid to the stratigraphic relationships between "types" or to the real variation within each.

Figure 8. Histogram of log M_1 width for 75 modern humans of both sexes from Dickson Mound. Data from Wolpoff (1971).



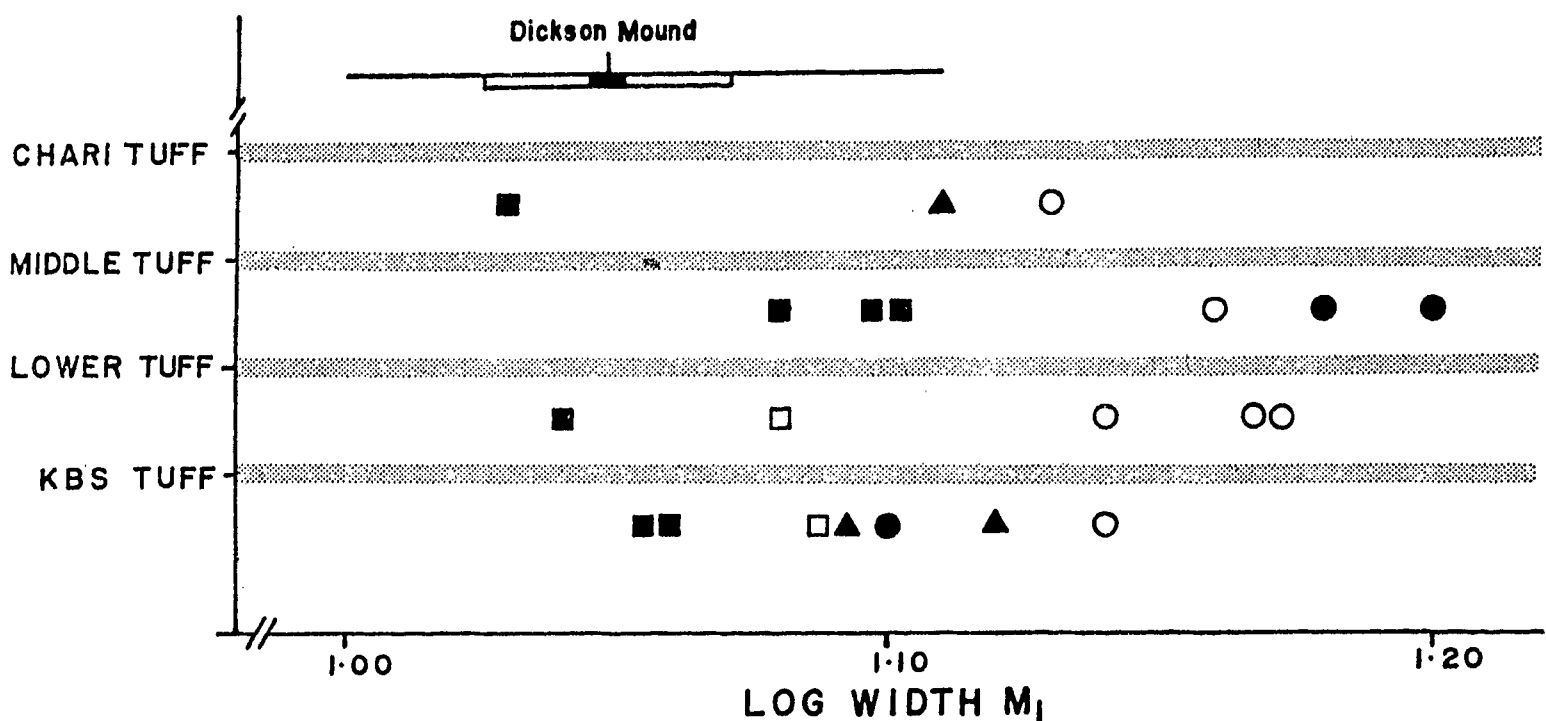
A recent publication by Eldredge & Tattersall (1975, p. 236) illustrates a highly arbitrary and typological analysis of fossil hominids. For example, discussing *Australopithecus* they state, "We have chosen here to lump Olduvai hominid 7 and its lower Bed I paratypes into *A. africanus*; if a distinction were to be made, *A. africanus* and *A. habilis* would form a primary sister group divided by a single character: possession by the latter of a brain greater than 600 cm³ in size", and it is not surprising that they conclude: "To be quite blunt, then, *A. africanus* is so primitive that it tells us nothing . . . about human evolution". If an evolutionary pattern were sought from the actual fossils and their stratigraphic distribution rather than temporally heterogeneous artificial groups lumped or divided by choice to satisfy arbitrary morphological criteria (e.g. "a brain greater than 600 cm³ in size"), we doubt that the primitiveness of *Australopithecus africanus* would tell us *nothing* about human evolution.

Early hominids and stratigraphy

Hominid fossils have rarely been studied in stratigraphic context because, until recently, very few were known from a significant stratigraphic context. Pilbeam & Zwell (1972) attempted to date various Plio-Pleistocene hominids to the nearest 0.5 m.y. and plotted histograms of tooth measurements for samples from each successive time interval. We have undertaken a more modest analysis here which is limited to the East Rudolf fossil hominids to illustrate again the stratophenetic approach to phylogeny reconstruction. Significantly, our results appear not to differ greatly from those of Pilbeam & Zwell.

Before proceeding with analysis of the East Rudolf fossils, it is necessary to consider briefly the distribution of tooth measurements in a single modern human population for comparison with the fossil samples. The distribution of the width of M_1 in a sample of 75 modern humans from Dickson Mound is presented in Figure 8 (data from Wolpoff, 1971). A measure of M_1 size is used to characterize the size of individuals because this tooth is usually one of the least variable in size within a given mammalian population, and it is thus usually the best tooth on which to base attempted diagnoses of closely related species from the same stratigraphic intervals (Gingerich, 1974c). Only the width of M_1 is used here to avoid possible variability in tooth size introduced by interproximal wear against adjacent teeth. The width of M_1 has been plotted on a logarithmic scale to facilitate later comparison with other samples from populations of larger body and tooth size.

Figure 9. Stratigraphic distribution of fossil hominids at East Rudolf, Kenya. Log M_1 width is plotted for samples from four successive stratigraphic intervals separated by tuffs. Dickson Mound sample at top gives comparative scale for interpreting East Rudolf hominids at each level: horizontal line is range, vertical slash is mean, open bar is one standard deviation, solid bar is standard error of mean (see Figure 8). In East Rudolf samples squares represent *Homo* sp. of authors, circles represent *Australopithecus* sp. of authors, triangles represent undetermined specimens. Open figures are all estimated from other tooth measurements for those specimens via regressions, and thus they are less reliable than solid figures. Note particularly the well separated modes in the two middle levels, suggesting the probable presence of two hominid lineages.



As expected, the distribution of M_1 widths in the Dickson Mound sample is approximately normal, with most specimens falling near the mean of 1.05. Other human populations might show a wider range of variation, but it is very unlikely that any would show significant bimodality in a measurement like the width of M_1 . Plotting tooth measurements of highly dimorphic gorillas in the same way (data from Mahler, 1973) yields a distribution with a greater range of variation than the Dickson Mound population used here, but even highly dimorphic gorillas still show no significant bimodality in the width of M_1 . Sampling specimens at random from normally distributed populations like these, most would fall near the mean value although occasionally an outlying specimen might be sampled. One would expect the same unimodal distributions of this trait to characterize populations of fossil hominids.

The fossil specimens from East Rudolf are important to any discussion of hominid evolution since the stratigraphic sections there include several secondarily deposited volcanic tuffs dividing the sequence into four separate time intervals, each containing a number of fossil specimens. Various parameters of the fossil hominids could be plotted in this stratigraphic context to see if any significant pattern of distribution or change emerges. For illustrative purposes we have plotted in Figure 9 the log of the width of M_1 (solid symbols) for specimens from each of the four stratigraphic intervals at East Rudolf. Teeth are by far the most common hominid remains at East Rudolf and elsewhere, and they are in fact the only skeletal elements preserved in sufficient numbers

and from a sufficient number of stratigraphic intervals to permit a significant stratigraphic analysis.

Open symbols in Figure 9 are estimated widths of M_1 for additional specimens, estimated from regression equations relating M_1 width to the width of P_3 , P_4 , M_2 or M_3 . All hominid specimens plotted were collected at East Rudolf between 1968 and 1973, and subsequently described in a series of papers by Day & Leakey (1973), Day *et al.* (1975), Leakey (1970, 1971, 1972, 1973*a,b*, 1974), Leakey, *et al.* (1971, 1972), Leakey & Walker (1973), Leakey & Wood (1973, 1974*a,b*). The stratigraphic context is that outlined by Brock & Isaac (1974). The range of variation in the Dickson Mound sample of 75 specimens described in Figure 8 is also plotted at the top of Figure 9 for comparison with the East Rudolf sample. Squares in Figure 9 represent the specimens identified by authors as *Homo* sp., circles represent *Australopithecus* sp. of authors, and triangles represent specimens considered a third, sometimes a fourth lineage, or specimens which are too incomplete to permit generic determination. Dr Milford Wolpoff generously made his original measurements of all of the East Rudolf hominids discussed here available to us, and we have thus had the advantage of comparing measurements made by a single scholar.

Interpretation

Considering the sample illustrated in Figure 9 as a whole, no pattern is obvious. However, when the specimens are organized into stratigraphic intervals and each interval analyzed in turn, a pattern does begin to emerge. The lowest interval includes specimens placed in *Homo* and *Australopithecus* as well as two additional specimens. Considering only the width of M_1 , and comparing the distribution of this character with the distribution of the Dickson Mound sample, it is not clear that more than a single biological species is being sampled from below the KBS tuff. In the next highest interval, between the KBS and Lower tuffs, the distribution includes two widely spaced clusters suggesting that two hominid lineages were present at this level. Similarly, in the next higher interval, between the Lower and Middle tuffs, the two widely spaced clusters suggest two distinct hominid lineages at that time. In the highest interval sampled, between the Middle and Chari tuffs two clusters are present which might represent two lineages, although they could possibly be sampled from both tails of the distribution of a single evolving lineage.

The simplest hypothesis, that a single hominid lineage was evolving through the course of the Plio-Pleistocene in the area of Lake Rudolf seems an unlikely one, judging from the pattern of Figure 9, if the variability of the Dickson Mound comparative population is in any way representative of the variability of populations of fossil hominids. Furthermore, considering their bimodality, it appears rather improbable that the distributions of measurements in the middle two intervals in the East Rudolf sequence were sampled from normally distributed populations of a single hominid lineage.

The possibility of two coexisting evolutionary lineages, one large and one small, is the next simplest hypothesis to be entertained. The distribution of data points in the two middle intervals of Figure 9 appears to accord well with this hypothesis, the squares representing the smaller lineage ("*Homo*") and the circles representing the larger lineage ("*Australopithecus*").* If the lowest interval includes variants of only a single

* See note added in proof.

hominid lineage or two very recently separated lineages, there is in addition a strong suggestion of character divergence through the course of the lower three intervals. Adaptive differences in morphology permitting two hominid lineages to coexist in the East African Plio-Pleistocene have not yet been demonstrated, but it should be noted that body size itself is perhaps the most important single component of an animal's adaptation, and the differences in body size between the small and large hominid lineages might have been sufficient to permit their coexistence with a considerable degree of sympatric overlap.

Interpretation of the M_1 measurements for the interval above the Middle tuff is as yet unclear because the distribution of the few specimens from this level does not yet link well to the interval below. It is possible that by this time the large lineage had become extinct, and that only the lineage of smaller specimens leading to modern humans remained. Considering the variability of the modern Dickson Mound population and the pattern of tooth measurements in Figure 9, there seems no reason to suggest the presence of more than two hominid lineages in the East African Plio-Pleistocene.

We recognize that the available sample sizes utilized in Figure 9 are too small to permit any definitive answer to the question of how many hominid lineages are represented at East Rudolf, and offer the above interpretations chiefly to illustrate the kind of information available when fossils are considered in their stratigraphic context. Large samples are sometimes not really as important as the pattern that emerges from a stratigraphic diagram like that of Figure 9, although larger samples will of course inspire more confidence in the stability and reality of any pattern emerging.

The East African fossil record is unique in preserving abundant fossil hominid material in a reasonably detailed stratigraphic context. In the interest of discovering actual evolutionary patterns of change in dental parameters, brain size, or any other character of interest, we urge that this unique material be studied explicitly in stratigraphic context. Only in this way can spatial and temporal variation be analyzed and the evolutionary complexity of early hominid evolution elucidated.

5. Summary and Conclusions

The stratophenetic method of reconstructing the phylogeny of a group of mammals with a good fossil record involves: (1) organization of all fossils in their stratigraphic context, (2) linking phenetically similar mammals present in adjacent stratigraphic intervals, (3) cladistic, geographic, etc., testing to determine whether the given phylogeny makes sense in terms of character evolution, geographic dispersal, etc. Much of the confidence inspired by a given pattern of phylogenetic linking depends on the density and continuity of the fossil record supporting the linking.

Fossil tarsiiiform and plesiadapiform primates appear to form a closely linked group of aberrant Paleocene and Eocene primates, while fossil adapoids and early anthropoids form another tightly linked group. Fossil, paleogeographic, and faunal evidence suggests that the initial radiation of anthropoids from an adapoid ancestry occurred in Africa or Asia in the Late Eocene, with protoplatyrrhines reaching South America by the early Oligocene via North America.

Teeth are by far the most common Plio-Pleistocene hominid remains at East Rudolf and they are the only skeletal elements preserved in sufficient numbers to permit a significant stratigraphic analysis of evolutionary change. Analysis of hominid tooth

size for specimens from four successive stratigraphic intervals at East Rudolf, and comparison of the resulting pattern with variation in a modern human population suggests that two hominid lineages probably coexisted through a significant portion of the East African Plio-Pleistocene, but more importantly, this analysis illustrates the value of studying hominid fossils in their stratigraphic context.

Finally, we should emphasize again that it is not sufficient to collect fossil primates from different intervals of the Tertiary, or fossil hominids from different intervals of the Plio-Pleistocene if their stratigraphic context is then ignored when the fossils are studied and compared. Fossils are the only historical documents bearing on phylogeny reconstruction, a science which is essentially historical.

The methodology outlined here is an outgrowth of detailed stratigraphic studies of Early Eocene *Hyopsodus*, *Pelycodus*, etc., collected by recent Yale expeditions directed by E. L. Simons, and we are indebted to Professor Simons for free access to these collections and for numerous discussions on phylogeny reconstruction and primate evolution. We are also indebted to Professors C. L. Brace and M. H. Wolpoff for discussions relating to this paper. Dr Wolpoff generously gave free access to his extensive measurements of the dentition of East Rudolf fossil hominids. Krystyna Swirydczuk drew Figures 5 and 6, and assisted with Figure 4. Gladys Newton typed the manuscript, and Karoly Kutasi assisted with photography. This research was supported in part by a Faculty Research Grant from the Rackham School of Graduate Studies, University of Michigan. Drs Wolpoff, Brace, E. Delson, and N. Eldredge read the manuscript and their comments have improved it greatly.

Note added in proof

The final revised version of this paper was submitted in January 1976. Since then Leakey & Walker (*Nature* **261**, 572–574) have described a new hominid cranium KNM-ER 3733 from the stratigraphic interval above the KBS tuff at East Rudolf (now “east of Lake Turkana”). The new cranium has an endocranial volume estimated at about 800–900 cm³ and is strikingly like that of Peking *Homo erectus*. It occurs in the same stratigraphic interval as robust *Australopithecus* and provides a dramatic confirmation of the coexistence of two contemporaneous hominid lineages in East Africa, the point we have tried to make also in Figure 9.

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