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Diagnosis and Differentiation of the Order Primates

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ABSTRACT We contrast our approach to a phylogenetic diagnosis of the order Primates, and its various supraspecific taxa, with definitional procedures. The order, which we divide into the semiorders Paromomyiformes and Euprimates, is clearly diagnosable on the basis of well-corroborated information from the fossil record. Lists of derived features which we hypothesize to have been fixed in the first representative species of the Primates, Euprimates, Strepsirhini, Haplorhini, and Anthropoidea, are presented. Our classification of the order includes both holophyletic and paraphyletic groups, depending on the nature of the available evidence.

We discuss in detail the problematic evidence of the basicranium in Paleogene primates and present new evidence for the resolution of previously controversial interpretations. We renew and expand our emphasis on postcranial analysis of fossil and living primates to show the importance of understanding their evolutionary morphology and subsequent to this their use for understanding taxon phylogeny. We reject the much advocated "cladograms first, phylogeny next, and scenario third" approach which maintains that biologically founded character analysis, i.e., functional-adaptive analysis and paleontology, is irrelevant to genealogy hypotheses. Unlike the cladistic rules of operations demand, we advocate and use a priori weighting of characters.

We discuss the evidence for the various proposed relationships of the earliest euprimates, the Adapidae and Omomyidae, and show that linking the former with living Strepsirhini and the latter with living Haplorhini does not depend on the assumption of the presence of soft-anatomical characters in the fossils. On the contrary, it is the sharing of derived hard anatomical features of the fossil taxa with the living groups which makes their possession of either strepsirhine or haplorhine "soft" attributes probable.

We discuss the relative merits of the use of the grade concept (with its widely recognized implication of polyphyly) in attempts to group primates and maintain that there exists no evidence for either an "archaic primate" or a prosimian or an anthropoid grade. All the characters in the literature attributed to these are inherited from the first representatives of either the semiorder Paromomyiformes or the semiorder Euprimates or the semisuborder Anthropoidea. Consequently, we find neither descriptive nor didactic merit in gradal arrangements, the goals of which can be much better served by a phylogenetic (not cladistic) classification.

INTRODUCTION

In this study, we aim to show that evolutionary (or phylogenetic) diagnosis of the order Primates, including both the semiorder Paromomyiformes and the semiorder Euprimates, is eminently feasible. Furthermore, we will show that attempts to demonstrate that the order is only properly "definable" from the perspective of *living* forms or that the diagnosis of the order is only stratigraphically and "gradally" feasible are views based on theoretically unacceptable perspectives. The failure to recognize that a phylogenetic diagnosis of the order is possible stems from (1) a disregard for paleontological evidence, (2) differing interpretations of basicranial evidence, (3) the nonusage of postcranial and dental information, and (4) an emphasis on a concept of "grades."

Given the fact that primates are interesting animals (but, clearly, more importantly because they are our closest kin) the literature dealing with the "nature" of the taxon is often more about polemics than scientific reappraisals of sundry studies dealing with the subject. For example, seeking a "definition" of Primates often leads to an exercise in listing literature-derived facts and views. Similarly, there is a point of view, developed from the early days of cladistics, that the proper starting point for such a definition is the living species of primates (e.g., Martin, 1986). This is a "neontology-centered" and "fossil phobic" perspective without acceptable logical foundations. This is a view which, as Gingerich (1986) so aptly commented, cannot grapple with the very philosophical problems it engenders, such as which of the living primates is "more" of a primate than the other. We concur with Gingerich (1986) that a paleobiological perspective is equal to any neontological effort. Paleobiology provides a rare and unique perspective on living species, just as the study of the living brings powerful falsifiers into any paleobiologically based hypothesis.

For authors, particularly nonmorphologists or nonsystematists (see Glossary), who view fossils as yielding only the rudimentary anatomical observations, as is often the case in preliminary reports of new fossils, morphology has only limited significance. We suspect, however, that this perspective on form allows an equally limited appreciation of the form-function attributes of living taxa. For paleobiologists, however, who attempt to fathom both a historical and adaptive meaning, collections of fossil primates hold somewhat different potential. Gingerich (1986, p. 40) and Fleagle (1986) make a similar point concerning the importance of paleobiology. Thus, the numerous ways to study the intricate details of teeth and their mechanics, cranial shape, brain proportions, and the increasingly better-known and -appreciated evolutionary morphology of postcranials affords a vastly different perspective of the fossil record than the more limited views some have advocated (e.g., Martin, 1986).

THE ORDER PRIMATES: PROBLEMS OF DEFINITION AND GRADAL DIAGNOSIS

Definition vs. diagnosis of the Primates

What may seem at first a trivial distinction between the two concepts, definition and diagnosis, can have profound implications. As students of phylogeny (evolutionary history, and not sister group relationships only) we hold to the simple theoretical perspective that the last common ancestor of a monophyletic group (be it either paraphyletic or holophyletic) is not likely to transmit all of its characteristics in an unchanged form to its sundry descendants. It is not reasonable, therefore, to expect descendants of this common ancestor to share clear-cut (needing no interpretation) defining features, although this may occur. The notion of "definition," which Martin (1986) explored, is, we believe, geared toward the "key" mentality of practical guides, i.e., an attempt at a "technology" to use for the allocation of future or existing fossils rather than an interpretation of fossils. In Martin's (1986) view species are granted membership in taxa only by the virtue of their possession of certain defining synapomorphous attributes. But to expect terminal branches (species today, or in any other time-slice) of clades or phena of various lineage segments to have virtually unaltered "key" or "defining" characters is often very unrealistic in light of what we understand of the evolutionary process, stasis included. This attitude is referred to by many as "objective," in the same manner as the phenetic school of the 1960s considered its perspective to be free from any assumption of evolution. Anthropoids certainly inherited orbital rings but transformed them into posteriorly closed orbits, and hominids have transformed the *diagnostic* pedal grasping ability of the protoeuprimates and ape ancestors. Yet we do not exclude these latter taxa from the Euprimates.

To "define" a taxon like a large order is to assume that *all* of the descendants of the last common ancestor retained the characters of that morphotype, which, however, must have instantly evolved from its respective ancestry. While such a concept of definitions rigidly involves both the notions of punctuation and stasis as possible evolutionary processes, the origin of real species, or at least morphologically recognizable entities, appears to be different (see particularly Godinot's, 1985 , subtle and provocative analysis of this problem).

The point is simple. Phylogeny is the adaptive and nonadaptive change (the path of this change is genealogy) and, unfortunately, there is no perfect way to reflect this history in a reductionist exercise like classification. But a phylogenetic perspective, compared to one centered on the "living" alone, demands a transformationist view of homologous characters. The consequence of this view rids one of a "definitional," static attitude toward characters (see especially Simpson, 1961, 1975). The artiodactyls are members of their order not because they all have double-pulleyed astragali but because they originated from a form which had one. Whether all artiodactyls retained this feature or merely indications (to be interpreted) of its constraining influence upon subsequently altered homologous conditions is precisely what we attempt to judge empirically and conceptually in order to discover their phylogenetic ties. This corroborated history becomes the basis of our best-tested classification (Bock, 1977). In a recent review Ghiselin (1986, p. 653), in essence reiterating Simpson's (1961) views, stated that "Classifications ought to be based upon a scientific evaluation of any data that happen to be germane; that is upon scientific knowledge as a whole . . . . It means thinking like a historian, asking what has happened and why, and formulating hypotheses and gathering data to test them . . . . Good science generally wins out over bad philosophy, but it takes a long time."

A definition-based system of classification (and the phylogeny supposedly derivable from it) generates a discrete set of traits and groups which become interchangeable in a circular fashion. Groups are identified by traits, homologs of which can only be found in group members. If these disappear because they have transformed into another condition then the philosophy of such a definitional approach renders the taxonomic identity of forms showing these features (derived forms of the homologs) unresolvable, and their evolution unknowable.

Using the fossil record, along with rigorous character analysis and an a priori weighting scheme, both steeped in biology and paleontology (see Neff's 1986, important although somewhat differently phrased views), we make vertical comparisons which allow a transformational understanding of the characters. This is not accomplished through the so-called "stratophenetic" ordering of attributes (a degree of precision often unattainable in paleontology), but the transformation sequences are hypothesized and tested through a corroborative morphological analysis, just as one would study contemporary morphoclines, coupled with a fundamental consideration of time value of the features studied (Bock, 1977, 1979; Szalay, 1977; Cartmill, 1981; Gingerich, 1984b; Neff, 1986).

What then is a diagnosis? Quite simply, in the diagnosis of a monophyletic taxon, which may be either paraphyletic or holophyletic (depending resolvability and adaptive considerations; see especially Lemen and Freeman, 1984, on the genus in the Mammalia), we include those characters which (with high probability) represent the ancestral state of the designated taxon. Such diagnostic characters are only useful if they represent the conditions derived from another putative ancestor. Thus, in the diagnosis of the Primates or Euprimates, the unique features of the ancestors are listed, although their other features, primitive on another taxonomic level, are equally valid but less useful in this particular taxonomic context. To list the presence of a series of features shared with other eutherians when diagnosing the Primates would be redundant.

In diagnosing a higher taxon like the order Primates, we offer suites of characters which were, with a high degree of probability, present in the last common ancestor of the members included. This probability is ascertained through the analysis of both the functional and adaptive aspects of features and the fossil record (character analysis, *fide* Bock, 1981; Szalay, 1981a; Neff, 1986). Character distributions are important sources for recognizing character correlations; therefore they give insight into the nature of constraints; and thus they aid in the formulation of alternative transformation hypotheses. As Bock (1981) has rigorously discussed, "outgroup" approaches are circular and lack validity. This does not mean, of course, that character states of groups other than the one under study (a concept distinct from a "cladistic outgroup") should not be investigated as possibly suitable antecedent conditions.

Thus, studies geared toward understanding the phylogenetic, functional-adaptive, and developmental constraints (all of these are being aspects of all organisms; Reif et al., 1985) of characters lead to an understanding of uniquely shared form-function solutions and sequentially sensible character sequences, and not mere enumeration of "concrete characters." Such efforts, yielding the only meaningfully acceptable synapomorphies, and not mere distribution analysis, make it highly probable that a particular feature was uniquely acquired in the common ancestor. It follows from this evolutionary diagnosis (as opposed to "key-type" definitions of a higher category) that characters of some taxa which were demonstrably altered through later evolution do not invalidate the inclusion of such taxa in that higher-level taxon.

Grades as expressions of evolutionary relationships

Systematists continue to debate the ideal form of a classification, including that of the Primates. Although there has been a noticeable shift toward a phylogenetic (but decidedly not limited to a cladistic) emphasis (e.g., Szalay and Delson, 1979, and many other works) some continue to advocate different approaches. While Archer and Aplin (1984) made liberal use of the rankless category "Plesion" (anything that is a fossil) in their cladistic classification, the notion of "grades" has figured largely in the definition and delineation of the Primates by MacPhee et al. (1983).

It is essential that we first briefly examine the notion and usage of the grade concept in systematics. We believe that the original concept of an evolutionary grade is based on a nonevolutionary, pre-Darwinian notion of the Scala Naturae, a notion of hierarchy without any phylogenetic content. Since Darwin, however, the notion of progressive evolutionary change as the cause of diversity has predominated in taxonomic efforts to group organisms, but due to the overwhelming task, for a long time a gradistic approach (i.e., based on broad and poorly tested homologies) had to suffice. In the literature Huxley's (1958) now-classic usage of the grade and clade concepts is widely followed. Gould (1976, p. 119) has also accepted Huxley's notion of the grade, paraphrasing it as: "grades are levels of structural organization that may be reached independently by different lineages."

Matters, however, have become complicated around the grade concept when, in order to win advocacy for exclusively holophyletic classifications, many cladistic classifiers have come to refer to nonholophyletic, or, as properly called, paraphyletic, taxa as grades. Whereas paraphyletic taxa are monophyletic (but not including all the descendants of the last common ancestor in the taxon, as for example, in the case of the Pongidae without the Hominidae), grades, by definition, are not. This studiedly confusing use of grades, when in fact paraphyletic taxa are referred to, robs the grade concept of its uniquely descriptive nature, which implies multiple independent evolution of taxa (and not characters) into a similar adaptive zone and therefore polyphyly. The recent rash of usages of the term monophyly often imply the loaded notion of a taxon which includes all of the common ancestor's descendants, the more restricted concept of monophyly, holophyly. Monophyly, as Ashlock (1971) clearly redefined it, only means that the last common ancestor of all included forms is also contained in that taxon. Therefore, paraphyly and holophyly represent alternate forms of monophyly. Although Huxley (1958), as we noted above, has supplied the post-Synthesis era with a somewhat better-defined notion of grades and clades, clearly, even to him, grades represented stages of evolutionary progression in a poorly defined phylogenetic context. We find that the notion of analysis by grade is prevalent when phylogenetic constraints exhibited by organisms seem to get in the way of a particular mode of analysis or when exact evolutionary relationships (on any taxonomic level) are considered unresolvable.

We will now briefly examine the more controversial areas of evidence for the monophyly of the Primates, Euprimates, Strepsirhini, Haplorhini, and Anthropoidea. In Table 1 we present a classification used in this paper, one which we will justify within the text below.

ON THE DIAGNOSTIC FEATURES OF THE PRIMATES (OR: THE UNIQUE ATTRIBUTES OF THE LAST COMMON ANCESTOR OF THE ORDER)

As long as remains of early primates have been objects of scientific scrutiny there has never been a paucity of efforts by students of living taxa to demonstrate how cranial, dental, and postcranial features of the early representatives of the order were really "generalized," i.e., like those of primitive therians or eutherians (see especially Lewis, 1980a,b; and Martin, 1986) and not diagnostically primate. In a recent study on the basicranial morphology of the archaic paromomyiform *Ignacius*, MacPhee et al. (1983) stated that there are no clearly definable unique specializa-

TABLE 1. An outline classification of the Order Primates, employing the new category subdivisions semiorder and semisuborder[1]

- Order Primates Linnaeus, 1978
  - Semiorder Paromomyiformes Szalay, 1973
    (including superfamilies Paromomyoidea and Plesiadapoidea)
  - Semiorder Euprimates Hoffstetter, 1977
    - Suborder Strepsirhini E. Geoffroy, 1812
      - Infraorder Adapiformes Szalay and Delson, 1979
      - Infraorder Lemuriformes Gregory 1915b
        (including superfamilies Lemuroidea and Lorisoidea)
    - Suborder Haplorhini Pocock, 1918
      - Semisuborder Tarsiiformes Gregory, 1915b
        (including the families Omomyidae and Tarsiidae)
      - Semisuborder Anthropoidea Mivart, 1864
        - Infraorder Platyrrhini E. Geoffroy, 1812
        - Infraorder Catarrhini E. Geoffroy, 1812

[1] The prefix semi-, added to an existing category, ranks a taxon without the necessity of adding new hierarchical designations. Addition of the prefix semi- to a widely accepted category means a subdivision of that rank, and thus the prefix and the root word designate a rank below that of the root word.

TABLE 2. Diagnostic primate characters[1]

1. Auditory bulla inflated and formed by the petrosal
2. Meatal tube formed by ectotympanic which is extrabullar or "aphaneric," and large as in *Phenacolemur* or *Plesiadapis*
3. Promontorium centrally located in middle ear cavity, and a large hypotympanic sinus separates it from the basisphenoid
4. Carotid enters bulla posterolaterally and is tube enclosed
5. Molar teeth with the following combination of characters: high trigonid and wide talonid, combined with a characteristically low paraconid; reduced stylar shelf; long protocone apex to gumline distance; emphasized postportocone fold on upper molars; upper molars, particularly the second one, transversely wide
6. Dental formula probably containing the full eutherian complement with the possible derived absence of one pair of incisors
7. The archontan pedal morphology further modified by the hypertrophy of the flexor fibularis
8. Although digits are sharply clawed, broad and sellar entocuneiform-hallucial joint suggests considerable ability for the hallux to abduct and for the foot to grasp
9. Nearly spherical humeral capitulum (this feature probably also present in the archontan morphotype)

[1] Derived features which occur in the given combination in the last common ancestor of the taxa included in the order Primates.

tions which can diagnose the common ancestor of all primates—more specifically, the protoparomomyiform. In another review, Martin (1986) has stated that in his opinion there are no shared derived features that link these archaic primates to euprimates. Accordingly, by his "definition," plesiadapiforms are not primates. Martin's views of a "definition," which would exclude the evolutionarily most important and earliest remains of an order are unacceptable to us. We will therefore review the nature of the evidence concerning the diagnostic features of primates (Table 2).

Dental evidence

Few statements can be made as categorically as the assertion that no other aspect of primate anatomy reflects and informs about the feeding diversity reached by the order like the dentition, or even just parts of it. We can confidently add to this that paleontology supplies us with an incomparable view of this dietary diversity because of the proverbial predilection of teeth to become fossilized.

Defining the dental attributes of the last common ancestor of the order (not considering here such relatively uninformative features for our present purpose as the dental formula) from a neontological perspective is fraught with considerable difficulty. The simple reason for this is that teeth tend to evolve (but not always) extremely rapidly in mammals, closely tracking behavioral and environmental shifts as they relate primarily to food hardness and texture encountered in various feeding strategies. They certainly do not seem to have anything to do with specific reproductive isolating mechanisms, which are one of the central aspects of species formation, and therefore with the numerical diversity of species. Nevertheless the morphological diversity of dental taxa known from any one time along with the paleoenvironmental information supply hints about the limits of diversity. Martin (1986) has published views on the "expected number of species" in the Paleogene that assume a diversity much less than today. Given the variety of morphological types and the greater extent of known favorable habitats for primates (a far more equable world-wide climate, and tropical and subtropical forests) this is a perception with which we cannot concur. For similar paleontological and for simple empirical reasons we cannot endorse Martin's claim that primates have relatively "simple" teeth, and that *Tarsius* "possesses molars that are very close to the hypothetical ancestral condition for placental mammals generally" (p. 16). We suspect that such a view (in light of a rather good early placental dental fossil record) is the outgrowth of an a priori conviction that a living, small, nocturnal predator is likely to have retained ancestral primate attributes.

Martin (1986) also states that molar features do not uniquely "define" primates. The teeth of lemurs (many kinds), tarsiers, or hominoids certainly do not retain attributes recognizably present in their putative euprimate common ancestor. But the teeth of taxa not separated by the equivalent time interval which divides these living forms, those in the Paleocene and early Eocene, will readily reveal to diligent students of their form-function the unmistakable shared attributes derived from their last common ancestor. The extremely complex, highly species- and genus-specific, historically layered form-function attributes of primate dentitions are not only our best clues to the feeding preferences of these animals but they clearly mirror their ancestral morphology in spite of the adaptive plasticity of the dentition. It should be understood that it is not something special about the dentition which makes it adaptively plastic. It is rather that the feeding mechanism is the primary target area of selection whenever new survival strategies are pursued, and these strategies most often involve a change in the dietary regime. The confidence in the recognition of such ancestral constraints in the dentition is clearly rivaled by the same trust we have in the more conservative areas, such as some aspects of the postcranium or some cranial features. Nevertheless, as much tested practice suggests, a good fossil record can make the dental evidence as fully relevant to the diagnosis of a higher taxon as any other area of hard anatomy.

Judged from the Paleogene dental evidence of primates (see Szalay and Delson, 1979, for an overview, and for labelled figures of upper and lower primate molars) the last common ancestor of the order probably displayed the following *combination* of characters: (1) trigonids relatively high-crowned while the talonid was considerably widened; (2) an emphasis on the postprotocone fold of the upper molars and a reduced stylar shelf; (3) an unusually long gum line (cervix)–protocone apex distance, related to the hypertrophy of the talonid (i.e., an elongated lingual protocone slope); (4) angulation and lowering of the crest in between the paraconid and protoconid, related to the emphasis on the postprotocone fold; (5) characteristic mesial shift of the protocone, with strong para- and metaconules present, all this occlusally related to the mesial "tilt" of the trigonids; and (6) upper molars, particularly the second one, transversely wide.

The sorting of teeth and their phylogenetic interpretation, involving the best functional-adaptive analytical procedures available, like those of all other cranioskeletal elements obtained from the geological record, have been and continue to be the source of the robust data base supplied by paleontology. The valid methods, those which are consistent with our understanding of the evolutionary process and the constraints derived from phylogeny, development, and adaptation (see especially Bock, 1981), utilize the remains of the skeletal system (with its obvious relationship to other parts of the organism) to fuse neontology and paleontology as alternate sides of a conceptually unified discipline.

Basicranial evidence

The basicranial evidence is of utmost importance in the delineation of the Primates, and several reviews in the past have dealt with this topic. An outstanding recent overview is that of MacPhee and Cartmill (1986). There are, however, some critical disagreements between the interpretations advanced by MacPhee et al. (1983) and MacPhee and Cartmill (1986) and our own interpretation of the archaic primate evidence. We elaborate these differences below.

Two character complexes are commonly considered as supplying critical information for assessing relationships in the study of living and fossil primates: the composition of the bulla and the pattern of intrabullar carotid circulation. A petrosal-derived bulla and canal-enclosed stapedial and promontory branches of the intrabullar internal carotid have long been considered as primitive characteristics for the order Primates.

Composition of the bulla in early primates

In 1983, after introducing new information on the basicranium of *Ignacius*, MacPhee et al. reasoned that identifying the ossified bulla of known archaic primates as a petrosal is inappropriate because there is no guarantee that the bulla is a petrosal derivative. Although the absence of sutures between the bulla and petrosal bone in fossils is usually interpreted to mean that the bulla is of petrosal origin, the only way to be certain is to observe the ontogenetic development of the auditory region. The latter is possible in extant species only. Accordingly, the attribution of petrosal origin to the bullae of archaic primates is a questionable practice. In MacPhee et al.'s opinion, the best that can be said, given this and the lack of a bulla in microsopids like *Cynodontomys*, is that primate bullae in the Paleogene must have been variable.

Our criticism of these conclusions is threefold. First, we do not place much value on deductions regarding *primate* anatomy that are based on *Cynodontomys*. Although there are dissenting views, we believe that the nonprimate status of microsyopids is very strongly supported by our studies on basicranial and dental morphology (Szalay, 1969, 1977; Szalay and Delson, 1979), by the recognition of their dermopteran pedal morphology (Szalay and Drawhorn, 1980), by their dermopteranlike basicranial morphology (Rosenberger and Szalay, in preparation), and by recent unpublished evidence by Krishtalka and Stuckey (personal communication). That

Cynodontomys lacks a bulla, then, is important only if it is a primate. Our detailed work shows microsyopids to be nonprimates.

Secondly, we think that the absence of ontogenetic information about the bullae of fossil primates does not, of itself, impair the usefulness of the auditory region in determining archaic primate relationships. On the one hand we agree with MacPhee et al. (1983) that ontogeny provides a precious repertoire of characters for the testing of homology hypotheses. Clearly, when available, ontogenetic information is most valuable and greatly extends the available data base. Nevertheless, developmental evidence (virtually unattainable in fossil mammals) does not carry more weight in testing homology hypotheses than the usually available morphological evidence. For this reason, the absence of ontogenetic information does not preclude our ability to accept homologies of adult structures. For example, no juvenile stages in omomyids, adapids, or Fayum catarrhines document their bullar homologies, yet the details of morphological resemblance in all known areas, the ear region included, strongly support the obvious conclusions regarding homologies (Cartmill et al., 1981). In plesiadapids (judged to be primates by dental and postcranial criteria, independently from the bulla) and all other primates the bullar floor and walls are completely ossified as a continuous expansion of the petrosal bone.

Our third reason for challenging MacPhee et al.'s view on the lack of certainty about the petrosal origins of archaic primate bullae is empirical. There *are* data that suggest the bulla is derived from the petrous bone. The evidence obtains from the basicranial remains of a young specimen of *Plesiadapis*, MNHN No. CR 7377. Figures 1 and 2 show that the gap between the ossified bullar floor and the basisphenoid in this specimen is not composed of a basisphenoid lamina. Also, the flange formed by the basioccipital-basisphenoid which overlaps the medial bullar wall in *Plesiadapis*, *Ignacius*, and such euprimates as *Rooneyia* and *Tarsius* would not be expected to occur together with another deeper flange coming off of the middle section of the basicranium. This leaves only the entotympanic, the alisphenoid, petrosal, and the ectotympanic to form an ossified bulla. The ectotympanic is universally confined to the meatal region in all primates. There is no evidence of any sort to suggest either entotympanic or alisphenoid homologies for the bulla.

MNHN CR 7377 (Fig. 2) clearly shows its midcranial suture with the squamosal and also provides strong evidence that the bulla was not of entotympanic derivation. There is no sign of any suture which would indicate that the ventrally curved beginning of the medial bullar wall is of the entotympanic—the beginning of the bulla is pristinely continuous with the inner-ear-bearing petrosal. The clear presence of the intracranial squamosal-petrosal suture, the clear suturing between the ectotympanic and petrosal, and the lack of any sign of a suture at the very area which should indicate a bulla of entotympanic homologies, all on one specimen, is the clearest confirmation that a petrosal bulla was present in *Plesiadapis*.

Pattern of intrabullar carotid circulation

In our reassessment of the basicranium we will now concentrate on the evidence for the entry of the carotid into the bulla and the pattern of intrabullar circulation in the archaic primates. Our realization that the basic architectural pattern of the archaic forms was essentially similar to the strepsirhines is a by-product of this investigation. We have restudied the specimen that was examined by MacPhee et al. (1983) and MacPhee and Cartmill (1986), and our interpretation differs in a fundamental way from theirs.

The skull, a juvenile, is characterized by extreme fractures and separation of bones. There are two obvious areas of separation: (1) the right parietal from the occipital complex, and (2) the basisphenoid from the basioccipital. In our view an anteriorly and dorsally oriented force crushed the buried cranium in such a way that separation at some of the sutures occurred. These distortions are responsible for our conflict with existing interpretations of the basicranial structure of this important specimen.

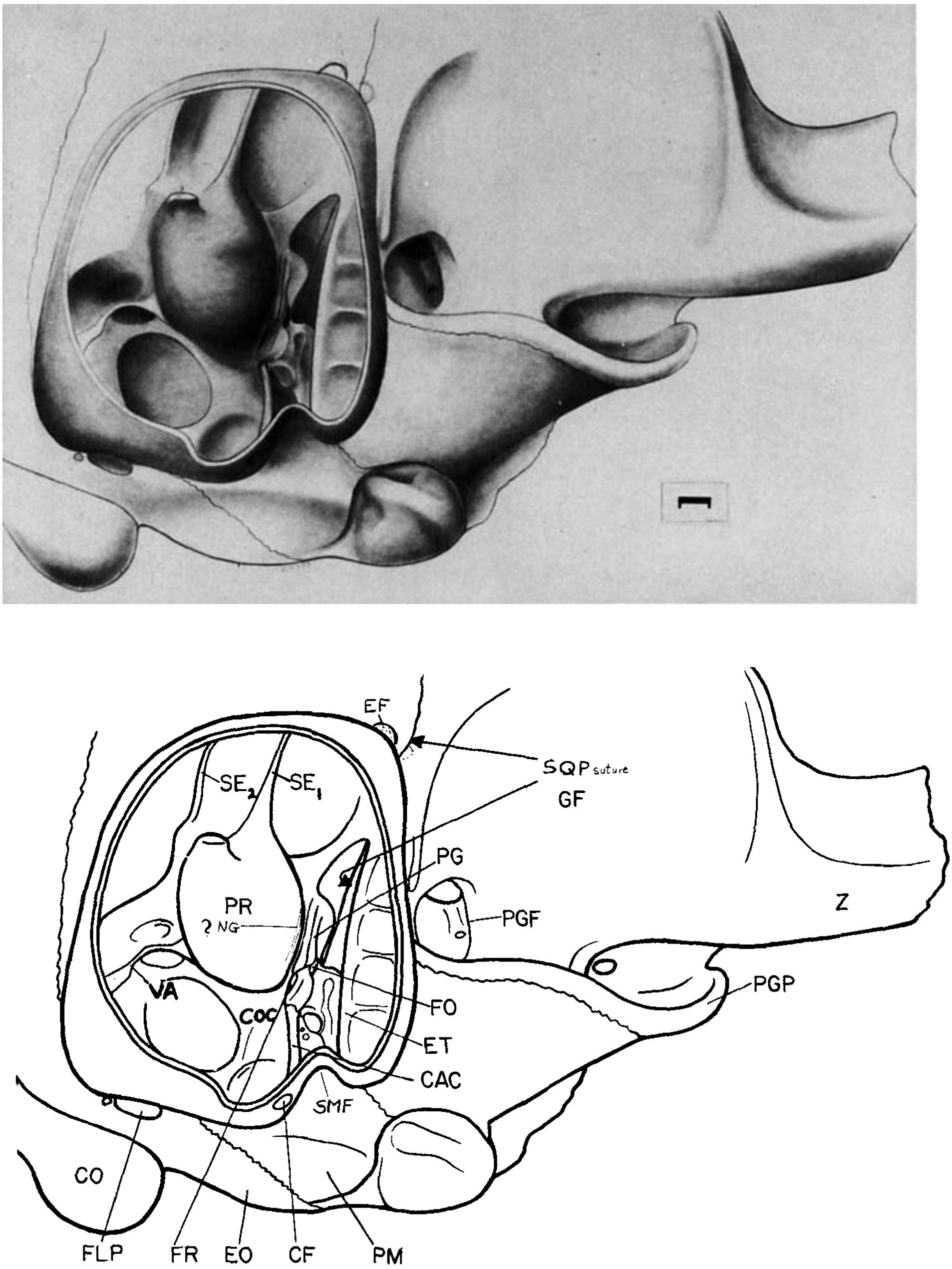
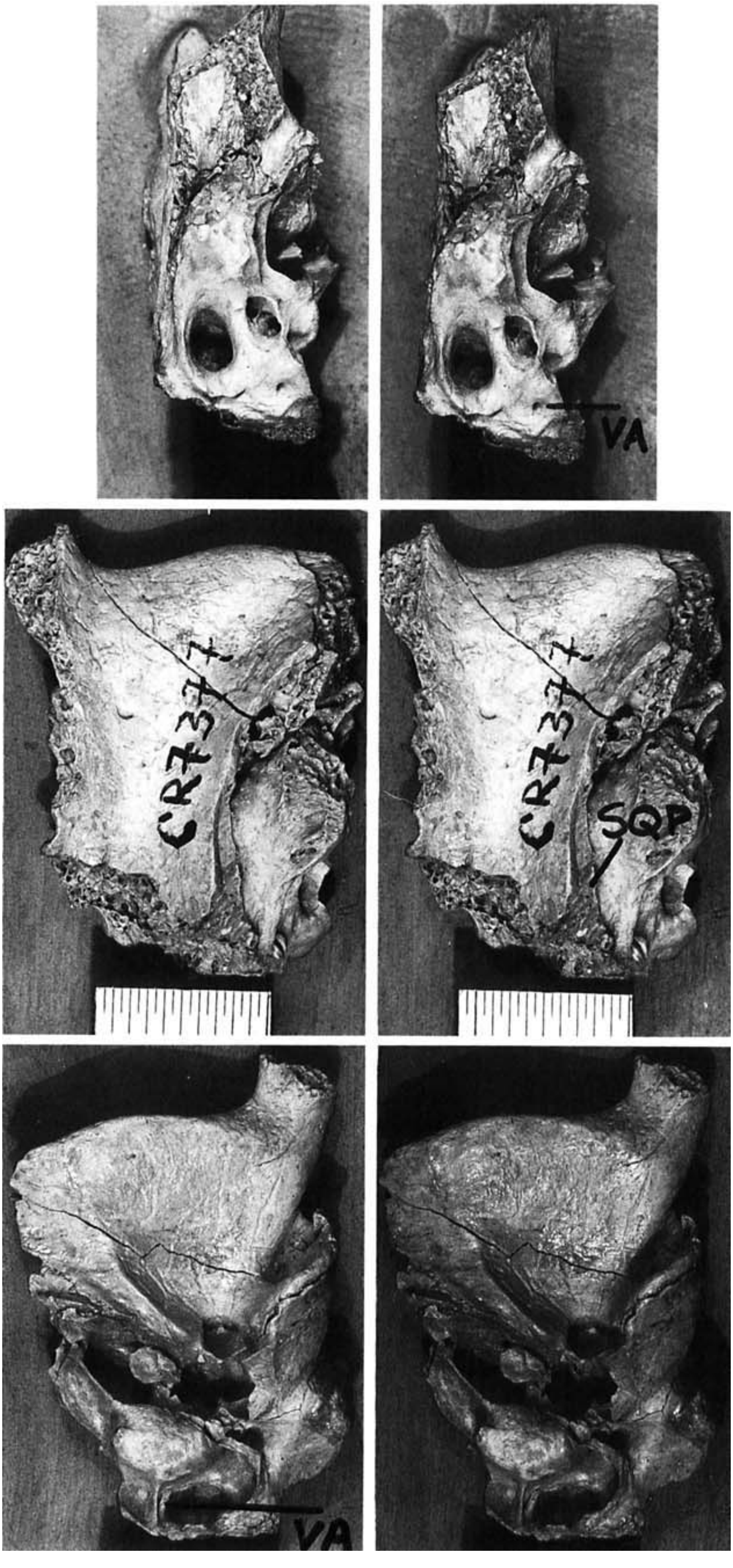


Fig. 1. Reconstruction of the left basicranium in the late Paleocene European *Plesiadapis tricuspidens*, based on MNHN Nos. CR 125 and CR 7377. The following abbreviations are used: CAC, carotid canal; CoC, cochlear canaliculus; CF, carotid foramen; CO, condyle; EF, eustachian foramen; EO, exoccipital; ET, ectotympanic; FLP, posterior lacerate foramen (jugular foramen); FO, fenestra ovale; FR, fenestra rotunda; GF, glenoid fossa; PC, promontory canal; PG, promontory groove; PGF, postglenoid foramen; ?NG, groove for nerve?; PGP, postglenoid process; PM, petromastoid; PR, promontorium, SE1 and SE2, septa; SQP, squamosopetrosal suture; SMF, stylomastoid foramen; VA, vestibular aqueduct; Z, zygoma. Scale represents 1 mm.


VA
CR7377
SQP
VA

The separation of the basisphenoid and basioccipital is an unquestionable fact. The basisphenoid is simply more rostral and dorsal to the rostral edge of the basioccipital (see Fig. 3, areas designated as X1 and X2). Given this fact, the examination of the area identified as the "middle lacerate foramen" by MacPhee et al. (1983) and MacPhee and Cartmill (1986) suggests that this "foramen," unlike such foramina in living species, has a dorsally ascending wall. This condition, on both sides, can be explained, on closer examination, as an expression of the separation of the alisphenoid from the petrosal bulla. In fact the alleged foramen, if there was one, is an artifact of the crushing documented above. The ascending wall of the alleged "middle lacerate foramen" is the closely conforming portion of the alisphenoid to the ventrally curving shell of the bulla itself.

We have also identified the fenestra rotunda, the carotid canal, and the possible promontory canal. The apical forward extension of the promontorium in *Ignacius* is almost certainly homologous to the conditions displayed in *Plesiadapis* and adapids. The remnant of the carotid canal in *Ignacius*, as in the other two known archaic primate taxa with good basicranial information, is clearly discernible on the left petrosal promontorium. This was not identified by MacPhee et al. (1983) or by MacPhee and Cartmill (1986), nor were the fenestra rotunda, and the promontory groove or possibly a canal. We believe, consequently, that their reconstruction of the vascular anatomy, although a bold hypothesis, is contradicted by the specimen itself. MacPhee et al. refer to a ridge, we believe correctly, on the posteromedial region of the cavity, as the cochlear canaliculus. We may add to this that this condition, the visibility of the canaliculus, is exactly what one sees in other archaic primates and *Adapis*, a point of significant similarity.

Ignacius displays one of the most telling synapomorphies of the Primates, strongly uniting the semiorders Paromomyiformes and Euprimates, which has not been previously noted. In that genus, as in *Phenacolemur* and *Plesiadapis*, and exactly like adapids, the promontorium is displaced laterally and the middle ear cavity is extended as a diverticulum in the shape of a half-doughnut medially, anteriorly, and posteriorly. This is in a diagnostic contrast to such other archontans as tupaiids and microsyopids which have the promontorium (and the cochlea it houses) in the primitive eutherian position close to the basioccipital-basisphenoid suture. It is very important to understand the functional significance of this, possibly related to an inflated bulla, but even without such an understanding we believe it to be an extremely important synapomorphy linking the archaic primates with modern ones.

As far as *Plesiadapis* and other archaic primates are concerned, we have no doubt that a functional carotid canal existed which went as far as the fenestra rotunda (see Fig. 1). This is in direct opposition to the assessment of MacPhee and Cartmill (1986). In specimens of *Plesiadapis* (Saban, 1963; Szalay, 1972) an area resembling a blister on the ventral and anterior margin of the fenestral rotunda, is, we believe, the incipient homolog of the ventral shield in adapids and lemuroids. It receives the carotid artery and its associated nerves, and channels these past the ventral margin of the fenestra rotunda as it sends off the stapedial branch dorsally and the promontory one anteriorly and dorsally into the intracranial cavity. This is evident in MNHN No. CR 7377 (see Fig. 2, ventral view). Given the fact that this bony blister also has an opening which is external to the fenestra rotunda itself, it is not improbable that it represents the lumen of a promontory canal. In our view the condition in *Plesiadapis*, even in these intricate details of the promontory entry into the petrosal, bears special similarities to the adapids and lemuroids. Another interesting and potentially significant similarity, possibly a synapomorphy, is between the well-defined raised ridge on the posteromedial roof of the middle ear cavity of both *Plesiadapis* and adapids and lemuriforms (see Figs. 1, 2, 4). This visible struc-

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Fig. 2. Stereophotos of part of the left basicranium of *Plesiadapis tricuspidens*, MNHN No. CR 7377. Ventral (below), dorsal (middle), and medial (above) views, respectively. Abbreviations as in Figure 1. Scale represents 1 cm.

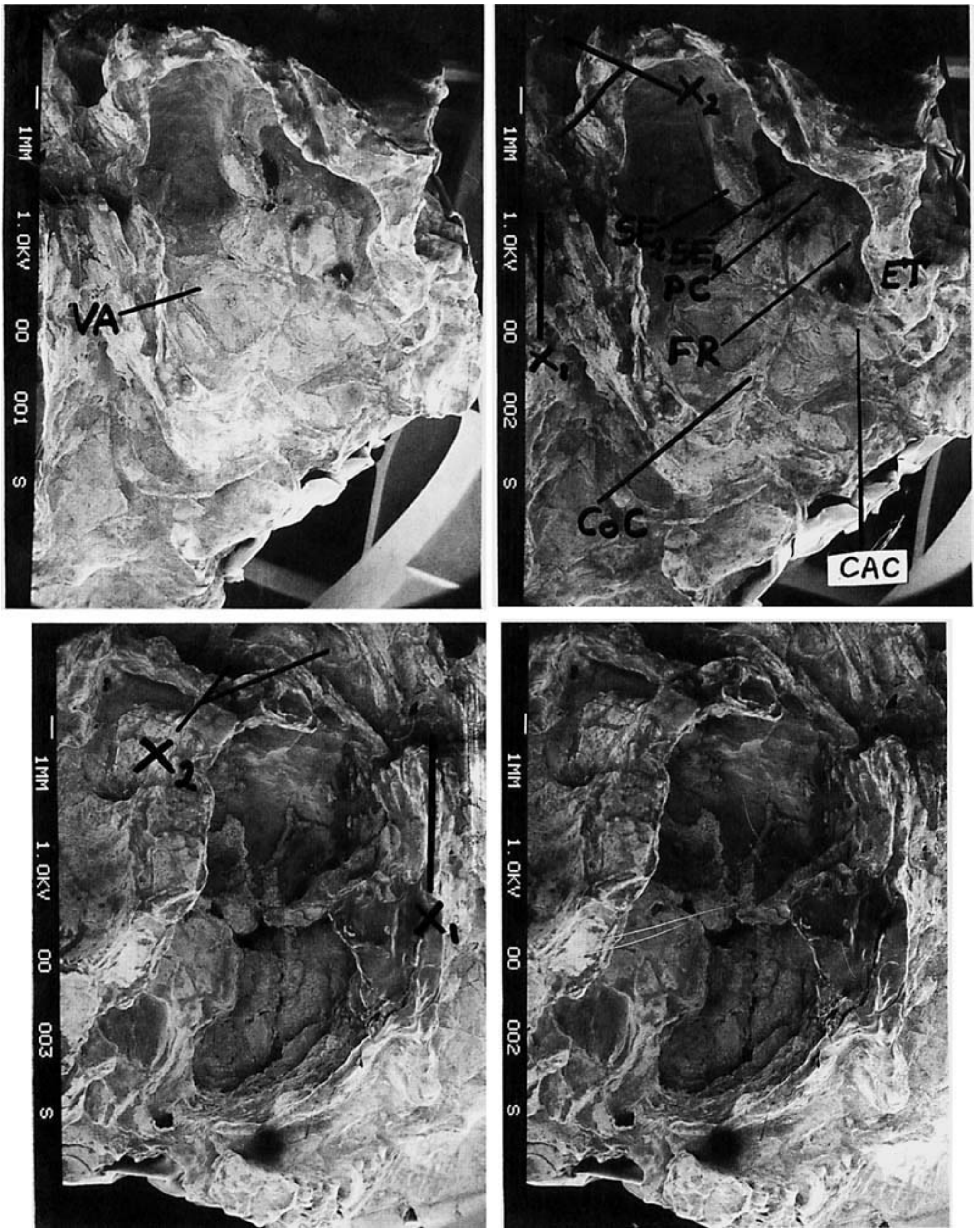

Fig. 3. Stereophotos of left (above) and right (below) basicranial regions of *Ignacius graybullianus* from the Early Eocene of Wyoming, UMMP No. 68006. Abbreviations as in Figure 1. Note postmortem separation of cranial elements in areas designated as X1 and X2. ×1, basisphenoid-basioccipital separation; ×2, petrosal bulla-alisphenoid separation.

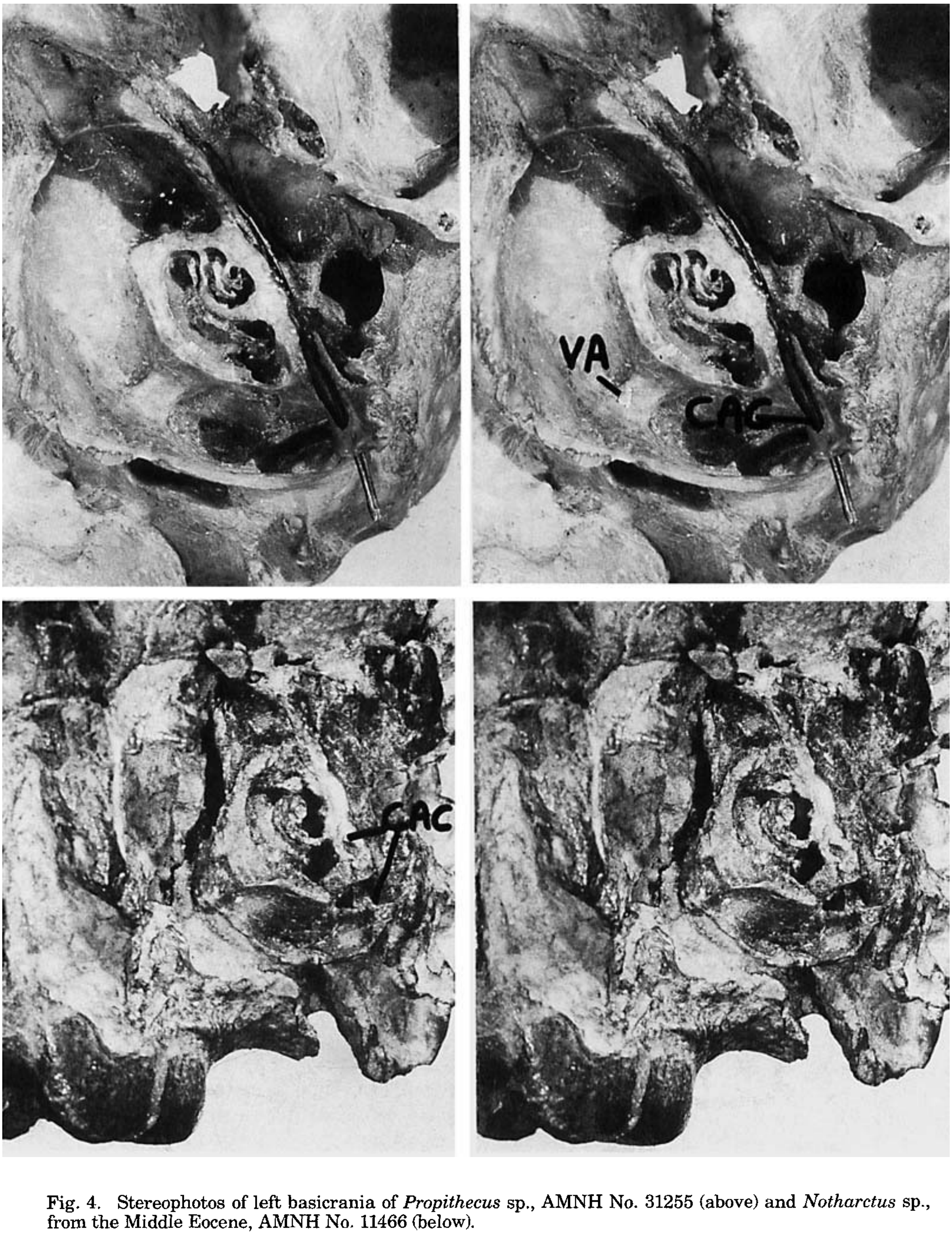

Fig. 4. Stereophotos of left basicrania of *Propithecus* sp., AMNH No. 31255 (above) and *Notharctus* sp., from the Middle Eocene, AMNH No. 11466 (below).

ture is the vestibular aqueduct, and its lumen is clearly discernible on the intracranial surface of the MNHN CR 7377 near the subarcuate fossa and internal auditory canal, shown in Figure 2.

In commenting on the area homologized as the promontory canal on the only described basicranium of *Phenacolemur*, AMNH No. 48005 (Szalay, 1972), MacPhee et al. note that "as the 'canal' is imperforate in both *Phenacolemur* and the related genus *Ignacius*, the paromomyid forebrain must have been supplied by vessels other than the promontory artery" (p. 509). In our view this observation is without any justifiable foundation, since both specimens are remarkably poorly preserved: every area which should be "perforate" is messily "imperforate." On the other hand, the pristine specimen of *Plesiadapis*, MNHN No. 7377, on which we base the important details of our reconstruction (see Fig. 1), clearly shows the carotid foramen, the carotid canal, and at least a possible channel for the promontory canal. It is also noteworthy that we have carefully studied the basicranial remains of MNHN CR 125, the complete skull of *Plesiadapis tricuspidens*, and were unable to find any opening which could have been interpreted as a medial lacerate foramen in the sense used by MacPhee et al. (1983) or MacPhee and Cartmill (1986). In spite of our disagreement with MacPhee and Cartmill (1986) on the interpretation of archaic primate specimens (and a few other points pertaining to the haplorhines), we strongly urge the corollary reading of their detailed review of basicranial morphology in primates.

In assessing the basicranial evidence of the members of the semiorder Paromomyiformes, we have some definite observations and conclusions. Plesiadapids have definite carotid canals and almost certainly a promontory canal. The promontory canal of *Phenacolemur* is still more reasonably interpreted as just that, as designated by Szalay (1972). At minimum our observations suggest that the relationship of basicranial openings of *Ignacius* has been misinterpreted by MacPhee et al. Given our interpretation of the often painfully inadequate morphology of the specimens, we see their vascular reconstruction of *Ignacius* as unsupported by the preserved morphology of any of the known paromomyiform basicrania. Consequently such a reconstruction is not a "character," and aids in no diagnosis, be it either definitionally "key-type" or phylogenetic.

To sum up this section, we have restudied in considerable detail the Paleogene primate evidence, as well as relevant specimens of extant strepsirhines, and have established detailed primate synapomorphies between the archaic primates (*Plesiadapis*, *Phenacolemur*, and *Ignacius* (microsyopids are unquestionably dermopterans cranially)[1] and the Eocene euprimates.

Postcranial morphology and inferred substrate preference

Both MacPhee et al. (1983) and Martin (1986) have questioned the value of postcranial evidence linking archaic primates to euprimates. Their objections are based on two assumptions: (1) that most primate postcranial features are primitive therian or eutherian features (following Lewis, 1980a,b) and (2) that shared features are likely to be convergent. In several long contributions (Szalay and Decker, 1984; Szalay et al., 1975; Szalay, 1977; Szalay and Drawhorn, 1980) Szalay and others have shown that on the bases of numerous character complexes the form-function solutions in Paromomyiformes resembled euprimates and other archontans (tree shrews and colugos, but not the highly derived archontan bats) in special taxon-specific ways. These features do not resemble an undefined eutherian or therian morphotype.

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[1] Rosenberger and Szalay (in preparation) have made detailed comparisons between living colugo basicrania and the evidence for microsyopids published in Szalay (1969). The presence of a tympanic process on the medial surface of the promontorium in AMNH 55286 (Szalay, 1969, pl. 42) strongly suggests that the bulla, as in colugos, was attached there, and medial to this point, as in the living dermopterans, a rostral entotympanic was present (Hunt and Korth, 1980). In addition to the probable bulla homology, there are two unique dermopteran features present in skull of *Cynodontomys*: a flat and circular expansion of the petromastoid, and evidence of the squamosal air spaces discussed in detail by Hunt and Korth (1980). The cranial evidence, dental features such as the twinned entoconid and hypoconulid, and the pedal evidence published by Szalay and Drawhorn (1980) make it extremely likely that the Microsyopidae are an early family of the archontan Dermoptera.

More recently, Szalay (1984) documented the reasons why the constraints of the upper ankle joint structure inherited by archaic primates from their ancestry resulted in specific character acquisitions related to inversion of the foot, a pattern shared with euprimates. This evidence and discussion will not be repeated here. The objections by Lewis (1980a), that the archontan and primate features of the foot are ancient therian features, can no longer be maintained. The morphological evidence unequivocally shows that marsupials and eutherian arborealists solve their substrate-related problems in such distinct ways that the phylogenetic constraints, and subsequent archontan and then primate specializations of the latter, are undeniable. We will emphasize some already noted and some new evidence gleaned from the osteology of the feet of archaic and modern primates, as well as information gleaned from the elbow joint. All of these lines of evidence point to grasping arboreality, developed beyond that seen in such archontans as tupaiids.

In contrast to tupaiids and dermopterans (both living and fossil) archaic primate calcanea (Szalay and Drawhorn, 1980) show a pronounced groove for the important digital flexor, the flexor fibularis. This has been pointed out by both Szalay and Decker (1974) and Szalay and Drawhorn (1980). This may indicate a greater emphasis, through the size of the tendon of this muscle and its more stable alignment, of grasping ability than is evident in other archontans. A rather important area of supporting evidence is the comparative morphology of the entocuneiform-first metatarsal joint in all archontans and eutherians. This joint clearly mirrors the range and nature of movements of the hallux. The problem and the evidence for primate grasping are pursued independently by two of us (Szalay and Dagosto, in press), but some of the evidence has clear bearing on the issue of primate ordinal characteristics, so we will briefly discuss it.

That *Plesiadapis* had five toes on the hindfeet and a well-developed hallux is a well-established fact.[2] Part of the skeleton of *Plesiadapis tricuspidens* described by Szalay et al. (1975) contains a right entocuneiform, undescribed in 1975 but illustrated by Szalay and Delson (1979: Fig. 35). A left entocuneiform, AMNH No. 92011, from the Paleocene Bison Basin Saddle locality, is virtually identical to that of *Plesiadapis* from France and almost certainly represents the same genus. Comparisons with condylarths and carnivorans in that size range (or any other size range) make it just as likely that it belongs to a primate, as would phenetic sorting of teeth of *Plesiadapis*, condylarths, or carnivorans. The most interesting aspect of these two archaic primate entocuneiforms is that they are in some important ways similar to tupaiids and euprimates, and yet they show no meaningful similarities to marsupial homologs. These Paleocene entocuneiforms are distally very long and broad, and in distal view show a remarkably wide and sellar platform for the movements of the hallucial metatarsal. The relative size and configuration of the hallucial articular facet reflects a powerful but not as wide-ranging grasp as we see in Paleogene euprimates. The relative importance of the distal end suggests an equally important habitual loading through the hallux. A hypertrophied plantar process on the entocuneiform of the plesiadapids (its homolog occurs both in tupaiids and Paleogene euprimates) suggests an enlarged tibialis posterior, an important pedal invertor and plantarflexor, and a well-developed tunnel for powerful flexors of the digits (flexor tibialis and flexor fibularis). While there is no suggestion in the only known skeleton of *Plesiadapis* that anything like the graspleaping-related mechanics in the postcrania of Paleogene euprimates (except in *Adapis*, see Dagosto, 1983) was present, a powerful and habitual grasp as part of locomotion is not contradicted.

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[2] There has been an unfortunate and inadvertent misrepresentation of the critical nature of the hallux in *Plesiadapis*. Martin (1986, p. 23) has recently cited Gingerich (1986), claiming that this author "now believes that the hallux might have been totally lacking. This, of course, would represent a complete departure from the typical primate condition." Gingerich (1986, p. 38), however, clearly states in the same symposium that the right hallux of the Menat specimen of *Plesiadapis*, although disarticulated from the rest of the foot in the block, "now lies just below and parallel to metatarsals of the left foot."

ON THE DIAGNOSTIC FEATURES OF THE SEMIORDER EUPRIMATES

There is wide-ranging consensus among students of the subject that the living primates (excluding the Tupaiidae) and the Paleogene families of Adapidae and Omomyidae all share a common ancestor later than any of these shares with any archaic primate. This is what is expressed in the monophyletic group semiorder Euprimates, and this node in phylogeny is relatively easily supported.

There has been a fundamental restructuring, albeit with clear indications of continuity, from an archaic primate to the first Euprimates. The skull, the orbits in particular, and the postcranial morphology have undergone a reorganization which still leaves its strong influence on the descendants. Curiously, this transformation, which perhaps primarily reflects a feeding-related locomotor change, was not accompanied by an equally dramatic change in the basic construction of the molar teeth.

Until quite recently the large number of cranial, dental, as well as postcranial synapomorphies of high phylogenetic valence were either rejected or ignored when arguing for special ties between the archaic paromomyiforms and the tarsiiforms (Gingerich, 1974, 1975, 1978; Gingerich and Schoeniger, 1977; Schwartz et al., 1978). This is important to emphasize here because that view was based not on the total available suite of cranial, dental, and postcranial features, the polarity of which could be resolved, but on one low weight character, the enlargement of one pair of incisors in arbitrarily chosen representatives of the "plesitarsiiforms." We judge this a character of "low" weight from an a priori weighting procedure based on a processually judged perspective (somewhat different from the a priori weighting scheme advocated by Neff, 1986). Size alone, and not details of similarity, were the defining aspect of this alleged synapomorphy. The more complex and more unique shared similarities (which are therefore less likely to be convergent) and also the more important (high weight) features (such as aspects of the hip, and complex form-function attributes of the foot) were not rejected or devalued—they simply were not considered in these phylogenetic analyses. Although this assumption-laden avoidance of postcranial features is not unique in paleomammalogy, its continued practice can only result in unnecessarily incomplete phylogenetic and classificatory assessments.

The monophyly of the Euprimates has long been strongly supported by such cranial features as a well-developed postorbital bar and by dental synapomorphies shared between the Adapidae and Omomyidae such as the postprotocone crest (protocone fold or nannopithex fold) of the upper molars, a mesiodistally compressed trigonid on M/3 (less so on M/2), and a trigonid which is widely open lingually on M/1. On close comparison the details are more intricate than can be succinctly described here. What is important is that the similarities of the molars of the known representatives of these two families (Simpson, 1940; Szalay, 1976; Gingerich, 1986) are supported by the uniquely shared similarities of the nailed cheiridia, innominate bone, elbow morphology, and the perhaps more complex special similarities of the upper ankle joint and the various joints of the tarsus (see Dagosto, 1986, for detailed discussion of the transformation sequences of various tarsal features in strepsirhines). From these complex sets of similarities, the morphotypes of living higher taxa (Lemuriformes, Tarsiiformes, the Anthropoidea) can be more convincingly transformed than from any other known phenon. This is the reason for the highly corroborated nature of the concept Euprimates.

CONTROVERSIES SURROUNDING THE RELATIONSHIPS OF PALEOGENE EUPRIMATES

There is no agreement on the special affinities of the omomyids and adapids to the living infraorders. The reasons for this are much clearer than the relatively late acceptance of the primate status of the archaic primates, or of euprimate monophyly. The intricate cranial, dental, and postcranial similarities of early adapids and omomyids, paradoxically, allowed ample room for disagreement (e.g., Gingerich, 1978 vs. Szalay, 1976).

In reviewing this area of phylogenetics, Rasmussen (1986) has recently suggested that "unproven phylogenetic assumptions" have weighed heavily in the view of students who attempted to sort out the threads of affinity between the Paleogene and Recent euprimates. This issue is clearly an outgrowth of various studies on the evolutionary history of the early euprimates and therefore we will discuss it here.

Gingerich (1978) and Rasmussen (1986) maintain that (1) paleontological evidence favors adapid-anthropoid relationships. Rasmussen also suggests that (2) the omomyid-tarsiid-anthropoid clade is dependent on the assumption that adapids and lemuriforms are sister groups, or more precisely, that the latter is a descendant of the former (a hypothesis Rasmussen considers unproven or uncorroborated); (3) adapids and omomyids form a clade; (4) tarsiids and omomyids form a clade and this latter shares a common ancestor with Adapidae (which he and Gingerich consider to be the ancestral source of the Anthropoidea) while the common ancestor of Omomyidae and Adapidae is the sister of the Lemuriformes (as defined by Szalay and Delson, 1979); (5) soft anatomy and biochemistry cannot be used to evaluate the adapid-anthropoid hypothesis because the haplorhine condition of *Tarsius* is irrelevant to the evaluation of the omomyids.

The issues raised are intriguing and complex. Nevertheless, an evaluation of the characters cited and an examination of the assumptions advanced in the literature and summarized by Rasmussen in making his arguments can hopefully resolve or perhaps simplify both the nature of the evidence and the theoretical underpinnings of the various interpretations.

Given the robust documentation of euprimate monophyly, the questions which seem important are as follows: (A) Are adapid-anthropoid similarities primitive primate or euprimate features, or "anthrolemuroid" level shared derived similarities, or convergences? (B) What is the nature of omomyid-tarsiid-anthropoid similarities, and to what degree do omomyid-anthropoid special resemblances depend on the assumption of omomyid ancestry for tarsiids, or on the assumption of haplorhinism for the omomyids. (C) Are adapid-lemuriform similarities euprimate or adapid level (i.e., strepsirhine in a formal systematic sense) synapomorphies or convergent attributes? (D) Are omomyid-adapid similarities primitive or advanced euprimate features? (E) Is the haplorhine condition shared with the adapids (necessary for Rasmussen's phylogeny unless it evolved twice, in tarsiids and anthropoids), and are some or all omomyids strepsirhine in nasal structure?

A. *What do adapid-anthropoid similarities mean?*

We will now examine the list of similarities first provided by Gingerich (1975, 1976, 1984a–c) and reiterated by Rasmussen (1986) which they considered as being supportive of ancestor-descendant adapid-anthropoid ties. These features, according to them, are absent from omomyids (or by implication, the morphotype of omomyids). We assess these hypotheses in the light of our judgment of the polarities of the characters. The characters we list are those published by these authors and the comments following each are our assessment of them.

(1) Small, vertically implanted, spatulate incisors. This morphological designation is, we believe, too broadly and simplistically defined to have resolving power. Such taxa as *Teilhardina* and *Chumashius*, and probably others, leave no doubt that the omomyid morphotypic condition could also be characterized as having this general type of anterior dentition. It appears that the designation describes not only the morphotypic adapid condition (which we believe was already diagnostically strepsirhine) but probably the primitive omomyid and euprimate conditions as well. Other interpretations, more precise and therefore potentially vulnerable, have been offered by Rosenberger et al. (1985).

(2) Upper canine with honing wear facet against enlarged anterior lower premolar. The evidence is so spotty on the anterior dentition of most relatively primitive archaic primates, as well as omomyids, that this feature is of little significance, especially in light of this honing combination being absent in four-premolared adapids. Loss of P1 in taxa with large canines is likely to crowd the postcanine

dentition and result in conditions preadapted for canine honing. This is a functionally highly canalized complex, very likely prone to parallel evolution.

(3) I/2 larger than I/1. This may well be a primitive euprimate feature, and hence of no value in sorting out anthropoid ties. In addition, since the occlusion of the second incisors with one another and the occlusion of the upper canine with lower I/2 differ in adapids and anthropoids (see Rosenberger et al., 1985), size ratios, per se, can only suggest the most ambiguous homologies. *Washakius* has an I/2 alveolus which is larger than that for I/1, and similar proportions are likely to turn up elsewhere. All euprimate incisors may represent I2 and I3, and therefore these designations may not be correct.

(4) Fusion of the mandibular symphysis. This is a common and plastic feature in mammalian lineages which are undergoing masticatory transformation. This character is the result of the necessity for increasing resistance at the symphysis (for often different biological roles, or even distinctive mechanical requirements as far as either the incisors or cheek teeth are concerned); hence we consider this of very low weight phylogenetically. The notharctines, adapines, indriids, and megaladapids, among the strepsirhine primates, have independently fused the mandibular symphysis. So the likelihood of some adapid sharing this feature synapomorphously with the ancestral anthropoid is similar to that of *Megaladapis* sharing it with an adapid homologously. If *Tarsius* is the sister taxon of omomyids or anthropoids, its unfused symphysis is representative of the primitive haplorhine condition, unless one wishes to advocate an ontogenetically mediated reversal from a fused adapid (?haplorhine) condition. Rosenberger et al. (1985) have suggested why it is likely that adapids and anthropoids achieved symphysial fusion independently.

(5) Sexual dimorphism in body and canine size. It is unclear to us why dimorphism may not be a primitive mammalian feature, in a way similar to how it occurs in the nocturnal Didelphidae, for example. Clearly this is an area of inquiry where the morphological consequences of various behavioral strategies have not been adequately analyzed. It appears extremely sensitive to convergence, given the facility and consequences of size-related changes both within a biological species or in a lineage. A serious complicating factor is that in the cryptic *Tarsius*, a secondarily nocturnal habitus may have come to mask the original, diurnally-related intersexually (epigamic) and intrasexually correlated dimorphic paraphernalia.

(6) Annular ectotympanic. Although ectotympanics of adapids and platyrrhines can both be described as annular, the actual details of shape and their ontogeny are so dissimilar that the hypothesis that they are homologous is not supported. It is probable that the ectotympanic configuration of platyrrhines (and early anthropoids), a ribbonlike form, was derived from an extrabullar, tube-like construction, and the adapids independently evolved their ring-like condition. Thus, in our opinion, the "annular" designation of the ectotympanic is merely a vaguely descriptive term, without any support for a "simiadapid" relationship.

(7) Calcaneus and navicular not elongated. All early euprimates show moderate lengthening of the tarsals compared to most other contemporary mammals or to the known archaic primates. This is likely a diagnostic attribute of the first euprimates, and thus any similarity between adapids and anthropoids in this respect cannot be cited as a specially shared character between them. The implication of this character as it is usually used is that the derived, more extensively elongated tarsals of omomyids and *Tarsius* compared to adapids preclude their last common ancestor from being the source of anthropoids. What is usually not appreciated here is that most known omomyids are not galago- or tarsier-like in this respect. Tarsal lengthening in known omomyids (except for the necrolemurines) is only moderately longer than in adapids (Szalay, 1976). But most importantly, we consider changes in the length of tarsal elements of low weight phylogenetically. There is indirect evidence for the evolutionary plasticity of such a general character. It appears probable to us that the transition from a relatively small-bodied graspleaper to a larger-bodied protoanthropoid would have been accompanied by the shortening of the tarsals (Szalay and Langdon, 1986).

The known tarsal specialization of a few known species of omomyids, while certainly suggestive of a morphotypic condition for the Omomyidae, is also consistent with the idea put forward by Szalay and Dagosto (1980) that the earliest euprimate common ancestor was an animal which could be broadly characterized as a grasp-leaper. Leaping is an almost certainly predicted biorole from all available remains of early euprimates, the probable secondary slow-climbing specialization of some adapinans (Dagosto, 1983) notwithstanding. The unique sculpting of euprimate hip morphology can be closely correlated with the powerful leaping-related mechanics of the gluteus medius muscle in many eutherians which modify it in a manner resembling the protoeuprimate condition. The gluteus medius arises from virtually the entire iliac blade, which is primitively the dorsolateral side of the triangularly shaped ilium in protoprimates and other relatively unmodified therians.

Notharctines probably broadly represent the retained and therefore ancestral euprimate postcranial proportions. The fact that known tarsiiforms, many omomyids probably included, have retained or accentuated their leaping-related foot mechanics beyond a protoanthropoid condition is not a compelling case against the more recent phylogenetic ties of such a probably paraphyletic family like the Omomyidae with the living haplorhines.

(8) Unfused tibia and fibula. This feature, like the last one, is also a primitive euprimate, primate, eutherian, therian, etc., attribute. If all known omomyids had a fused distal crus than none would be a likely ancestor to anthropoids. But as recently demonstrated by Dagosto (1985), with the exception of *Necrolemur*, omomyid distal crura were not fused.

In sum, there are no convincing shared and derived similarities between adapids and anthropoids; and no compelling hints that any of the noted homologous conditions in adapids were directly transformed to the protoanthropoid equivalent. Features 1, 3, 7, and 8 are euprimate or primate symplesiomorphies, and the ancestral omomyid was not any more derived in these respects than the known adapids. Features 2, 4, and 6 are, in our view, of low phylogenetic weight, and we judge them to be convergent between adapids and protoanthropoids.

B. The relationship of the Omomyidae, Tarsiidae, and the Anthropoidea

The close haplorhine affinities of these taxa are based on what we believe to be strong synapomorphies. Many of these characters, however, if one interprets them as Gingerich or Rasmussen do, were either shared with the Adapidae or evolved independently in the Anthropoidea. The biochemical similarities (Baba et al., 1975), presence of a retinal fovea (fovea centralis) with the yellow spot (macula lutea) and the assumed loss of a tapetum lucidum (all of these in a nocturnal primate), the complex similarities of the fetal membranes and a hemochorial placenta (Luckett, 1975), coupled with the emphasis of the promontory artery and the deemphasis of the stapedial one, are the outstanding attributes, probably all shared and derived at the level of the most recent common ancestor of the Tarsiidae and Anthropoidea. We must add to this for the living forms the sharing of a continuous, untethered upper lip and nonglandular rhinarium. It seems clear to us that none of these shared special similarities linking tarsiers and anthropoids supports an adapid-anthropoid ancestor-descendant relationship unless (1) we assume these to have been also present in the Adapidae or (2) they have been independently acquired by the Tarsiidae and Anthropoidea from adapid conditions antecedent to them. Assuming that adapids had haplorhinism does not of course rank as evidence which can support any hypothesis. Furthermore, until some very sophisticated osteologically anchored research can shed light on biochemistry, fetal membranes, and nose and lip structure and histology, many of these features will remain unavailable for study in the Adapidae and Omomyidae.

Past and present allocations of fossil families to living groups is not based on assumed soft anatomy based on poorly understood hard morphology. It is the recognition and interpretation of hard anatomy as either homologs or convergences at a given taxonomic rank which makes assignment either to Strepsirhini or Haplorhini possible. The "soft" characteristics of these groups have little to do with the *nomina* used.

We are clearly not advocating, like Cartmill and Kay (1978) or Cartmill et al. (1981), that *Tarsius* and anthropoids are one another's sisters, to the exclusion of the Omomyidae. This evidence has been reviewed by Rosenberger and Szalay (1980) and Packer and Sarmiento (1984), who favor the idea that the protoanthropoids did not resemble *Tarsius* in the ear region. In light of this, Aiello's (1986) contention that "the loss of the subtympanic recess is best considered as a robust synapomorphic feature" (p. 54) is puzzling. An alleged homologous disappearance of a space in an ear region (i.e., a loss of a character) sensitive to proportion changes which may occur cranially is hardly a feature we would weight highly, particularly in light of the highly modified and unusual middle ear of *Tarsius*.

On the other hand, let us review the characters which appear to be synapomorphously shared between the protoanthropoid and at least some omomyid taxa and assess to what degree the interpretation of these characters is dependent on the assumption of haplorhinism for the omomyids.

First of all, we should note that we obviously assume that the characters listed on Table 3, because they are shared by strepsirhines and haplorhines, were present in the first euprimate. We do, however, see with different degrees of probability, the following complex of similarities as special omomyid-anthropoid, and probably haplorhine, synapomorphies, even though the point noted below under number 5 is still not quite resolved in our minds.

(1) There is a deemphasis of the stapedial and hypertrophy of the promontory arteries along with the medial entry of the carotid artery into the bulla.

(2) There is a strong suggestion in the respective morphologies that the enlarged "hypotympanic sinus" of the known omomyid basicrania is homologous with the pneumatized anterior portion of the anthropoid bulla. The hypertrophied petromastoid of some omomyids (but absent in tarsiids) and the protoanthropoid may be part of a specially shared homologous complex within a larger taxon which includes the tarsiids also.

TABLE 3. Diagnostic euprimate characters[1]

1. Continuous postorbital rings
2. Orbital convergence
3. Enlarged brain compared to known archaic primates, suggested by increased neurocranial part to the facial skull, and an increased relative height of the occiput in adapids compared to *Plesiadapis*
4. Stapedial and promontory arteries subequal, and like the carotid, enclosed in a bony canal; this may be a primitive primate trait
5. Postprotocone fold on upper molars (probably also present in archaic primate ancestry); lowers with relatively low trigonids; trigonids are increasingly compressed mesiodistally from M/1 to M/3
6. On all digits of the manus and pes the protoprimate claws (falculae) are replaced by nails, except for the probably secondary toilet claws of the second pedal digit
7. General elongation of tarsals compared to archaic forms
8. Upper ankle joint equally deep medially and laterally with a greater arc of rotation than in archaic forms; calcaneocuboid joint sellar and spherical, with a well-developed pivot on the cuboid; peroneal process drastically reduced as the calcaneus is elongated; posterior elongation of the astragalar tibial trochlea
9. Powerful grasping and "opposable" hallux; this is primarily realized by entocuneiform-hallucial joint which is sellar with a great arc for abduction and adduction and limited motion for dorsiflexion and plantarflexion; joint is displaced to the medial and distal side of the entocuneiform; large hallucial peroneal process
10. Innominate bone with flattened illium for hypertrophied gluteus medius
11. Patellar groove long and narrow
12. The spherical humeral capitulum of archontans is coupled with transversely wide trochlea, cylindrically shaped and separated from the capitulum by a marked groove

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[1] Derived features which occur in the given combination in the last common ancestry of the taxa included in the semiorder Euprimates.

(3) There are special similarities in the shape and conformation of the incisors of protoanthropoids and some of the omomyids in which these are known (see Rosenberger and Szalay, 1980).

(4) There is a similarity in the downturning of the medial edge of the humeral trochlea in omomyids and of platyrrhines and Fayum primates (see Szalay and Dagosto, 1980).

(5) As we reiterate in this paper, Dagosto (1985) has also shown that certain features of the upper ankle joint, reflected not only on the astragalus but on the crus as well, sort out into a strepsirhine and a haplorhine dichotomy, even though it may not be certain which of these is the primitive euprimate condition. This makes the distal tibia of unclear significance in this problem. However, if the haplorhine distal crural condition is derived, then these features would certainly negate the adapid-anthropoid argument and support haplorhine monophyly. If the noted shared similarity of the distal tibia between omomyids and anthropoids is a primitive euprimate condition, then the adapid-lemuriform similarity is a synapomorphy supporting special ties of these taxa, and anthropoids cannot be derived from this strepsirhine group based on these characters. Either way, the close phyletic association of adapids with anthropoids cannot be supported by tarsal features.

(6) We consider an aspect of cranial morphology discussed by Cave (1967) and Cartmill (1972) and emphasized by Szalay and Delson (1979) a feature of exceptional significance in supporting the concept of Haplorhini. The fact that the olfactory process of the brain passes below the interorbital septum in strepsirhines but above a septum formed by the orbitosphenoid in all known omomyid skulls and in living haplorhines is a powerful indication that the haplorhines fundamentally reorganized the development of the skull due to some hitherto poorly understood adaptive shift involving vision and olfaction. Because a similar change did not occur in short-faced strepsirhines (lorisids), any argument which would tend to point to independent acquisition of developmental constraints is considerably weakened. Clearly, however, without agreement among systematists on the importance of weighting this feature will not be fully appreciated or studied.

None of the features on which we base our view that omomyids, or phyletic sisters of omomyids, are more recently related to anthropoids than to adapids is dependent upon an assumption that haplorhinism existed in the fossils (contra Rasmussen, 1986, p. 3). These osteological features, cited above and detailed in Table 4, continue

TABLE 4. Diagnostic haplorhine characters[1]

1. Shortened facial skull
2. Olfactory process above the interorbital septum
3. Reduced olfactory lobe and enlarged temporal lobe
4. Probable presence of fovea centralis and macula on the retina, and absence of tapetum lucidum
5. Carotid artery enters skull medially; promontory artery is hypertrophied, and at least its bony canal is absolutely larger than the stapedial one
6. Auditory meatus formed by ectotympanic which is elongated and partly outside of the auditory bulla or "phaneric," possibly a retention of the archaic primate condition
7. Petromastoid and squamosal pneumatized with a trabecular bony lattice, and the lack of this condition in *Tarsius* (which completely lacks petromastoid inflation) is probably secondary from an omomyid ancestry
8. Tarsal modifications include a less-cupped astragalar medial astragalotibial facet, and a reduction of the astragalar tibial shelf, compared to the condition seen in the Strepsirhini; this may be a primitive euprimate retention rather than a derived haplorhine feature
9. Inferior tibiofibular joint is relatively rigid and the tibial medial malleolus is less rotated
10. Naviculocuboid articulation offset and not in contact with the naviculomesocuneiform facet on the navicular, a feature which may prove to be an archontan retention
11. Naviculoentocuneiform articulation shortened transversely, a feature which could be, although unlikely, a primitive archontan feature
12. Incisor morphology slightly spatulate and mesiodistally aligned, unlike the *en echelon* arrangement of adapids
13. Humeral trochlea medially downturned

[1] Derived features which occur in the given combination in the last common ancestor of the taxa included in the suborder Haplorhini.

to be open to testing by the fossil record. If these characters continue to be corroborated as synapomorphies on the level designated, then the haplorhinism of the omomyids will become increasingly probable. We do think it is probable that omomyids were nasally haplorhine because they had a more recent common ancestor with tarsiers and anthropoids than any of these strepsirhines. Because we see no evidence which would indicate tarsier-anthropoid monophyly in exclusion of omomyids, haplorhinism was probably present in the common haplorhine ancestor—a probabilistic and not a parsimony-based assessment. If haplorhinism could somehow be refuted in omomyids, it would only necessitate a reevaluation of the internal relationships within the Haplorhini, not negate the existence of this clade. On the basis of high-weight shared derived features listed in Table 4 we believe that the monophyly of the Haplorhini, including not only tarsiers and anthropoids but omomyids as well, is highly probable and remains unrefuted.

C. What is the nature of similarities between adapids and lemuriforms?

It should not be considered curious that the adapid-lemuriform ancestral tie has been so widely accepted. It is important to point out some of the methodological reasons for this, as these have a close bearing on the features themselves on which these views are based.

In order to consider some similarities as convergences, as does Rasmussen (1986), one cannot, or should not, at the same time reject a homology explanation which accounts for these similarities. Before one rejects the homology hypothesis one should at least attempt to show that the similarity is due to alternately and differently achieved morphological pattern or form-function solutions or to differing developmental constraints. If the student who claims convergence cannot document the nature of similarities to be so, then the homology hypothesis was not successfully rejected, and subsequently it is unreplaced by the convergence explanation. The pervasive similarities between adapids and omomyids and the strong suggestion of these resemblances in the ancestries of later primates leave little doubt that we are probably looking at primitive euprimate traits. Most of the similarities between adapids and lemuriforms, although many are primitive euprimate features, are such detailed similarities that trying to explain them as convergences will require the type of testing advocated above, which has not even been attempted so far.

Nothing appears to be more parallel an acquisition than such alleged adapid-anthropoid synapomorphies suggested by Rasmussen (1986) as the "quadrate" teeth of *Adapis* and *Propliopithecus*, "quadrateness" being the vague consequence of numerous independent transformations of mammalian teeth. To imply that such a character is more of a special similarity between these taxa than the intricate resemblance between, for example, the molars of some adapids and *Lepilemur* or *Hapalemur*, is to ignore a clear hierarchy of similarities which are decisive in transformation determinations, or at least in the initial ordering of resemblances. Similarly, Rasmussen's claim, citing Charles-Dominique and Martin (1970) and Cartmill (1982) as his sources for the notion that the small cheirogaleids represent the primitive lemuriform postcranial condition, is without any foundation in the character analysis of the skeleton (see Dagosto, 1986).

It is admittedly difficult to establish that the great variety of osteological features which are known to be part of the morphotypic condition of lemuriforms (and are specifically found among the extant Lemuridae and Indriidae) are strepsirhine synapomorphies, acquired after the split of the Adapidae and Omomyidae. Yet, to state that adapids are more recently related to tarsiiforms and anthropoids (haplorhines) than to the tooth-combed strepsirhines requires a methodological bias which would disregard the uniformity of such special strepsirhine complexes as the basicranial morphology along with cranial and postcranial similarities. There is not one undisputed, high-weight character which would suggest a theoretical preference for an adapid-anthropoid transformation rather than special ties between adapids and lemuriforms.

Cartmill and Kay (1978) and Rasmussen (1986) claim that there are no recognized shared derived features linking adapids with living tooth-combed lemuriforms. In Table 5 we list four such characters. We think, unlike others (e.g., MacPhee and Cartmill, 1986), that the annular and intrabullar nature of the ectotympanic in strepsirhines is unique among primates and is probably derived from the condition seen in archaic primates. The primitive haplorhine condition, as seen in the known omomyids, probably reflects this ancient primate heritage. Clearly, however, this is only a tenuous interpretation.

The anterior dentition of strepsirhines displays an en echelon alignment of the first and second upper incisors in which the latter are staggered behind the former. In this strepsirhine pattern the lower incisors occlude with the central upper one. Persistence of this pattern in the last common ancestor of the Lemuriformes strongly suggests a strong and unique phylogenetic constraint restricted to the strepsirhines since there seems to be no evidence for it among the omomyids and other haplorhines.

In addition to those cited, two postcranial features link adapids and lemuriforms. The astragalofibular facet on the astragalus slopes gently laterally for its entire extent in all known strepsirhines (Dagosto, 1986; Gebo, 1986). In contrast, in *Tarsius* omomyids, and anthropoids the facet is very flat until it develops an abrupt lateral flare at its plantar end. The condition seen in strepsirhines is unique among the primates (and possibly among other mammals), whereas the haplorhine character is also found in paromomyiforms and other mammals. Thus, it appears that the strepsirhine condition is a synapomorphy.

Strepsirhines also share a unique naviculocuboid contact (Fig. 5; Dagosto, 1986). In these animals the navicular and cuboid have a broad articulation which results in the facet lying plantar to both the naviculoentocuneiform and the naviculomesocuneiform facet. In haplorhines, like in other eutherians, the naviculocuboid facet only contacts the naviculoectocuneiform facet. The polarity of this morphocline is admittedly unclear to us (but see Dagosto, 1986).

It is not unlikely that the Adapidae, as it is constituted now, is paraphyletic, a perfectly satisfactory arrangement given the level of our understanding of their structural details. This does not mean that such a taxon, a paraphyletic one, is the equivalent of a grade (see more on this above and below). Some adapids were most probably more recently related to lemuriforms than to omomyids, but none shows signs of special relationships to protoanthropoids. The use of the concept of "lemuroid" and "tarsioid" grades by Rasmussen (1986, Fig. 2) to advance a proposed phylogeny is methodologically unsound, and these grades are empirically undefined. What is the evidence that the character constellations in these two "grades" have been achieved independently at least twice? If there is no evidence, then we have a clade, holophyletic or paraphyletic. Rasmussen speaks of close similarity between Adapidae and Omomyidae. Rather than acknowledging that this suite of similarities represents the euprimate character constellation (and there is no evidence that would suggest the Euprimates to be a grade rather than the clade it almost certainly is) or, more properly stated, that these attributes are primitive euprimate similarities, Rasmussen implies in his Figure 2, but does not demonstrate in the text, that the similarities of adapids and omomyids are synapomorphies. Similarly, he does

TABLE 5. Diagnostic strepsirhine characters[1]

1. Ecotympanic annular and intrabullar or "apheneric," and the auditory meatus is formed by petrosal; this may represent the primitive euprimate condition derived from that described for protoprimates (see Table 2)
2. *En echelon* alignment of the first and second upper incisors (the latter staggered behind the former), and occlusion of lower incisors with the central upper one
3. The astragalar fibular facet with large amount of flare and a gentle slope in contrast to the haplorhine condition (see Table 4)
4. Navicular naviculocuboid facet in contact with naviculomesocuneiform and naviculoentocuneiform facets

[1] Derived features which occur in the given combination in the last common ancestor of the taxa included in the suborder Strepsirhini.

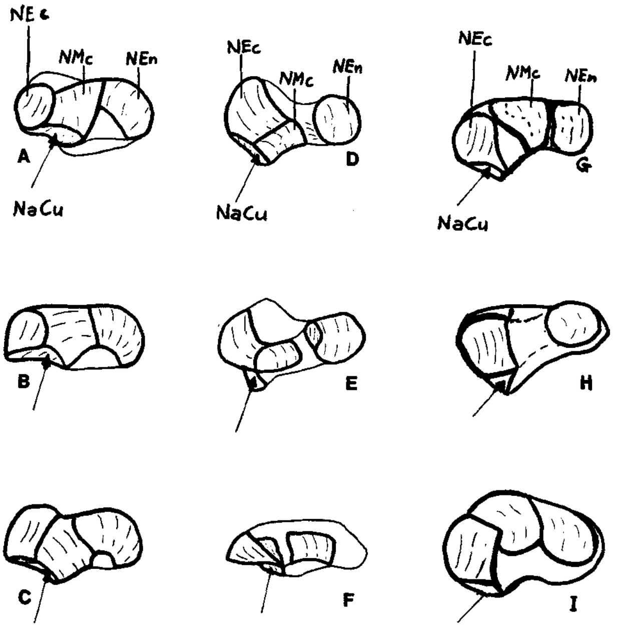

Fig. 5. Comparison of the distal end of the navicular bone from the tarsus in primates. This is one of the several complexes of postcranial features which align the Omomyidae with the Anthropoidea and the Adapidae with the Lemuriformes. Although the haplorhine condition (G–I) is similar to Paleogene eutherians in having the naviculocuboid (NaCu) facet in contact only with the naviculoentocuneiform (NEc) facet, it is distinct from both other primates and eutherians in having the naviculomesocuneiform (NMc) facet retract from both the adjacent NEc facet and the plantar surface of the bone. Strepsirhines are equally derived compared to other eutherian patterns in having the NaCu facet bordering both the NEc and NMc facets. We do not know what the primitive primate condition was. A, *Lemur*; B, *Propithecus*; C, *Cheirogaleus*; D, *Microcebus*; E, *Galago*; F, *Nycticebus*; G, *Hemiacodon*; H, *Tarsius*; I, *Cebus*. Arrows point to the NaCu facets.

not demonstrate that the "lemuroid grade" features have evolved in parallel or convergently.

This procedure is unacceptable juggling of the systematic meaning of empirically established similarities. Similarities exist throughout all of these taxa, but their sorting out as to the level of recency of their origin is dependent on evenly applied criteria. The proper scientific procedure in this case, given a working hypothesis, is to show in the framework of an empirical study that these attributes are indeed not monophyletic; i.e., they resemble each other in parallel or convergent fashions. Reference to the various suites of characters as gradal rather than cladal is a literary rather than a properly biosystematic procedure. Given the unique distribution of these features within the taxa Strepsirhini and Haplorhini, the burden of proof that these are nonsynapomorphous features rests on those who claim such a position.

D. What is the nature of adapid-omomyid similarities?

The pervasive similarities between adapids and omomyids, and the strong suggestion of these resemblances in the ancestries of both lemuriforms and anthropoids leave little doubt that we are probably looking at primitive euprimate traits. To state that adapids are more recently related to omomyids than to lemuriforms means that the various strong special resemblances between the ear regions and cranial anatomy of the omomyids and of anthropoids and the list of adapid-lemuriform similarities established by Gregory (1920) are being simply dismissed. In our view no convincing shared and derived features have been advanced to support a clade consisting of adapids and haplorhines to the exclusion of the Lemuriformes.

TABLE 6. Diagnostic anthropoid characters[1]

1. Hypotympanic sinus (an anterior accessory cavity) shifted anteriorly and partly separated from the promontorium by a transverse septum
2. Hypertrophied (beyond known omomyid condition) carotid artery enters bulla medially into the transverse septum, and the stapedial is known only as an embryonic vessel
3. The ventral petrosal bulla, the hypotympanic sinus (the anterior accessory cavity), and the petromastoid are filled with a trabeculated network of bone (pneumatized)
4. Ectotympanic ribbon-like (not annular as in primitive strepsirhines) and extrabullar ("phaneric") with a ventral component wider than the two dorsal horns, not similar to the strepsirhine condition
5. Complete postorbital plate (secondarily open in *Aotus* due to the hypertrophy of eyes)
6. Mandibular symphysis fused
7. Incisors transversely mesiodistally in contact and transversely oriented
8. Hallux and the peroneal process of the first metatarsal reduced compared to omomyids or strepsirhines
9. Entocuneiform-hallucial joint is modified ovoid, rather than sellar in construction
10. The following derived fetal membrane attributes are known in living species: discoidal, hemochorial placenta; invasive attachment of placenta; primordial amniotic cavity; no choriovitelline placenta; body stalk; rudimentary allantois

[1] Derived features which occur in the given combination in the last common ancestor of the taxa included in the semisuborder Anthropoidea.

New fossils are continuously being described which will undoubtedly increase our ability to judge the complex similarities and differences of Paleogene euprimates. In addition to new evidence either from fossils or extant species, there are some efforts to reinterpret some of the known evidence. Schwartz (1984, 1986), in two recent assessments of omomyid taxa, has attempted to demonstrate that the concept of the Omomyidae is nonmonophyletic. One representative example of his numerous views on primate phylogeny in these papers is his case for the European microcherine *Pseudoloris* actually being a galagid. This view is developed further, and he suggests a tarsioid-lorisoid sister group relationship. In spite of Schwartz's systematics, we believe that the Omomyidae is a monophyletic, probably paraphyletic, tarsiiform group.

Although Rasmussen (1986) uses the broadly accepted concept of Omomyidae, we dispute his views on the nature of attributes of this family. We reluctantly conclude that much of the evidence has been misunderstood in exactly those subtle details which must be functionally understood to be decisive in the determination of polarities of the various morphoclines. Not only *Teilhardina*, but also *Omomys*, *Chumashius*, very likely *Anaptomorphus*, *Washakius*, and probably many others (estimated by the phyletic distance between these taxa) possessed unhypertophied lower incisors and relatively larger lower canines. It is clear that the morphotype omomyid did not differ significantly from its adapid relative (or ancestor) in incisor hypertrophy and canine reduction, and consequently the nature of similarity of the protoanthropoid in these features to what possibly were euprimate attributes forces no choices in regard to either of these earliest two families of euprimates.

E. Were adapids haplorhine and omomyids strepsirhine in their nasal structure and physiology?

Rasmussen (1986) raised these two questions and suggested possible answers to this query. The phylogeny advocated by him necessitates that either the adapids were haplorhine in nasal and related morphology or that haplorhinism evolved independently in *Tarsius* and anthropoids. We cannot find any traces in the morphology of living or fossil taxa which make such conditions likely. From what we know from endocasts of the relative size of the olfactory lobes (with their real although unspecifiable connection to rhinarial function and bioroles) and of the large and complex system of olfactory turbinals in *Adapis* (Rosenberg and Strasser, 1985), adapids do not have the comparable reduction of the olfactory system seen in omomyids. Until some new correlation of the skull and teeth and the nose in living primates aids the evaluation of fossils (considering caveats such as the one noted below concerning the gap between the upper incisors) this will remain a moot, unprovable point. The important correlates of haplorhinism, i.e., the continuous upper lip and nonglandular nose (the primitive strepsirhine retention of the shape of the nostrils in *Tarsius* notwithstanding, as noted by Hofer, 1979), are very likely synapomorphies between tarsiids and anthropoids, and the assessment of omomyid ties to anthropoids and *Tarsius* is entirely independent from this.

We briefly examine here various suggestions concerning the prediction of strepsirhinism vs. haplorhinism in fossils. Martin (1973) has argued that a rhinarium is necessarily associated with the separation of the upper incisors, basing this view on the hypertrophied tethering philtrum seen in extant lemuriforms, which is accompanied by a wide separation of the upper central incisors. However, the simple fact that such rhinarium possessing taxa like the Canidae, Viverridae, and Hyaenidae, to list only a few eutherians, and marsupials like the phalangerids (*Gymnobelidius*, *Petaurus*, etc.) have tightly connecting central incisors, invalidates such a simple predictive scheme (for various views on paleobiological prediction see Kay and Cartmill, 1977; and Szalay, 1981b). A number of Paleocene groups of mammals, including the various arctocyonids known by skulls, have relatively enormous olfactory lobes and tightly fitting upper incisors, and it is not unreasonable to suggest that they were nasally strepsirhine.

In living lemurs, although they do have an extensive philtrum connecting the rhinarium and the vomeronasal organ (possibly hypertrophied from a primitive euprimate condition) the gap may be a consequence of the extraneous (or possibly connected, see Rosenberger and Strasser, 1985) factors of occlusion. As Rosenberger and Strasser (1985) point out, the adapid upper incisor conformation with the lower counterparts suggests that the gap above is not tooth-comb related. The tooth comb has certainly altered the relationship of the occluding teeth and their spacing, yet the nature of similarities and differences between the adapids and lemuriforms (a detailed functional-adaptive analysis, along the lines advocated by Bock, 1981, is much needed) has not as yet been explained satisfactorily. We must conclude from this, tentatively, that a correlative assessment of upper incisor relationships in the tooth-combed lemuriforms is not a reliable guide with which to predict the structure of the nose in other mammals or specific primates. It is for this reason that we cannot endorse Schmid's (1983) and Aiello's (1986) arguments, based on Martin's (1973) analysis, that the Microchoerinae were strepsirhine. Surely the unique incisor occlusion, even with convincing evidence of fur combing (Schmid, 1983), coupled with the greatly reduced frontal lobe in omomyids (*Necrolemur* included), makes a tooth-gap-related assessment of the nose in the Microchoerinae highly equivocal.

As far as we know, there is no evidence to support Rasmussen's (1986, Fig. 2) scheme in which a haplorhine adapid would be the predecessor of the anthropoids. If the "3rd" hypothesis of Gingerich and Schoeniger (1977) is correct, as Rasmussen (1986) advocates, then we must accept the common ancestors of omomyids and adapids to have been haplorhine unless we evoke its independent evolution twice, and we also have to accept the independent evolution of a foveate retina, unless we have adapids with such features.

What is indeed remarkable about the scheme which Rasmussen (1986) proposes is that we have come full circle concerning soft anatomical evidence. He claimed that implications of soft anatomical features for fossils are necessary for the Strepsirhini and Haplorhini subdivisions of the Euprimates. We attempted to show that the assessment of adapid and omomyid ties is dependent only on features associated with hard anatomy. For the hypothesis Rasmussen endorses, however, assumptions about rhinarial morphology and eye anatomy are necessary, and these have no corroborating evidence in their favor—only negative evidence which can never be tested.

ON THE USE OF GRADES AND CLADES IN DEALING WITH DIVERSITY AND EVOLUTION

Earlier in this paper we noted the meaning and use of the grade concept in systematics, and expressed the opinion that various workers sometimes seem to resort to analysis by grade when they believe that exact evolutionary relationships cannot be established. An example of this approach is given by MacPhee et al. (1983), who adopted a gradal arrangement of the order Primates. We have already dealt with the grade concept itself above; now we will comment on the specifics of their arrangement.

We believe that MacPhee et al. (1983) have also misapplied the concepts of grades, paraphyly, and holophyly. These authors recommend a reversion to a three-tiered classification of the order into grade I (the Plesiadapiformes), grade II (the Prosimii), and grade III (the Anthropoidea). Their rationale for such an action is that grade I can accommodate groups of uncertain affinities, and grade II can conveniently hold such taxa as Lemuroidea, Lorisoidea, and Tarsiiformes, whose affinities they believe to be doubtful.

What do MacPhee et al. (1983) imply by their unique concept of grades of primate evolution? We believe that their "grades," in which they strive for monophyly, represent an anthropoid-centered construct/phylogeny cum classification of the primates. We find no adaptive common denominators (other than those based on shared synapomorphies, and therefore cladal), and the authors offer no clue for the biological justification of these grades.

Grade I includes both groups whose locomotor propensities are unknown (Mixodectidae), and also so obviously different forms as the volant dermopterans (to which we believe the Microsyopidae belonged; see Szalay and Drawhorn, 1980) and the scansorial (some more terrestrial than others) but nonvolant tupaiids. If, as they express it in the paper, attempts to show the archaic primates to have been arboreal were "failures" (as also implied by Martin, 1986), then why group terrestrial, arboreal, and gliding forms in the same "grade"? If there is, on the other hand, a "phylogenetic" similarity among these forms, why then should the grade concept be used at all?

What holds grade II together as a grade? We cannot think of a single characteristic of this group which is not one of the features found in the morphotype of the semiorder Euprimates. This "new" group is, of course, the monophyletic Prosimii, dating back to a time when the more precise ties of its members could not be sorted out. Beyond that we are puzzled by the use of the grade concept in a manner which groups in the "same" grade animals as distinct as *Microcebus* and *Archaeoindris*, or *Daubentonia* and *Tarsius*. How does this scheme satisfy the views advanced by Cartmill and Kay (1978) and Cartmill et al. (1981) of *Tarsius*, the only surviving tarsiiform genus, which according to these authors is the sister group of the Anthropoidea?

Although we find no convincing support for this view, we do find that two of the most convincing phylogenetic features of grade III—a foveate retina with the lack of an enveloping tapetum lucidum, as well as a postorbital septum—are also found in grade II—in *Tarsius*! If *Tarsius* is secondarily nocturnal (or "prosimian"?) as Cartmill et al. (1981), among others, have forcefully argued, then why not keep the taxon with its phyletic sisters? To extend the reasoning behind such an arrangement, we are surprised that *Aotus*, a nocturnal form, is not included in grade II. Clearly, grade II is defined by the lack of anthropoid cladal characters, thus strongly supporting our view that this gradal scheme is not based on the traditional notions of independently attained biological levels of organization, but on a purely anthropoid perspective of the order.

While we applaud the expressed views of MacPhee et al. (1983) that evolutionary explanations are necessary for the understanding of grade boundaries, we are puzzled by their neglect of the information of postcranial adaptations found in grade I. While we consider their groupings a very imprecise phylogenetic arrangement, we find no other biological reasons for their composition either. In producing a polyphyletic group in grade I, they seem to deny (in that paper) one of the most fruitful and integrative of biological research objectives of evolutionary biology, that of the mutually reinforcing search for adaptive and evolutionary hypotheses which yield the most probable taxon phylogeny.

It is quite obvious to us that gradal arrangements, such as they may be, are just as arbitrary as any poorly supported phylogenetic arrangement. The latter, however, have the merit of being refineable along the same conceptual foundations on which the better-corroborated taxa are based. As new information becomes tested we believe that a phylogenetically and adaptively (different sides of the same coin) well understood order Primates, accommodating both the archaic and modern primates, will be firmly established.

CONCLUSIONS

It is our firm conclusion, after reviewing the literature and the evidence for the early descent and branching of the order Primates, that the understanding of the evolutionary path of various groups depends on the understanding of character transformations. Transformation hypotheses of character complexes, involving distributional, functional, developmental and adaptive assessments, are the most vulnerable and therefore most scientific bases of taxon phylogeny. It is paleontological and functional-adaptive research into characters, rather than parsimony-based schemes (based on distribution alone) divorced from biology and the fossil record, which holds out the greatest promise to resolve character conflicts which bedevil the taxon phylogeny of primates and other groups.

GLOSSARY

A ready source of information on the evolutionary history of groups of primates and a classification of the order is in Szalay and Delson (1979). Another older but highly reliable and authoritative book on primate evolution is that of Le Gros Clark (1959).

The following brief definitions are included at the suggestion of the editor for those not familiar with these morphological and systematic concepts. A detailed glossary is found in Szalay and Delson (1979).

Adapidae family of Paleogene primates.

Archonta cohort of eutherian mammals consisting of the Scandentia (tupaiids or tree shrews), Primates, Dermoptera (colugos or flying lemurs), and Chiroptera (bats).

Artiodactyla order of even-toed ungulate eutherian mammals.

clade a monophyletic segment of the evolutionary tree of life, a phyletic lineage.

Condylarthra order of ancient mammals which very likely gave rise to such diverse modern descendants as the artiodactyls, perissodactyls, and whales.

Dermoptera (see Archonta).

grade level of biological organization attained independently by two or more lineages (see text).

haplorhine the vernacular form of the formal taxonomic name Haplorhini.

haplorhinism the set of conditions in common which characterize the nose and related complex in the living haplorhines. These include the presence of fur to the margins of the nostrils; nostrils widely separated by a hair-covered internarial septum; presence of a continuous mobile upper lip.

holophyletic a monophyletic taxonomic group which includes all the descendants of the last common ancestor of that group (Hennig's concept of monophyly).

Microsyopidae family of Eocene mammals, probably member of the gliding Dermoptera.

Mixodectidae family of Paleocene-Eocene mammals, either of dermopteran or scandentian (tupaiid) affinities.

monophyletic a group whose most recent common ancestor is included in that group. Both holophyletic and paraphyletic groups are monophyletic.

neontology the study of aspects of living organisms, as opposed to the study of fossils (paleontology).

Omomyidae Tertiary family of primates.

paraphyletic a monophyletic taxonomic group which does not include all the descendants of the last common ancestor of that group.

phenon (phena, pl.) a morphologically relatively uniform sample of a taxon; a morphologically, but not necessarily specifically or generically, distinct sample.

phenetic school systematic approach in which groups are created based, ideally, solely on the degree of resemblance among individuals without any assumptions of evolutionary descent.

philtrum the median groove on the upper lip of humans and other living haplorhines; the term also applies, as it is developmentally homologous, to the median part of the rhinarium that is connected to the gum, after passing through between the two halves of the upper lip in the more primitive lemuriform and eutherian conditions. The remnant of this can be felt with the tongue as the tethering of the upper lip to the gum.

polyphyletic a group whose most recent common ancestor is not included in that group.

stratophenetic reconstruction of phylogeny based on the stratigraphic superposition of similar fossils.

strepsirhine the vernacular form of the formal taxonomic name Strepsirhini.

strepsirhinism the set of conditions in common which characterize the nose and related complex of the strepsirhine primates and many other groups of therian mammals. Traits include the presence of a naked, moist patch of skin surrounding the nostrils; slitlike nostrils; upper lip bound down to the gum.

symplesiomorphy shared ancestral (primitive) characters.

synapomorphy homologously shared derived (advanced) characters.

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