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Tarsiers — "These animals are astonishingly deliberate and stupid-appearing in behavior, so much so that it seems a miracle that they can survive." D. Dwight Davis, 1962

Tarsius, whatever its aptitude, has managed to survive, and its phylogenetic relationships, classification, and evolutionary significance remain among the most interesting unsolved problems in primatology. First classified as a lemur, when that term included all prosimians, then separated in a group distinct from the other primates, *Tarsius* is now sometimes ranked with anthropoids. Thus the tarsier has achieved in a century of classificatory revision what most "lemurs" failed in 50 million years of evolution!

The phylogenetic position of *Tarsius* is fundamental to any consideration of either its classification or its evolutionary significance, and the phylogenetic relationships of the genus will receive most attention in the following discussion. First, it is necessary to outline and justify the methodology of phylogeny reconstruction advocated here (not because it is a new methodology, but because it has rarely been stated explicitly and it has recently fallen out of favour with a vocal majority of systematists). Second, it is necessary to review briefly the fossil record of primates, with emphasis on the early Tarsiiformes. Finally, a comment will be added concerning both the classification and the evolutionary significance of *Tarsius*.

It should be noted at the outset that it is impossible in a paper of this length to deal specifically with individual criticisms of my earlier conclusions regarding the relationships of *Tarsius* and the origin of anthropoid primates, such as those recently put forward by Szalay (1976) and others. These will be discussed at length in a monograph on the evolution of Eocene Adapidae now in preparation. Suffice it to say that I think most disagreement is due to differences between stratophenetic and "cladistic" approaches to phylogeny reconstruction, and this is the problem I wish to discuss at greatest length here.

PHYLOGENY RECONSTRUCTION

A phylogeny is generally understood to be the history of the various lines of evolution within a group of organisms. The very concept of *history* implies a time dimension, and only historical data, records of past times, can be used to reconstruct history with any confidence. This is as true of the study of animal phylogeny as it is of the study of 'prehistory' or the history of Victorian England. The historical data of animal phylogeny, fossils, are the objects of research of a branch of science, paleontology, which is uniquely suited to the study and reconstruction of phylogeny. If there is an "undesirable" characteristic of paleontological methodology, it is the following: when historical data are inadequate to permit determination of the lines of

evolution within a given group, paleontology yields no phylogeny. When the fossil record is inadequate, sound paleontological methodology has often been abandoned in favour of analytical algorithms that do yield answers, whether the available raw data are adequate to solve the particular problem or not. Thus, it is little wonder that recently proposed phylogenies based chiefly on the comparative anatomy of living primates have proven so unstable and so controversial.

The essence of phylogeny reconstruction based on paleontology ("stratophenetics" see Gingerich 1976b) has been described and applied, explicitly or implicitly, many times (see Simpson, 1961, for example) but I am not aware that anyone else has stated the method quite so simply as it is presented here. Three steps are involved: (1) data organization, (2) linking, and (3) testing.

Data organization, simply stated, involves arranging the available fossil specimens in chronological order (i.e., stratigraphical order). This is conveniently done in a diagram, where morphological attributes of the oldest fossils are recorded at the bottom and attributes of successively more recent ones are recorded in sequence, with the youngest known (Recent, if there are any living members of the group) being plotted at the top.

Phenetic linking joins the different species in any one time interval to the most similar species samples in adjacent intervals. Ideally, the criterion of acceptable linking would be near identity of population samples in adjacent intervals, and this is sometimes possible (Gingerich, 1976a, b). In other cases gaps in the fossil record introduce varying levels of uncertainty, depending on the size of the gap and the morphological distinctness of the two species populations being linked. The pattern of phenetic linking derived from this step itself constitutes the principal phylogenetic hypothesis.

Critical testing requires that a high level of uncertainty be placed on a phylogeny lacking a dense and continuous fossil record. Once the pattern of stratophenetic linking is worked out, it is possible to go back over it and study the evolution of individual morphological characters. Links based largely on characters seen to be retentions of primitive morphology (as between the Adapidae and living lemurs, see below) are somewhat weaker than links based on newly acquired characteristics. However, the crucial test falsifying a phylogenetic hypothesis constructed stratophenetically is usually the discovery of new fossil evidence that cannot be accommodated into the pattern of phenetic linking previously advanced. It is a positive characteristic of phylogenies constructed stratophenetically that they do tend to be relatively stable.

In view of the wide use of "cladistics" to reconstruct phylogenetic history, some specific criticisms will here be directed toward that approach to phylogeny. To put this into perspective, the approach outlined above and advocated here can be summarized as follows:
1. Fossils are collected from different stratigraphic intervals.
2. These fossil taxa are linked together based on their overall similarity and stratigraphic proximity.
3. If a fairly dense and continuous pattern of linking is found, the whole pattern is accepted as the probable phylogeny of the group under study. Several additional steps are usually taken to establish evolutionary patterns and erect a classification:
4. Individual characters are studied to trace their change through time, giving some idea of the relative importance of character divergence, convergence, parallelism, and other patterns in evolution.

5. Individual lineages are grouped into clades at various levels, based on common ancestry. Morphological characters held in common by species within each clade are used to diagnose various clades from each other, and verbal classifications are constructed from this.

The end result is an understanding of the phylogenetic history of the group being studied, better knowledge of how evolution works, and finally a verbal classification that can be used to organize species and discuss them in groups at whatever level is preferred.

In contrast to this approach, cladistics requires *a priori* assumptions about the phylogenetic history of the group under study and about the evolutionary patterns of individual characters. Cladistics attempts to provide conclusions comparable to those of steps 4 and 5 above, without any independent means of constructing the phylogeny from which the conclusions must be derived. This problem arises because cladistics is basically a method of classification, and not a method of phylogeny reconstruction. Clades themselves are parts of a phylogeny, not something with an independent existence that can be used to construct a phylogeny. In other words, clades have no existence until the desired phylogeny is already constructed.

Circularity is manifest at every stage of cladistic analysis as it is currently being used to reconstruct phylogenies. As presented by numerous authors, cladistic analysis involves:

1. Identification of the alternative states of homologous characters.
Comment: However, homologous characters are characters that can be traced back to the same feature in a common ancestor — which can only be done *after* the phylogenetic history of the group is known.

2. Arrangement of alternative states into a "morphocline" for each character.
Comment: The only justification for a bipolar morphocline is an operational one — this simplistic, one way, primitive-to-derived ordering is *assumed* in order to make the subsequent analysis manageable. Examples of evolutionary radiations including both evolutionary reversals and multipolar character radiations have been documented in the fossil record (see Gingerich, 1976b) and are undoubtedly both common and important in evolution.

3. Assignment of "polarity" to the morphocline, i.e. one end of the morphocline is identified as primitive, the other as derived.
Comment: For every rule used to assign polarity to a morphocline there is an equally valid converse: a widely distributed character state (such as the presence of hair in mammals) is assumed to be primitive, whereas it may only be the result of a secondary radiation within the group (nails on the terminal phalanges of most primates are an example of a widely distributed, but probably derived character state, claws being primitive or sometimes probably secondarily derived), illustrating that widely distributed character states are not necessarily primitive. Character states that appear early in ontogeny are assumed to be primitive because ontogeny usually recapitulates phylogeny, but neoteny is a well known and important developmental process leading to the converse.

4. Species sharing large numbers of "derived" character states are clustered together in a cladogram.
Comment: Even when two living species are known to possess derived character states, it is often not possible to demonstrate that these are shared because of common inheritance — adaptation, unfortunately for the comparative anatomist, has been very effective in moulding similar morphological patterns independently, whether convergently or in parallel.

5. The resulting cladogram is used to infer phylogenetic relationships.

Comment: Cladograms represent an attempt to summarize the most parsimonious possible classification of animals according to the distribution of morphological character states — they contain no historical information beyond that assumed in their construction.
To repeat a conclusion of the preceding paragraph, cladistics is a method of classification and not a method of phylogeny reconstruction.

FOSSIL RECORD OF TARSIIFORMES

Turning to the fossil evidence, it is interesting to note that among the most respected evidence discussed at the 1918 Zoological Society symposium on the relationships of *Tarsius* was the apparent dental similarity of the Oligocene primate *Parapithecus* to the tarsier. "*Parapithecus* retains sufficient of the primitive traits to establish the truth of the Tarsioid ancestry of the Apes, ..." (Elliot-Smith, 1919). However, the most striking similarity of *Parapithecus* to *Tarsius* has since been shown to be an artifact of breakage (Simons, 1972): the mandible of *Parapithecus* appeared to have a V-shaped mandible, a mobile mandibular symphysis, and retain but a single pair of incisors only because the symphyseal region and the central incisors were broken away before the left and right rami were found and reassembled (see Fig. 1). *Parapithecus* is still considered a very primitive anthropoid, but its morphology, as now known, supports the stratophenetic hypothesis that higher primates originated from Eocene Adapoidea, leaving the tarsier in a much different phylogenetic position (see below).
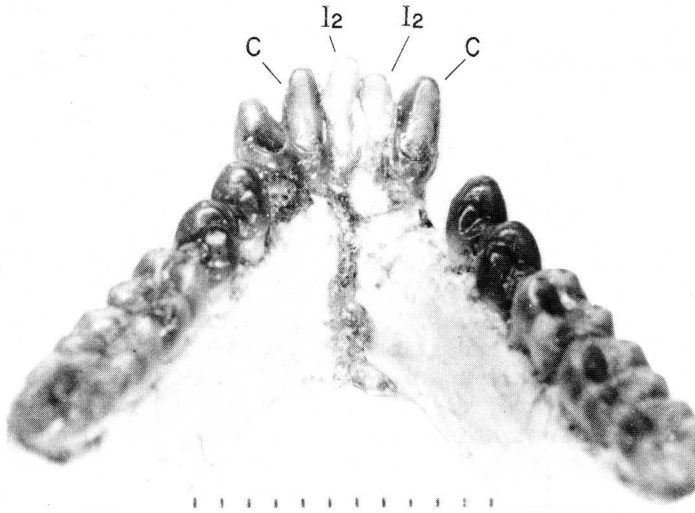

Figure 1. *Type and only mandible of the primitive anthropoid primate Parapithecus fraasi from the Fayum Oligocene of Egypt. Note breakage between left and right rami causing the specimen to falsely resemble tarsioid primates by making it appear to have had a V-shaped mandibular arch, unfused symphysis, and only one pair of lower incisors (the left and right lateral incisors). Photograph of specimen in Stuttgart Natural History Museum, Ludwigsburg; scale is in mm.*

It is an unfortunate accident of biogeography and paleontological discovery that no fossils are known that closely resemble *Tarsius* from strata younger than 35 million years before present. In the Eocene, two such subfamilies of Tarsiiformes are known, the Omomyinae (recently reviewed by Szalay, 1976) and the Microchoerinae (reviewed by Simons, 1961, and more recently by Sudre). Some members of both of these subfamilies are known from relatively complete skulls and dentitions, and there is general agreement that both groups are tarsiiform — stratophenetically they link more closely to the living tarsier than to any other mammalian group. Close resemblances in dentition (see Figure 2), and cranial and basicranial structure are sufficient to constitute a strong link between Eocene Omomyinae-Microchoerinae and *Tarsius*, in spite of a 35 my gap in the fossil record. Furthermore, Eocene tarsiiform primates link closely stratophenetically with Paleocene plesiadapiform primates. Their close stratigraphic proximity, similar dentition (especially the enlarged lower central incisors), and similar auditory region (especially the tubular ectotympanic) being the strongest evidence favouring this close linking (Gingerich, 1976b).
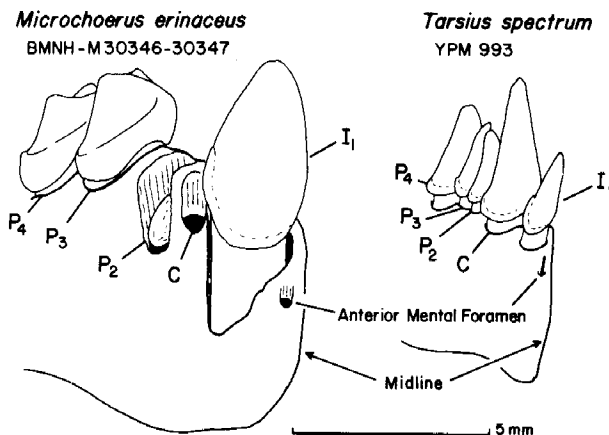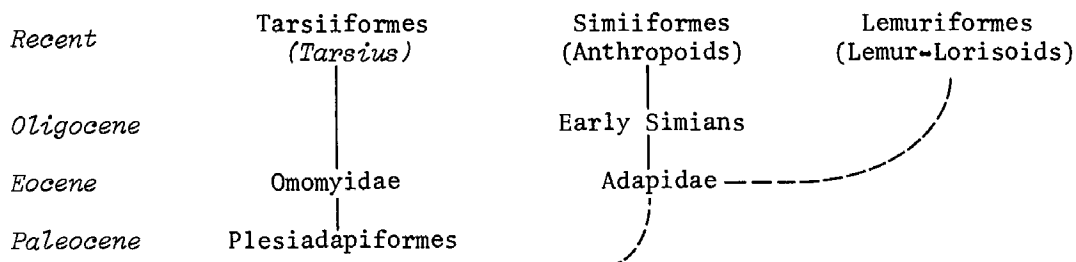

Figure 2. Comparison of the herbivorous late Eocene microchoerine *Microchoerus*, with the insectivorous Recent *Tarsius*. Note especially the unfused mandibular symphysis and large pointed central incisors found in both — these are important characteristics by which both differ from Eocene adapids and primitive anthropoids. (Figure from Gingerich, 1976b.)

How do the remaining living primates relate to this broad plesiadapiform-tarsiiform evolutionary pathway? Living lemuriform primates are, like *Tarsius*, separated from their closest possible ancestors in the fossil record by a nearly complete gap of some 35 my. The only Eocene primates possibly ancestral to the living Lemuriformes are the Adapidae, which share with modern lemurs certain cranial features thought to be primitive for primates (annular ectotympanic) and lack other important derived features of living Lemuriformes (such as the tooth comb; but see Gingerich, 1975).

It was mentioned above that the anterior dentition of *Parapithecus*, as now known, supports an adapoid rather than tarsioid origin for higher primates. This linking between primitive anthropoids and Eocene adapoids is one of the strongest in all of primate phylogeny. The Oligocene anthropoids from the Fayum can hardly be distinguished from late Eocene adapids in any morphological

characters yet known, i.e., in molar structure, in their anterior dentitions, or in middle ear morphology. *Amphipithecus* is a late Eocene primate of particular importance to this discussion because authorities disagree about whether it is anthropoid or adapoid in morphology — further substantiating the broad linking of these two groups.

The general pattern of stratophenetic linking in primates can be diagrammed as follows, where solid lines indicate relatively strong linkings and dashed lines indicate relatively weaker linkings:

Recent   Tarsiiformes   Simiiformes   Lemuriformes
                   (Tarsius)   (Anthropoids)   (Lemur-Lorisoids)

Oligocene   Early Simians

Eocene   Omomyidae   Adapidae — — — — —

Paleocene   Plesiadapiformes

This phylogenetic pattern is discussed in more detail in Gingerich and Schoeninger (1976). It should be noted that cladistic testing of the above pattern shows that many of the similarities shared by recent Lemuriformes and Eocene Adapidae are characteristics (such as the free annular ectotympanic) thought to be primitive in primates, thus weakening this link between the two groups.

CLASSIFICATION AND EVOLUTIONARY SIGNIFICANCE OF *TARSIUS*

Several different classifications could be proposed for the pattern of phylogenetic relationships diagrammed above. Classification of Tarsiiformes and Plesiadapiformes together in one suborder, and Simiiformes and Lemuriformes together in another seems to be the most natural classification since both halves of this dichotomy appear to be strictly monophyletic. If it is found that in fact modern Lemuriformes were not derived from the Adapidae, then adapids should probably be ranked as primitive Simiiformes, and the Lemuriformes retained as a third suborder. Inclusion of Tarsiiformes and Simiiformes as a single suborder, with Plesiadapiformes and/or Lemuriformes excluded, makes the resulting "Haplorhini" polyphyletic or paraphyletic, depending on which group or groups are excluded.

To conclude, it appears that *Tarsius* should properly be regarded as a side branch derived from the earliest and most primitive primates, rather than a close relative of early anthropoids. The few distinctive "derived" characters of soft anatomy shared by *Tarsius* and anthropoids may have evolved independently, or they may prove in fact to be primitive characters of primates. Without a fossil record to document successive stages in the evolution of a given anatomical character, it is very difficult (perhaps impossible) to use the character to infer relationships within a group of mammals.

ACKNOWLEDGEMENTS

REFERENCES

Davis, D.D. (1962). *Bull. Singapore natn. Mus.*, 31, 1-129.
Elliot Smith, G. (1919). *Proc. Zool. Soc. Lond.*, 1919, 465-475.
Gingerich, P.D. (1975). *In* "Lemur Biology", (I. Tattersall and R. Sussman, eds), pp. 65-80, Plenum, New York.
Gingerich, P.D. (1976a). *Am. J. Sci.*, 276, 1-28.
Gingerich, P.D. (1976b). *Univ. Mich. Pap. Paleont.*, 15, 1-140.
Gingerich, P.D. and Schoeninger, M.J. (1976). "The fossil record and primate phylogeny", *J. Human Evolution*, 6, 483-505.
Simons, E.L. (1961). *Bull. Br. Mus. nat. Hist.*, Geol. 5, 43-65.
Simons, E.L. (1961). "Primate Evolution", Macmillan Co., New York.
Simpson, G.G. (1961). "Principles of Animal Taxonomy", Columbia University Press, New York.
Szalay, F.S. (1976). *Bull. Am. Mus. nat. Hist.*, 156, 157-450.

DISCUSSION

Kay: It seems to me that most of the features that we use to recognize extant
primates are shared by adapids and omomyids: namely, orbits that are frontated
and somewhat enlarged, small interorbital breadths, small infraorbital foramina
nails rather than claws, and so on. If plesiadapoids were ancestral to tarsi-
oids but not to adapids, then all of those characters would have had to be
evolved in parallel in the two Eocene groups. Why do you think that's more
probable than evolving enlarged incisors in parallel?

Gingerich: Throughout the Eocene, we can separate tarsioids very clearly
from adapids. But in the late Paleocene and early Eocene we get forms like
Berruvius and *Navajovius* (and even *Plesiadapis* at one time) being confused
with omomyids; whereas, to my knowledge, there are no forms intermediate
enough to confuse them between plesiadapiform primates and adapids.

Kay: *Plesiadapis rex*, which I believe was mistaken for an omomyid, is known
from one isolated tooth. I believe *Berruvius* is only known from two lower
teeth. I don't think anyone today would make the mistake of assigning species
of *Anemorhysis* or *Teilhardina* to the plesiadapoids. Where we have adequate
fossils, it seems to me that the distinctions between plesiadapoids and omo-
myids are quite great.

Gingerich: You haven't mentioned the tubular ectotympanic, which we see in
Tarsius, in the Eocene tarsioids, and then again in the plesiadapiform pri-
mates. We don't have a lot of evidence to go on, but what we have seems to
tie the omomyids back into the plesiadapiform stock.

Luckett: You list a free ectotympanic ring as a primitive primate character.
But the ring isn't free in the earliest primates, the plesiadapoids. How does
that fit in with your stratophenetic method?

Gingerich: Microsyopids seem to be an early branch of the main plesiadapiform
stock. The microsyopid ectotympanic isn't known, but it clearly wasn't tubular
like that of the other plesiadapiform primates, and it may have been a free
ring. It is known to have been free and intrabullar in leptictid insectivores,
which I think are very closely related to microsyopids.