

Dental Development, Homologies and Primate Phylogeny

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ABSTRACT Comparison of sequences of dental development and eruption of fossil and extant primates as well as insectivores strongly suggests that the commonly accepted dental homologies, the reconstruction of the ancestral primate morphotype as well as the phylogenetic relationships of primates should be revised. It is suggested that various primates (e.g. Tarsius) have retained the primitive mammalian characteristic of five premolar loci, but lost the incisors and developed the canine at the front of the jaw. Other primates (e.g. Strepsirhini) retained the primitive incisor-canine complex and lost premolars. In addition, it appears that the molar region of Catarrhini is not homologous with that of other primates.

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Introduction

Recent descriptions of fossil Eutheria which unquestionably possessed five pairs of premolars (Clemens, 1973; Lillegraven, 1969; McKenna, 1975) demand a revision of the dental formula (3.1.4.3/3.1.4.3) commonly accepted as primitive for eutherians and identification of the loci which may have been involved in reduction of premolar number within the various mammalian groups (cf. McKenna, 1975). Specimens of Kennalestes (McKenna, 1975) and Gypsonictops (Clemens, 1973; Lillegraven, 1969) clearly demonstrate loss of a premolar from within the set of five premolars. McKenna (1975) has argued that this tooth was dP3.

Inherent in the need to recognize that premolar loss may occur at different loci within or at the extremities of the premolar set is that of determining mechanisms which produce such dental reduction, i.e., tooth "loss." From developmental studies of tooth replacement in the multi-toothed, polyphyodont reptile Lacerta vivipara (Osborn, 1971), it is clear that tooth "loss" is not just the non-development and, thus, non-appearance of a structure. It involves forces or fields of inhibition which prevent either total growth and eruption or proper calcification of the tooth (Butler, 1939; Grüneberg, 1952, 1963; Osborn, 1973). With regard to incomplete calcification, the vestigial structure is resorbed (Grüneberg, 1952, 1963; Osborn, 1971) and thus, for all intents and purposes, has been "lost." Simplistically, the reptilian condition (i.e. multiple successive waves of replacement of large numbers of teeth) could have been converted to that of mammals by inhibiting most waves of dental development as well as the number of successfully developing teeth. That teeth, more accurately, are inhibited from complete development rather than strictly "lost" (and thus potential tooth loci of the dental lamina are not "lost") is implied by the secondarily derived multi-toothed condition of cetaceans.

Contrasted with reptiles, mammals are characterized by having maximally two sets of post-natal teeth: deciduous predecessors and permanent successors (Peyer, 1968). The molars are the result of the same interactions which produce deciduous incisor, canine and premolar teeth (Butler, 1939, 1956; Kindahl, 1957, 1958a, 1958b, 1959a, 1959b, 1967; Osborn, 1970, 1971, 1973;

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Peyer, 1968). Therefore, a permanent set of teeth that would have replaced the molars has been inhibited. Furthermore, with regard to deciduous incisors, canines and premolars that are succeeded by permanent teeth, there are variations of the common one-to-one replacement which should be noted.

Differential Tooth Replacement and Tooth Loss. When there is a difference between the number of deciduous and replacing permanent teeth of the same set during ontogeny, the decrease has been in the number of permanent teeth. An extreme example is found in Lepilemur (the sportive lemur) in which a pair of deciduous upper incisors develop and erupt but are ultimately shed and unreplaced (Schwartz, 1974a). Other examples of differential tooth replacement are: 1) the indriines (Propithecus, Indri and Avahi), in which four deciduous lower premolars are shed and replaced by only two permanent premolars (Schwartz, 1974b); 2) Elephantulus (Kindahl, 1958a), Talpa (Kindahl, 1958b), Notharctus (Gregory, 1920) and Adapis (Stehlin, 1912), in which only the posterior three of four deciduous premolars are replaced by permanent premolars; and 3) Tarsius (Fig. 1) in which the teeth usually defined as the upper lateral incisor, the lower incisor and the upper and lower anterior premolars do not replace teeth nor are replaced (Dahlberg, 1948; Schwartz, 1974a). With regard to the non-replacing-unreplaced teeth of Tarsius, they should be viewed as deciduous, not permanent teeth, because they are the first to develop and erupt and therefore function with both "proper" deciduous and permanent sets of teeth (cf. Dahlberg, 1948; Schwartz, 1974a, 1975a).¹ This is similar to the situation in Notharctus, Adapis, Elephantulus and Talpa, in which it is the anteriormost deciduous premolar which not only functions with the other deciduous teeth but is retained with the permanent set.

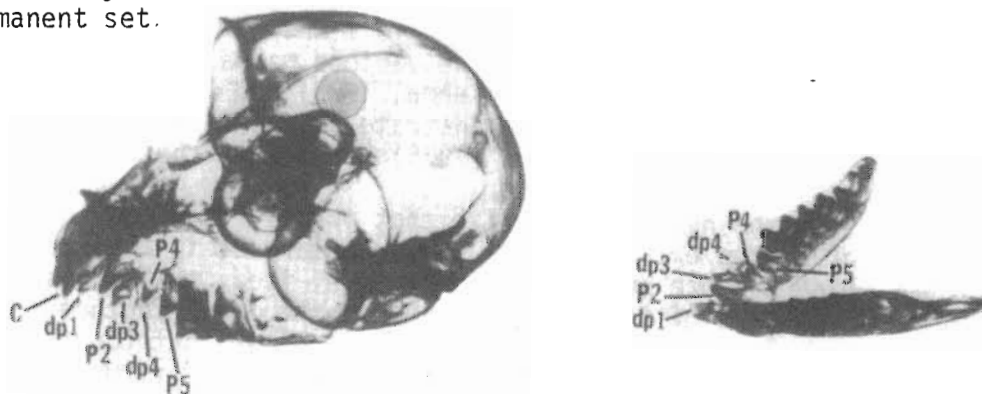


Figure 1: Positive print of radiograph of a juvenile Tarsius spectrum (RM 1892d; approx. X2) showing relative states of dental development and eruption. dp1 and dp3 are retained and will function with the variously developing and erupting permanent teeth; as defined here, the permanent premolars develop and erupt in the order $P2 \rightarrow P5 \rightarrow P4$.

¹Cartmill and Kay (1978) have argued that the occasional development in fetal tarsiers of rudimentary dental nubbins at the loci of what are here regarded as deciduous teeth indicates that the fetal "teeth" are really deciduous teeth and that the latter are permanent teeth. In reviewing this phenomenon in Tarsius and other mammals, Schwartz (ms.b) pointed out that there is a fundamental difference between fetally initiated dental nubbins and post-natally erupting teeth: the former are developmentally very incomplete and do not function, whereas the latter have complete crowns and roots and do function in mastication. There may be two sets of post-natally functioning teeth, which are the deciduous and permanent dentitions, and the variably initiated dental nubbins are pre-natal or pre-deciduous teeth, as they are commonly referred to in Homo sapiens.

From the above, two significant generalizations can be made. First, in the adult Talpa, Elephantulus, Notharctus, Adapis (and, presumably, other four-premolar adapids) and Tarsius, the antemolar teeth are a mixed (deciduous and permanent) dentition. These teeth are not serially homologous and cannot be undifferentially lumped together for purposes of either biological or phylogenetic consideration. Thus, simple dental formulae such as 2.1.4.3/2.1.4.3 for most adapids, or unmodified statements such as "...the three premolars of Tarsius..." are misleading.

The second generalization concerns the evidence for tooth "loss." Various studies (e.g. Butler, 1939, 1956; Gruneberg, 1952, 1963; Osborn, 1971, 1973) clearly demonstrate that the non-appearance of a tooth (tooth "loss") is caused by fields of inhibition which, at some stage of tooth development (e.g. follicle, bud, crown) interfere with the proper growth of a tooth, resulting in its resorption. If a tooth subjected to forces of inhibition does develop to a certain minimum threshold (the "quasi-continuous" trait of Gruneberg (1952, 1963)) sufficient for it to erupt, it will be diminutive, stunted or malformed (*ibid.*; also Butler, 1939, 1956, 1963). On a macroscopic level, observation of the latter (i.e. a stunted tooth) would indicate a locus of tooth inhibition and, perhaps eventually, tooth "loss." However, tooth "loss" can occur without necessarily observing a preceding diminution of a tooth (Schwartz, 1974c). The first generalization--occurrence of a mixed (deciduous and permanent) dentition in the adult--implies that tooth "loss" can occur phylogenetically in the following fashion by: 1) developing and erupting a deciduous tooth and inhibiting its permanent successor; 1a) possibly retaining the deciduous tooth to function with the permanent members of its set; and 2) inhibiting the deciduous tooth (see Kindahl, 1967).² Step "1a" need not necessarily occur. This model applies, for example, to the derivation of the sister-taxa Lepilemur and Megaladapis.

The majority of strepsirhines and Anthropoidea develop two pairs of deciduous upper incisors that are replaced by two pairs of permanent teeth; this represents the primitive state. The condition in Lepilemur could have been derived by: 1) eruption and subsequent shedding of two pairs of deciduous upper incisors (e.g. dI^a and dI^b) and inhibition of one pair of the permanent replacements (I^a for example); 2) complete inhibition of the

²This sequence follows from the developmental dependence of the permanent tooth on its deciduous predecessor (cf. Gruneberg, 1952, 1958; Kindahl, *op. cit.*; Peyer, 1968): i.e., 1) the development of a deciduous tooth is seen as a "bud" at the free edge of the dental lamina; 2) as the deciduous tooth develops, it sends off a "stalk" (the gubernaculum) at the end of which the permanent successor develops. Molars, for example, are deciduous teeth in that they develop from the free edge of the dental lamina and are not replaced by other teeth; obviously, development of permanent successors has been inhibited. Kindahl's (*op. cit.*) work on various insectivores beautifully illustrates the developmental interplay between permanent and deciduous teeth. In Talpa and Elephantulus, the tooth Kindahl identifies as the first premolar develops from the free edge of the dental lamina but, unlike the other deciduous teeth, does not send off a gubernaculum and, thus, does not develop a permanent successor; this tooth is retained and functions with the "adult" dentition. The data presented in this paper are congruent with Kindahl's (especially 1967) conclusion that permanent teeth are "lost" first, and then the deciduous teeth are inhibited. Of course, it is possible that all development at a tooth locus could be simultaneously inhibited.

originally affected pair of deciduous-permanent incisors (dI^a and I^a) with normal development and eruption at the remaining incisor locus ($dI^b - I^b$); and, finally, eruption of the deciduous incisors (dI^b) with inhibition of the permanent set. The condition in Megaladapis--lack of incisors--is further derived by inhibiting the remaining pair of deciduous incisors.

Loci of tooth "loss" in other taxa are: 1) in Tarsius, the sites of the teeth usually defined as the upper lateral incisor, the lower incisor and the upper and lower anteriormost premolar--these are all retained, unreplaced deciduous teeth; 2) in Talpa, Elephantulus, Notharctus and Adapis (and, presumably, other four-premolar adapids), the anteriormost premolar is a deciduous tooth--complete inhibition at this locus most likely occurred in the evolution of three-premolar adapids, such as Protopadapis; and 3) in Gypsonictops and Kennalestes (McKenna, 1975), the "loss" of $dP3$ resulted in the reduction from five to four premolars.

THE SIGNIFICANCE OF TOOTH REPLACEMENT IN TARSIUS

Dental Development and Premolar Homologies.-- Elsewhere it has been suggested that the order of development and eruption " $P2 \rightarrow P4 \rightarrow P3$ " may be primitive for primates (Schwartz, 1975b). This sequence is observed in most strepsirrhines (Schwartz, 1974a, 1975b), as well as many cebids (cf. Johnston, Dreizen and Levy, 1970; O. della Serra cited in Hill, 1960; Schwartz, unpublished data), the parapithecids (Conroy, Schwartz and Simons, 1975) and some fossil and extant insectivores (cf. Kindahl, *op. cit.*; Osborn, 1970; Slaughter, Pine and Pine, 1974; West, 1972) (Figs. 2 and 3). In addition, in these and

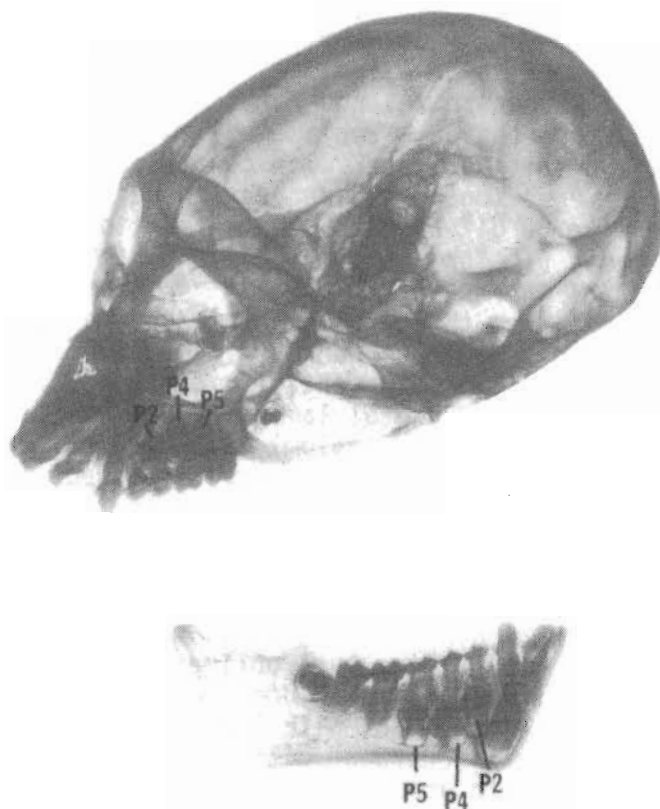


Figure 2: Positive print of radiograph of a juvenile Cebus albifrons (AMNH 46507; natural size). In Cebus, the permanent premolars develop and erupt in the order $P2 \rightarrow P5 \rightarrow P4$; this is the most common sequence in three-premolar primates (toothcombed or not) and is also seen in fossil and extant insectivores.

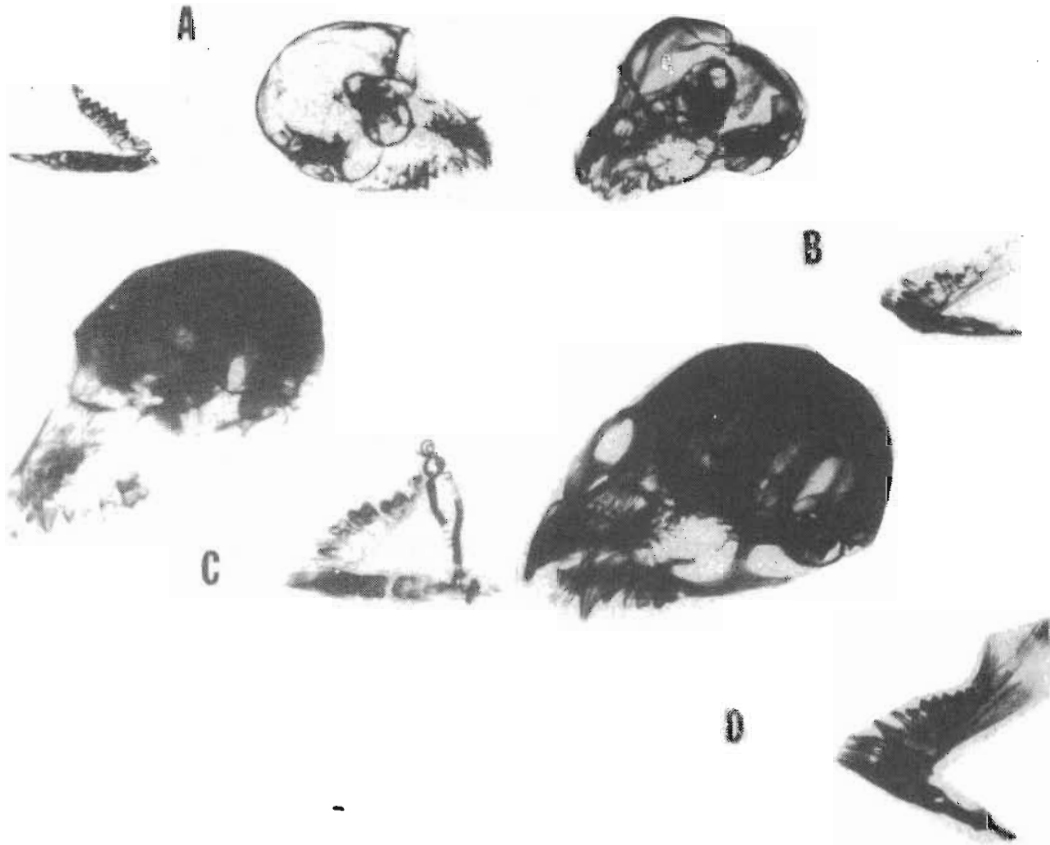


Figure 3: Comparison of (A) Tarsius spectrum (RM 1892d) with (B) Perodicticus potto (AMNH 51023), (C) Galago crassicaudatus (MNHN A-3.014), and (D) P. potto (AMNH 51024). Note the development/eruption of dental triads. In Tarsius, this unit is composed of the upper anterior "incisor," and the upper and lower "canine." In the others, these teeth are the upper canine, "P2" and "P2" as in all lorises and some lemurids.

other taxa, regardless of the order in which the three permanent premolars appear, each permanent premolar is always preceded by a deciduous counterpart. These forms obviously differ from Tarsius in that, in the adult, "P2," "P3" and "P4" are all permanent teeth and do not represent a mixed dentition. It is therefore not possible to homologize the teeth of Tarsius with those of other taxa in the traditional manner. Inter-taxon comparison of patterns of dental development and eruption, however, does appear to be a viable method of determining dental homologies (see Gazin, 1958: 73-74).

In 1952, Gazin (p. 24) described a juvenile specimen of Absarokius noctivagus (USNM 19198; see Fig. 4, this paper) which "...exhibits Dp₄ with what appears to be P₂, as well as P₄ and M₃, just erupting...The first two molars are in position and unworn...If one may judge by the positions of the two erupting premolars, P₃ is yet buried beneath the long slender roots of Dp₃." Later, Gazin (1958: 73-74) revised the dental homologies of this specimen:

"The dental formula for the more typical anaptomorphids was previously regarded (Gazin, 1952, p. 24) as including three lower premolars. In the Absarokius jaw from the Knight showing replacement of the deciduous premolars..., the first of the three permanent cheek teeth in the antemolar series...appears to be the first erupting, and for this reason was interpreted as P₂.

This would be closely followed or nearly coincident in time with P₄, and followed later by P₃. P₃ does not actually show in the illustration but its presence within the jaw (unerupted) has been verified...in the case of the modern tarsiers, while P₂ and then P₄ follow the permanent incisors, it was not certain that P₃ always precedes the canine, and the canine may well be erupting with P₄. Omitting from consideration the...very early erupting P₂ of Tarsius it is at once seen that an approximation is made to the situation evident in the Absarokius jaw. As a result, the interpretation suggested, in which the tooth in question is regarded as P₂ instead of the canine, cannot be considered as conclusive."

Gazin's observations are quite significant: demonstration of congruous patterns of development and eruption of the "canine," "P₃" and "P₄" of Tarsius with the three unerupted teeth of the juvenile Absarokius noctivagus (compare Figs. 1 and 4) illustrates the importance of data on dental development and eruption for determining homologies. It is thus significant that the comparable states of development and eruption in Tarsius and A. noctivagus, as well as the total sequences of development and eruption of the "canine," "P₃" and "P₄" of Tarsius (cf. Dahlberg, 1948; Schwartz, 1974a, 1975a), are the same as the prevalent order of premolar development and eruption, "P₂" → "P₄" → "P₃" (compare Figs. 1, 2, 4). In addition to congruous patterns of premolar development and eruption, all of the teeth involved replace deciduous predecessors. Therefore, I suggest that not only are the three erupting teeth of A. noctivagus homologous with the "canine," "P₃" and "P₄" of Tarsius, but these teeth, respectively, are homologous with "P₂," "P₃" and "P₄" of, for example, ceboids, parapithecids, lorises and lemurids. These latter primates have totally inhibited the premolar locus between "P₂" and "P₃" whereas this locus is present in Tarsius; and this tooth should be identified as dP₃ (see Fig. 5).

Dental Development and Canine Homologies.-- In all species of lorises, galagines and cheirogaleines, development and eruption of the upper canine is so intimately coordinated with that of the upper and lower P₂ that these teeth may be regarded as an integrated, functional unit (Schwartz, 1974a) (Fig. 3). Although lemurines do not maintain this dental triad through eruption, in many, the upper C-P₂ unit is unmistakable during development (Schwartz, 1974a).

With regard to Tarsius, all three species display a complex in which the upper anterior "incisor" and upper and lower "canine" (=P₂ of other extant primates) develop and erupt in intimate association (Schwartz, 1974a) (Figs. 1 and 3A). If not for their positions in the jaw, the teeth of this dental triad could easily be accepted as homologous with these of the remarkably similar developmental complex (C-P₂) of lorises and lemurids. Nevertheless, these homologies seem warranted because: 1) the integration of the dental triad persists from development through completed eruption in Tarsius, lorises, galagines and cheirogaleines; and 2) the previously discussed premolar developmental data also indicate that the "canine" of Tarsius is homologous with the "P₂" of other primates. The morphologies of the teeth in question also support this interpretation: the upper canine of lorises and lemurids and the upper anterior "incisor" of Tarsius are demonstrably the most robust and caniniform teeth of the respective dental triads (cf. Clark, 1962; Gregory, 1922; Hill, 1955, 1958; James, 1960; Simons, 1961a, 1961b; Tattersall and Schwartz, 1974). Therefore, I suggest that the upper anterior "incisor" of Tarsius should be identified as a

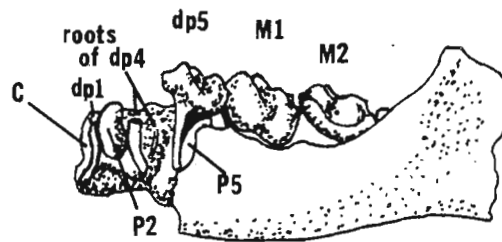
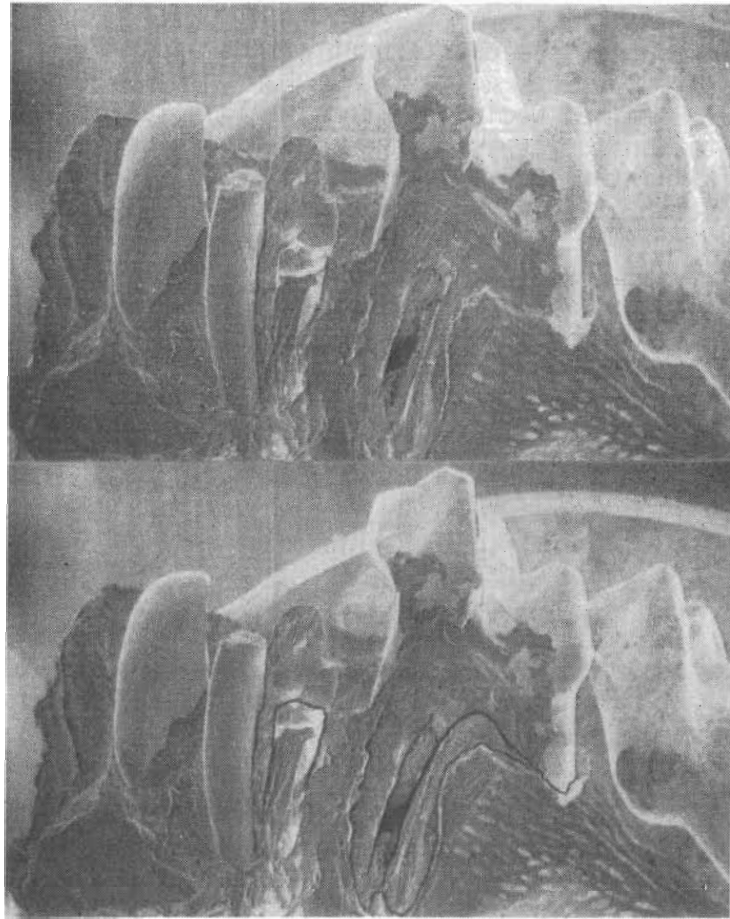


Figure 4: Scanning electron stereomicrograph and drawing (from Gazin, 1958) of left mandible of a juvenile *Absarokius noctivagus* (USNM 19198; approx. X12) showing alveoli for the canine and dp_1 , the roots of dp_3 (partially outlined) and the crowns of P_2 and P_5 (partially outlined). The teeth are identified according to discussion in the text.

canine. In the lower jaw, the counterpart of the upper caniniform tooth has been "lost."

Homologies of Retained Deciduous Teeth.-- This leaves but two antemolar teeth of Tarsius to consider: i.e., the small tooth between the upper canine and P_2 and the small anteriormost lower tooth (Figs. 1 and 5); both are retained deciduous teeth.

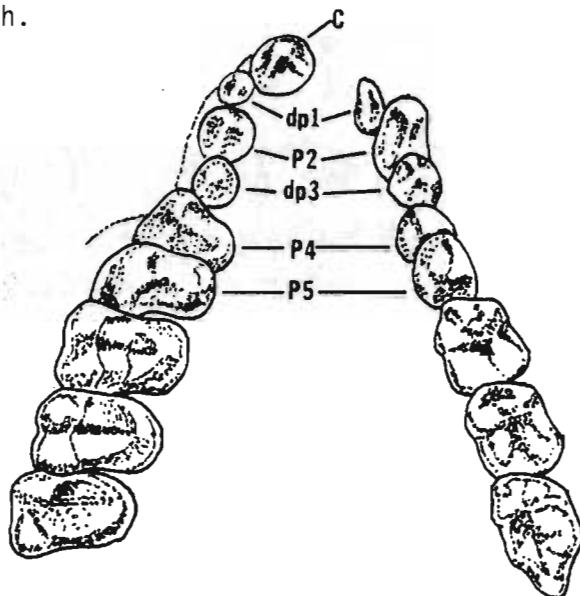


Figure 5: Upper half and lower half of dental arcs of Tarsius spectrum with revised dental homologies; the deciduous premolars are retained, unreplaced teeth as illustrated in Fig. 1 (Redrawn from Clark, 1962).

Since comparison of dental development in primates indicates that the upper anterior "incisor" and the upper and lower "canine" of Tarsius should be identified as the upper canine and P_2 , respectively, the obvious conclusion is that the deciduous teeth here-discussed are the upper and lower dp_1 . Morphologically, these teeth would be described as premolariform. Retention of a deciduous premolar between the canine and P_2 has also been reported by Adapis (Stehlin, 1912) and Notharctus (Gregory, 1920). Analysis of patterns of eruption in these adapids indicates that their deciduous premolar is homologous with the suggested dp_1 of Tarsius and that the dp_3 locus has been inhibited.

The dental formula of Tarsius is thus: $C \ dp_1^1 \ P_2^2 \ dp_3^3 \ P_4^4 \ P_5^5 \ M_1^1 \ M_2^2 \ M_3^3$ (Figs. 1 and 5). The premolars of ceboids, lorids, lemurids, archæolemurines, parapithecids, as well as the three permanent premolars of adapids and the unerupted teeth of Absarokius noctivagus (USNM 19198) are P_2 , P_4 and P_5 (see Figs. 2, 3 and 4).

Dental Homologies in Various Plesiadapiforms and Tarsiiforms.-- Correlation of relative size with morphology of the premolars of Tarsius permits description of the posterior two as semi-molariform, with P_4 somewhat less so than P_5 . dp_1 and dp_3 are rudimentary and bound the larger, premolariform P_2 . In the upper jaw, these teeth are bounded by M_1 posteriorly and the canine anteriorly. In the lower jaw, the anterior caniniform tooth is absent but would have been present primitively. Thus, the primitive antemolar dental state from which that of Tarsius would have been derived can be reconstructed as $C_1^1 \ dp_1^1 \ P_2^2 \ P_3^3 \ P_4^4 \ P_5^5$.

DENTAL DEVELOPMENT AND PRIMATES

With remarkable concordance, this antemolar dental state, in number of teeth as well as relative size and morphology, applies to the upper, lower or both jaws of various plesiadapoids, microsyopids, anaptomorphines, and omomyines (e.g. Bown, 1974; Bown and Gingerich, 1972; Gazin, 1952, 1958, 1962; Gingerich, 1975a, 1975b, 1976; Kay and Cartmill, 1975; McKenna, 1966; Robinson, 1967; Simons, 1961b; Simpson, 1940; Szalay, 1969a, 1972a, 1973, 1976; Wilson and Szalay, 1972) (Figs. 6, 7B-D).

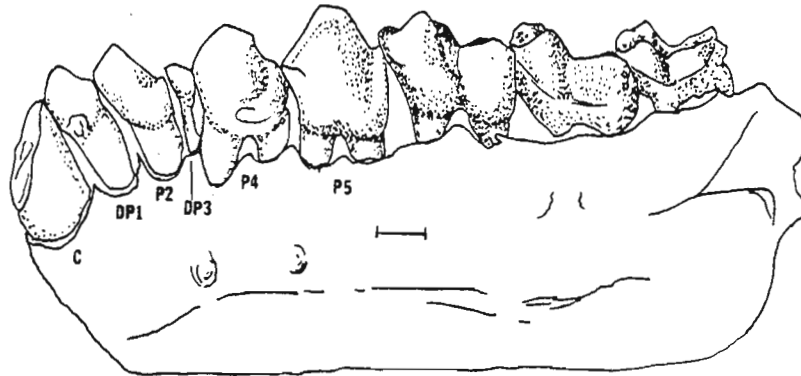


Figure 6: Left mandible of ?Tetonoides (= Tetonius homunculus) with reference to revised dental homologies; the bar represents 1 mm. (Redrawn from Robinson, 1967).

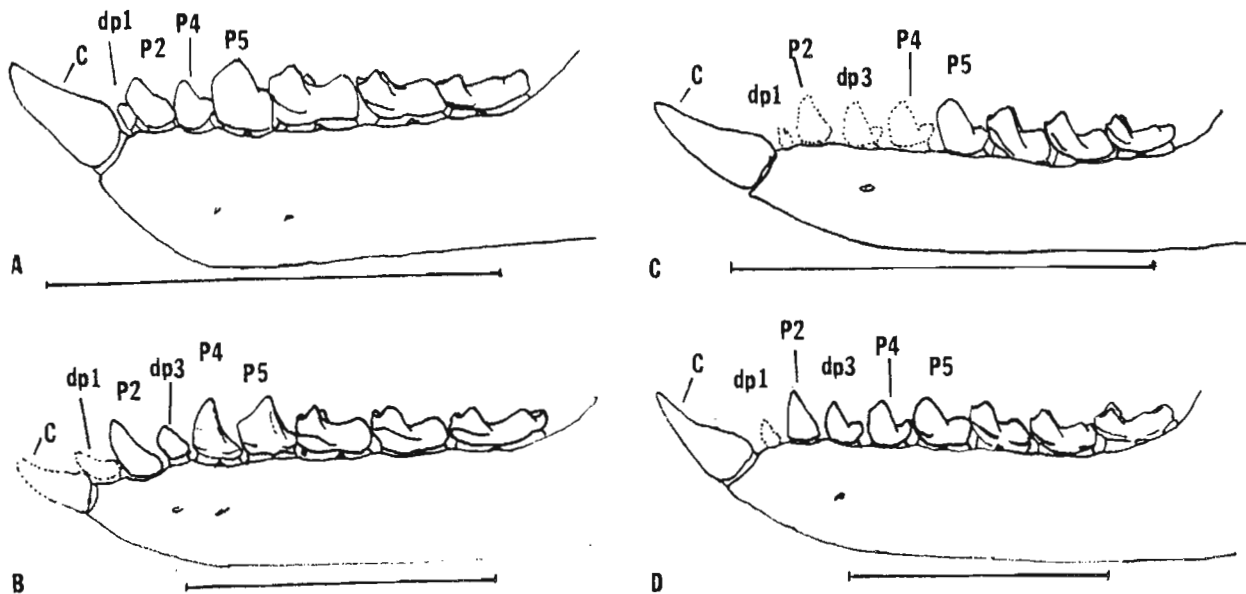


Figure 7: Lower dentitions of (A) Nannopithec, (B) Omomys, (C) Palenochtha and (D) Plesiolestes, with reference to the dental homologies suggested in the text. (Redrawn from Gingerich, 1975a; the bar represents 1 cm.).

The most striking similarities with Tarsius are seen in the lower dentition of the omomyine Omomys and the paromomyid Plesiolestes. The only difference between the latter two and Tarsius is that Omomys and Plesiolestes also possess a large caniniform tooth. This tooth anteriorly bounds the set of antemolar teeth, as does the upper canine of Tarsius. The lower jaw of both Omomys and Plesiolestes thus possess five premolar loci which are bounded anteriorly by a canine. Considering the degree of congruity, tooth for tooth, between Omomys, Plesiolestes and Tarsius, I suggest that the lower dental formula of the former two primates is $C\ dP_1\ P_2\ dP_3\ P_4\ P_5\ M_1\ M_2\ M_3$. Furthermore, from what is known of the upper dentition, in conjunction with Szalay's (1973) reconstruction, I suggest that the upper dentition of Plesiolestes contains the same teeth as does the lower. This identification may also hold true for the upper dentition of Omomys (cf. Gazin, 1958; Szalay, 1976).

The condition in Omomys and Plesiolestes--five premolar loci bounded anteriorly by a large caniniform tooth--is also noted, for example, in Pronothodectes, Palaechthon, Palenochtha, Tetonius, Chlororhysis, Anemorhysis, Hemiacodon, Washakius, Ourayia, Loveina, Macrotarsius and Absarokius abbotti (cf. Bown, 1974; Bown and Gingerich, 1972; Gazin, 1952, 1958, 1962; Gingerich, 1975a; Robinson, 1967; Simons, 1961b; Simpson, 1940) (Fig. 7B-D). In most of these primates, the teeth in the P1 and P3 loci are relatively small, as they are in Tarsius, Omomys and Plesiolestes, and are here identified as deciduous teeth (Figs. 5, 6, 7B-D). In Tetonius (Fig. 6), the tooth in the P3 locus is incredibly diminutive and should be identified as dP3. Although the tooth at the P1 locus of Tetonius is not as small as that, for example, in Omomys or Plesiolestes, it is here tentatively identified as dP1. For the lower jaw of these primates I suggest that the dental formula is $C\ dP_1\ P_2\ dP_3\ P_4\ P_5\ M_1\ M_2\ M_3$. Although I have reservations about the upper jaw assigned to Ourayia (Simons, 1961b), I suggest that this primate possessed a canine at the front of the premaxilla and five premolar loci. Judging from the known upper dentition of Absarokius abbotti (Bown and Gingerich, 1972) and Hemiacodon and Washakius (Gazin, 1958), the small tooth at the P3 locus should be identified as a deciduous tooth as in Omomys and Plesiolestes. If we extrapolate from Tarsius, in which the upper dP1 develops and erupts in concert with the lower dP1, we would expect the same to apply to these primates as well. Similarly, as is seen in microsyopids (McKenna, 1966; Szalay, 1969a, 1969b) and as Matthew (1915) reconstructed for Tetonius, one would expect that an upper canine opposed the lower anterior caniniform tooth. Therefore, I suggest that the upper dental formula for these paromomyids and omomyids is $C\ dP_1\ P_2\ dP_3\ P_4\ P_5\ M_1\ M_2\ M_3$.

DENTAL TRANSMUTATION

Debates on the Dentition of the Microchoerines-- The dental formula of the microchoerines (Necrolemur, Microchoerus, Nannopithecus and Pseudoloris) is generally accepted as 2.1.3.3/0.1.4.3 (e.g. Simons, 1961a, 1972) but Gingerich (1974a) has recently argued that it is 2.1.3.3/1.1.3.3, the same as is commonly cited for Tarsius. Simons (1961a) concluded that the enlarged, robust lower anterior tooth was a canine, and that the incisors had been lost, because some specimens of Microchoerus erinaceus possessed what he identified as alveoli for small incisors, whereas the majority of microchoerines did not display this feature. Gingerich (1974a), on the other hand, comments that a mental foramen sometimes is present in Tarsius in the position of what Simons

identified as the alveolus in some Microchoerus, and, thus, the "alveolus" is really a "foramen." It must be pointed out, however, as did Gingerich, that the presence of such an extremely anteriorly situated mental foramen is quite variable in Tarsius, and its presence is but a few specimens of Tarsius is therefore insufficient evidence to totally discount Simons' interpretation.

With regard to the large lower anterior tooth, Gingerich (1974a) identifies it as an incisor for the unjustified reason that "...the left and right lower canine do not contact in any mammal" (p. 277-278). In addition, Gingerich identifies the small, rudimentary tooth situated immediately posterior to the enlarged lower anterior tooth as the canine and not a premolar because he feels that "...the probability is small that there were ever more than three lower premolars in this subfamily" (p. 278).

I contend that the reason the lower anterior teeth of Tarsius appear as "very differently specialized" is because they are different teeth. To call the large lower anterior tooth of microchoerines an incisor because right and left canines are not supposed to contact each other is not only circular reasoning, but totally eliminates the possibility of recognizing such a specialization. Similarly, to identify the rudimentary tooth immediately posterior to the large lower anterior tooth as a canine because of a feeling that microchoerines probably did not have more than three premolars is hardly the type of evidence upon which to revise the very dental homologies which are then used in the reconstruction of phylogenies.

Homologies of the Large, Caniniform Anterior Tooth of Various Primates.-- Above, I have argued that the large anterior upper tooth of Tarsius as well as the large lower teeth of anaptomorphines, omomyines and various plesiadapoids are canines and not incisors, as they are commonly identified. I would extend this to include all Paleocene and Eocene primates which, regardless of the number of premolars, display upper and/or lower caniniform teeth at the front of the jaw.

It is commonly accepted that, regardless of morphology, upper incisors are defined as those teeth contained in the premaxilla and the upper canine is that tooth immediately behind the premaxillary-maxillary suture (e.g. Bown and Gingerich, 1972; Gazin, 1958; Gingerich, 1974a; Gregory, 1922; Peyer, 1968; Tomes, 1914). Identification of the lower canine is based on occlusion with the upper dentition, i.e. the lower canine is that tooth which occludes in front of the upper canine (*ibid.*). Lower incisors, then, are those teeth anterior to the lower canine and the premolars would be bounded anteriorly by the canine and posteriorly by M1. This may have been the way the teeth of primitive mammals differentiated (i.e. with large, distinct upper and lower canines which bounded the smaller, more gracile, somewhat spatulate incisors posteriorly and the less trenchant premolars anteriorly); many taxa, fossil and extant, (albeit with reduction in number of teeth of various tooth sets) have retained this basic mammalian pattern of dental differentiation and position. However, while this may have been the primitive mammalian condition, it must, as such, be recognized as a general substrate from which obvious as well as unexpected variations may be derived. Recall, once more, the secondarily derived condition of the cetacean dentition.

With regard to the lower anterior tooth of plesiadapoids, anaptomorphines, omomyines and microchoerines, it is a large, robust, variably trenchant tooth, which may be flared laterally and whose emplacement may be orthal or variably procumbent (Figs. 6, 7, 8). Various authors (e.g. Gingerich, 1974a, 1974b, 1975a; Simons, 1961b; Szalay, 1972a) have made a point of the similar morphology of the large lower anterior tooth of

various Paleocene and Eocene primates in support of the interpretation that these teeth are homologous. As illustrated in Figs. 6, 7 and 8, this conclusion does not seem unreasonable. However, accepting these lower anterior teeth as incisors introduces the problem of explaining how and why they have become enlarged and "caniniform" as well as how and why the "second incisor" (if present) and the "canine" are small and "premolariform" (cf. Bown, 1974; Bown and Gingerich, 1972; Gazin, 1952, 1958; Gingerich, 1974a, 1974b, 1975a; Robinson, 1967; Simons, 1961b; Szalay, 1972a, 1973). As reasoned above, comparison of development and eruption, functional associations, as well as morphology, strongly indicates that the teeth posterior to the large lower anterior tooth are best interpreted as premolars, some of which may be retained deciduous teeth. With this understanding, it is not surprising that the so-called "second incisor" and/or the "canine" (depending on different interpretations) can be small-to-rudimentary and variably "premolariform." Recognizing these teeth as premolars also obviates the need to offer explanations as to how their function radically changed and why a tooth, such as the canine, would be greatly remodelled from a large trenchant structure to one which is small and somewhat "premolariform." The explanation is simply that they are premolars.

Similarly, the robust lower anterior tooth of plesiadapoids, anaptomorphines, omomyines and microchoerines is not an incisor but a canine: it is morphologically the most "caniniform" tooth in the jaw and is in front of the anteriormost premolariform tooth (dP1). Positionally and morphologically, then, the lower anterior tooth presents features which would be developmentally characteristic of a canine. The only significant difference, therefore, between the lower dentition of a microchoerine and that of, for instance, a "four-premolar" adapid is that the canine of the latter is bounded anteriorly by recognizable incisors. In fact, in both "four-premolar" adapids and microchoerines, the four teeth between the caniniform tooth (=the canine) and M₁ are three definite premolars which are preceded by a small rudimentary tooth. Given that small, rudimentary teeth can be interpreted as retained deciduous teeth and evidence, as with "four-premolar" adapids, supports the interpretation that these deciduous teeth are premolars, the obvious conclusion is that the lower dental formula of Microchoerinae is $\bar{C}$ dP₁ P₂ P₄ P₅ M₁ M₂ M₃ (Fig. 7A). Furthermore, recognition of the lower anterior tooth of microchoerines as well as plesiadapoids, anaptomorphines, and omomyines as a canine and not an incisor obviates the need to hypothesize extreme remodelling and enlarging of what is otherwise (e.g. in primitive mammals, adapids, Anthropoidea) a small, non-trenchant, somewhat spatulate tooth.

Rather than remodelling an incisor not only to look like, but to functionally utilize the robusticity and trenchantness of a canine, it appears to be simpler and biologically more conservative to retain the canine and inhibit ("lose") the incisors. For, although sutures and other anatomical landmarks may appear to be post-natally correlated with tooth position, both tooth loci and dental morphology are determined fetally well in advance of the differentiation of these ultimately surrounding features (Kollar and Baird, 1971; Miller, 1971; Tonge, 1971). Osteogenesis then proceeds around these dormant dental sites which are activated by the much later developing hormonal system (*ibid.*). Thus, the post-natal association of teeth and bony landmarks is actually accidental, and should not be taken as an immutable constant among diverse groups of mammals. Therefore, if selection was operating for large, robust "caniniform" teeth to function at the front of the jaw, it would seem more reasonable to repress incisor development and the incisor "field" (cf. Butler, 1939, 1963; Patterson, 1956; Van Valen, 1970) and

initiate canine development anteriorly, than to genetically revise the constitution of the various morphogenetic fields. In other words, why remodel an incisor to look and function like a canine, as well as remodel an incisor and the canine to look and function like premolars, if the position of initiation of the proper canine and premolars can be shifted forward with little more disturbance than simply "losing" the incisors? With regard to plesiadapoids, anaptomorphines, omomyines and microchoerines, the reasonable conclusion is that the lower anterior tooth is a canine behind which lie the premolars. Furthermore, since the lower anterior tooth of Tarsius is a retained deciduous tooth and is neither large and "caniniform" nor "incisiform," it would appear that this primate has "lost" the entire complement of anterior teeth (i.e. incisor and canine) during its evolution.

The same argument applies to the interpretation of the homologies of the anterior teeth of the upper jaw. For, although the upper jaw is ultimately composed of two bones (the premaxilla and the maxilla), tooth position and morphology are determined much earlier than the differentiation and initial ossification of these features. The main difference, then, between the upper and lower jaws is that, in the former, there is a suture. However, this suture, regardless of its functional and developmental significance, is neither in whole or in part responsible for the initiation nor morphological determination of the neighboring dentition. Therefore, it need not be true in every case that the teeth contained in the premaxilla are incisors and that the tooth immediately posterior to the premaxillary-maxillary suture is the canine.

Consider the upper anterior tooth (if it has been preserved) of various plesiadapoids, microchoerines and Tarsius. It is, to paraphrase Simons (1961a: 58), larger, longer, and more robust than the commonly presumed upper canine (see also Bown and Gingerich, 1972; Gingerich, 1974a, 1974b; Russell, 1964; Simons, 1961b; Simpson, 1935, 1940, 1955; Szalay, 1968, 1972a). In short, the upper anterior tooth is certainly more "caniniform" than is the presumed canine (Figs. 5, 8), and, as argued for the large lower anterior tooth, should be identified as a canine behind which are some number of premolars. With regard to microchoerines, the large upper anterior tooth is a canine with, proceeding posteriorly, the rudimentary tooth being a deciduous premolar, the presumed canine a premolar, the reduced so-called P² a deciduous premolar, and the two posterior premolars as such. Thus, the upper dental formula of microchoerines is: C dP¹ P² dP³ p⁴ p⁵ M¹ M² M³.

The upper anterior tooth of plesiadapoids, although it may be adorned with finger-like projections as in Plesiadapis tricuspidens (cf. Gingerich, 1974a, 1974b, 1976; Simpson, 1935, 1955), is nonetheless large, long and markedly the most robust antemolar tooth.

Therefore, in accordance with the arguments above, the upper anterior tooth of plesiadapoids should be identified as a canine and, if present, the supposed second incisor and the canine are premolars.

Morphocline Polarity and the Plesiadapoid Anterior Tooth.--Gingerich (1974a) has suggested that the evolution of the plesiadapoid upper anterior tooth proceeded from a fully tricuspid morphology (as seen in Pronothodectes). From this state further adornments were added. However, according to Gingerich's (1974a) scheme, much if not all cuspidate elaboration was then "lost" in the evolution of the supposed "terminal" plesiadapids, i.e. Nannodectes gidleyi, Chiromyoides major and C. campanicus, and, most notably, Platychaerops daubrei (ibid.: 228-232). This morphocline, especially in light of the preceding discussion, seems unnecessarily complex. For, since it appears most likely that the upper anterior tooth is not an incisor but a canine, one would expect that its primitive state would be characterized

by little, if any, elaboration of the basic large, robust, trenchant canine morphology as seen, for example in Platychaerops, Chiromyoides, Plesiolestes, microsyopids (e.g. Microsyops lundeliusi) (McKenna, 1966), as well as those forms (primate and non-primate) in which the canine is situated in its "expected" position (i.e. behind the premaxillary-maxillary suture). Therefore, I suggest that the morphocline of plesiadapid upper canine morphology is not from complex-to-more-complex-to-markedly-less-complex, but from simple-to-complex.

PREMOLAR "LOSS" AND DENTAL HOMOLOGIES

Plesiadapiformes.-- The preceding discussion has dealt with: 1) mechanisms of tooth "loss," 2) loci (dP1 and dP3) at which tooth "loss" from a five-premolar state has occurred in various Paleocene and Eocene primates as well as Tarsius, and 3) the homologies of the large, robust upper and lower anterior teeth. Reduction from five to four premolars during the evolution of the adapids and microchoerines, although parallel and independent events, is best seen as the "loss" of dP3 with the retention of dP1, P2, P4 and P5. Some adapids possess only three premolars, the derivation of which could occur by the "loss" of dP1. Although reduction from four to three premolars appears to have occurred independently in strepsirhines versus Anthropoidea, reduction from five to four premolars by total inhibition of the dP3 locus would appear to have characterized the common ancestor of these two groups. With regard to proper three-premolar primates--as are most strepsirhines, the platyrrhines and parapithecids--retention of the primitive sequences of premolar development and eruption indicates that the locus of dP1 had been inhibited. In addition, reduction to three premolars may have occurred more than once in the strepsirhines. For, if the adapids are not "basal" or near the ancestry of lemurs and lorises (e.g. Cartmill, 1975; Clark, 1962; Gregory, 1915, 1920; Martin, 1972; Simons, 1961b, 1972) but form a sister-group only with the derived Hapalemur-Lepilemur-Megaladapis group (Schwartz, 1974a, 1975b; Schwartz and Tattersall, in press), reduction to three premolars must have occurred independently in the other strepsirhines. Although reduction from five to three premolars in the strepsirhines and Anthropoidea is the result of "loss" of dP1 and dP3, various plesiadapoids and anaptomorphines have decreased the number of premolars at different loci while retaining dP3.

As Gingerich (1974a, 1976, but on different criteria) has pointed out, there is a dichotomy between the plesiadapoids and tarsiiiforms, on the one hand, and Anthropoidea and Strepsirhini, on the other. Within the realm of dental homologies presented here, the latter group (i.e. Anthropoidea and Strepsirhini) can be characterized by the presence (and thus retention) of incisors and canines in their "expected" positions with reduction from five to three premolars occurring at the dP1 and dP3 loci; the plesiadapoids and tarsiiiforms have inhibited the incisors, developed the canine at the front of the jaw (shared derived character complexes) (the lower canine has been "lost" in Tarsius) and, in many cases, have retained the primitive primate premolar region, dP1 P2 dP3 P4 P5. However, with regard to premolar "loss," the plesiadapoid-tarsiiiform group differs from the strepsirhine-anthropoid group.

Review of the data on the plesiadapids (Gingerich, 1974a) indicates that the tooth called P2 (at least in the lower jaw) is a deciduous tooth. This is based on the observation that the non-appearance of this tooth (especially in the lower jaw) is quite frequent and that, when this tooth is present, it is most often a stunted, rudimentary tooth (Gingerich, 1974a, 1976). This is

further substantiated by partial data on development and eruption (*ibid.*: 250-253). First, it is only in three species of *Plesiadapis* (*P. rex*, *P. praecursor* and *P. insignis*) that the small "P₂" is consistently present whereas this tooth is only variably present in the majority (*P. fodinatus*, *P. churchilli*, *P. anceps*, *P. walbeckensis* and *P. remensis*) (Gingerich, 1974a). In other *Plesiadapis* (*P. cookei*, *P. dubius*, *P. tricuspidens* and *P. russelli*), as well as in the plesiadapids *Chiromyoides* and *Platychoerops daubrei*, "P₂" is never present (*ibid.*). Considering the (albeit punctuated) morphocline of the appearance-"loss" of "P₂" within not only the plesiadapids but each of many species of *Plesiadapis*, it is apparent that this represents a locus of tooth inhibition. Therefore, as argued in the model presented earlier, this tooth ("P₂") is best regarded as a deciduous tooth whose permanent successor had been inhibited.

This interpretation gains further support from evidence of dental development as seen in the mandibular fragment of a juvenile *Plesiadapis rex* figured by Gingerich (1974a: 252). In this specimen, M₁₋₂, "dP₃₋₄" and the so-called P₂ had fully erupted, the alveolus for the enlarged lower anterior tooth is preserved, and the crowns of "P₃" and "P₄" are fairly well developed. It can be noted, then, that, aside from being rudimentary, the so-called P₂ has erupted such that it functions with not only the posterior deciduous premolars but also with the two permanent premolars which erupt much later. Therefore, the logical conclusion is that this "P₂" is a deciduous tooth which occurs in a position of tooth inhibition and tooth "loss." Furthermore, it is interesting that this deciduous premolar is in the same position (three places anterior to M₁) as is the dP₃ of *Kennalestes*, *Gypsonictops*, *Tarsius*. I suggest, therefore, that the "P₂" of plesiadapids are instead dP₃ and the "P₃" and "P₄" are P₄ and P₅, respectively.

Among the plesiadapids, the tendency is to retain more upper than lower premolars (cf. Gingerich, 1974a, 1976; Szalay, 1972a). With regard to the morphocline of specific tooth "loss" other than the variable "loss" of dP₃ previously discussed, dP₁ is generally the first lower premolar inhibited (e.g. in *Nannodectes*), followed by P₂ "loss" (e.g. in *Plesiadapis praecursor*, *P. anceps*, *P. rex*), and lastly by intermittent (e.g. in *P. churchilli* and *P. fodinatus*) and then complete "loss" of dP₃ (e.g. *P. tricuspidens*, *P. dubius*, *Chiromyoides* and *Platychoerops*). In the upper jaw, P₂ is the only premolar "lost," (although *Chiromyoides* may have "lost" dP₁ as well), but its "loss" is observed only after that of dP₁ and P₂ and its absence noted in but a few plesiadapids, i.e. *Plesiadapis tricuspidens*, *P. cookei* and perhaps *Chiromyoides*. Thus, the plesiadapids may be seen to "lose" premolars so as to create a semi-diastematic condition: i.e. 1) the lower premolars are "lost" antero-posteriorly, thus creating a diastema behind the large lower canine; 2) the rather diminutive dP₁ and the small P₂, which (relative to the upper canine and dP₃) are widely spaced in the upper jaw, become, with "loss" of lower anterior premolars, even more functionally isolated; and 3) "loss" of P₂, in conjunction with the absence of lower anterior premolars and the demonstrable isolation of dP₁, effectively creates an upper diastema behind the upper canine (Fig. 8).

In similar fashion, albeit with somewhat limited data (especially with regard to the upper jaw), the plesiadapid mode of premolar "loss" and subsequent creation of a semi-diastematic condition also applies to the carpolestids (cf. Clark, 1962; Gazin, 1962, 1971; Rose, 1975; Simons, 1972, 1974). In the carpolestid premolar "loss" morphocline, however, the semi-diastematic condition is produced by continual diminution in size of the (deciduous) premolars anterior to the retained P₄₋₅ and P₅, which become

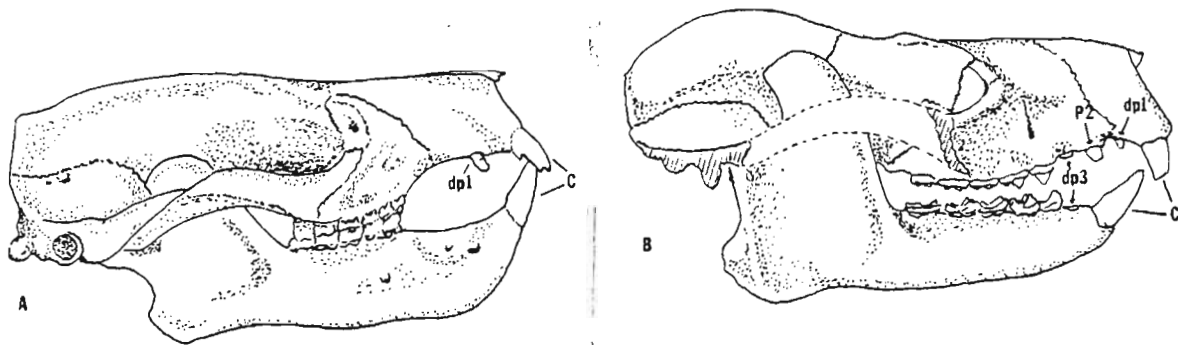


Figure 8: Comparison of (A) *Plesiadapis* and (B) *Microsyops* (both XI) with reference to the dental homologies suggested in the text. (Redrawn from McKenna, 1966).

 increasingly enlarged and elaborate (especially seen with the plagiaulacoid P₅). In addition, the microsyopids (see Bown and Gingerich, 1973; Bown and Rose, 1976; Gingerich, 1974a), exhibit the plesiadapid type of premolar reduction; this is seen, for example, by comparison of *Microsyops* and *Cynodontomys* (McKenna, 1966; Szalay, 1969a) with *Utasorex* and *Niptomomys* (Szalay, 1969b) (Fig. 8).

The paromomyids (e.g. Schwartz and Krishtalka, 1977; Simpson, 1940, 1955; Szalay, 1972, 1973; Wilson and Szalay, 1972), for the most part, retain the primitive five premolar region. However, the plesiadapid mode of premolar reduction, to a certain extent, must have been involved in the evolution of *Phenacolemur* (Simpson, 1955).

Tarsiiformes.-- With regard to the anaptomorphines, *Trogolemur* (Gazin, 1958; Matthew, 1909, 1915) and *Pseudotetonius* (Bown, 1974) possess four, rather than five, premolariform teeth between the large lower anterior tooth (i.e. the canine) and M₁; (the upper dentition of these two taxa is not known at present). In *Pseudotetonius*, the posteriormost premolar (=P₅) and M₁-2 (the only known molars) are virtually indistinguishable from those of *Tetonius*, whilst the tooth anterior to P₅ differs from that of the latter in that it is single-, not double-rooted and distinctly smaller in size; between this small tooth and the large canine are two alveoli, presumably for two more single-rooted diminutive teeth (Bown, 1974). In *Trogolemur*, the four teeth between M₁ and the canine are all single-rooted with the posterior two teeth distinctly premolariform and the anterior two demonstrably diminutive in size; (the size of the most anterior of these four teeth is inferred from the small root which is preserved (Gazin, 1958; Matthew, 1909, 1915)). To explain the differences between *Tetonius* and *Pseudotetonius*, Bown (1974) has proposed a rather complicated series of structural modifications involving "loss" of the large anterior tooth, enlargement of (what is here defined as) dP₁, reduction of P₂ (the so-called canine) and "loss" of the anterior root of P₄ (the so-called P₃). Such a series of structural modifications, however, seems hardly necessary when it is equally possible to inhibit various features (e.g. size, number of roots) during the development of the premolars or to simply retain small deciduous teeth. Although a definite identification of all dental homologies must await larger sample sizes, I would suggest that the large lower anterior tooth of *Pseudotetonius* and *Trogolemur* is the canine and the tooth immediately anterior to M₁ is P₅. In *Trogolemur*, the tooth anterior to P₅ is P₄ while the two rudimentary anterior teeth are probably deciduous premolars (dP₂ and dP₃?). In *Pseudotetonius*, the three rudimentary teeth anterior to P₅ may all be retained deciduous premolars (dP₂₋₄?). The diminution in premolar size from

posterior to anterior as well as the decrease in the number of roots of posterior premolars (especially in *Pseudotetodonius*) suggests that dP_1 was "lost" and the mechanisms of (and functional reasons for) premolar "loss" are at least analogous to those seen in plesiadapids, microsyopids and especially the carpolestids.

Rooneyia, one of the few North American primates known from the Oligocene, was described by Wilson (1966), who tentatively allocated it to the family Omomyidae (=Omomyinae). Primary characters which prompted Wilson to align *Rooneyia* with omomyines were the presence of para- and meta-conules on the upper molars. However, the morphology of the premolars and molars (especially the disposition of the paraconules, metaconules and hypocone (cf. Stehlin, 1916)), the nature of the auditory bulla and tubular ectotympanic (Szalay, 1975), the bony contributions to the enlarged orbit, the features of the brain as well as general craniofacial relationships are cladistically microchoerine (cf. Simons, 1961a; Simons and Russell, 1960) (see also Thenius, 1969). Although the crowns themselves are not preserved, Wilson (1966) suggested that the premaxillary alveoli housed two "powerful" teeth; posterior to the premaxillary-maxillary suture there is a small, single-rooted tooth followed by two distinctly premolariform teeth and then the molars. While indicating that the diminutive tooth posterior to the premaxillary suture could be a premolar rather than a canine, Wilson opted for the latter interpretation. Given that the data are limited, I suggest that the two premaxillary teeth are the canine (anteriorly) and P_2 (posteriorly), and the other antemolar teeth are dP_3 , P_4 and P_5 . If this interpretation is correct, development of two "powerful" teeth in the premaxilla could have been achieved by simply inhibiting the dP_1 of a five-premolar upper dentition similar to that seen in the microchoerines, C dP_1 P_2 dP_3 P_4 P_5 M_1 M_2 M_3 .

Catarrhini.-- With regard to premolar "loss" in the evolution of the catarrhines, reduction to two premolars can be seen to have proceeded from a premolar region homologous with that of three-premolar Anthropoidea and Strepsirhini (i.e. P_2 , P_4 and P_5). Various interpretations of such "loss" have previously been given: Gregory (1922) suggested that reduction of premolars occurred antero-posteriorly; Osborn (1973) briefly commented that perhaps M_3 was inhibited and the molariform posterior deciduous premolar retained as the first of the three posterior molariform teeth; and I (1974c) argued that the posterior premolar was "lost" in the lower jaw while the anterior premolar was "lost" in the upper jaw. However, data on so-called supernumerary molars in catarrhines, in concert with an appreciation of the mechanisms of determination of tooth position and morphology, is most supportive of Osborn's (1973) suggestion.

Interestingly, the catarrhines are the only anthropoid group which develop and erupt so-called anomalous "fourth" molars (e.g. Bennejeant, 1936; Colyer, 1936; Schultz, 1935, 1941, 1944, 1950; Delson, personal communication, for *Paradolichopithecus*). These "fourth" molars are commonly interpreted as "Supernumerary permanent teeth, probably due to localized twinning or splitting of a tooth bud in early development..." (Schultz, 1950: 239). An alternative interpretation is that a "fourth" molar is not anomalous but simply the result of relaxation of forces of inhibition on a tooth which otherwise would develop at that locus. A similar phenomenon occurs in the callitrichids: although the third molar has been "lost," initial development of this tooth sometimes occurs (Hershkovitz, 1970). Thus, if the last molar can be "lost" by forces of inhibition created, for example, by shortening of the jaw and subsequent crowding (e.g. Hershkovitz, 1970, for callitrichids; Pederson, 1949, for Eskimos), then, when there is sufficient developmental space, the tooth which had been "lost"

may reappear (Grüneberg, 1952, 1963). I suggest, therefore, that reduction in premolar number during the evolution of catarrhines was the result of inhibition of P5, retention of dP5 as the first molariform tooth, and concomittant "loss" of M3. The post-incisor dental formula of Catarrhini is: C P2 P4 dP5 M1 M2; (incisor homology will not be discussed at this time). From these conclusions, it is obvious that the three molars of Catarrhini are not homologous with the three molars of other primates and that reduction to two molars in the callitrichids was by "loss" of M3 whereas in Homo sapiens it is by "loss" of M2.

Indriidae.-- Lastly, mention must be made of the indriines and palaeopropithecines, which possess only two premolars. Reduction of premolar number in these two groups has been suggested to be the result of "loss" of anterior premolars (Gregory, 1922), "loss" of the middle of a primitively three-premolar dentition (Friant, 1935), or by inhibition of the upper anterior and lower posterior premolars (Schwartz, 1974c). It also could be that reduction to two premolars occurred as in the catarrhines. Although I have not seen specimens nor reports of any indriine or palaeopropithecine with "fourth" molars, data on development and eruption as well as comparative morphology of the premolar region of indriids (Lamberton, 1938; Schwartz, 1974a, 1974c, 1975b; Tattersall, 1973a, 1973b; Tattersall and Schwartz, 1974) is suggestive of the latter interpretation. At this time, however, the homologies of the indriine and paleopropithecine premolar (and molar?) region must remain in doubt.

PHYLOGENETIC RELATIONSHIPS

Dental Complexes.-- The phylogenetic relationships suggested by the preceding discussion of dental homologies and consequent shared derived character states are reflected in the accompanying cladogram (Fig. 9). The dotted lines in the cladogram reflect the uncertainty of determining how many derived states are shared because of recency of ancestry or are independently attained. From the above, it has become apparent, at least with regard to modes of premolar "loss," that parallelism is more the rule than is the principle of parsimony. Indeed, whether or not selection in the plesiadapoid-tarsiiform group for robust anterior teeth and variable "loss" of premolars to create semi- or fully-diastematic conditions can be seen as the result of competition with rodents and multituberculates, there is no reason to exclude the possibility that these primates were competing among themselves. Aside from some degree of parallelism in modes of premolar "loss," the tarsiiforms and plesiadapoids form a natural group through sharing the derived character complexes whereby the incisors have been "lost" and the canine is developed as the most anterior tooth in the jaw. The microsyopids also share this derived character complex and, thus, as is indicated by dental morphology (Bown and Gingerich, 1973; Bown and Rose, 1976; Gingerich, 1974a; McKenna, 1966; Szalay, 1969a, 1969b), form a sister-group with the plesiadapoid-tarsiiform clade. Although retaining the primitive emplacement of incisors and canines, the common ancestor of Anthropoidea and Strepsirhini has "lost" dP3; independent "loss" of dP1 in each group is indicated by its presence in the adapids. With regard to the primates as a whole, the ancestral morphotype would have been characterized by the complex whereby, of the retained five premolars, P1 had been inhibited and dP1 retained.

The Ear Region.-- The sister-groups indicated by dental characters are also consistent with data on other morphological features. This can be seen,

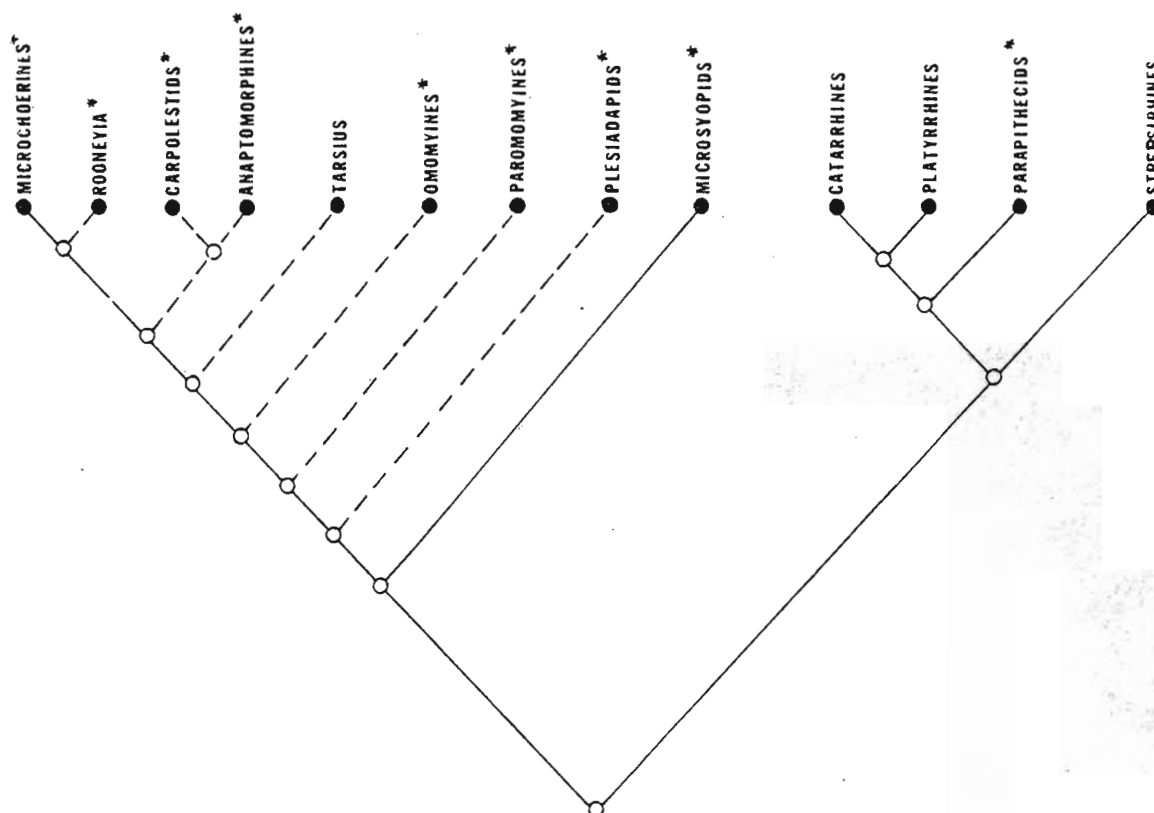


Figure 9: Tentative theory of relationships among the Primates; the asterisks denote extinct taxa while distances of divergence are schematic and do not reflect time. Since reclassification of the primates seems warranted but is not dealt with here, commonly accepted referents to taxa are used in their familiar sense.

for instance, in the bony ear, the differences which exist in the bulla and the disposition of the tympanic bone.

The primitive primate ear region has been generally accepted as that seen in the lemurs, i.e. a large, inflated petrosal bulla which extends laterally beyond the inferior edge of the tympanic ring (e.g. Cartmill, 1975; Clark, 1962; Simons, 1972; Tattersall and Schwartz, 1974). However, while Anthropoidea and Strepsirhini may be characterized by a totally petrosal bulla (e.g. Major, 1899; Van Kampen, 1905), recent studies of the development of the bulla of *Tarsius* (Schwartz, ms. a; R. D. Martin, personal communication) show that there is a distinct entotympanic contribution which fuses with the petrosal (Fig. 10). In the adult tarsier, all sutural evidence of such a contribution is obliterated. It, therefore, can be appreciated that if the bullae of Anthropoidea and Strepsirhini are totally petrosal, this is a shared derived character. Since the bulla of *Tarsius* is composed of an entotympanic contribution, it would appear that this character state was derived from a condition in which the bulla was totally entotympanic as seen, for example, in microsyopids and leptictids (McKenna, 1966). Thus, it would seem that the ancestral primate would have possessed an entotympanic bulla (also suggested by Bown and Gingerich, 1973) which may not, however, have been totally ossified (McKenna, 1966). It is unfortunate that evidence of a compound bulla may be obliterated in the adult, for such a contribution may well be present in the few plesiadapoids and tarsioids for which bullae are known (i.e. *Plesiadapis*, *Phenacolemur*, *Tetonius*, *Necrolemur* and *Rooneyia*); nonetheless, its conformation in *Tarsius* does lend support to McKenna's

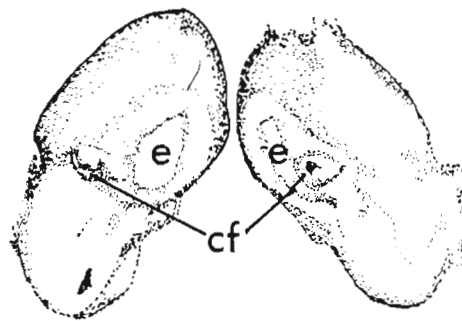
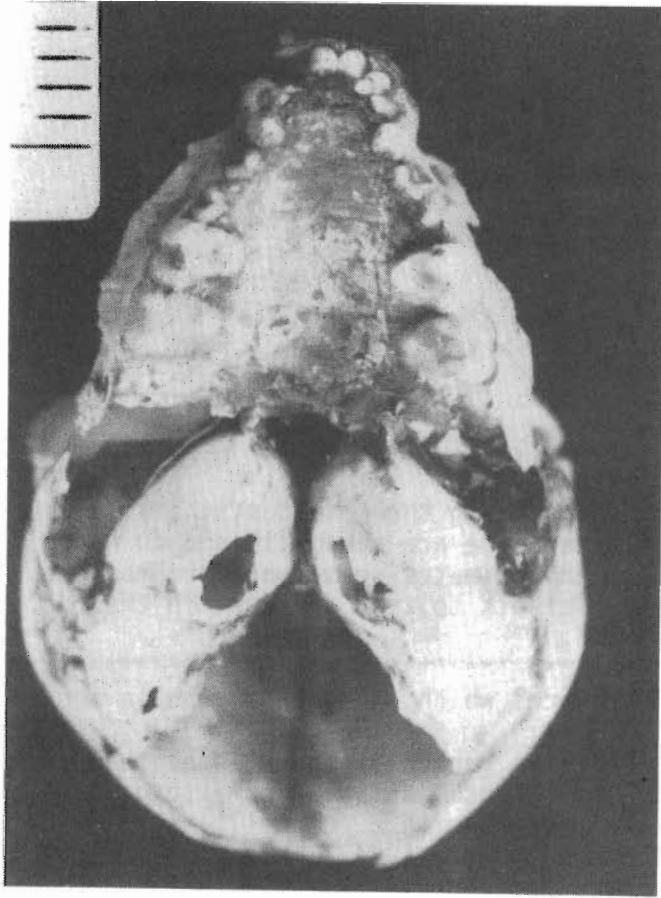


Figure 10: Basicranial view of skull of juvenile *Tarsius* (RM c). Right and left auditory bullae both have a "hole" in the medial wall of the hypotympanic sinus (detailed in drawing) whose subtending edges show morphological evidence of contact (not unlike the cranial squamosal suture) with a distinct and

separate contribution to the bulla: an entotympanic element (cf. Kampen, 1905; McDowell, 1958; McKenna, 1966); (for further discussion see Schwartz, ms.a). Scale is in mm. e = entotympanic, cf = carotid foramen.

(1966) suggestion that this may be the case in Plesiadapis.

Herskovitz (1974a) and Szalay (1972b) have recently argued that the primitive primate condition is with the tympanic bone external to the bulla. In reviewing available data on the ontogeny of the bulla, Schwartz, Tattersall and Eldredge (1978) concluded similarly; obviously, any modification of this configuration would constitute a derived condition. Interestingly, one derived condition, in which there is a tubular ectotympanic but the ring lies within the bulla, is seen in Tarsius, Necrolemur, Rooneyia, Tetonius, Plesiadapis and apparently Phenacolemur. If these taxa are reflective of their less well-known sister taxa, it is most likely they share this derived character because of common ancestry.

It is generally accepted that the ancestral primate lacked the medial branch of the internal carotid artery and possessed a stapedia branch which was larger than the promontory (e.g. Clark, 1962; Gregory, 1920; McDowell, 1958; McKenna, 1966, 1975; Simons, 1961b, 1972; Szalay, 1975; Tattersall and Schwartz, 1974). However, many primates--plesiadapoids (at least Plesiadapis (Russell, 1959) and perhaps Phenacolemur (Szalay, 1972b)), tarsii-forms (Tarsius, Necrolemur (Simons and Russell, 1960) and perhaps Tetonius (Szalay, 1975)), Anthropoidea and a number of strepsirhines (Saban, 1963) as well as microsyopids (McKenna, 1966)--are characterized by the promontory artery being larger than the stapedia branch. It, thus, would appear that this is the primitive primate condition, whereas that in which the stapedia is larger than the promontory is derived. Therefore, this primitive condition is not indicative of increased circulation to an increasingly sophisticated brain, as has, for example, been claimed for Apidium (Gingerich, 1973). Furthermore, since microsyopids possessed the medial branch of the internal carotid artery, this artery must have been present in the ancestral primate. Although absence of this artery would have characterized the ancestor of plesiadapoids and tarsii-forms and the ancestor of strepsirhines and Anthropoidea, loss of this feature would have been independently achieved in each case.

CONCLUSIONS

The phylogenetic relationships suggested by the complexes of tooth "loss" and subsequent dental homologies as well as the states of some non-dental characters support Pocock's (1918) and later Hill's (1953, 1955) contention that Tarsius should not be grouped with lemurs and lorises phylogenetically or taxonomically. However, it is apparent that the tarsier clade not only is significantly different from the lemur/loris group (i.e. Strepsirhini) but is equally distinct from Anthropoidea. Consequently, the notion of a "Tarsius stage" in the evolution of Anthropoidea becomes meaningless. From this point of references, similarities between Tarsius and Anthropoidea in such characters as the absence of a rhinarium (Pocock, 1918), the presence of a postorbital bar and some degree of post-orbital closure (e.g. Herskovitz, 1974b; Simons and Russell, 1960), as well as aspects of fetal membrane morphogenesis (Luckett, 1974) are the result of parallel evolution (Schwartz, 1978a). That such seemingly diagnostic characters of higher primates could have evolved independently in Tarsius while others set it distinctly apart is paralleled in the composi-

tion of blood serum proteins: while Tarsius resembles Homo sapiens in hemoglobin and adenylate kinase patterns "... these similarities are offset by marked differences in albumin and PGM (phosphoglucumutase)" (Barnicot and Hewett-Emmett, 1974: 901). As Barnicot and Hewett-Emmett further pointed out, "... it would not be particularly surprising to find phenotypic resemblances for a few proteins even in forms that are in fact only distantly related" (*ibid.*).

Another consequence of the conclusions reached here is that there are a number of derived complexes which clearly attest to the primate affinities of plesiadapoids and microsyopids. Therefore, no longer is there a need for preoccupation with the notion of a "wastebasket" taxon (e.g. Cartmill, 1972) to deal with these forms.

Some of the characters, then, which can be attributed to the ancestral primate would be: 1) five premolars, of which the first and third are retained deciduous teeth; 2) lack of a postorbital bar; 3) fissured claws; 4) an entotympanic bulla (ossified?) with the tympanic ring external to it; 5) a medial branch of the internal carotid artery; and 6) small, somewhat spatulate incisors (more than two pairs?) and a trenchant canine in their "expected" positions. Aside from molar morphology (cf. Simpson, 1935), only character 1 represents a derived condition. Notably absent from this discussion have been aspects of molar morphology and various specializations of premolars (e.g. carpolestids, anaptomorphines, cercopithecids). To some extent, derived versus primitive character states of these morphologies were taken into consideration in constructing the cladogram. Obviously, it would seem in order to re-evaluate the commonly accepted phylogenetic relationships of and among primates as well as the significance of the morphologies upon which they are based.³

SUMMARY

Among other aspects of morphology, Tarsius differs from other extant primates in that: 1) it does not possess any recognizably incisiform teeth in either the upper or lower jaw; 2) the most caniniform upper tooth is the one at the front of the jaw (the so-called central incisor), and there is no similarly caniniform tooth in the lower jaw; 3) the lower antemolar dentition is composed of five teeth which can best be described as premolariform, as is also the case with the five antemolar teeth behind the large, anteriormost upper tooth. The question, then, is what are the antemolar teeth of Tarsius--are they premolars and transmuted canines and incisors, or are they identifiable as the teeth they morphologically most resemble?

To test this two-tailed hypothesis, aspects of dental development and eruption in Tarsius and other extant primates with presumably similar dental formulae were compared. It was found that: 1) in post-natal tarsiers, all of the antemolar teeth do not replace predecessors or are themselves replaced, as typifies other primates--thus, the "adult" dentition of Tarsius differs from that of other extant primates in retaining what appear to be deciduous teeth along with proper permanent teeth; 2) those teeth which are

³Since this paper was written, Krishtalka and Schwartz (in press) have pursued further the relationships among plesiadapiform-tarsiiform primates suggested here. Of the hypotheses presented in Fig. 9, we have corroborated the suggestion that the microsyopids (in part) are the most primitive members of the clade, Rooneyia is cladistically a microchoerine, and the relationship of Tarsius lies nested within the clade; the reader is referred to this reference for detailed morphological discussion.

retained and unreplaced in post-natal tarsiers are the upper "lateral incisor," and the upper and lower "P2"; 3) of the permanent teeth of Tarsius, the so-called canine, P3 and P4 are not only morphologically most relatable to the "P2," "P3" and "P4" of other extant primates, but these teeth develop and erupt in the order in which the three premolars of other primates are frequently seen to appear ("P2" → "P4" → "P3"); and 4) the upper "central incisor" and "P₂" of Tarsius develop and erupt as an integrated unit, as do the upper canine and "P₂" of most strepsirhines--and these teeth, respectively, are also morphologically comparable.

From these correlations, it is concluded that: 1) the remarkable similarity in relative times of development and eruption of the "canine," "P3" and "P4" of Tarsius and the "P2," "P3" and "P4" of other extant primates, as well as the comparable morphology of the teeth involved, indicates that these teeth, respectively, are homologous; 2) the coordinated development and eruption of the upper "central incisor" and "P₂" of Tarsius is similar to the integrated appearance of the morphologically similar upper canine and "P₂" of strepsirhines because these teeth, respectively, are homologous; 3) the unreplaced antemolar teeth of Tarsius are retained deciduous premolars and the antemolar dental formula of Tarsius is thus best represented as $\underline{C} \text{ dP}_1 \text{ P}_2 \text{ dP}_3 \text{ P}_4 \text{ P}_5$; and 4) the other extant primates to which Tarsius is compared possess P2, P4 and P5, as a result of the P1 and P3 loci having been completely inhibited. The correlation of dental morphology with commonly observed patterns of dental development and eruption is, therefore, taken to be more reflective of homology than tooth position and occlusion. It is further suggested that our current knowledge of odontogenesis--tooth position and morphology are established well before the differentiation of bony landmarks--is compatible with the interpretation that the canine can be the first tooth in the jaw. Thus, dental transmutation, at least in the case of Tarsius, need not be invoked to explain divergences from the dental picture of incisiform, caniniform and premolariform teeth being in their expected positions.

A juvenile specimen of Absarokius noctivagus (USNM 19198) lends itself to this type of analysis. It was found that the appearance of this primate's "canine," "P3" and "P4" is similar to the sequence in which "P2" (=P2), "P3" (=P4) and "P4" (=P5) of many extant primates develop and erupt; and it is suggested that these teeth, respectively, are homologous. The most caniniform tooth of Absarokius is the one at the front of the jaw (at least as is known for the lower dentition), and this tooth is taken to be the canine, not a transmuted incisor.

Developmental data for other fossil primates (especially plesiadapiform and tarsiiform primates, which have traditionally been interpreted as having transmuted incisors and canines) are rare and not as complete. However, one can characterize primates as having either a relatively large, robust tooth or a set of recognizably incisiform teeth at the front of the jaw. Those which display the former condition are interpreted as having a canine at the front of the jaw behind which are five or fewer premolars, as seen in the upper jaw of Tarsius and the lower of Absarokius; some of the premolars may be retained deciduous teeth, as in Tarsius. Those which share this derived configuration are the plesiadapiform and tarsiiform primates. Strepsirhines and anthropoids, for the most part, have retained the primitive condition in which the incisors, canines and premolars are in their expected positions.

PART II

[Since this paper was first presented and manuscript copy circulated some years ago, and various authors have discussed the text in print, I have edited this version to maintain as much semblance to the original as can be expected. Major alterations are presented as footnotes. In this brief section, I will discuss further some aspects of my argument and address a few recent contributions.]

In part I, I have discussed (admittedly, somewhat laboriously) how one might approach determining dental homologies when there is rather acute disparity between the actual morphology and identification of a tooth. In doing so, I have played down the role and magnitude of dental transmutation in phylogeny, at least primate phylogeny. I do not suggest that morphological modification of teeth does not, or has not, occurred. Rather, I question how frequently it has happened, and urge that as many avenues of analysis--paleontological and neontological--be pursued prior to firm decisions of homology versus modification. However, lest I be accused of ruling out altogether the occurrence of dental transmutation, I shall discuss some instances wherein this can be elucidated by the approach detailed in part I.

Phaner, an extant Malagasy primate, is described as having, in contrast to other strepsirhines, a rather caniniform anterior upper premolar (e.g. Tattersall and Schwartz, 1974, and references therein). This tooth is not the most caniniform tooth in the upper jaw. The tooth which is, is situated in the expected position of a canine and anterior to it are two teeth which can reasonably be seen as incisors. The "caniniform premolar" and the two demonstrably premolariform teeth posterior to it develop and erupt in the sequence "P2" → "P4" → "P3" (see Schwartz, 1975b), the sequence commonly seen in other three-premolar primates. The "caniniform premolar" also develops and erupts in concert with the most caniniform upper tooth and the anterior lower premolar (see Schwartz, 1974a)--and this is similar to the developmental/eruptional dental triad of $C - P_2^1$ of the majority of strepsirhines. Thus: 1) on the basis of relative morphology, the most caniniform tooth can be isolated and suggested to be the canine; and 2) with the addition of developmental/eruptional data, this identification is further supported and the other (but less) caniniform tooth is seen to correspond well to the unquestionably premolariform tooth (P_2^2) of other primates, with which it can be homologized. The conclusion is that the upper anteriormost premolar of Phaner has been somewhat morphologically altered. (This may have appeared obvious from the beginning, primarily because the teeth of Phaner are in their expected positions. However, it should also be obvious that this example has broader implications.)

A second, but more complicated, example lies in the identification of the teeth of strepsirhine toothcombs.

Lemurids and lorids possess six lower procumbent anterior teeth behind which lie three premolariform teeth; there is no lower tooth which compares in caniniformity with the upper canine. The lateral teeth of the toothcomb are distinct from the four central teeth in that they are more robust, more convex buccally, laterally flared, and have marked margocristids (Gingerich, 1977; Martin, 1972; Schwartz, 1974b, 1978b); the central teeth are slenderer and more straight-sided. Extant indriids and the subfossil indriid Archaeolemur also possess a toothcomb behind which are two (in the former) or three (in the latter) premolariform teeth; in contrast to the lemur/loris toothcomb, that of indriids is

composed of only four teeth. However, similar to the toothcombs of lemurs and lorises, the lateral teeth of the indriid toothcomb are morphologically distinct from the central set of teeth, and they are distinguished from the central pair by the same criteria which separate the lateral from the central teeth of the lemur/loris toothcomb (*ibid.*). Thus, solely on the basis of morphology, it seems reasonable to conclude that the lateral teeth of all strepsirhine toothcombs are homologous, as would also appear to be true of the central teeth (although it is not certain which of the two pairs of central teeth of the lemur/loris toothcomb is the homologue of the central teeth of the indriid toothcomb).

To pursue further the study of the homologies of the strepsirhine toothcomb, Schwartz (1974b, 1978b) analyzed features of development and eruption of the teeth concerned. It was found that, regardless of the number, the central teeth appeared markedly in advance of the lateral teeth; the lateral teeth of all toothcombs are developmentally and eruptionally distinct from the central set of teeth. The congruence of morphologic and ontogenetic data, thus, adds considerable weight to the conclusion that the lateral teeth of all strepsirhine toothcombs are homologous, as would also be the case for the central teeth (although, again, it is not possible to homologize the central set of teeth of the indriid toothcomb with one of the pairs of central teeth of the lemur/loris toothcomb). And it would also seem that the toothcombed state, with its morphologic and ontogenetic peculiarities, was inherited from the common strepsirhine ancestor, but the question still remains: what are these teeth?

On the basis of tooth position and occlusion, I originally concluded that the lateral teeth are canines and the central set incisors (Schwartz, 1974b). Since I no longer believe that these criteria alone are sufficient for such identifications, I retreat in part from this position, but maintain that if the lateral tooth of any toothcomb is a canine, then all are canines; similarly, if the central teeth of any strepsirhine toothcomb are incisors, then all are incisors. That this is most probably the case is strongly suggested by overall dental similarities with anthropoids and adapids, in contrast to plesiadapiform and tarsiiform primates. More specifically, the implication of the phylogenetic relationship of the adapids to the strepsirhines (whether it is basal in some way (e.g. Clark, 1962; Gingerich, 1975b; Gregory, 1920; Simons, 1972) or restricted to a few taxa (Schwartz and Tattersall, in press)), and the relationship of, for example, Hadropithecus to extant indriids, is that lower canines and incisors were retained by the extant members of this clade. Further support of this interpretation derives from Stehlin's (1912) analysis of eruption patterns in juvenile Adapids: the lower anterior dentition appears sequentially uninterrupted by the eruption of other teeth, but the eruption of the canines is distinctly retarded relative to the emplacement of the incisors. And this pattern of eruption characterizes the lower anterior dentition of all extant toothcombed primates.

Recently, Gingerich (1977) has argued that only the lemur/loris toothcomb possesses canines and incisors, whereas the lateral teeth of the indriid toothcomb are incisors which have come to look like the canine of the lemur/loris toothcomb because of similar function. In light of the above, of which Gingerich was aware, the logic of this escapes me. It is the case, however, that Gingerich's conclusions were based rather heavily on his erroneous analysis of a juvenile specimen of Avahi (see Schwartz, 1978b). What is further disturbing is that Gingerich totally ignores the developmental/eruptional data: "... ontogenetic development

cannot be used in any deterministic way to rediscover phylogenetic history" (p. 389). Yet, in direct contradiction to this rather dogmatic statement, Gingerich (p. 390) proceeds to invoke Osborn's (1973) work on the development of tooth buds to support his model of incisor loss and, therefore, which incisors remain in various taxa.

It is obvious that Gingerich's approach to homology is fraught with serious problems--which basically stem from a lack of appreciation of ontogenetic studies in phylogenetic studies and a seeming disregard for or use of data as it serves his purposes. Since it is upon our identification of structures (as homologous or otherwise) that we base our phylogenetic hypotheses, it is of paramount importance that we take advantage of and pursue as many avenues of analysis as possible.

The approach to interpreting dental homologies and the subsequent revisions presented here no doubt will fall on few immediately sympathetic evolutionary biologists. This seems inevitable when a long-standing tradition is questioned. Of course, it would be the best of all possible worlds if we could also follow Gingerich's (1977: 389) suggestion that "to prove that a given tooth in a specialized mammal is homologous with the canine tooth in a generalized mammal requires that the tooth be traced phyletically back to the canine in a generalized mammal"; (I believe one could substitute incisor, premolar, etc. for "canine"). However, it is often not the case that this is possible. And it is also not uncommon that we are confronted with a group of mammals which are dentally "specialized" at even the earliest record of them.

It might be argued that, since other mammals have "specialized" their anterior dentition (e.g. phalangeroid marsupials, soricid and solenodontid insectivores), this is also true for plesiadapiform and tarsiiform primates. However, this is certainly circular reasoning and invalid as falsification--few have questioned, much less tested, the identification of the teeth of these taxa. I further suggest that other groups of mammals are similar to primates in that some sub-clades retained the primitive topography of teeth (i.e. unless lost, incisors, canines, etc., in their expected positions), in contrast to other but related sub-clades which lost incisors (in one or both jaws) and developed the canine at the front of the jaw. In the latter instance, as with plesiadapiform-tarsiiform primates, the commonly-thought-of occlusal relationship of the upper and lower canine is disrupted; the teeth which develop in the expected positions of canines occlude as canines would because it is a characteristic of cheek teeth (regardless of which teeth they are or how we identify them) that a lower tooth occludes anteriorly with its upper counterpart.

It might also be claimed (as one anonymous reviewer wrote) that there is no proof that teeth other than incisors will or can develop in the premaxilla. Cartmill and Kay (1978) pursued this disagreement by suggesting that, since there are separate premaxillary and maxillary dental laminae, those teeth which appear in the premaxilla are the same, i.e. incisors. However, it must be pointed out that, while the dental lamina may be fleetingly associated with tooth bud formation, its role is merely one of providing the necessary cellular environment and interaction for this process; and this phase of ontogeny must not be confused with the much earlier stage at which tooth position and morphology are determined (see part I, citations to Kollar and Baird, Miller, and Tonge, and references therein). The role of the dental lamina is even more dramatically elucidated by experiments wherein: 1) a suspected tooth locus is extirpated from a very young embryo (usually a laboratory rodent); 2) it is placed in a mesodermal environment such as the back of a developing chick or frog; and 3) if a tooth locus had

been successfully transplanted, a recognizable tooth eventually develops (*ibid.*). Therefore, if a tooth (e.g. a rodent molar or "incisor") can successfully grow in such a foreign location as the back of a frog, where there is no dental lamina, premaxilla, or maxilla, it would appear that, if need be, the canine could develop at the front of the jaw. The evidence for this having happened, in various primates at least, comes from the earlier discussed correlation of dental morphology and developmental/eruptional patterns. And it is this body of data, especially the developmental information, and the interpretation thereof, which must be dealt with in attempts to either falsify or corroborate the conclusions reached here.

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REFERENCES

- Barnicot, N. A. & Hewett-Emmett, D., 1974. Electrophoretic studies on prosimian blood proteins. In Martin, Doyle & Walker, Prosimian Biology. London: Duckworth.
- Bennejeant, Ch., 1936. Anomalies et variations dentaires chez les Primates. Paris: Clermont-Ferrand.
- Bown, T. M., 1974. Notes on early Eocene anaptomorphine primates. Univ. Wyo. Contrib. Geol., 13: 19-26.
- Bown, T. M. & Gingerich, P. D., 1972. Dentition of the early Eocene primates *Niptomomys* and *Absarokius*. Postilla, Yale Peabody Mus., 158: 1-10.
- Bown, T. M. & Gingerich, P. D., 1973. The Paleocene primate *Plesiolestes* and the origin of Microsyopidae. Folia primatol., 19: 1-8.
- Bown, T. M. & Rose, K. D., 1976. New early Tertiary primates and a reappraisal of some plesiadapiforms. Folia primatol., 26: 109-138.
- Butler, P. M., 1939. Studies of the mammalian dentition. Differentiation of the post-canine dentition. Proc. Zool. Soc. Lond., B109: 1-36.
- Butler, P. M., 1956. The ontogeny of molar pattern. Biol. Rev., 31: 30-70.
- Butler, P. M., 1963. Tooth morphology and primate evolution. In Brothwell, Dental Anthropology. London: Pergamon Press.
- Cartmill, M., 1972. Arboreal adaptations and the origin of the order Primates. In Tuttle, The Functional and Evolutionary Biology of Primates. Chicago: Aldine-Atherton.

- Cartmill, M., 1975. Strepsirhine basicranial morphology and the affinities of the Lorisiformes. In Lockett & Szalay, Phylogeny of the Primates. New York: Plenum Press.
- Cartmill, M. & Kay, R. F., 1978. Craniodental morphology, tarsier affinities, and primate suborders. In Chivers & Joyce, Recent Advances in Primatology, Vol. 3, Evolution. London: Academic Press.
- Clark, W. E. LeGros, 1962. The antecedents of man; 2nd ed. Edinburgh: Edinburgh University Press.
- Clemens, W. A., 1973. Fossil mammals of the Type Lance Formation Wyoming, Part III. Eutheria and summary. Univ. California Publ. Geol. Sci., 94: 1-102.
- Colyer, F., 1936. Variations and diseases of the teeth of animals. London: Bale and Daniels, Sons.
- Conroy, G. C., Schwartz, J. H. & Simons, E. L., 1975. Dental eruption patterns in Parapithecidae (Primates, Anthrozoidea). Folia primatol., 24: 275-281.
- Dahlberg, A. A., 1948. The milk and permanent dentitions of the Tarsius philipensis (abstract). Amer. J. Phys. Anthropol., 6: 239-240.
- Friant, M., 1935. Description et interpretation de la dentition d'un jeune Indris. C. R. Assoc. Anat., 1935: 205-213.
- Gazin, C. L., 1952. The lower Eocene Knight Formation in western Wyoming and its mammalian faunas. Smithsonian Misc. Coll., 117: 1-82.
- Gazin, C. L., 1958. A review of the middle and upper Eocene primates of North America. Smithsonian Misc. Coll., 136: 1-112.
- Gazin, C. L., 1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. Smithsonian Misc. Coll., 144: 1-98.
- Gazin, C. L., 1971. Paleocene primates from the Shotgun member of the Fort Union Formation in the Wind River Basin, Wyoming. Proc. Biol. Soc. Wash., 84: 13-38.
- Gingerich, P. D., 1973. Anatomy of the temporal bone in the Oligocene anthropoid Adapidae and the origin of Anthrozoidea. Folia primatol., 19: 329-337.
- Gingerich, P. D., 1974a. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Ph.D. thesis, Yale University. University Microfilms, Ann Arbor.
- Gingerich, P. D., 1974b. Dental function in the Paleocene primate Plesiadapis. In Martin, Doyle & Walker, Prosimian Biology. London: Duckworth.
- Gingerich, P. D., 1975a. Systematic position of Plesiadapis. Nature, Lond., 263: 111-113.
- Gingerich, P. D., 1975b. Dentition of Adapis parisiensis and the evolution of lemuriform primates. In Tattersall & Sussman, Lemur Biology. New York: Plenum Press.
- Gingerich, P. D., 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Univ. Mich., Mus. Paleontol. Pap. Paleontol., no. 15: 1-141.
- Gingerich, P. D., 1977. Homologies of the anterior teeth in Indridae and a functional basis for dental reduction in Primates. Amer. J. Phys. Anthropol., 47: 387-394.
- Gregory, W. K., 1915. On the relationship of the Eocene lemur Notharctus to the Adapidae and other primates. 2. On the classification and phylogeny of the Lemuroidea. Bull. Geol. Soc. Amer., 26: 419-446.
- Gregory, W. K., 1920. On the structure and relations of Notharctus, an American Eocene primate. Mem. Amer. Mus. Nat. Hist., (n.s.) 3(2): 49-243.

- Gregory, W. K., 1922. The origin and evolution of the human dentition. Baltimore: Williams and Wilkins.
- Grüneberg, H., 1952. The genetics of the mouse; 2nd ed. The Hague: Martinus Nijhoff.
- Grüneberg, H., 1963. The pathology of development. New York: John Wiley & Sons.
- Hershkovitz, P., 1970. Dental and periodontal diseases and abnormalities in wild-caught marmosets (Primates, Callithricidae). Amer. J. Phys. Anthropol., 32: 377-394.
- Hershkovitz, P., 1974a. The ectotympanic bone and origin of higher primates. Folia primatol., 22: 237-242.
- Hershkovitz, P., 1974b. A new genus of late Oligocene monkey (Cebidae, Platyrrhini) with notes on postorbital closure and platyrrhine evolution. Folia primatol., 21: 1-35.
- Hill, W. C. O., 1953. Primates, Comparative anatomy and taxonomy, vol. I, Strepsirhini. Edinburgh: Edinburgh University Press.
- Hill, W. C. O., 1955. Primates, Comparative anatomy and taxonomy, vol. II, Haplorhini: Tarsioidae. Edinburgh: Edinburgh University Press.
- Hill, W. C. O., 1960. Primates, Comparative anatomy and taxonomy, vol. IV, part A, Cebidae. Edinburgh: Edinburgh University Press.
- James, W. W., 1960. The jaws and teeth of primates. London: Pitman Medical.
- Johnson, G. W., S. Dreizen & B. M. Levy, 1970. Dental development in the cotton ear marmoset (Callithrix jacchus). Amer. J. Phys. Anthropol., 33: 41-48.
- Kampen, P. N. van, 1905. Die Tympanalgegend des Säugetierschädel. Morph. Jb., 34: 32-1722.
- Kay, R. F. & M. Cartmill, 1974. Skull of Palaeochthon nacimienti. Nature, Lond., 252: 37-38.
- Kindahl, M. E., 1957. On the development of the tooth in Tupaia javanica. Ark. Zool., 10: 463-479.
- Kindahl, M. E., 1958a. Some observations of the development of the tooth in Elephantulus myurus Jamesoni. Ark. Zool., 11: 21-29.
- Kindahl, M. E., 1958b. Notes on the tooth development in Talpa europaea. Ark. Zool., 11: 187-191.
- Kindahl, M. E., 1959a. On the tooth development of Soricidae. Acta Odont. Scand. 17: 203-237.
- Kindahl, M. E., 1959b. The tooth development in Erinaceus europeus. Acta Odont. Scand., 17: 467-489.
- Kindahl, M. E., 1967. Some comparative aspects of the reduction of premolars in Insectivora. J. Dent. Res., 46: 805-808.
- Kollar, E. J. & G. R. Baird, 1971. Tissue interactions in developing mouse tooth germs. In Dahlberg, Dental Morphology and Evolution. Chicago: University of Chicago Press.
- Krishtalka, L. & J. H. Schwartz, in press. Phylogenetic relationships of plesiadapiform-tarsiiform primates. Ann. Carnegie Mus.
- Lamberton, Ch., 1938. Dentition de lait de quelques lemuriens subfossiles Malgaches. Mammalia, 2: 57-80.
- Lillegraven, J. A., 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada and review of marsupial-placental dichotomy of mammalian evolution. Univ. Kansas Paleontol. Contr., art. 50, vert. 12: 1-122.
- Luckett, W. P., 1974. Comparative development and evolution of the placenta in primates. In Luckett, Contr. Primatol., vol. 3, Reproductive Biology of the Primates. Basel: S. Karger.

- Major, C. I. F., 1899. (Exhibition of, and remarks upon, some skulls of fetal Malagasy lemurs.) Proc. Zool. Soc. Lond., 1899: 987-988.
- Martin, R. D., 1972. Adaptive radiation and behavior of the Malagasy lemurs. Phil. Trans. Roy. Soc. Lond., 264: 295-352.
- Matthew, W. D., 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Amer. Mus. Nat. Hist. Mem., 9: 289-567.
- Matthew, W. D., 1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part IV. Entelonychia, Primates, Insectivora (part). Amer. Mus. Nat. Hist. Bull., 34: 429-483.
- McDowell, S. B., 1958. The Greater Antillean insectivores. Bull. Amer. Mus. Nat. Hist., 115: 113-214.
- McKenna, M. C., 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. Cal. Publ. Geol. Sci., 37: 1-130.
- McKenna, M. C., 1966. Paleontology and the origin of the Primates. Folia primatol., 4: 1-25.
- McKenna, M. C., 1975. Toward a phylogenetic classification of the Mammalia. In Lockett & Szalay, Phylogeny of the Primates. New York: Plenum Press.
- Miller, W. A., 1971. Early dental development in mice. In Dahlberg, Dental Morphology and Evolution. Chicago: University of Chicago Press.
- Osborn, J. W., 1970. New approach to zahnreihen. Nature, Lond., 225: 343-346.
- Osborn, J. W., 1971. The ontogeny of tooth succession in Lacerta vivipara Jacquin (1787). Proc. Roy. Soc. Lond., B179: 261-289.
- Osborn, J. W., 1973. The evolution of dentitions. Amer. Sci., 61: 548-559.
- Patterson, B., 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana Geol., 13: 1-105.
- Pederson, P. P., 1949. The East Greenland Eskimo dentition. Numerical variation and anatomy. Medd. Gronl. Cop., 142: 1-256.
- Peyer, B., 1968. Comparative odontology. Chicago: University of Chicago Press.
- Pocock, R. I., 1918. On the external characters of the lemurs and of Tarsius. Proc. Zool. Soc. Lond., 1918: 19-53.
- Robinson, P. C., 1967. The mandibular dentition of ?Tetonoides (Primates, Anaptomorphidae). Ann. Carnegie Mus., 39: 187-194.
- Rose, K. D., 1975. The Carpolestidae, early Tertiary primates of North America. Bull. Mus. Comp. Zool., 147: 1-74.
- Russell, D. E., 1959. Le crâne de Plesiadapis. Bull. Soc. Geol. France, ser. 7, 1: 213-214.
- Russell, D. E., 1964. Les mammifères Paleocènes d'Europe. Mem. Mus. Nat'l. Hist. Nat. (n.s.), 13: 1-324.
- Saban, R., 1963. Contribution à l'étude de l'os temporal des Primates. Mem. Mus. Nat'l. Hist. Nat., ser. A, Zool., 29: 1-378.
- Schultz, A. H., 1935. Eruption and decay of the permanent teeth in primates. Amer. J. Phys. Anthrop., 19: 489-581.
- Schultz, A. H., 1941. Growth and development of the orangutan. Contr. Embryol., XXIV, Carnegie Inst. Wash. Publ., 525: 57-110.
- Schultz, A. H., 1944. Age changes and variability in gibbons: a morphological study on population sample of man-like apes. Amer. J. Phys. Anthrop., 2: 1-129.
- Schultz, A. H., 1950. Morphological observations on gorillas. In Gregory, The anatomy of the gorilla. New York: Columbia University Press.

- Schwartz, J. H., 1974a. Dental development and eruption in the prosimians and its bearing on their evolution. Ph.D. thesis, Columbia University.
- Schwartz, J. H., 1974b. Observations on the dentition of the Indriidae. Amer. J. Phys. Anthropol., 41: 107-114.
- Schwartz, J. H., 1974c. Premolar loss in the primates: a re-investigation. In Martin, Doyle & Walker, Prosimian Biology. London: Duckworth.
- Schwartz, J. H., 1975a. Re-evaluation of the morphocline of molar appearance in the primates. Folia primatol., 23: 290-307.
- Schwartz, J. H., 1975b. Development and eruption of the premolar region of prosimians and its bearing on their evolution. In Tattersall & Sussman, Lemur Biology. New York: Plenum Press.
- Schwartz, J. H., 1978a. If Tarsius is not a prosimian, is it a haplorhine? In Chivers & Joyce, Recent Advances in Primatology, vol. 3, Evolution. London: Academic Press.
- Schwartz, J. H., 1978b. Homologies of the toothcomb. Amer. J. Phys. Anthropol., 49: 23-30.
- Schwartz, J. H., (ms.a). Entotympanic contribution to the bulla of Tarsius.
- Schwartz, J. H., (ms.b). Dental uniquenesses of Tarsius: a source for re-thinking dental homologies.
- Schwartz, J. H. & L. Krishtalka, 1977. Revision of Picrodontidae (Primates, Plesiadapiformes): dental homologies and phylogeny. Ann. Carnegie Mus., 46: 55-70.
- Schwartz, J. H. & I. Tattersall, in press. The phylogenetic relationships of Adapidae (Primates, Lemuriformes). Anthrop. Pap. Amer. Mus. Nat. Hist.
- Schwartz, J. H., I. Tattersall & N. Eldredge, in press. Phylogeny and classification of the Primates revisited. Yrbk. Phys. Anthropol., 21: 95-133.
- Simons, E. L., 1961a. Notes on Eocene tarsiods and a revision of some Necrolemurinae. Bull. Brit. Mus. (Nat. Hist.), Geol. Ser., 5: 45-69.
- Simons, E. L., 1961b. The dentition of Ourayia: its bearing on the relationships of omomyid prosimians. Postilla, Yale Peabody Mus., 54: 1-29.
- Simons, E. L., 1972. Primate evolution. New York: MacMillan.
- Simons, E. L., 1974. Notes on early Tertiary prosimians. In Martin, Doyle & Walker, Prosimian Biology. London: Duckworth.
- Simons, E. L. & D. E. Russell, 1960. Notes on the cranial anatomy of Necrolemur. Breviora, Mus. Comp. Zool., 127: 1-14.
- Simpson, G. G., 1935. The Tiffany fauna, upper Paleocene, II. Structure and relationships of Plesiadapis. Amer. Mus. Nov., no. 816: 1-30.
- Simpson, G. G., 1940. Studies on the earliest primates. Bull. Amer. Mus. Nat. Hist., 77: 185-212.
- Simpson, G. G., 1955. The Phenacolemuridae, a new family of early primates. Bull. Amer. Mus. Nat. Hist., 105: 411-442.
- Slaughter, B., R. H. Pine & N. E. Pine, 1974. Eruption of cheek teeth in Insectivora and Carnivora. J. Mamm., 55: 115-125.
- Stehlin, H. G., 1912. Die Säugetiere des schweizerischen Eocäns. Kritischer Katalog der Materialien, 7. Teil, erste Hälfte Adapis. Abh. Schweiz. Pal. Ges., 38: 1165-1298.
- Stehlin, H. G., 1916. Die Säugetiere des schweizerischen Eocäns. Kritischer Katalog der Materialien, 7. Teil, Zweite Hälfte, Caenopithecus-Necrolemur. Abh. Schweiz. Pal. Ges., 41: 1297-1552.
- Szalay, F. S., 1968. The beginning of primates. Evolution, 22: 19-36.
- Szalay, F. S., 1969a. Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bull. Amer. Mus. Nat. Hist., 140: 1-288.

- Szalay, F. S., 1969b. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). Amer. Mus. Nov., no. 2362: 1-36.
- Szalay, F. S., 1972. Paleobiology of the earliest primates. In Tuttle, The Functional and Evolutionary Biology of Primates. New York: Aldine-Atherton.
- Szalay, F. S., 1972b. Cranial morphology of the early Tertiary Phenacolemur and its bearing on primate phylogeny. Amer. J. Phys. Anthrop., 36: 59-76.
- Szalay, F. S., 1973. New Paleocene primates and a diagnosis of the new suborder Paromomyiformes. Folia primatol., 19: 73-87.
- Szalay, F. S., 1975. Phylogeny of primate higher taxa: the basicranial evidence. In Lockett & Szalay, Phylogeny of the Primates. New York: Plenum Press.
- Szalay, F. S., 1976. Systematics of the Omomyidae (Tarsiiformes, Primates): Taxonomy, phylogeny, and adaptations. Bull. Amer. Mus. Nat. Hist., 156: 157-450.
- Tattersall, I., 1973a. Cranial anatomy of the Archaeolemurinae (Lemuroidea, Primates). Anthrop. Pap. Amer. Mus. Nat. Hist., 52(1): 1-110.
- Tattersall, I., 1973b. Subfossil lemuroids and the "adaptive radiation" of the Malagasy lemurs. Trans. N.Y. Acad. Sci., ser. II, 35: 314-324.
- Tattersall, I. & J. H. Schwartz, 1974. Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). Anthrop. Pap. Mus. Nat. Hist., 52(3): 141-192.
- Thenius, E., 1969. Phylogenie der Mammalia. Stammesgeschichte der Säugetiere (einschliesslich der Hominiden). Berlin: W. de Gruyter.
- Tomes, C. S., 1914. A manual of dental anatomy. Philadelphia: P. Blakiston's Son.
- Tonge, C. H., 1971. The role of mesenchyme in tooth development. In Dahlberg, Dental Morphology and Evolution. Chicago: University of Chicago Press.
- Van Valen, L., 1970. An analysis of developmental fields. Devel. Biol., 23: 456-477.
- West, R. M., 1972. Upper deciduous dentition of the Oligocene insectivore Leptictis (=Ictops) acutidens. Ann. Carnegie Mus., 44: 25-44.
- Wilson, J. A., 1966. A new primate from the earliest Oligocene, West Texas, preliminary report. Folia primatol., 4: 227-248.
- Wilson, R. W. & F. S. Szalay, 1972. New Paromomyid primate from middle Paleocene beds, Kutz Canyon area, San Juan Basin, New Mexico. Amer. Mus. Nov., no. 2499: 1-18.