THE PHYLOGENETIC RELATIONSHIPS
OF ADAPIDAE
(PRIMATES, LEMURIFORMES)

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ABSTRACT

The Eocene Holarctic primates of the family Adapidae have generally been considered to be close to the ancestry of the lemurs of Madagascar, themselves conceived of as a homogeneous group. Reexamination of available evidence reveals, however, that the adapids appear to be more closely related to *Lepilemur*, *Megaladapis*, and *Hapalemur* than they are to *Lemur* and *Varecia*. This phylogenetic relationship implies that a split prior to earliest Eocene occurred between the common ancestor of *Lepilemur-Megaladapis-Hapalemur*-Adapidae and that of *Lemur-Varecia* and, in turn, implies earlier dates yet for the divergences establishing the major taxa of the modern Malagasy primate fauna.

INTRODUCTION

The consensus regarding the phylogenetic relationships of the Eocene primate family Adapidae has changed remarkably little in the more than half-century since Gregory (1920) published his exhaustive monograph on *Notharctus*, the best-known North American representative of the group. Although Gregory's contention that the adapid subfamily Notharctinae contained the ancestor of the New World monkeys has not survived into the recent literature, his basic concept of the adapids as primitive lemuroids has been almost universally adopted.

This basic assessment has remained largely unchanged even while suggestions as to the affinity of the adapids with other primate groups have multiplied. Thus Gingerich (1973, 1975a, 1975b), whilst proposing that the origin of the "higher" primates is to be sought within Adapidae, nonetheless emphasized the relationship of this family with the Malagasy lemuroids. Szalay (1974), however, has expressed his belief that "The Eocene lemurs have a more primitive dentition, with less specialized teeth and the tritubercular molars of early Tertiary primates, than any of the Madagascan species . . . which . . . puts them closer to the ancestor of the catarrhines than any Madagascan lemur" (p. 53). Cartmill and Kay (1978) have departed yet further from orthodoxy in arguing that no characters can be distinguished which indicate any particular relationship between the adapids and any other group of primates, haplorhine or strepsirhine.

Evidently, then, such shifting as there has been away from the classical viewpoint of adapid relationships has been in the direction of emphasizing the affinity of these Eocene forms to non-Malagasy primate groups, or of denying any special relationship whatever to other primate taxa. In contrast, however, our own preliminary investigation of relationships among the so-called lower primates has suggested that the adapids are not "basal" lemuriforms, and that in fact they form a sister-group with only *Hapalemur* and *Lepilemur* among the extant Malagasy lemurs.[1] It is this relationship, and its implications, that we wish tentatively to explore here.

ACKNOWLEDGMENTS

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[1] We use the vernacular term "lemur" solely to mean "Malagasy primate."

The following abbreviations are used in the text for names of institutions: AMNH: the American Museum of Natural History; USNM, the Smithsonian Institution; BM (NH), British Museum (Natural History).

THE MORPHOLOGICAL EVIDENCE

THE DENTITION: MOLAR MORPHOLOGY

In support of his contention that the adapids, or at least the adapines, were near the ancestry of the lemurs and lorises, Gregory (1915, 1920, 1922) repeatedly called attention to similarities in molar morphology between *Adapis parisiensis* and *Lepilemur*; he thus regarded the latter as representing the primitive strepsirhine condition. More recently Gingerich (1975a) has chosen to compare *A. parisiensis* instead with *Hapalemur*. Gingerich chose *Hapalemur* for comparison because it is supposedly "intermediate" in the range of variation exhibited by other extant lemurs, and "because of its relatively generalized nature . . . which . . . may closely approximate the condition of the ancestral lemur stock" (p. 70). We have, however, recently determined that *Lepilemur* and *Hapalemur* exhibit a number of derived character states in their dental morphology which are not shared with other extant strepsirhines and which are otherwise seen among the lemurs only in the subfossil *Megaladapis* (Tattersall and Schwartz, 1974). Derived features of upper molar morphology of *Hapalemur*, *Lepilemur* and *Megaladapis* include: (1) a reduction of lingual, especially cingular, development; (2) a protocone which, although large, does not dominate the trigon; (3) buccolingually compressed (and hence with subcrescentic-crescentic cross sections) paracones and metacones which are connected by marked para- and metacristae; and (4) a strikingly developed preprotocrista on M^{1-3} which passes anterior to the paraconule and connects with a crest or shelf extending from the parastylar region.

The lower molars also display derived characters not shared with other Malagasy forms or with primates in general. These teeth are char-

acterized by: (1) cuspal compression with sharp, almost continuous (except for the region of the entoconid) intercusp cresting; and (2) a cristid obliqua confluent with the paracristid.

All of these derived states are also seen in the adapids (cf. Gingerich, 1975a; Gregory, 1915, 1920; Stehlin, 1912). In the notharctines they are less pronounced than they are in the adapines, amongst which their degree of expression is very close to that found in the *Lepilemur-Megaladapis-Hapalemur* group.

Some specimens of *Adapis parisiensis* (Stehlin, 1912) and of *Notharctus* (Gregory, 1920) yield information on patterns of dental eruption and some *Notharctus* also contribute data on dental development. From Stehlin's and Gregory's descriptions and illustrations and our study of juvenile specimens, it appears that in both of these adapids, M^1 and then M^2 erupt first; M^3 comes into place later, somewhat after the anterior dentition. In *Adapis* and *Notharctus*, the anteriormost premolar (which is most probably a retained deciduous tooth [Schwartz, MS]), erupts well ahead of the posterior three premolars which, in turn, replace their predecessors in the sequence $P^4 \rightarrow P^3 \rightarrow P^2$. Study of maxillary (AMNH 13025) and mandibular (AMNH 13029) remains of *Notharctus tyrannus*, in which the posterior three deciduous premolars have not been shed, reveals a developmental pattern for the permanent premolars of $P^2 \rightarrow P^4 \rightarrow P^3$. The sequence of eruption of the permanent premolars thus differs from the developmental sequence.

Amongst strepsirhines, the only taxa which also convert a $P_2 \rightarrow P_4 \rightarrow P_3$ developmental pattern to $P_4 \rightarrow P_3 \rightarrow P_2$ in eruption are *Lepilemur* and *Megaladapis* (Lamberton, 1938; Schwartz, 1974a, 1975a). This is in marked contrast to the majority of lemurs and lorises which possess the primitive sequence of premo-

lar appearance ($P_2 \rightarrow P_4 \rightarrow P_3$) in both development and eruption. *Hapalemur, Lemur catta*, and the archaeolemurines are similar to *Lepilemur, Megaladapis*, and adapids in that their premolars erupt in a posteroanterior sequence but differ in that this is also the order in which these teeth develop (Schwartz, 1974a, 1975a). Other aspects of craniodental morphology indicate that the sequence $P_4 \rightarrow P_3 \rightarrow P_2$ in development and eruption arose independently in *L. catta*, the archaeolemurines and *Hapalemur* (cf. Tattersall and Schwartz, 1974).

The early appearance of M1 followed by M2 also represents a derived character state (Schwartz, 1974a, 1975b); the primitive state is marked by the eruption first of the anterior dentition. The only other strepsirhines to display early eruption of M_1^1, followed by M_2^2, are *Megaladapis, Lepilemur, Galago demidovii*, and, to some extent, *Microcebus murinus*. Again, wider comparisons indicate the acquisition independently of this feature in the *Megaladapis-Lepilemur*—(and presumably also, with subsequent loss)—*Hapalemur* group.

The evidence of both molar and premolar eruption sequences thus rules out the possibility that adapids (or at least those in which the characters can be discerned) were ancestral to the lemurs as a whole, and strongly suggests a sister relationship between *Megaladapis-Lepilemur-Hapalemur* and Adapidae.

THE DENTITION: EVOLUTION OF THE TOOTHCOMB

With the exception of *Daubentonia*, all extant strepsirhines possess a toothcomb. Comparative morphological, as well as development/eruption studies have shown that, while there are fewer teeth in the indriine toothcomb than in that of other lemurs and lorises, the lateral procumbent teeth (canines) of all these forms are homologous as are the teeth of the central set (incisors) (Martin, 1972; Schwartz, 1974b). It thus seems virtually certain that the toothcomb was not acquired independently, but was present prior to the major strepsirhine divergences (Martin, 1972; Schwartz, 1974b; Tattersall and Schwartz, 1974). Similarly, since except among the larger subfossil lemurs the

toothcomb is invariably associated with an unfused mandibular symphysis, it is likely that these two character states were present together in the ancestral form (cf. Tattersall and Schwartz, 1974).

Many authors have suggested that the toothcomb (and, by implication, an unfused symphysis) was derived from a condition similar to that seen in most adapids, in particular *Adapis*, wherein the lower anterior teeth are orthally emplaced and associated with a fused mandibular symphysis (e.g., Stehlin, 1912; Gregory, 1920, 1922; Hill, 1953; Clark, 1962; Martin, 1972; Cartmill, 1975; Gingerich, 1975a). Simons (1972), however, has correctly remarked that *Adapis*, at least, could not have given rise to modern strepsirhines precisely because its fused symphysis is a specialization. In the light of this observation, it would be extremely questionable to view the adapid condition as predating the acquisition of an unfused symphysis in association with a toothcomb, as this would imply that the unfused symphysis, at least, was secondarily derived, and not a primitive retention.

Although most known adapids possessed a fused symphysis in association with orthally emplaced lower teeth, the well-represented early Eocene adapid *Pelycodus*, found in both North America and Europe (Russell, Louis and Savage, 1967), possessed an unfused symphysis (Gregory, 1920) and (possibly) procumbent lower anterior teeth (Simons, 1972). As Gregory (1920) pointed out, the unfused symphysis, at least, is primitive for Adapidae.

In arguing for *Adapis* as ancestral to lemurs and lorises, Gingerich (1975a) pointed out that the lower canines of *A. parisiensis* are functionally incisors, i.e., that the anterior dentition functioned as a unit, as is the case with the toothcomb (or "dental scraper"). Gingerich suggested that, with the modification of this dental complex to form a toothcomb, symphyseal fusion would no longer be necessary and, thus, would not occur during ontogeny. This argument, however, could equally well apply the other way around to explain the transition from a toothcomb to an orthal anterior dentition (as happened, for instance, in the evo-

lution of the Malagasy subfossil *Hadropithecus* [Tattersall, 1973b; Tattersall and Schwartz, 1974]). Indeed, such a transition would make better sense functionally; certainly, when other characters are considered, indications are that the possession of a toothcomb, in association with an unfused symphysis (as suggested in *Pelycodus* and possibly *Pronycticebus* [Simons, 1972]), was primitive for Adapidae.

MANDIBULAR MORPHOLOGY

In a review of relationships among the Malagasy lemurs (Tattersall and Schwartz, 1974), we proposed that a relatively long and slender mandibular corpus, in association with a hooked gonial region, represents the primitive condition for strepsirhines. *Pelycodus* and *Notharctus* retain this primitive condition, whereas the other adapids tend to have a relatively shorter and deeper mandibular corpus (cf. Gazin, 1958; Gregory, 1920; Stehlin, 1912).

With regard to the mandibular condyle, we distinguished three discrete morphologies among the lemurs: (1) the primitive condition, as seen in *Lemur*, in which the condyle is broad transversely, and the somewhat posteriorly directed articular facet is distinct from, rather than confluent with, the posterior surface of the condylar neck; (2) a derived condition seen in the indriines, in which the condyle may be broad transversely, but is also more or less strongly curved in the coronal plane, and where the articular facet is confluent with the posterior aspect of the condylar neck; and (3) a different derived condition, seen among the lemurs only in *Lepilemur*, *Megaladapis*, and some *Hapalemur* (e.g., USNM 63355) in which a distinct articular facet descends, medial to the condylar neck, from the posterior aspect of the transversely broad condyle. This last configuration is elsewhere found only in the adapids, amongst which the posteromedial extension of the articular facet is most pronounced in *Notharctus* (e.g., AMNH 21960, 21864 and 13230), *Smilodectes* (e.g., USNM 17995 and 21815) and *Adapis* (e.g., BM(NH) 1633 and 7506); it is present, but slightly less pronounced, in *Pelycodus* (e.g., AMNH 15019).

BASICRANIAL STRUCTURE: THE BONY EAR

The character which is perhaps most commonly adduced to indicate for the adapids not only affinities with, but also a position near the ancestry of, the Malagasy lemurs, is the structure of its bony ear. In essence, this argument involves the presence of an enlarged auditory bulla, of petrosal formation, which extends laterally beyond the inferior border of the tympanic ring. This configuration is characteristic of the adapids and also of most of the lemurs with the notable exception of the highly modified *Megaladapis* and the palaeopropithecines; in the latter, this may well be a size-related modification (Tattersall, 1973a).

Although this type of bullar conformation has been argued by many to represent the primitive primate condition (e.g., McDowell, 1958; Clark, 1962; Szalay and Katz, 1973; Tattersall and Schwartz, 1974; Cartmill, 1975) recent work on the ontogeny of the bulla (Cartmill, 1975; MacPhee, 1977) indicates otherwise. Rather it appears that possession of an extrabullar tympanic ring—as in earlier ontogenetic stages—is primitive and that the condition wherein the lateral edge of the bulla has grown laterally beyond the ectotympanic is derived (Schwartz, Tattersall and Eldredge, in press). Common possession of this apomorphy by adapids, *Lemur*, *Varecia*, *Lepilemur*, *Hapalemur*, *Daubentonia*, and indriids most certainly bespeaks their common ancestry but indicates nothing about relationships among these taxa.

BASICRANIAL STRUCTURE: THE CAROTID CIRCULATION

Considerable emphasis has been placed on the pattern of carotid circulation in the determination of the phyletic relationships of mammals. The diversity of taxa characterized by an internal carotid artery which sends off three major branches (medial, promontory, and stapedial), with the promontory larger than the stapedial, suggests strongly that this condition is primitive for Eutheria (cf. McDowell, 1958; McKenna, 1966; Szalay, 1975). Since this condition is also characteristic of the microsyopid

primates (McKenna, 1966), it is reasonable to regard it as having been present in the ancestral primate. Within Primates, deviations from this condition thus represent derived states.

One such derived state is where the medial branch of the internal carotid is absent, and the stapedial is larger than the promontory artery. This occurs in adapids, *Lemur*, *Varecia*, *Hapalemur*, the indriines, the archaeolemurines, and, to some extent, in the palaeopropithecines (Saban, 1963; Szalay, 1975; Szalay and Katz, 1973; Tattersall, 1973b). *Lepilemur* and *Megaladapis* possess different conformations: in the former the stapedial artery is feebly developed, whilst in the latter it is entirely absent.

STRUCTURE OF THE ORBITAL FOSSA

Another character which has received much attention in discussions of the relationships among "lower" primates is the structure of the medial orbital wall. In both North American and European adapids in which this feature is preserved, contact between the frontal and maxilla separates the palatine from the lacrimal, while contact between the palatine and frontal separates the orbitosphenoid from the maxilla (Clark, 1962; Gregory, 1920; Piveteau, 1957). This configuration is also seen in the indriines, *Palaeopropithecus*, *Daubentonia*, *Plesiadapis*, and occasionally in *Phaner*, *Hapalemur*, and *Lepilemur* (Cartmill, 1975; Genet-Varcin, 1963; Kollman, 1925; Tattersall and Schwartz, 1974); it also characterizes many extant Lipotyphla—soricids, talpids, tenrecids, and chrysochlorids (Butler, 1956). In *Archaeolemur*, while the maxilla separates the palatine and lacrimal, the fronto-maxillary suture is appreciably longer—presumably as a result of secondary loss of the prenasopalatine portion of the palatine (Kollman, 1925)—and the absence of this portion of the palatine permits a broad contact between the maxilla and orbitosphenoid, thus separating the palatine from the frontal. In non-primates, this particular pattern is seen, for example, in *Leptictis* (representative of the late Cretaceous-early Tertiary ernotherian leptictids [McKenna, 1975]), as well as erinaceid and solenodontid lipotyphlan insectivores (Butler, 1956).

In contrast to each of these configurations is that seen in *Lemur* and *Varecia*: the palatine broadly contacts the frontal and lacrimal and thus separates the maxilla from both of these bones (Clark, 1962; Kollman, 1925); when *Phaner*, *Hapalemur*, and *Lepilemur* do not display the configuration discussed above, they have this one. This pattern also characterizes tupaiids, marsupials, Dermoptera and Macroscelidea, although some specimens are seen to have part of the ethmoid exposed between the palatine and the lacrimal (Evans, 1942; Muller, 1934; Saban, 1956). *Tarsius* has a similar disposition of the ethmoid vis-à-vis the palatine and lacrimal; lorisids, cheirogaleids and Anthropoidea display variants of this configuration (see Cartmill, 1975, for further discussion).

Whilst not explicitly stating this, Clark (1962) implied that the palatine-lacrimal configuration, as seen in *Lemur* and *Tupaia*, is primitive for primates. This interpretation is tied to the multifaceted belief that "insectivores" are generalized, primitive mammals, *Tupaia* represents the ancestral primate condition, and *Lemur* is the most primitive primate; therefore, whatever *Tupaia* and *Lemur* share must have been present in the ancestral primate. Adapids do not have this configuration of the medial orbital wall. On the other hand, Cartmill (1975) has argued that, since shrews and hedgehogs are probably closely related to primates, the pattern shared by these taxa reflects the primitive primate state, and that the pattern seen in adapids is primitive. However, while shrews, hedgehogs, and some primates show contact between the frontal and maxilla, soricids and erinaceids themselves *do not* share the same total configuration of the medial orbital wall. Furthermore, the "diversely adapted Madagascar lemurs," which Cartmill (1975, p. 340) cited in support of his argument, include *Phaner*, *Lepilemur*, and *Hapalemur*, which variably develop the pattern seen in *Lemur*. Thus those taxa which consistently display the same conformation of the entire medial orbital wall as do the adapids are the indriines, *Palaeopropithecus*, *Plesiadapis*, and non-erinaceid-solenodontid lipotyphlan insectivores; the palatine is much reduced in *Daubentonia* (Kollman, 1925). Erinaceids, solenodontids, and

leptictids share the same pattern with *Archae-olemur*.

From the available evidence it is obviously not easy to decide which of the above configurations of the medial orbital wall is primitive for Primates. In addition to the claims of Clark (1962) and Cartmill (1975), Martin (1968) reasoned that the ancestral primate had the ethmoid exposed, as in *Tarsius*, Anthropoidea, most lorisids and cheirogaleids, and sometimes in marsupials, macroscelidids, and Dermoptera. Whether Clark's hypothesis or Martin's is correct, the pattern seen in the adapids emerges as an autapomorphic condition. Cartmill's argument rests heavily on the assumption that shrews and hedgehogs are closely related to primates. While this may be a viable hypothesis (Krishtalka, 1976 and personal commun.), we believe it unwise to use preconceived notions of phylogeny to determine the derived-primitive polarity of the morphologies which are then supposed to indicate relationships.

If wide distribution—"communality of possession" (e.g., Hennig, 1966; Schaeffer, Hecht and Eldredge, 1972)—of a character among the taxa under consideration as well as in an array of taxa of varied affinities bespeaks primitiveness, we must agree with Martin (1968) that the ancestral primate had the ethmoid exposed. On the other hand, development of different configurations of the medial orbital wall in members of the same genus (e.g., *Phaner*, *Lepilemur*, *Hapalemur*) may reflect more accurately the futility of using this character complex in phylogeny reconstruction.

PHYLOGENETIC RELATIONSHIPS

It is apparent from the preceding survey that the closest affinities of the adapids lie with the *Lepilemur-Megaladapis-Hapalemur* group. As we have seen, some of the classical features which have traditionally been focused upon by primate paleontologists do not help to clarify the issue of adapid relationships; but it does seem to us that the dental evidence, in particular, is compelling. At this stage, unfortunately, the details of the relationships within this entire assemblage of fossil and living forms are not entirely clear, as the dotted lines in figure 1

imply. The basis for the formation of this theory of relationships, and the uncertainties involved, are perhaps best discussed by characterization of the branching-points on the diagram.

The common ancestor of the entire assemblage under consideration (node 1 in fig. 1) was highly derived in many ways relative to the ancestor it shared with the *Lemur-Varecia* group. Its molars were characterized by buccolingual compression of the cusps and by marked intercuspal cresting; in the lower molars this cresting was interrupted lingually between the metaconid and the entoconid. The talonid heel of M_3 was elongate. The premolars appeared in a posteroanterior sequence, at least in eruption, and the anterior molars came in early. The posteromedial aspect of the mandibular condyle was prolonged inferiorly to provide a secondary articulation with the postglenoid process. There was a marked posterior convergence of the temporal lines.

But if it is relatively easy to characterize the ancestor represented by node 1 (a reflection of the distinctiveness of the assemblage), there exist considerable problems in determining relationships within the group. The common ancestor possessed a toothcomb as a primitive retention from an earlier ancestor (see fig. 2). Known adapines uniformly possessed orthally implanted anterior lower teeth, as did all the notharctines with the possible exception of *Pelycodus*. If this derived trait is shared because of ancestral retention in the adapines and notharctines, then the relationships of these two groups are as expressed by node 2b (fig. 1). If *Pelycodus* indeed possessed procumbent anterior lower teeth, this would strongly suggest that the primitive conformation had been lost independently in the two groups. Such an interpretation accords better with molar morphology, which favors the phylogeny represented by node 2a (fig. 1). This common ancestor would have possessed further buccolingual compression of the molar cusps, and sharper intercuspal crests; it would also have shown the development of a small hypocone on the upper molars. It is the relationship expressed by node 2a (fig. 1) which we find to be the more plausible.

FIG. 1. Hypothesis of evolutionary relationships within Lemuroidea.

Node 3 (fig. 1) is the hardest of all to locate within the scheme because *Hapalemur* is characterized principally by its retention of features primitive for the clade (although, of course, it is highly derived relative to its common ancestor with the *Lemur- Varecia* group). A striking autapomorphy resides in the loss in most *Hapalemur* of the derived condition of the temporomandibular joint.

The common ancestor of *Lepilemur* and *Megaladapis* (node 4 in fig. 1) had lost the upper permanent incisor teeth, and possessed a highly unusual pattern of development and eruption of the premolars whereby the developmental sequence P2 → P4 → P3 yielded to a sequence of eruption of P4 → P3 → P2.

We fully realize that comparison of genera with higher taxa is an unsatisfactory process, although the reconstruction of ancestral morphotypes helps avoid the problem. However, it is possible that careful evaluation of relationships within the Adapinae may reveal that the Malagasy forms are more closely related to some adapines than to others. For instance, the loss of the anteriormost premolar in *Lepilemur*, *Megaladapis*, and *Hapalemur* may more specifically align them with *Mahgarita*, *Caenopithecus* and *Protoadapis*, as opposed to *Adapis* and its four-premolared allies. This question will be explored in a future, more detailed, study.

But despite the fact that relationships *within* this assemblage of primates have yet to be worked out, there seems to be little question about the alignment of the adapids with the *Lepilemur-Megaladapis-Hapalemur* group, to the exclusion of the other genera conventionally assigned to Lemuridae. That this relationship has not been recognized before is presumably largely due to the pervasive notion that the Malagasy lemurs constitute a single homogeneous, monophyletic grouping—an assumption which has only very recently begun to be challenged. This realignment of relationships, although apparently well-grounded, is thus somewhat radical, and carries profound im-

plications not only for the classification of the lemuriforms, but also for the times of phyletic divergence within the strepsirhines and for the history of the geographical dispersion of these primates.

While a popular view of mammalian, and in particular primate, dispersal would have waves of northern forms migrating southward (e.g., Van Couvering and Van Couvering, 1975; Walker, 1972), the implications of our suggested relationships among strepsirhines (fig. 2) instead favor the hypothesis that Africa was the source of forms which subsequently invaded Madagascar and Holarctica. The importance of Africa as a center of early primate diversification and dispersal is thrown into even more dramatic focus precisely because the well-known Holarctic Paleogene primate fauna lacks many elements (particularly indriiform ances-

tors) which we know must have been extant at that time. This is certainly more compelling than citing the absence of adapids in Africa as evidence for a southerly migration of strepsirhine ancestors; there exists at present *no* appropriate African (or Malagasy) fossil primate record.

Since Africa emerges as the only credible source of such invading forms, adapids must have been present on that continent at a time when faunal interchange was still possible with Laurasia. While such interchange prior to the closure of the Tethys seaway in the early Neogene seems to have been possible during the mid-late Eocene and mid-late Oligocene (Adrover and Hugueney, 1975; McKenzie, 1970; Van Couvering, 1972; Van Couvering and Van Couvering, 1975), the presence of adapids in the earliest Eocene of Euramerica
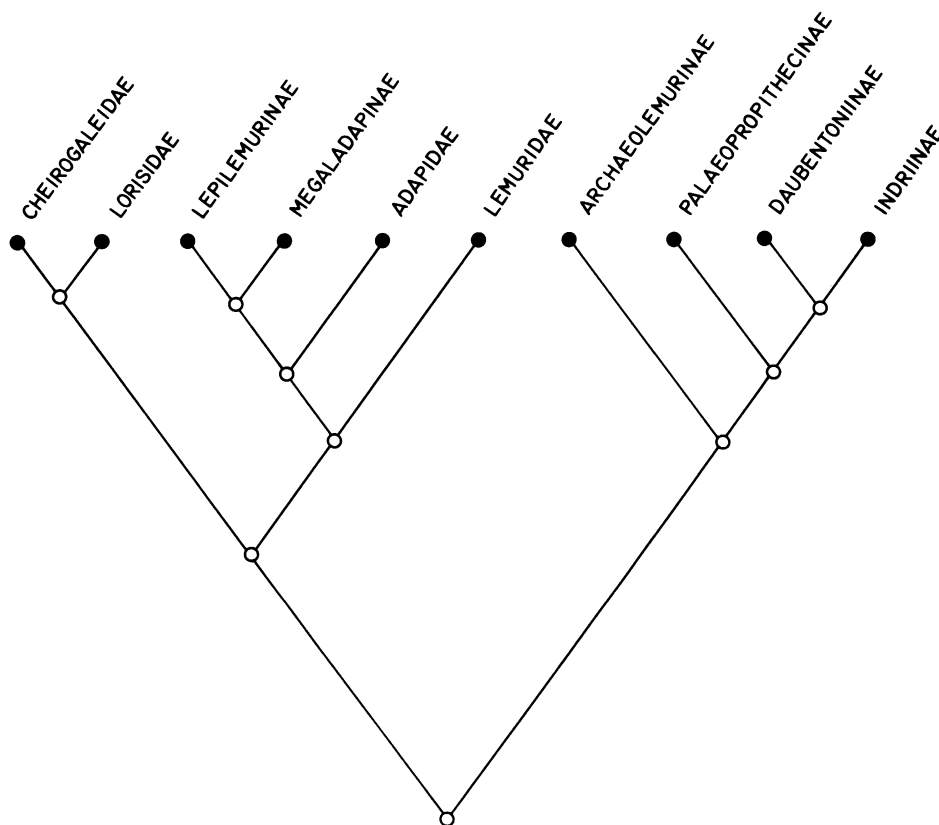

FIG. 2. Hypothesis of evolutionary relationships within Strepsirhini.

had to have resulted from a northward invasion during the latest Cretaceous-early Paleocene regression (cf. Van Couvering and Van Couvering, 1975). If our theory of relationships is correct, the split between the *Lemur-Varecia* ancestor and the ancestor represented by node 1 in figure 1 occurred before the ear- liest appearance of any adapid, which lends added weight to our suggestion (Tattersall and Schwartz, 1974) that the last common ancestor of all the lemurs was very early in date, and reinforces the hypothesis that the Malagasy pri- mate fauna is the result of multiple early invas- ions, not of *in situ* diversification.

LITERATURE CITED

Adrover, R., and M. Hugueney
   1975. Des rongeurs (Mammalia) africains dans une faune de l'Oligocène élevé de Major- que (Baléares, Espagne). Nouv. Arch. Mus. Hist. Nat. Lyon, vol. 13, pp. 11-13

Butler, P. M.
   1956. The skull of *Ictops* and the classification of the Insectivora. Proc. Zool. Soc. London, vol. 126, pp. 452-481.

Cartmill, M.
   1975. Strepsirhine basicranial structures and the affinities of the Cheirogaleidae. *In* Luck- ett, W. P., and F. S. Szalay (eds.), Phy- logeny of the primates: a multidisciplinary approach. New York, Plenum Press, pp. 313-353.

Cartmill, M., and R. F. Kay
   [In press] Craniodental morphology, tarsier affini- ties, and primate suborders. *In* Chivers, D. J. and K. A. Joysey (eds.), Recent advances in Primatology, vol. 3: Evolu- tion. London, Academic Press, pp. 205-213.

Clark, W. E. LeGros
   1962. The antecedents of Man (2nd ed.). Edin- burgh, The University Press.

Evans, G. F.
   1942. The osteology and relationships of the ele- phant shrews (Macroscelididae). Bull. Amer. Mus. Nat. Hist., vol. 80, pp. 85-125.

Gazin C. L.
   1958. A review of the middle and upper Eocene primates of North America. Smithsonian Misc. Coll., vol. 136, pp. 1-112.

Genet-Varcin, E.
   1963. Les Singes actuels et fossiles. N. Boubée et Cie, Paris.

Gingerich, P. D.
   1973. Anatomy of the temporal bone in the Oligocene anthropoid *Apidium* and the ori- gin of Anthropoidea. Folia Primatol., vol. 19, pp. 329-337.
   1975a. Dentition of *Adapis parisiensis* and the evolution of lemuriform primates. *In* Tat-

tersall, I., and R. W. Sussman (eds.), Lemur Biology. New York, Plenum Press, pp. 65-80.
   1975b. A new genus of Adapidae (Mammalia, Primates) from the late Eocene of southern France, and its significance for the origin of higher primates. Univ. Mich. Contrib. Mus. Paleon., vol. 24, pp. 163-170.

Gregory, W. K.
   1915. 1. On the relationship of the Eocene lemur *Notharctus* to the Adapidae and other pri- mates. 2. On the classification and phy- logeny of the Lemuroidea. Bull. Geol. Soc. Amer., vol. 26, pp. 419-446.
   1920. On the structure and relations of *Notharctus*, an American Eocene primate. Mem. Amer. Mus. Nat. Hist., new ser., vol. 3, pt. 2, pp. 49-243.
   1922. The origin and evolution of the human dentition. Baltimore, Williams and Wilkins.

Hennig, W.
   1966. Phylogenetic systematics. Urbana, Univer- sity of Illinois Press.

Hill, W. C. O.
   1953. Primates, comparative anatomy and taxon- omy, vol. 1: Strepsirhini. Edinburgh, The University Press.

Kollman, M.
   1925. Etudes sur les lémuriens: la fosse orbito- temporale et l'os planum. Mém. Soc. Linnéenne Normandie (Zool.), new ser., vol. 1, pp. 3-20.

Krishtalka, L.
   1976. Early Tertiary Adapisoricidae and Erinaceidae (Mammalia, Insectivora) of North America. Bull. Carnegie Mus. Nat. Hist., no. 1, pp. 1-40.

Lamberton, C.
   1938. Dentition de lait de quelques lémuriens subfossiles malgaches. Mammalia, vol. 2, pt. 2, pp. 57-80.

Martin, R. D.
   1968. Towards a new definition of Primates. Man, vol. 3, pp. 377-401.

1972. Adaptive radiation and behaviour of the Malagasy lemurs. Phil. Trans. Roy. Soc. London, vol. 264, pp. 295-352.

McDowell, S. B.
1958. The Greater Antillean insectivores. Bull. Amer. Mus. Nat. Hist., vol. 115, pp. 113-214.

McKenna, M. C.
1966. Paleontology and the origin of the Primates. Folia Primatol., vol. 4, pp. 1-25.
1975. Toward a phylogenetic classification of the Mammalia. *In* Luckett, W. P., and F. S. Szalay (eds.), Phylogeny of the Primates: a multidisciplinary approach. New York, Plenum Press, pp. 21-46.

McKenzie, D. P.
1970. Plate tectonics of the Mediterranean region. Nature, vol. 226, pp. 239-243.

McPhee, R. D. E.
1977. Ontogeny of the ectotympanic-petrosal relationship in strepsirhine primates. Folia Primat., vol. 27, pp. 245-283.

Muller, J.
1935. The orbitotemporal region of the skull of Mammalia. Arch. Néerl. Zool., no. 1, pp. 118-259.

Piveteau. J.
1957. Primates. Paléontologie humaine. Traité de Paléont., vol. 7, pp. 1-675.

Russell, D. E., P. Louis, and D. E. Savage
1967. Primates of the French early Eocene. Univ. California Publ. Geol. Sci., vol. 73, pp. 1-46.

Saban, R.
1956. Les affinitiés du genre *Tupaia* Raffles 1821, d'après les caractères morphologique de la tête osseuse. Ann. Paléont., vol. 42, pp. 169-224.
1963. Contribution a l'étude de l'os temporal des Primates. Mém. Mus. Natl. Hist. Nat. Paris, ser. A, Zool., vol. 29, pp. 1-378.

Schaeffer, B., M. Hecht, and N. Eldredge
1972. Phylogeny and paleontology. *In* Dobzhansky, T., M. Hecht and W. C. Steere (eds.), evolutionary biology, vol. 6. New York, Appleton-Century-Crofts, pp. 31-46.

Schwartz, J. H.
1974a. Dental development and eruption in the prosimians and its bearing on their evolution. Doctoral Thesis, Columbia Univ. Ann Arbor, University Microfilms, Inc.
1974b. Observations on the dentition of the Indriidae. Amer. Jour. Phys. Anthrop., vol. 41, pp. 107-114.

1975a. Development and eruption of the premolar region of prosimians and its bearing on their evolution. *In* Tattersall, I., and R. W. Sussman (eds.), Lemur Biology. New York, Plenum Press, pp. 41-63.
1975b. Re-evaluation of the morphocline of molar appearance in the primates. Folia Primatol., vol. 23, pp. 290-307.
[MS] Entotympanic contribution to the bulla of *Tarsius*.

Schwartz, J. H., I. Tattersall, and N. Eldredge
[In press] Phylogeny and classification of the primates revisited. Yrbk. Phys. Anthrop.

Simons, E. L.
1972. Primate evolution. New York, Macmillan.

Stehlin, H. G.
1912. Die Saugetiere des Schweizerischen Eocäns. Kritischer Katalog der Materialien, 7 teil, erste Hälfte *Adapis*. Abh. Schweiz. Pal. Ges., vol. 38, pp. 1165-1298.

Szalay, F. S.
1974. A review of some recent advances in paleoprimatology. Yearbook Phys. Anthrop., vol. 17, pp. 39-64.
1975. Phylogeny of primate higher taxa: the basicranial evidence. *In* Luckett, W. P., and F. S. Szalay (eds.), Phylogeny of the Primates: a multidisciplinary approach. New York, Plenum Press, pp. 91-125.

Szalay, F. S., and C. C. Katz
1973. Phylogeny of lemurs, galagos and lorises. Folia Primatol., vol. 19, pp. 88-103.

Tattersall, I.
1973a. Subfossil lemuroids and the "adaptive radiation" of the Malagasy lemurs. Trans. New York Acad. Sci., vol. 35, pp. 314-324.
1973b. Cranial anatomy of the Archaeolemurinae (Lemuroidea, Primates). Anthrop. Papers Amer. Mus. Nat. Hist., vol. 52, pt. 1, pp. 1-110.

Tattersall, I., and J. H. Schwartz
1974. Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). Anthrop. Papers Amer. Mus. Nat. Hist., vol. 52, pt. 3, pp. 141-192.

Van Couvering, J. A.
1972. Radiometric calibration of the European Neogene. *In* Bishop, W. W., and J. Miller (eds.), Calibration of hominoid evolution. Edinburgh, Scottish Academic Press, pp. 247-272.

Van Couvering, J. A., and J. A. H. Van Couvering
1975. African isolation and the Tethys seaway.

In VIth Congress Regional Committee on Mediterranean Neogene Stratigraphy, Proceedings. Bratislava, Slovak Acad. Sci., pp. 363-367.

Walker, A.

    1972. The dissemination and segregation of early primates in relation to continental configuration. *In* Bishop, W. W., and J. A. Miller (eds.), Calibration of hominoid evolution. Edinburgh, Scottish Academic Press, pp. 195-218.