CRANIODENTAL MORPHOLOGY
AND THE SYSTEMATICS
OF THE MALAGASY LEMURS
(PRIMATES, PROSIMII)

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ABSTRACT

The conventional classification of the Malagasy lemurs, which implies that these prosimians are the result of a single adaptive radiation restricted to the island, has never received adequate examination. Indeed, a comparative description of the craniodental morphology of these forms has never been undertaken. Based on such a comparison, we attempt here a cladistic analysis of lemur relationships, relying heavily on the construction of ancestral morphotypes for the various groups involved. Among the entire lemur fauna, fossil and subfossil, we recognize three infraorders: Indriiformes (including Indriinae, Palaeopropithecinae, Archaeolemurinae, and *Daubentonia*); Lemuriformes (Lemurinae, Lepilemurinae, and Megaladapinae); and Lorisiformes (Cheirogaleidae). The precise relationships of the indriiforms remain obscure, although it appears to us most likely that Lorisiformes and Lemuriformes share a common ancestry more recently than either does with Indriiformes. We conclude that the Malagasy prosimian fauna does not represent the result of a single monophyletic radiation on Madagascar; the latest common ancestor of the Malagasy prosimians probably existed in Africa during the early or middle Paleocene, i.e., subsequent to the separation of Madagascar (probably during Maestrichtian times) from the mainland. The ancestors of the various groups represented in Madagascar today arrived independently on the island, probably by rafting, at any time between the early Paleocene and the middle Eocene.

INTRODUCTION

The Malagasy lemurs, perhaps to a greater extent than any other primate group, have been the victims of what might be termed "zoogeographical typology." On the one hand, ever since its description by Linnaeus in 1758 *Lemur catta* has been regarded as not only the type but also the stereotype of the group; on the other, because of their restriction to the island of Madagascar, the lemurs have been seen as the results of a single circumscribed adaptive radiation. When a dichotomy has been drawn in the Malagasy primate fauna, it has generally been drawn either between the living and subfossil forms (despite the fact that Standing pointed out as long ago as 1908 that the extinct and extant lemurs all belong to a single contemporaneous fauna), or between *Daubentonia* and the other lemurs.

The presently accepted view of lemur systematics, unchanged in its essentials for fifty years, could only have persisted in the absence of detailed comparative studies of the Malagasy prosimian fauna as a whole. Even those recent publications (e.g. Charles-Dominique and Martin, 1970; Tattersall, 1973a, 1973b) which have hinted that the lemurs might form a less homogeneous group than currently supposed, have done little more than merely make the suggestion. In the present paper we make an attempt, albeit an extremely preliminary and tentative one, to fill this critical gap. But in virtually all areas, even within our limited scope of craniodental morphology, studies providing the depth of detail required are lacking. Our observations are made in the hope that they will stimulate students in pertinent areas of primate biology to provide the data required and to evaluate them within the context of Prosimii as a whole.

We should note here that we understand "lemurs" to be the common term denoting the Malagasy primates; i.e., we regard it as a combination taxonomic/zoogeographic, rather than as a specifically taxonomic, term. Throughout our descriptions and discussion of relationships, for reasons that will become obvious, we have avoided, where possible, referring to taxa higher than the subfamily. In following generally accepted terminology, we speak of Cheirogaleinae (*Cheirogaleus, Microcebus, Phaner*); Lemurinae (*Lemur, Varecia, Hapalemur, Lepilemur*); Indriinae (*Indri, Propithecus, Mesopropithecus, Avahi*); Archaeolemurinae (*Archaeolemur, Hadropithecus*); and Palaeopropithecinae (*Palaeopropithecus, Archaeoindris*).

METHODS

Our theory of lemur relationships (expressed in fig. 23) is based exclusively on the criterion of recency of common ancestry of the various sister-groups involved. These monophyletic groupings have been determined on the basis of mutual possession of character states which we take to be derived, as the common possession of primitive states by organisms of a given group has no relevance to relationships within that group. Among the lemurs, at once a diverse yet generally conservative array of animals, perception of primitiveness or derivedness in a given character state is not always easy, and many of our assignments must be considered provisional. We have taken as primitive those character states that are widely shared within a taxon, and, particularly, are shared with members of closely related taxa; derived states are those showing any departure from the condition inferred to be primitive for the group.

In discussing the phylogenetic relationships of the lemurs, we have leaned heavily, where possible, on the construction of hypothetical ancestral morphotypes for the various sister-groups defined in figure 23. We have done this because it appears to be the simplest way of expressing our views on the distribution of primitive and derived character states within and between such groups. Those character states used to define the ancestral morphotype of a given assemblage are those considered primitive for that assemblage. They are, however, derived with respect to the common ancestor of the next larger grouping. States considered primitive for more inclusive groupings are usually not listed where they persist in the ancestral morphotypes of subgroups of such larger assemblages.

CRANIODENTAL MORPHOLOGY OF THE LEMURS

GENERAL CRANIAL CONFORMATION

Although superficially the morphological distance between *Microcebus* and *Megaladapis* may seem enormous, the lemurs in fact present a high degree of evolutionary conservatism in their cranial morphology, a conservatism that extends, in many cases, to very fine details of cranial construction. In general, the indriines are distinguished from the lemurines by the possession of somewhat more globular braincases, more closely integrated anteriorly with the facial skeleton. However, because of the biomechanical relationship between facial and neurocranial length (Tattersall, 1973a, 1973b, In press; Roberts and Tattersall, 1974), two taxonomically distant long-faced forms may bear a greater resemblance to each other in general cranial proportions than each other in general cranial proportions than either does to a more closely related, but shorter-faced, species. Figure 1 serves to illustrate this point.

Nonetheless, a few generalizations may be made. Whereas the indriines (including *Avahi*, with its large, and probably therefore, more closely approximated orbits), *Daubentonia*, the archaeolemurines, *Archaeoindris* and even, to some extent, *Palaeopropithecus*, share a ventrally broad, high nasal region, the nasal region of the lemurines and *Megaladapis* tends to be narrower and more pinched ventrally (except in the short-faced *Hapalemur*). The indriines, archaeolemurines, palaeopropithecines, and *Daubentonia* are united in possessing considerable facial depth, largely although not entirely due to maxillary development; this contrasts with the shallower,
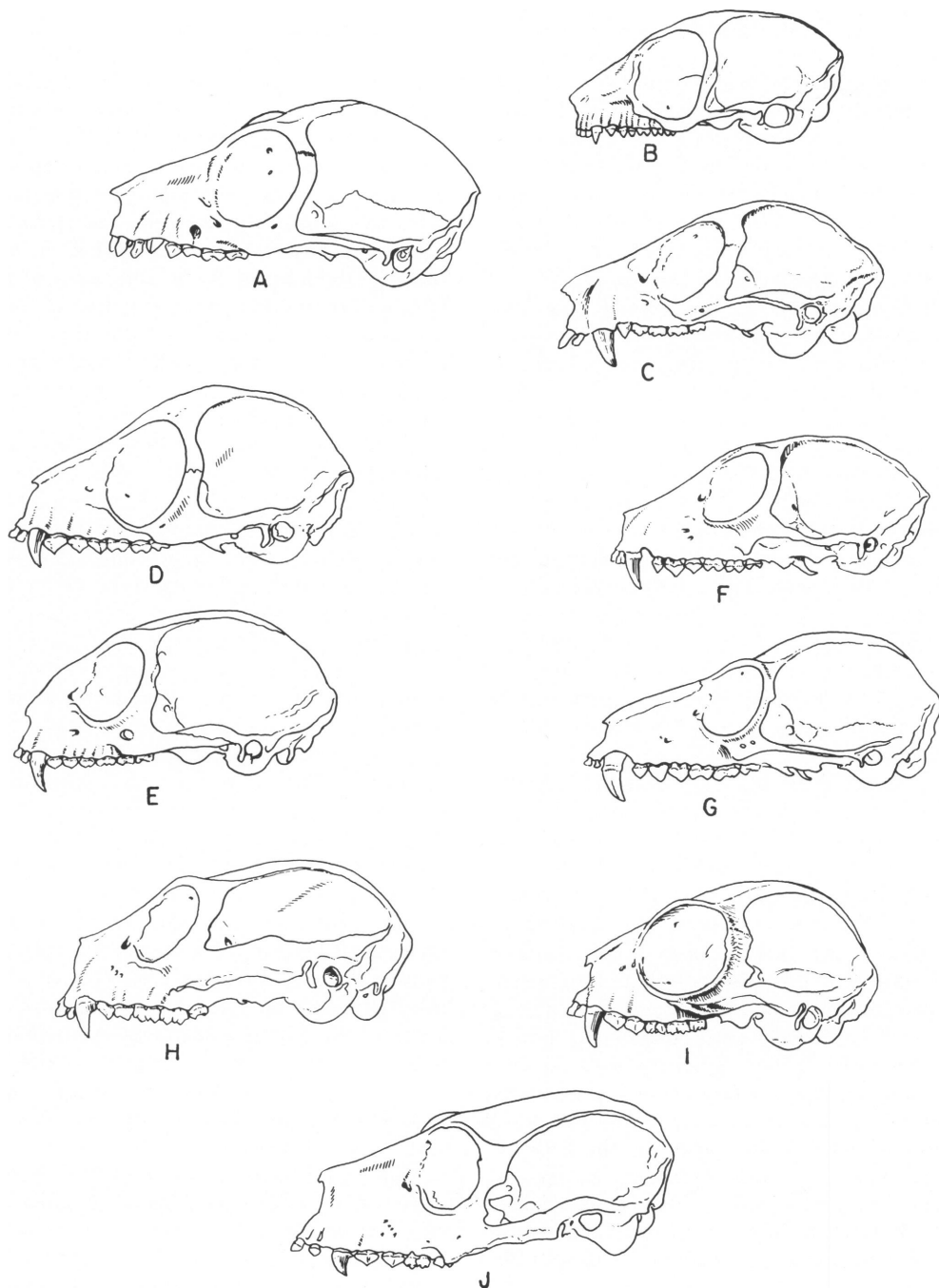
FIG. 1. Crania of the living Malagasy lemurs in lateral view. A. *Cheirogaleus major* (slightly sub-adult). B. *Microcebus murinus*. C. *Phaner furcifer*. D. *Lepilemur mustelinus*. E. *Hapalemur griseus*. F. *Lemur rubriventer*. G. *Varecia variegatus*. H. *Propithecus verreauxi*. I. *Avahi laniger*. J. *Indri indri*. Not to scale.

lower facial region of the lemurines and cheiro-galeines, and correlates with the much greater depth of the mandible. It also correlates with the more robust development of the zygomatic arch, and of other areas supporting the masticatory musculature, in the former than in the latter. The facial skeleton is tucked farther beneath the neurocranium in the indriines, archaeolemurines, *Archaeoindris* and *Daubentonia*, than it is in the lemurines, cheirogaleines, and *Megaladapis*.

Generalizations about the cranial base are limited because the proportions of this area are strongly influenced by the degree of posterior cranial expansion dictated by the length of the face, a highly variable factor in all subfamilies, and by the position and orientation of the occipital condyles and foramen magnum. It is true, however, that the indriid cranial base is relatively considerably broader than that of the lemurines and cheirogaleines; *Daubentonia* falls close to the indriids in this regard. The relative sizes of the medial and lateral pterygoid laminae vary widely among the lemurs, but this variation is discordantly distributed between the various groups. The pterygoid foramen is consistently much larger in the indriines than in the lemurines and cheirogaleines.

The palaeopropithecines, although sufficiently distinctive to have been regarded by Gregory (1915) as "gross and swinelike," are actually much closer in cranial morphology to the indriines than has been supposed. *Palaeopropithecus*, whose long, low cranial contour disguises a substantially deep face, quite closely recalls *Indri*; the most obvious differences between these two genera in cranial proportions can be traced to the relatively small size of the orbits and cranial cavity in the former. *Propithecus* differs from *Indri* almost solely in those characters of the face and neurocranium directly related to the anteroposterior abbreviation of the former. The departures of *Avahi* from the condition represented by *Propithecus* are largely associated with the substantial enlargement of its orbits and the development of considerable lateral mastoid sinuses.

Although even recent authors (e.g. Mahé, 1972) continue to discover a "monkeylike" *Gestalt* in the crania of the archaeolemurines, it is difficult to see why (Tattersall, 1973a). These animals are, in fact, despite their relatively large sizes, highly reminiscent of *Propithecus*. The cranium of *Archaeolemur majori*, in particular, remains extraordinarily *Propithecus*-like, although its dental arcade is somewhat posteriorly shifted, slightly shortening the prezygomatic face and, posteriorly, crowding the structures of the cranial base. Facial shortening, in concert with the diminution of the anterior dentition, is yet further evident in *Hadropithecus*, and the concomitant anteroposterior abbreviation of the neurocranium has yet further accentuated the tendency toward basicranial crowding, compressing the bullae anteroposteriorly.

Within Lemurinae, *Lemur* and *Varecia* differ relatively little in general cranial proportions, although the latter lacks the large frontal sinuses developed in the former. *Hapalemur* and *Lepilemur* approach each other more closely than either does *Lemur*, although some similarities between the two genera may be attributed to facial reduction. Thus, for instance, the temporal lines in these genera converge posteriorly, whereas in *Varecia* and *Lemur* they tend to be subparallel. *Hapalemur* is unique in its sister-group in possessing a long, slender, sometimes hooked paroccipital process. Many, if not most, of the distinctions separating *Megaladapis* from Lemurinae may, on the other hand, be attributed to facial lengthening in the large genus (Tattersall, 1973b). The effects of facial elongation on the construction of the postfacial cranium are nowhere more dramatically illustrated than in *Megaladapis*. The combination of a relatively tiny brain with the need to accommodate a large and horizontally accentuated posterior temporalis muscle necessitated the development of truly enormous frontal sinuses to bridge the gap between the necessary positions of the functional portion of the neurocranium and the face.

Cranial proportions, despite considerable size differences, do not vary widely within Cheirogaleinae, although the smaller forms have relatively larger orbits; in profile *Phaner* bears a remarkable similarity to the similarly sized *Lepilemur*, but possesses a somewhat narrower nasal region and braincase. The large, single posterior palatine foramen in all the cheirogaleines is

formed in a manner strongly reminiscent of that of the lorisids and divergently from the lemurines.

Alone among the lemurs, *Lepilemur* and *Daubentonia* possess interparietal bones.

LOWER JAW AND
TEMPOROMANDIBULAR JOINT

In the morphology of the mandible the accepted lemur subfamilies remain in general far more homogeneous within themselves than they do in cranial form.

The indriine lower jaw is very strongly distinguished from the lemurine by the great depth of the horizontal ramus, the rounding-out and posteroventral expansion of the angle, the long and obliquely oriented symphysis with a well-excavated genial fossa and pronounced inferior tubercle, and by various other, less obvious, characteristics. The most striking of these last is the very extensive attachment area of the anterior belly of the digastric. Although this leaves no scar in *Varecia*, *Lemur*, and *Lepilemur* and but a limited impression in *Hapalemur*, in the indriines the muscle shows a well-marked insertion, increasing in relative size through the enlarging series *Avahi→Propithecus→Indri*. In the last of these genera, indeed, a distinct lamina projects ventrally from the inferior mandibular margin; there is an homologous swelling in *Propithecus*.

These features all bind the indriine mandible closely to that of the archaeolemurines, although the mandible of the latter is more robust and possesses a shorter, fused symphysis of decreasing obliquity in the series *Archaeolemur →Hadropithecus*. The palaeopropithecine mandible is even closer to the indriine, particularly in its extreme depth relative to width and the obliquity of its long, fused symphysis.

Within Lemurinae there is somewhat more variability in mandibular conformation. The long, shallow horizontal rami of *Lemur* and *Varecia* are closely similar to each other, whereas *Hapalemur* possesses a better filled-out and more ventrally protruding mandibular angle and a narrow but posteriorly hooked coronoid. *Lepilemur* is intermediate in exhibiting a *Lemur*-like crescentic angle that protrudes ventrally like that of

Hapalemur; the body of the mandible is slightly deepened at the symphysis. All the lemurines are united in possessing rather ovoid symphyses that lack the genial pit and pronounced inferior tubercles of the indriines. The inclination of the symphysis is not dissimilar to that seen in the indriines, but its internal margin fails to reach as far posteriorly because of the limited depth of the mandibular body.

In *Megaladapis* the lower jaw is large and robust, but the corpus is not notably wide relative to its depth. The large angle is not hooked as in the lemurines, but neither is it posteroventrally protruded as in the indriines. The fused symphysis has a long, sloping planum alveolare, with twin genial pits at its posteroventral extremity; it does not, however, possess an inferior transverse torus such as is found in the indriines and their allies. The attachment of the anterior belly of the digastric is very strongly marked, although, relative to size, it is somewhat less highly developed than in the archaeolemurines. The posterior belly of the muscle attached to an elongated, gutter-like, paroccipital process.

The mandible of *Daubentonia* is, of course, very highly modified, but does resemble that of the indriines in possessing a deep, narrow corpus and a swelling of its ventral margin in the area of digastric insertion.

In general, the mandibles of the cheirogaleines are reminiscent of that of *Lemur*; the angle and the coronoid are both somewhat crescentic. The coronoids of *Phaner* and *Cheirogaleus* are broader anteroposteriorly than that of *Microcebus*; that of *Cheirogaleus* is higher than that of *Phaner*, in which the angle is better filled out. The symphysis is ovoid in all three.

Within Indriinae there is a tendency toward increasing subcircularity of the mandibular condyle with size. Thus in *Avahi* the condyle remains relatively broad transversely but is strongly curved in the coronal plane. The curvature remains in *Propithecus*, but the width is relatively decreased. In *Indri* the condyle is virtually globular. The articular surface of the condyle appears to be carried onto the posterior aspect of the condylar neck (fig. 2) in all indriines; at the very least, this region conforms extremely closely to the shape and curvature of the anterior face of
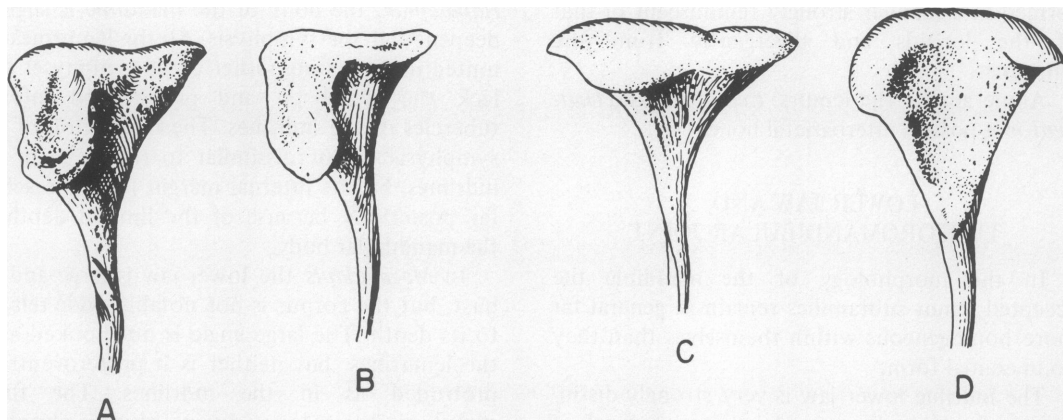
FIG. 2. Posterior view of the mandibular condyle. A. *Megaladapis edwardsi* (AMNH 100643). B. *Lepilemur mustelinus* (AMNH 100643). C. *Lemur fulvus* (AMNH 100528). D. *Propithecus verreauxi* (AMNH 170473). Right side; not to scale.

the postglenoid process. In the lemurines, on the other hand, the condyle is broad transversely (fig. 2), and, although the axis of the articular surface points more posteriorly than in the indriines, the condyle is generally better differentiated from its neck. In *Lepilemur*, however, a definite articular surface descends posteriorly, not along the line of the neck but distinctly medial to it (fig. 2). This surface is matched on the anterior face of the postglenoid process and is found elsewhere among the lemurs only in *Megaladapis*.

The rather broad condyles of the archaeolemurines show some degree of coronal curvature, but are generally more reminiscent of those of *Lemur* than of those of *Propithecus* or *Avahi*. The structure of the postglenoid process, at least in *Archaeolemur*, is also more *Lemur*-like, in that there is generally better differentiation from the bulla than is found among the indriines. In both *Palaeopropithecus* and *Archaeoindris* the structure of the components of the temporomandibular joint is strongly reminiscent of the condition seen in *Propithecus*, although precise anatomical relationships in the glenoid area are, of course, affected in the large genera by the modification of the ear region.

The extensive modification of the temporomandibular joint in *Daubentonia* vitiates the usefulness of detailed comparison of this region with the other lemurs. It is striking, however, that the anteroposteriorly elongated condyle of this an-

imal is not altogether unreminiscent of that of *Indri*.

EXTERNAL MORPHOLOGY OF THE BRAIN

It is clear from the studies of Smith (1903, 1908) and Radinsky (1968, 1970) that the external morphology of the brain is of limited utility in elucidating prosimian relationships above (and sometimes even below) the subfamily level. Given the wide variation in size between members of the various lemur subfamilies, there is fairly close similarity in sulcal pattern and proportion within Cheirogaleinae, Lemurinae, and Indriinae. The indriines are distinguished from the lemurines by the possession of such features as broader frontal lobes (probably in correlation with greater orbital frontation) and stronger development of the lunate and central sulci; the cheirogaleines, predictably, show less sulcal detail with decreasing size, but even the largest, *Phaner*, lacks the postcruciate sulcus and possesses only a short postsylvian sulcus (Radinsky, 1968, In press).

Daubentonia, in correlation with the extensive structural modification of its cranium, possesses an atypically shaped brain; uniquely among living prosimians its frontal lobes lack orbital impressions, but this is also true of the extinct *Palaeopropithecus* and *Megaladapis*, and is due in each case to extrinsic factors of cranial geometry (Radinsky, 1968; Tattersall, 1972, 1973b).

The endocast morphology of the extinct Mal-

agasy lemurs serves to place them firmly within the range of modern prosimians. Despite the observations of Clark (1945) and Piveteau (1950, 1956), the studies of Smith (1908) and Radinsky (1970) emphasize the affinities of the archaeolemurines with the indriines. The endocasts of *Palaeopropithecus* and *Megaladapis* tie these forms less closely to Indriinae and Lemurinae, respectively, but many differences may plausibly be associated with their much greater size and (primarily size-associated) cranial specializations.

Lorisids are clearly distinguished from any Malagasy form by greater cerebral overlap of the cerebellum; according to Radinsky (1968, In press) the olfactory bulbs and frontal lobes protrude farther forward between the orbits in galagines than in lorisines, whereas lorisines possess more highly convoluted brains.

Stephan and Andy (1969) have investigated the relative proportions of the various divisions of the primate brain. In general, the indriines (particularly *Indri*) show the greatest reduction of the olfactory bulbs, although *Hapalemur* falls within the indriine range. *Lepilemur* falls intermediate between the indriines and *Lemur* in this characteristic, whereas the lorisids show an enormous spread, *Loris* possessing olfactory bulbs slightly smaller than those of *Lemur*, but *Galago demidovii* exceeding even *Daubentonia*, the Malagasy form with the largest bulbs. The cheirogaleines fall about midway within the lorisid range. In terms of the index expressing the expansion of the neocortex, on the other hand, *Daubentonia* shows the highest degree of neocorticalization seen in any prosimian; *Hapalemur* and *Lepilemur* show the lowest. *Lemur*, however, follows *Daubentonia* closely, whereas the indriines occupy the middle ground, although the cheirogaleines separate *Indri* and *Propithecus* from the somewhat less neocorticalized *Avahi*.

STRUCTURE OF THE NASAL CAVITY

Although internal nasal structure remains fairly uniform throughout the Malagasy primates, some interesting variations may be noted despite our lack of comprehensive knowledge of the comparative anatomy of this region in prosimians. In contrast to that of the lorisids, the maxilloturbinal of *Lemur* is doubly rolled; in *Lepilemur* this element consists of but a single scroll. *Indri* and *Avahi* resemble each other in

possessing only an inferior maxilloturbinal scroll, whereas in *Propithecus* a superior scroll is additionally present. The basal lamina of the maxilloturbinal is reduced in the indriines and *Lepilemur*; it is more extensive in *Lemur* (Kollman and Papin, 1925). The maxilloturbinal of *Daubentonia*, morphologically divergent from that of the other lemurs, possesses a single (inferior) scroll.

The rolled portion of the nasoturbinal is well developed in *Lemur*, with extensions penetrating both frontal and maxillary sinuses. The scroll within the latter usually fuses with its wall, but, although this element is present in *Lepilemur*, such fusion does not occur (Kollman and Papin, 1925). Penetration of the sinuses fails to take place in *Daubentonia*. The (presumed) homologue of the human uncinate process is well developed, although it is rolled only posteriorly in the lorisids and *Lepilemur*. An anterior extension is present in all forms except *Lemur*. In *Indri* the upper part of the maxillary sinus is not closed off by fusion of the anterior border of the anterior lamina of the nasoturbinal with the lateral nasal wall; such fusion does occur in *Propithecus* and *Avahi*. The nasoturbinal of the lorisids, reduced anteriorly but enlarged over the remaining area, varies little within this group.

Most of the lemurs are sharply distinguished from the lorisids by the possession of a first endoturbinal, which, although well developed, fails to overlap the maxilloturbinal. Endoturbinal I of *Lepilemur*, however, resembles that of the lorisids in descending to cover the maxilloturbinal, as does that of *Microcebus*, and, probably, of the other cheirogaleines. Lemurines, cheirogaleines, and lorisids alike exhibit four endoturbinals, but there is variation within Indriinae, *Propithecus* and *Avahi* resembling the lemurines in this character, but *Indri* possessing a fifth. Like endoturbinal IV in the other indriines, endoturbinal V in *Indri* blocks the orifice of the sphenoid sinus. Besides *Indri*, only *Daubentonia* among the lemurs possesses a fifth endoturbinal; this animal is, further, unique in exhibiting an additional (third) ectoturbinal.

STRUCTURE OF THE ORBITAL FOSSA

The characteristic of this region traditionally of the greatest interest to primate taxonomists has been the presence or absence of an ethmoid

contribution ("os planum") to the medial orbital wall. But only in *Microcebus* and *Cheirogaleus*, among all the lemurs, does the ethmoid find expression in the orbit. In this these two genera resemble the lorisids, *Tarsius*, and the higher primates. As Simons and Russell (1960) and, more recently, Cartmill (1971) have pointed out, however, this character is not necessarily of direct phylogenetic significance; for developmental reasons, the os planum appears in the orbit in forms possessing large and/or closely approximated orbits.

There are, however, certain features of the arrangement of the bones in the medial orbital wall that do consistently distinguish the various lemur subfamilies (fig. 3). In the indriines, for example, where the prenasopalatine portion of the palatine bone is much reduced, the frontal descends anteriorly to contact the maxilla. This condition is also characteristic of *Daubentonia*, whereas in the lemurines the prenasopalatine intrudes anteriorly between the frontal and maxilla to contact the lacrimal. A similar prenasopalatine-lacrimal contact is made beneath the ethmoid in *Microcebus* and *Cheirogaleus*; this contrasts distinctly with the condition seen in

the lorisids. *Palaeopropithecus* shows the indriine condition, as, almost certainly do both the archaeolemurines. *Adapis* shows no frontomaxillary contact within the orbit, the prenasopalatine possessing the same topographic relationships as in the lemurines.

In most lemurs the lacrimal foramen is distinctly external to the orbit. In the archaeolemurines, however, the anterior and posterior lacrimal crests define the orbital margin (Tattersall, 1973a), a condition most closely approached among the living forms by *Avahi*. In *Megaladapis* the foramen lies anterior to the orbit, but the margin of the latter is interrupted by a strong channel running posteriorly from the foramen.

The suggestion originally made by Lamberton in 1937 (although as early as 1896 Major had expressed a belief that fragmentary fossils of *Archaeolemur* available to him had originally possessed orbital closure) that the archaeolemurines possess incipient orbital closure, still lingers in the recent literature (e.g. Mahé, 1972). In fact, this is emphatically not the case. The archaeolemurine postorbital bar is highly robust, but this element is a good deal more shelflike in forms such as *Varecia* and *Indri*. Beyond this
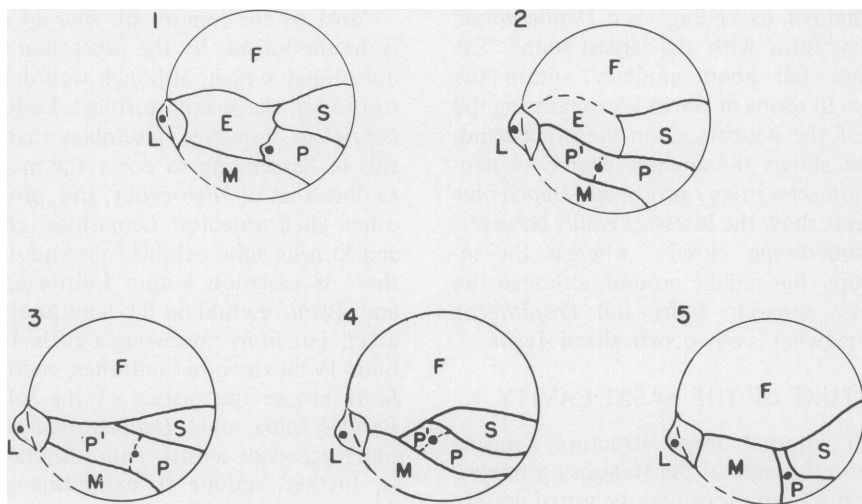

FIG. 3. Schema of the arrangement of the bones in the medial orbital wall of various prosimians. 1. Lorisids. 2. *Microcebus* and *Cheirogaleus*. 3. Lemuridae. 4. Indriidae. 5. *Daubentonia*. 1-4. Modified from Kollman (1925).

Abbreviations: E, ethmoid; F, frontal; L, lacrimal; M, maxilla; P, palatine; P', prenasopalatine portion of palatine.

the maxillary inflation, which in all other lemurs (except *Daubentonia*, which nonetheless possesses considerable maxillary sinuses) provides a more or less substantial bony floor to the orbit, is absent in the archaeolemurines. Strong bony development of the archaeolemurine maxilla, together with its marked backward extension, nonetheless compensates to a considerable extent for (and to the same extent is probably a cause of) the nondevelopment of maxillary sinuses.

Other features of the orbit, such as the arrangement of the foramina at the apex of the orbital cone and the architecture of the region of the nasopalatine foramen, are highly variable in a pattern not conforming to the distribution of the foregoing characters.

BASICRANIAL STRUCTURE

The anatomical details of the basicranium have long provided a wealth of information for taxonomists. This region in the lemurs has been magnificently and exhaustively described by Saban (1956, 1963), and more recently certain aspects have been reviewed, in the living forms, by Szalay and Katz (1973). Both inter- and intra-taxon variations are legion within Prosimii; many of these are quite discordantly distributed among the genera of the various subfamilies. We restrict our discussion here to a few major features.

Bony Ear

In virtually all living Malagasy primates, in contrast to the lorisids, the tympanic ring, attached above to the horizontal portion of the temporal squama, lies free within a prominent petrosal bulla. In *Microcebus* alone, and then far from invariably, does the ring make contact with the lateral wall of the bulla. Among the subfossil forms, the "normal" condition is shared by all genera assigned to extant subfamilies, and by Archaeolemurinae. But in Palaeopropithecinae and *Megaladapis* the tympanic ring connects to the exterior via a long ossified tube. Saban (1956, 1963) identified this conduit as a lateral extension of the ectotympanic, but Szalay (1972) regarded it as an outgrowth of the petrosal. We incline to agree with Szalay, at least in the case of *Megaladapis*. In the three large extinct forms, moreover, the prominent bulla disappears

(although a slight bulge remains in *Megaladapis*); this is a true regression, not to be compared with the condition seen in lorisids, where extensive pneumatization behind the bulla masks its salience posteriorly. Pneumatization of the temporal is rarely more than weakly developed among the lemurs (apart from the development of large lateral paratympanic sinuses in *Avahi*), although in general the indriines exhibit more extensive cellular development than do the lemurines or cheirogaleines.

It has been suggested (Tattersall, 1973b) that bullar regression (and presumably associated specializations) in *Megaladapis* and Palaeopropithecinae are related to the coincidence in these forms of large size and relatively small brains; the tympanic cavity and hypotympanic sinus necessarily remain capacious to minimize the damping effect on the tympanic membrane of the air in the cavity. In those forms where the bulla is present, its size relative to the cranial base naturally has profound effects on the appearance of this region; among the lemurs this relationship follows the observation among mammals in general that the relative size of the bulla is in inverse proportion to the size of the animal.

Since throughout Primates the auditory ossicles are generally homogeneous, it is not surprising to find relatively little variation in these elements among the Malagasy prosimians. Ardouin (1935) has attached considerable significance to the relationship of the long process of the incus to the axis connecting the end of the manubrium of the malleus to the tip of the anterior process of the incus. Indriinae and Lemurinae consistently differ in this characteristic, the long process protruding away from the axis in the former, while its tip just meets it in the latter. *Daubentonia* and *Palaeopropithecus* share the indriine condition; *Archaeolemur*, on the other hand, together with *Megaladapis*, more closely resembles the lemurines (Saban, In press). The lemurine stapes is consistently shorter and broader than its homologue in Indriinae.

Carotid Circulation

It has long been realized that a dichotomy exists between Cheirogaleinae and the other lemurs in the design of the carotid arterial system. In all lemurs a carotid foramen is situated in the

posterior wall of the bulla. In Lemurinae, Indriinae, Archaeolemurinae, and *Daubentonia* ("lemurine type"), this foramen is situated laterally, except in the smallest genera, *Lepilemur* and *Avahi*, where it is more medially positioned, possibly in correlation with the relatively larger size of the bullae. The cheirogaleine carotid foramen lies posteromedially, within the depression housing the posterior lacerate foramen; this arrangement is reminiscent of that found in lorisids.

More telling than this topographic similarity between the cheirogaleines and lorisids, however, is the organization of the carotid arterial circulation. In the lemurine type the common carotid artery sends the internal carotid, via the carotid sinus, into the bulla by way of the carotid foramen. Once on the promontory this artery divides into stapedial and promontory (entocarotid) branches (fig. 4). The larger stapedial artery (tiny in *Lepilemur*) courses laterally to cross the stapes, while the promontory artery continues
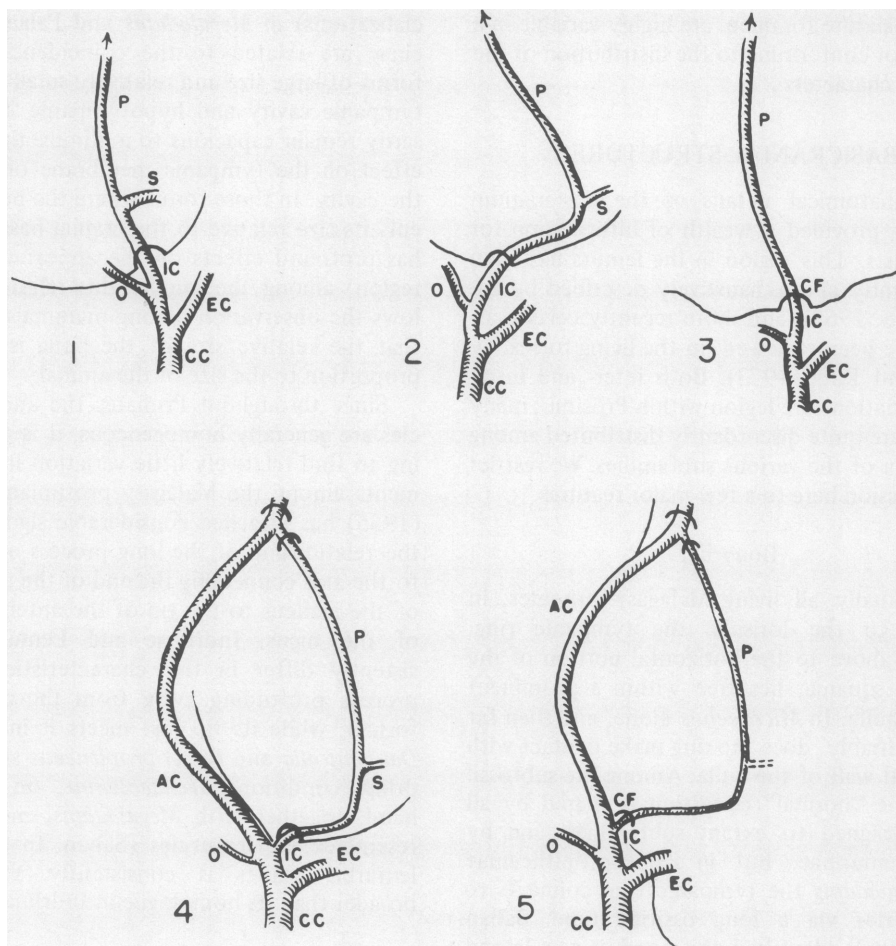

FIG. 4. Highly simplified schema of temporal carotid circulation in the lemurs and lorises. 1. *Lemur, Varecia, Hapalemur*, indriines, archaeolemurines, palaeopropithecines (essentially). 2. *Lepilemur*. 3. *Megaladapis*. 4. Cheirogaleines (*Phaner* lacks the stapedial branch). 5. Lorisids.
Abbreviations: AC, anterior carotid; CC, common carotid; CF, carotid foramen; EC, external carotid; IC, internal carotid; O, occipital artery; P, promontory artery (entocarotid); S, stapedial artery. Data from Saban (1956, 1963) and Szalay and Katz (1973).

forward to penetrate the endocranium. The cheirogaleine common carotid, on the other hand, gives off, before reaching the bulla, both internal and anterior carotid branches. The internal carotid enters the bulla through the carotid foramen, and, on the promontory, emits a tiny stapedial branch in *Cheirogaleus* and *Microcebus* (Saban, 1963). The stapedial artery is entirely lacking in *Phaner*. The more substantial promontory portion continues anteriorly to regain the exterior before joining the anterior carotid via the orifice of the auditory tube (fig. 4). The anterior carotid, equaling the internal carotid in size, follows the contour of the bulla anteriorly along the line of the petrobasisphenoid suture and, having anastomosed with the promontory artery, enters the endocranium via the anterior carotid foramen (the homology of which with the middle lacerate foramen is doubtful), an orifice absent elsewhere among the Malagasy prosimians.

In the lorisids, as in the cheirogaleines, the common carotid gives rise outside the bulla to both internal and anterior carotid branches. The feeble internal carotid enters the bulla through the carotid foramen, then, emerging from the carotid canal, skirts the round fenestra (instead of mounting the cochlea) and briefly becomes interiorized before anastomosing with the anterior carotid at the anterior carotid foramen (Saban, 1963). The latter artery, a major trunk, follows the internal contour of the bulla along its junction with the basioccipital and basisphenoid to the anterior carotid foramen; this vessel is considered by Adams (1957) and Bugge (1972) to be homologous with the ascending pharyngeal artery of human anatomy. What is clear, however, is that the principle of parsimony points to the common inheritance of the anterior carotid by the lorisids and cheirogaleines.

Among none of the three large subfossil genera, each of which lacks a salient bulla, does the general plan of temporal arterial circulation depart markedly from the lemurine type. The internal carotid in the palaeopropithecines entered the tympanic cavity through a posterolateral carotid foramen and branched into stapedial and promontory portions after emerging, on the cochlea, from the carotid canal; the promontory portions then ramified, the main branch emitting

two small rami to the endocranium via the orifice of the auditory tube, then anastomosing with the minor branches to continue toward the orbit. Saban (1956) interpreted the presence of a distinct foramen spinosum in *Palaeopropithecus* as indicating a significantly developed middle meningeal artery. In *Megaladapis* a carotid foramen on the posterolateral border of the slight bullar swelling admitted the internal carotid to the carotid canal. Without emitting a stapedial branch, the artery entered the endocranium near the longitudinal septum, and re-emerged on the alisphenoid (fig. 4).

Temporal arterial circulation in the adapids, and the arrangement of the associated foramina and canals, is very close to that of the lemurines (Stehlin, 1912; Gregory, 1920); and although, of course, there is no necessary connection between morphological primitiveness and stratigraphic ancientness, it appears overwhelmingly probable that this represents the primitive condition for Prosimii (although not necessarily for Primates). Various authorities, for instance Clark (1934) and Szalay (1972), have expressed a contrary opinion, but both these authors subsequently amended their views (Clark, 1971; Szalay and Katz, 1973). Indeed, it appears that the sequence "lemurine type"→"cheirogaleine type"→"lorisid type" presents a primitive-derived morphocline, as Szalay and Katz (1973) have also pointed out. This observation accords well with ontogeny in terms of the relationship of the tympanic ring to the bulla. Major (1899) has recorded that the lemurine type annulus, already completely ossified in the foetus, lies at this stage almost horizontally beneath the temporal squama. During ontogeny the ring rotates downward, until in the adult its medial inclination is no more than slight. The space between the free edge of the ring and the external auditory meatus is occupied by the annular cartilage and membrane, and Van Valen (1965) has suggested that calcification of this cartilage may have provided the initial step toward the exteriorization of the ectotympanic. But although this may conceivably, as Gregory (1920) proposed, be the mechanism leading to the development of an ossified tube in *Palaeopropithecus*, direct contact of the ectotympanic with the bulla, through continued rotation of the ring, appears to be a more likely percursor stage

to simple annular fusion, as seen in the lorisids. Indeed, this stage may well be approximated by the contact of the ring with the bullar wall frequently encountered in *Microcebus*. Beyond this, Jones (1929) has reported the occasional presence of an enclosed, ringlike ectotympanic in Galaginae.

The shift away from the primitive condition in temporal arterial circulation lies in the progressive de-emphasis of the stapedial artery (and, to a lesser extent, of internal carotid circulation in general), together with the increasing predominance of the anterior carotid. The reduction of the stapedial artery in *Lepilemur*, and its disappearance in *Megaladapis*, are events independent of this sequence and, as discussed later, probably of considerable phylogenetic significance in themselves.

MORPHOLOGY OF THE PERMANENT DENTITION

Throughout this discussion cusp nomenclature is purely topographic, without implications as to homology.

In lemurines the upper incisors are greatly reduced in size. In *Lepilemur,* indeed, as in *Megaladapis,* I^{2-3} are missing. In the indriines, on the other hand, these teeth are relatively large, showing a strong lateral flare except in *Avahi*, where they are small and peglike, especially in the case of I^2. In the lemurines I^2 is slightly larger than I^3, whereas this proportion is variable in the indriines. The cheirogaleines conform most closely to the indriine condition, with the exception of *Phaner*, where I^2 is relatively large, although not showing marked lateral flare. *Palaeopropithecus* falls close to the indriine condition in incisor morphology, but the lateral upper incisor is very distinctly reduced compared to the central. Known material of *Archaeoindris* lacks upper incisor teeth, but the evidence of the alveolae indicates that the same proportions obtained as in *Palaeopropithecus*. *Archaeolemur* exhibits a very strong development of the central upper incisors, which are closely approximated; I^3 is strong, but much smaller than I^2, against which it lies. *Hadropithecus*, by comparison, exhibits marked reduction of the upper incisors; I^2 remains, however, larger than I^3. Among the lorisids the upper

incisors, although high-crowned, are uniformly less flared, i.e., more cylindrical, than those of any lemur; where there is a size difference between I^2 and I^3, it is the latter which is reduced.

The anterior teeth in *Daubentonia*, apparently by analogy with rodents, have been regarded as incisors; however, we prefer to homologize them with the canine. Our reasons for so doing are as follows: in all prosimians, the developing permanent incisors lie well up in the premaxilla and erupt in line with the long axis of their precursors. Since the root of the enlarged anterior tooth of *Daubentonia* extends back to above the position of M^3, if this tooth is in fact an incisor the point of root growth would have to penetrate the premaxillary-maxillary junction during development, a linear direction of growth would have to become arcuate, and crown morphology would require drastic alteration. The situation is much simplified, however, if this tooth is in fact a canine. In prosimians the permanent canine begins to develop above and posterior to its deciduous predecessor. With growth this tooth arcs over the root of d$\underline{c}$, and follows a course along the maxillopremaxillary suture, eventually erupting anterior to the deciduous canine. Hyperdevelopment, such as is seen in the anterior teeth of *Daubentonia*, of the canine would continue this natural arc of development, but the increased size of the tooth would cause its tip to pass through the maxillopremaxillary suture; at the same time, the posteriorly moving point of root growth, already in the maxilla, would not have to penetrate the junction of two growth fields. The premaxilla, now containing the large canine crown and part of its root, would have to enlarge, as in *Daubentonia*, to accommodate this tooth. It should be noted here that the largely horizontal disposition of the canine root precludes the function, otherwise universal among extant primates, of transmitting forces through the facial skeleton to the anterior part of the neurocranium; this is presumably the reason for the considerable vertical enlargement, as a buttress, of the premaxilla of *Daubentonia*.

But beyond these morphogenetic reasons for regarding the anterior teeth of *Daubentonia* as canines, there remains the question of morphology. *Daubentonia* possesses anterior teeth that are large and compressed laterally, characteristics

of prosimian canines rather than incisors; less morphological alteration would thus be required of canines than of incisors to produce the condition typical of the anterior teeth of *Daubentonia*.

The upper canine is generally less pronounced and shows more mesiodistal elongation in the indriines than in the lemurines. The cheirogaleines and *Megaladapis* conform closely to the lemurine pattern, whereas *Palaeopropithecus* shares the indriine condition. The broad-based upper canine of *Archaeolemur* is low-crowned, whereas that of *Hadropithecus* is greatly reduced.

In Lemurinae there is some variation in the relative proportions of teeth within the upper premolar row. In *Lemur* and *Varecia* P^3 is the most salient tooth, and P^4 is not molariform, despite the development lingually of a protocone; in *Hapalemur* and *Lepilemur*, on the other hand, P^2 is the most high-crowned of the premolars, whereas in *Hapalemur* P^4 is distinctly molariform. Within Cheirogaleinae P^2 and P^3 are subequal in height in *Microcebus*, whereas in *Cheirogaleus* the former is somewhat higher than the latter.[1] *Phaner* is distinguished by its large "caniniform" P^2. In none of the cheirogaleines is P^4 molariform. P^2 of *Megaladapis* is higher than P^3; in upper premolar morphology *Megaladapis* most closely approximates *Lepilemur*.

The indriines, of course, are sharply distinguished by the possession of only two upper premolars, in which they resemble Palaeopropithecinae (but not Archaeolemurinae). *Indri* is distinguished from both *Propithecus* and *Avahi* by the possession of premolars of subequal length; in the latter P^3 is somewhat longer than P^4. P^3 of *Indri* lacks the greater height which distinguishes this tooth from P^4 in *Propithecus* and *Avahi*. In all indriines the premolars show less development lingually than do those of the lemurines; there is no hint, for example, of the protocone that characterizes P^4 in all lemurines.

In Palaeopropithecinae the wrinkled upper premolars show greater lingual development than

do their homologues in the indriines, although it is to the latter among all the lemurs that they show their greatest resemblance; lingual expansion is concentrated distally, as in the indriines, and no protocone is formed. P^3 is more salient than P^4, as in *Avahi* and *Propithecus*, and distinct discontinuous buccal cingula are developed on P^4 as in these two genera (but not in *Indri*).

The upper premolar series of *Archaeolemur* retains three teeth, and is highly modified into a continuous shearing blade. This blade is clearly derived from a premolar series of indriine type (but possessing, of course, P^2). The posterior moiety of P^4 is molarized, with a distinct paracone, but does not at all resemble the lemurine condition. The upper premolar series of *Hadropithecus*, derived yet further than in *Archaeolemur*, is modified still more: these teeth increase in size and complexity posteriorly, and all show, to a greater or lesser extent, the development of a protocone; P^4 is broader than M^1 and is completely molariform.

Daubentonia retains but a single, small, peg-like upper premolar.

M^1 and M^2 of the cheirogaleines resemble those of the lorisids (in particular the galagines) in possessing a notched posterior margin resulting from the posterior displacement of the hypocone; this relatively small cusp is rather shelflike and is confluent with a lingual cingulum in *Cheirogaleus* and *Microcebus*, whereas it is better differentiated in *Phaner* and the galagines. In the cheirogaleines and galagines the three cusps of the trigon are subequal in size and relatively evenly spaced, whereas in the lemurines the protocone dominates the trigon. M^3 in the cheirogaleines and galagines is subtriangular; in most lemurines it is rhomboidal, reflecting a more pronounced anteroposterior development of the protocone. *Varecia*, however, shows less development of the protocone in M^3.

M^1 and M^2 of *Lemur* are characterized by a prominent, continuous lingual cingulum from which a relatively large protostyle (except in M^1 of *L. catta*) and a relatively small hypocone are differentiated. In *Varecia* the hypocone is essentially lacking, and the protostyle is not greatly distinct, at least on M^2. The structures of the lingual molar moieties in *Lemur* and *Varecia* are shifted somewhat forward, the reverse of the

[1] As far as we can discover, *"Microcebus" coquereli* has been regarded as congeneric with *M. murinus* solely because, in contrast with species of *Cheirogaleus*, its P^2 is not noticeably higher than P^3. In virtually all other characters, however, *"M." coquereli* accords far better with *Cheirogaleus,* to which genus we prefer to allocate it.

condition seen in the cheirogaleines and galagines. In M^1 the metacone and paracone are subequal in size; in M^2 the former is slightly less salient, whereas in M^3 the metacone is greatly diminished.

The upper molar dentitions of *Hapalemur* and *Lepilemur* show less lingual development than do those of *Varecia* and *Lemur*. In *Hapalemur* the lingual cingulum diminishes from M^1 posteriorly; in *Lepilemur* there is only a trace of the cingulum in the position of the hypocone in M^1 and M^2, whereas even this has disappeared in M^3. In both genera the protocone, although the largest cusp, does not dominate the trigon as in *Lemur* and *Varecia*, and in neither is there any trace of a protostyle. In M^1 and M^2 of *Hapalemur*, however, there is an anterior displacement of the protocone, whereas in *Lepilemur* the greater development of the cingulum in the area of the hypocone shifts the emphasis of the lingual moiety of the tooth slightly distally. *Hapalemur* and *Lepilemur* possess molar paracones and metacones that are buccolingually compressed (although supported lingually by small buttresses), and are more distinctly connected to each other than in *Lemur* and *Varecia*, where these cusps are more conical. This produces a more bladelike appearance of the buccal molar margins in the former genera. *Hapalemur* and *Lepilemur* are yet further distinguished by the possession of a buccal molar cingulum with (in *Hapalemur*) a mesostyle on M^1, and (in *Lepilemur*) protostyles on all molars.

The upper molars of *Megaladapis* are most similar to those of *Lepilemur*, despite differences in the relative sizes of the teeth. In both genera the configuration of the lingual cingulum in the area of the hypocone is similar, whereas buccal cingula and parastyles are also shared. *Hapalemur* possesses the buccal cingulum, but lacks parastyles. In both *Megaladapis* and *Lepilemur* the paracone and metacone are lingually buttressed, and the lingual moieties of the upper molars are displaced distally. *Megaladapis* is distinguished from *Lepilemur*, however, by the presence of mesostyles on all molars.

The upper molar dentition of the indriids is totally distinct from that of the lemurines and cheirogaleines. Four main cusps are well developed. In M^1 the paracone is the dominant cusp,

displacing the mesiobuccal border of the tooth anteriorly; this effect is emphasized by the lesser development of the protocone. In *Indri* the metacone and hypocone are in transverse alignment and, as in the anterior cusp pair, the buccal cusp predominates; in *Propithecus* and *Avahi* the trigon is better defined, and the hypocone is displaced posteriorly. Although lacking a buccal cingulum, *Indri* possesses a distinct parastyle and mesostyle on M^1, as do *Propithecus* and *Avahi*, in which a buccal cingulum is present; the latter genera also exhibit metastyles. All three show metaconules and paraconules. The paracone of M^2 lies anteriorly, as in M^1, in both *Propithecus* and *Avahi*; in *Indri* the tooth is squarish, the buccal cusps lying almost opposite the lingual ones. Again, the trigon is better defined in *Propithecus* and *Avahi*, although the hypocone is less posteriorly displaced. Tiny metaconules and paraconules may be present on M^2 of all three genera, as may also be a small transverse crease representing the anterior fovea. Well-defined mesostyles are present in *Avahi* and *Propithecus,* and a trace of this structure may be seen in *Indri*. The parastyle is better developed in M^2 of *Propithecus* and and *Avahi* than in that of *Indri*; in M^3 of each genus the paracone and protocone are prominent and subequal in size. The posterior margin of the tooth is marked by a rim whose composition of a distobuccal metacone and a lingual hypocone is far more clearly evident in *Indri* than in *Propithecus* or *Avahi*. The talon basin is relatively much larger in *Indri* than in the other indriines. The general proportions of M^1 amd M^2 in *Mesopropithecus* are reminiscent of the condition displayed by *Indri*; however, in stylar development they are closer to *Propithecus*. M^3 is clearly most similar to that of *Propithecus,* as are the premolars.

The upper molar teeth of *Daubentonia* are greatly reduced in size and almost devoid of cuspal detail; in their generally squarish outline, however, they approach the indriine rather than the lemurine condition. They decrease in size posteriorly.

M^1 and M^2 of the palaeopropithecines are distinguished from those of the indriines primarily in that the area of the hypocone is not developed as a distinct cusp, but rather as a broad shelf. They most closely resemble those of *Propithecus*, especially in the buccal complication, including

stylar development, which they exhibit. The conules of *Propithecus* are, however, replaced by crests, and the protocone is rather more salient in the palaeopropithecines. M^3 is, in both its relative size and morphology, very similar to that of *Propithecus*. The enamel of all molars is fairly heavily wrinkled.

Although clearly derived from upper molars of indriine type, those of *Archaeolemur* are considerably modified. M^1 and M^2 are squarish, each corner bearing a well-defined cusp. These teeth are classically bilophodont, the paracone/protocone and metacone/hypocone pairs each being connected by a strong transverse crest. Distinct anterior, central, and posterior foveae are present, but there is no complication of the crown by conular or stylar development. M^3 may be round or triangular in outline, but is always reduced; most closely reminiscent of that of *Propithecus*, it bears a transverse crest linking the paracone and protocone, but lacks a posterior fovea.

Hadropithecus, too, possesses subsquare upper molars; M^1 is slightly larger than M^2, whereas M^3 is very strongly reduced. Although these teeth are totally uncharacteristic of the lemurs, they are in fact easily derivable from the *Archaeolemur* condition. The lingual portion of the upper molars, raised in *Archaeolemur* relative to the indriines, is yet further emphasized in *Hadropithecus*. The protocone and hypocone are continuous with a high, rounded crest bordering the mesial, lingual, and distal margins of M^1 and M^2; they are connected transversely with the paracone and metacone, respectively, by broad, inflated crests that are homologous with the lophs in *Archaeolemur*, but do not form sharp shearing crests as in the latter. Deep anterior, central, and posterior foveae are present, each open buccally. The small M^3, as in *Archaeolemur* and the indriines, is greatly reduced in its posterior moiety and lacks the posterior fovea.

All extant Malagasy lemurs, except, of course, *Daubentonia*, possess anterior dental combs, in which the outer teeth possess a lateral flare, whereas the internal teeth are narrow and virtually parallel-edged. A longitudinal ridge runs along the center of the ventral surface of each procumbent tooth in all prosimians possessing toothcombs and is bounded on each side by a shallow groove. In the outer tooth it is the lateral

groove that becomes most highly pronounced in producing the lateral flare to which we have referred.

In lemurines, cheirogaleines, and lorisids the dental comb consists of six teeth, i.e., two incisors and one canine on each side. In the indriines, however, only four teeth are present. Conventionally, these have all been identified as incisors, but developmental as well as morphological considerations suggest that the lateral tooth should, in fact be regarded as a canine (Schwartz, 1947a). It should be noted that all extant lemurs (except *Daubentonia*) and the galagines possess tooth combs composed of relatively more slender, more procumbent teeth than those of the lorisines.

Alone among the extant lemurs, *Daubentonia* lacks a dental comb. Its single large anterior tooth is best interpreted as a modified canine; bearing enamel only on its anterior surface, it grows continuously.

Of the subfossil lemurs, only *Mesopropithecus* and *Varecia insignis* possess toothcombs of totally conventional type. The former corresponds closely in this characteristic to the living indriines, and the latter to its extant congener. *Megaladapis*, however, displays a rather similar condition to the lemurines. Contrary to Lamberton (1938), we interpret the procumbent anterior dentition as consisting of a lateral canine, and two incisors; these teeth are relatively rather shorter and less slender than in the living lemurs, but they are of similar construction especially in that lateral tooth flares somewhat.

The palaeopropithecines possess, predictably enough, an anterior dental formula identical to that of the indriines. The incisor and canine are, however, somewhat short and stubby, and are obliquely implanted; but the lateral tooth flares distinctly, and both the incisor and canine show the longitudinal ridging characteristic of the procumbent teeth of the living lemurs and lorisids.

The lower canine and single lower incisor of *Archaeolemur* are longer and slenderer than those of *Palaeopropithecus*, but, likewise, are implanted obliquely. The relative proportions of these teeth remain as in the indriine dental comb, from which condition they are evidently derived. The lower canine and incisor of *Hadropithecus* are yet more orthally implanted, but are stub-

bier; the canine is somewhat larger than the incisor but shows little lateral flare.

In all living lemurs, except for *Daubentonia* in which lower premolars are lacking, and in the lorisids, the anterior lower premolar is caniniform. In the indriines this tooth tends to be less salient, but more mesiodistally elongated, than in the lemurines or cheirogaleines; this is especially true of *Avahi*, and, to a lesser extent, of *Indri*. The cheirogaleines and galagines are typified by particularly pronounced caniniform teeth. It should be noted that, despite the fact that the indriines possess but two lower premolars, we would identify the caniniform as P_2, as it is in the other lemurs and in the lorisids.

P_3 and P_4 in *Lemur* and *Varecia* are of increasing complexity posteriorly, although built on the same single-cusped pattern; in *Lemur*, however, an incipient metaconid is found internally on P_4. *Lemur* is further distinguished from *Varecia* in that P_4 is more salient than P_3; the reverse applies in the latter. In *Lepilemur* P_3 is slightly higher than P_4, whereas the latter possesses a less distinct, more laterally-compressed posterior fovea than is seen in the preceding genera. In *Hapalemur* P_3 is higher than P_4, which is heavily molarized, bearing five distinct cusps and deep anterior and posterior foveae. Both *Hapalemur* and *Lepilemur* lack the diastema between P_2 and P_3 found in *Lemur* and *Varecia*.

The cheirogaleine P_3 and P_4 resemble those of galagines; P_3 is subcaniniform, whereas P_4 shows some talonid development, except in *Phaner*.

In *Megaladapis* P_2 is very markedly caniniform, as in Lemurinae, and especially in *Lepilemur*. As in *Lemur* and *Varecia*, P_2 is separated from P_3 by a diastema; P_3 is similar to that of *Hapalemur* and *Lepilemur* in being more salient than P_4. The posterior premolars are relatively small, uncomplicated teeth; those of *M. grandidieri* bear a fairly close resemblance to those of *Lepilemur*.

The posterior premolar in the indriines is interpreted here as P_3, although it has conventionally been regarded as P_4. It consists of a single central cusp with crests descending mesially and distally. In *Avahi* this tooth is enormously elongated anteroposteriorly, whereas in this genus and in *Propithecus* the posterior moiety is deeply excavated.

The palaeopropithecines are identical with the indriines in premolar formula. Both lower premolars are elongate mesiodistally; the caniniform is low-crowned, whereas P_3 closely resembles that of *Propithecus*. In both palaeopropithecines a distinct diastema exists between P_2 and P_3; this is never found among the indriines.

In *Archaeolemur* the lower premolars, like those of the upper jaw, are highly modified but retain the primitive number. The caniniform is robust but not very high-crowned; the single cusp is situated anteriorly, while the posterior moiety forms the anterior portion of the continuous mesiodistally oriented shearing blade in which P_3 and P_4 participate. A lingually directed crest on the posterior portion of P_4 delimits the anterior edge of a small posterior fovea confluent with the anterior fovea of M_1. The caniniform of *Hadropithecus*, however, is greatly reduced, although continuous with the anteroposterior blade of P_3; P_4 is molariform (although nonetheless continuing the premolar blade), with crests radiating mesially, distally, buccally, and lingually from a centrally positioned protoconid. Foveae are formed between each pair of crests.

M_1 and M_2 in *Lemur* and *Varecia* are subequal in size, although the large talonid basin and anterior fovea are more open in the posterior tooth. The protoconid is the largest, most anterior cusp, and also the most distinctly formed, whereas the metaconid and hypoconid are barely raised from the encircling rim of the talonid. The area of the hypoconid projects laterally, contributing to the lateral waisting (more pronounced in *Lemur* than in *Varecia*) of the tooth. In *Lemur* no clear entoconid is discernible, and the talonid is somewhat open lingually; in *Varecia*, however, a small entoconid is present, and the talonid basin, relatively much larger than in *Lemur*, thus opens more posteriorly.

M_3 in both *Lemur* and *Varecia*, although relatively smaller than the anterior molars, nonetheless possesses four distinct cusps. In *Lemur* the metaconid remains the largest cusp, but the talonid basin is closed. M_3 of *Varecia*, however, shows buccal displacement of the entoconid, to the extent that this cusp is almost confluent with the hypoconid; the talonid basin is hence open lingually.

The anterior lower molar teeth of *Hapalemur*

and *Lepilemur* are mutually reminiscent, although they are more elongate in the latter. In both genera these teeth are readily distinguished from those of *Varecia* and *Lemur* by the presence of four distinct cusps; the entoconid in these forms is well developed, although more so in *Hapalemur*. In the former, however, the metaconid and entoconid are connected by a sharp crest, whereas the entoconid and hypoconid are not; thus this internal opening is posteriorly directed. In *Hapalemur*, on the other hand, it is the entoconid and hypoconid that are joined, with the result that the basin opens between the metaconid and entoconid, i.e., directly lingually, although in M_1 this opening is constricted anteriorly by the presence of a metastylid.

M_3 of *Lepilemur* is, uniquely among the lemurines, characterized by the presence of an elongated talonid heel, due largely to the presence of a very large, posteriorly displaced hypoconulid. This cusp is not linked to the small entoconid; the talonid basin thus opens posterointernally, as in the anterior molars. The anterior fovea of all the molars is not closed in *Lepilemur*, as it is in *Hapalemur* and the other lemurines. M_3 in *Hapalemur*, although smaller than the other molars, is morphologically reminiscent of them.

M_1 and M_2 in the cheirogaleines each possess four distinct cusps; only in *Phaner* is there no hypoconulid on M_3. M_1 and M_2 are less elongated than in all lemurines except *Lepilemur*; they resemble the lorisids in this as well as in possessing four cusps. The buccal cusps are more anteriorly displaced relative to the lingual ones, and are more salient, than in the lemurines; this, again, is a lorisid resemblance. Unlike the lemurines, the cheirogaleines lack a distinct anterior fovea, but a slight "paraconid" shelf may be present, as among the lorisids.

As in the case of the upper molars, the lower cheek teeth of the indriids are strongly distinct from those of the lemurines or cheirogaleines. Four distinct cusps are present on all lower molars (plus a paraconid on M_1), while a small hypoconulid is present on M_3. In *Avahi* and *Propithecus* the buccal cusps lie slightly anterior to the lingual ones; in *Indri* they are in transverse alignment. The lingual cusps of the lower molars of *Indri* are subequal in size, and are more rounded in outline, whereas in the other two genera the

hypoconid predominates and, with the protoconid, is more angular. The lower molars of all indriines are, however, more angular in outline than are those of all other living lemurs, with the single exception of *Lepilemur*. In striking contrast to the lower molars of the cheirogaleines and the lemurines, in which the reverse applies, the lingual cusps of the indriines are higher than the buccal ones.

M_3 in indriines is subequal in size with, or is larger than, the anterior molars, whereas in lemurines (except *Lepilemur*) it is smaller. The anterior, center, and posterior foveae (*Avahi* lacks the last of these on all teeth, as do the lemurines) are almost confluent in M_2 and M_3; the posterior fovea is reduced or absent on M_1.

The simple, reduced lower molars of *Daubentonia* resemble those of the indriines in being raised lingually.

M_1 and M_2 in the palaeopropithecines are similarly higher lingually than buccally, although to a lesser extent than in the indriines. These teeth bear, in other features, too, a strong resemblance to those of Indriinae, particularly *Propithecus*, but are relatively narrow, and possess distinct paraconids, as does M_3. M_3 in both genera is considerably reduced; its hypoconulid is weak or wanting.

The lower molar teeth of *Archaeolemur* are extraordinarily similar to the upper molars, except in being higher lingually than buccally, in which they agree with their homologues in Indriinae, Palaeopropithecinae, and *Daubentonia*. A similar observation applies to the lower molars of *Hadropithecus*, although the upper molars in this genus are more compressed mesiodistally.

The lower molars of *Megaladapis* display an extraordinary combination of features otherwise unique among the lemurids to *Hapalemur* and *Lepilemur*, although M_1 is distinctly smaller than M_2, a conformation not found in these two living forms. In M_1 and M_2 the metaconid bears a closely approximated metastylid and is not connected by a ridge to the entoconid; thus, as in *Hapalemur*, the talonid basin opens directly lingually. But on all lower molars and anteriorly directed crest arises from the protoconid, as in *Lepilemur* (although it should be noted that this crest increases in size—as do the teeth themselves—from front to back, whereas in *Lepilemur*

the reverse occurs). M_3 of *Megaladapis* shares with *Lepilemur* a well-developed hypoconulid and talonid heel. The talonid basin proper opens between the metaconid and the low entoconid, however, as does that of *Hapalemur*; a crest running to the entoconid from the postcristid, however, demarcates the heel from the basin, which opens separately in a manner analogous to that of the trigonid in *Lepilemur*.

MORPHOLOGY OF THE DECIDUOUS DENTITION

In all extant prosimians, except for *Tarsius*, *Daubentonia*, and *Lepilemur*, the deciduous upper incisors are small, but morphologically similar to their permanent successors. As a rule, *Tarsius* does not develop any deciduous upper incisors and, although *Daubentonia* and *Lepilemur* do develop such teeth, an adult pair never appear. Similarly, the deciduous upper canine is small but morphologically reminiscent of its permanent successor in all but *Daubentonia*; the latter possesses an unreplaced pair of continally growing canines.

The deciduous premolars of the cheirogalines and galagines are similar. In both groups dp^2 is caniniform, but less so than in the lorisines. dp^3 is primarily a single-cusped tooth that is triangular in outline at the base; in the lorisines this tooth is completely surrounded by cingulum, whereas in the cheirogaleines and galagines there frequently appears a small parastyle (not in *Cheirogaleus*), and the lingual moiety appears more prominent because the cingulum is discontinuous posteriorly. dp^4 is smaller than, but similar morphologically to, M^1; thus in *Microcebus* it is distinctly four-cusped and in *Phaner* and *Cheirogaleus* it is three-cusped.

In *Lemur*, *Hapalemur*, and *Lepilemur*, dp^2 is a small, simple, single-cusped tooth; it is the smallest of the deciduous premolars. In *Lemur*, dp^3 is similar to dp^2 in being small, single-cusped, and compressed laterally. In *Lepilemur* and *Hapalemur*, however, dp^3 has a distinct lingual moiety which is accentuated by slight waisting anteriorly and posteriorly. dp^4 is smaller but morphologically similar to M^1 and thus in *Lemur* possesses three distinct cusps, of which the protocone is the largest, and is adorned with a lingual cingulum (*L. catta*), or a small hypocone and

protostyle (other *Lemur*). In *Lepilemur* and *Hapalemur*, on the other hand, the metacone is the largest of the three cusps, extending posteriorly and, in *Hapalemur*, standing anterior to a large posterior basin.

In the indriines the anterior deciduous premolar is a simple, single-cusped tooth, compressed laterally, whereas the posterior is triangular in basal outline, possessing a distinct lingual bulge that is banded by cingulum and accentuated by waisting centrally; lingual styles are common on dp^4, the parastyle always being present.

Daubentonia possesses three deciduous premolars of which only the most posterior is replaced. The first is a small, peglike tooth well behind the premaxillary suture; this tooth might be considered the deciduous canine except that in all prosimians the deciduous canine is immediately posterior to, not separated from, the premaxillary suture. A large diastema isolates this anterior deciduous premolar from two that are deep in the maxilla; the anterior of these is small and peglike, whereas the posterior, although undifferentiated in crown morphology, is reminiscent of that of the indriines in being somewhat triangular, with the lingual moiety offset by slight waisting centrally.

Of the subfossil indriids, the deciduous premolars are known only in Archaeolemurinae. dp^2 and dp^3 of *Archaeolemur* are morphologically similar to their permanent successors and clearly form a bladelike unit; dp^4, on the other hand, is not like its permanent replacement but is morphologically similar to M^1 and thus is not fully incorporated into the premolar shearing blade. The deciduous upper premolars of *Hadropithecus* are, however, totally similar to the permanent ones although, not unexpectedly, they are slightly smaller.

The deciduous upper premolars of *Megaladapis* are recognizably similar to those of *Lepilemur* and *Hapalemur*: dp^2 is small and single-cusped; dp^3 is not compressed laterally, as it is in *Lemur*, but displays a distinct lingual moiety which, unlike *Lepilemur* and *Hapalemur*, is opposed by two buccal cusps; dp^4 has three distinct cusps of which the metacone is the largest, is extended posteriorly, and (intermediate between *Hapalemur* and *Lepilemur*) borders a small posterior basin.

In most prosimians the deciduous lower an-

terior teeth, whether procumbent or more vertically implanted, are morphologically the same as their permanent successors, but are smaller. *Daubentonia* and *Tarsius* are exceptions in that, in the former, the lower canines are persistent throughout life and, in the latter, the lower pair of incisors do not have deciduous predecessors.

The lower deciduous premolars of the cheirogaleines and galagines are virtually the same: dp_2 is caniniform with a small posterior heel; dp_3 is long and low, banded by a lingual cingulum that gives rise to small anterior and posterior stylids (which may be diminished in *Cheirogaleus*), and the large primary cusp may be closely associated with a smaller secondary cusp; dp_4 is extremely molariform, possessing four distinct cusps.

Although dp_2 is caniniform in *Lemur*, *Lepilemur*, and *Hapalemur*, in *Lemur* it is the least salient deciduous premolar, whereas in the last two it rises noticeably above the others. In all three taxa, dp^3 is a long, low, laterally compressed, primarily single-cusped tooth (in *Lemur*, except *L. catta*, a small secondary cusp may be closely applied to the primary), with a posterior basin. In *Lepilemur* and *Hapalemur*, however, dp_3 possesses a well-formed anterior stylid. In *Lemur* and *Hapalemur*, dp_4 is distinctly molariform; in addition to the four primary cusps, dp_4 possesses a paraconid. dp^4 in *Lepilemur* is not molariform but the disposition of the anterior moiety is the same as it is in M_1; the posterior portion is a large, excavated basin reminiscent of the molars in that it opens distally and internally.

The indriines, uniquely among prosimians, possess four lower deciduous premolars (Schwartz, 1974a). It was previously assumed that the first deciduous premolar is an unreplaced deciduous canine, but analysis of the wear facets indicates that this tooth occludes behind the upper deciduous canine and forms a functional unit with dp_2. dp_1 is a small, peglike tooth which, in an extremely young indriine, is situated close to the larger, caniniform, dp_2. Similar in shape to dp_1 is dp_3, which forms a functional unit with the molariform dp_4; not rectangular, dp_4 is constricted anteriorly.

Daubentonia possesses two deciduous lower premolars which are unreplaced. These teeth are situated well back in the mandible and, although with less differentiated cusp morphology, are similar in their basic shape to dp_3 and dp_4 of the

indriines and form a single functional unit.

The anterior lower deciduous premolar of *Archaeolemur*, although smaller, is morphologically similar to P_2. dp_3 is compressed laterally but lacks the lingual extension seen in its permanent successor, and forms a blade unit with dp_2. As with the upper posterior deciduous premolar, the lower is not fully part of the premolar shearing blade; although the cusps are more globular, the morphology and outline of this tooth is strikingly similar to the indriine dp_4. The lower deciduous premolars of *Hadropithecus* are smaller than, but morphologically similar to, the permanent ones. The lower deciduous dentition of Palaeopropithecinae is not known.

The lower deciduous premolars of *Megaladapis* are remarkably similar to those of *Hapalemur* although the anterior two are separated by a diastema.

DENTAL DEVELOPMENT AND ERUPTION

A generally neglected source of taxonomic information lies in the sequences of development and eruption of the permanent dentition. We make the distinction here between development and eruption because the time at which, relative to the other teeth, a given tooth begins to develop bears no necessary relationship to its place in the sequence of eruption. In addition, the relative timing of the initial eruption of a tooth may not coincide with its place in the sequence of completed eruption (Schwartz, 1974b, In press). The data on which the following discussion is based are presented in tables 1-3.

Although dental eruption and development sequences show some variation even at the species level, in most cases the accepted lemur subfamilies show a degree of homogeneity, their members sharing certain "hallmark" characteristics. Lemurinae, however, do not conform to this observation. In the first place, a distinct dichotomy exists within this group in the order of appearance of the premolars (table 1). In all lemurines with the exception of *L. catta* and *Hapalemur* the premolars develop in the order $P^2_2 \rightarrow P^4_4 \rightarrow P^3_3$; in these two exceptions the order of $P^4_4 \rightarrow P^3_3 \rightarrow P^2_2$ obtains. In both initial and completed premolar eruption *L. catta* and *Hapalemur* are joined by *Lepilemur* in showing the sequence

TABLE 1
SEQUENCES OF DENTAL DEVELOPMENT AND ERUPTION IN LEMURIDAE

	Development	Initial Eruption	Completed Eruption
Lemur mongoz	M1 C P2 I2 I3 M2 P4 M3 P3 M1 I2I3C P2 M2 P4 M3 P3	M1 I2I3 C M2 P2 M3P4 P3 M1 I2I3C M2 P2 M3 P4 P3	M1 I2I3 M2 M3 P2 C P4 P3 M1 I2I3C M2 M3 P2 P4 P3
Lemur fulvus	M1 C M2 I2I3 P2 P4 M3 P3 M1 I2I3C M2 P2 P4 M3 P3	M1 I2I3 M2 C P2 P4 M3 P3 M1 I2I3C M2 P2 P4 M3 P3	M1 I2I3 M2 P2 C M3 P4 P3 M1 I2I3C M2 P2 M3 P4 P3
Lemur macaco	M1 I2 C M2 I2I3 P2 P4 M3 P3 M1 I2 C M2 I2I3 P2 P4 M3 P3	M1 I2I3 M2 C P2 ?M3 P4 P3 M1 I2I3C M2 P2 ?P2 ?M3 P4 P3	M1 I2 I3 M2 ?C P2 ? M1 I2I3C M2 ?P2 ? ?
Lemur rubriventer	M1 C ? M1 I2I3C P2 ?		
Lemur catta	M1 I2I3 C M2 P4 M3 P3 P2 M1 I2I3C M2 P4 M3 P3 P2	M1 I2I3 M2 C M3 P4 P3 P2 M1 I2I3C M2 M3 P4 P3 P2	M1 I2I3 M2 M3 P4 ?P3 P2 C M1 I2I3C M2 M3 P4 ?P3 P2
Varecia variegatus	M1 I3I2 C P2 M2 P4 M3 P3 I2I3C M1 P2 M2 P4 M3 P3	M1 I3I2 M2 ?C P2 P4 M3 P3 M1 I2I3C M2 ?P2 P4 M3 P3	M1 I2I3 ? M1 I2I3C ?
Hapalemur griseus	M1 M2 I2I3 C P4 P3 M3 P2 M1 I2I3C M2 P4 P3 M3 P2	M1 I2I3 M2 P4 M3 P3 C P2 M1 I2I3C M2 P4 M3 P3 P2	(same as initial)
Lepilemur mustelinus	M1 M2 M3 C P2 P4 P3 M1 M2 I2I3C M3 P2 P4 P3	M1 M2 M3 P4 C P3 P2 M1 M2 I2I3C M3 P4 P3 P2	M1 M2 M3 P4 P3 P2 C M1 M2 I2I3C M3 P4 P3 P2
Ancestral Morphotype	(M1 I2I3) C P2 M2 P4 M3 P2 (M1 I2I3C) P2 M2 P4 M3 P2	(M1 I2I3) M2 P2 M3 P4 C P3 (M1 I2I3C) M2 P2 M3 P4 P3	(same as initial)
Megaladapis edwardsi and M. grandidieri	M1 M2 C M3 P2 P4 P3 ?		M1 M2 C M3 P4 P3 P2 ?

$P_4^4 \rightarrow P_3^3 \rightarrow P_2^2$; the others erupt their premolars in the order of development. In the lemurines (except *Varecia*), most cheirogaleines, and the galagines, the upper and lower M_1 are the first permanent teeth both to develop and to erupt. In *Varecia*, however, although the first molars are the earliest permanent teeth to erupt, they begin development after that of the dental comb has commenced. Whereas in most lemurines M_2^2 develop and erupt at some time after the toothcomb, in *Lepilemur* they do so immediately after M_1^1, i.e., prior to the toothcomb.

All lemurines display a relatively early development of $\underline{C}$ (but after the teeth of the dental comb have begun to develop), coupled with a very late eruption; this is the last, or almost the last, tooth in the sequence to appear fully in place. M_3^3 show an opposite trend, i.e., all those specimens providing pertinent data show a late development and a relatively earlier eruption. Thus in *Lemur mongoz*, *L. fulvus*, and, to a lesser extent, in *Hapalemur*, M_3^3 are almost the last teeth to develop, but complete eruption somewhere in the center of the sequence. In *Lemur mongoz*, *Varecia*, and *Lepilemur* the development and eruption of the upper canine are co-ordinated with those of P_2^2. As this is seen also in the cheirogaleines (except *Microcebus*), lorisines (except *Loris*), and all galagines, it is presumably best interpreted as a primitive retention. In *Hapalemur* and other species of *Lemur*, however, such co-ordination is not encountered.

The cheirogaleines are considerably less varied in characteristics of dental development and eruption than are the lemurines. In all genera the premolars develop and erupt in the order $P_2^2 \rightarrow P_4^4 \rightarrow P_3^3$. P_3^3 are the last teeth of all in both development and eruption; M_1^1 are the first. In all cheirogaleines, with the exception of *Microcebus murinus*, M_1^1 are followed by the teeth of the dental comb, and then by M_2^2, in development and eruption; in the lower jaw of the latter both M_1 and M_2 precede the dental comb. As indicated earlier, both development and eruption of $\underline{C}$ and P_2^2 are synchronous.

In *Cheirogaleus* (including "*Microcebus*" *coquereli*), $M_3^3 \rightarrow P_4^4 \rightarrow P_3^3$, in this order of both development and eruption, are the last teeth to appear. In *Phaner*, too, these teeth are the last to appear, but in the order $P_4^4 \rightarrow M_3^3 \rightarrow P_3^3$. In *Microce-*

bus only P_4^4 and P_3^3 consistently develop and erupt last; M_3^3 develop much earlier in the sequence, thus (at this stage) isolating P_2 from the $\underline{C}$-P_2^2 developmental unit. In eruption, however, M_3^3 regain their position in the $M_3^3 \rightarrow P_4^4 \rightarrow P_3^3$ sequence; P_2 is thus reassociated with P^2-$\underline{C}$. Further, both *M. murinus*, the smallest cheirogaleine, and *Galago demidovii*, the smallest galagine, are each unique to their subfamilies in developing and erupting M_2 prior to the toothcomb.

The indriines are united in developing the posterior premolar in each jaw prior to the anterior. In *Avahi* and *Propithecus* these teeth erupt in the same sequence; we lack data for premolar eruption in *Indri*, but suspect that the same pattern applies. In *Propithecus* and *Indri* $\underline{C}$ is not the last tooth to develop, but in the former is the last tooth to erupt; in *P. verreauxi* and in *Indri* $\underline{C}$ develops earlier in the sequence than in *P. diadema*. In *Avahi*, on the other hand, $\underline{C}$ is not the last tooth to develop, but is the last tooth to erupt. Despite considerable variation in the timing of dental development and eruption in Indriinae, these animals are, as a group, set distinctly apart from the other lemurs in these characteristics.

As in *Propithecus*, $\underline{C}$ of *Palaeopropithecus* is the last tooth to erupt. *Archaeolemur* and *Hadropithecus* are identical in dental development, and in eruption at the beginning of the sequence. *Hadropithecus* appears to differ from *Archaeolemur*, however, in erupting M_3 just before $\underline{C}$, the last tooth to erupt; in the latter $\underline{C}$ is also the last tooth to erupt, but immediately follows P_2^2.

The sequence of eruption is known only for the upper jaw in *Magaladapis edwardsi* and *M. grandidieri*. This sequence is virtually identical with that of *Lepilemur*; the only difference is that in *Lepilemur* $\underline{C}$ is the last tooth to erupt and in *M. edwardsi* and *M. grandidieri* it comes in closer to the middle of the sequence. Thus *Lepilemur* and *Megaladapis edwardsi* and *M. grandidieri* are alone among the lemurs (no information is available for the other species of *Megaladapis*) in possessing premolars that develop in the sequence $P_2^2 \rightarrow P_4^4 \rightarrow P_3^3$, but which erupt in the order $P_4^4 \rightarrow P_3^3 \rightarrow P_2^2$.

In the deciduous dentition, *Hapalemur* and *Lemur* (except some *L. rubriventer*) erupt the premolars in the order $dp_2^2 \rightarrow dp_3^3 \rightarrow dp_4^4$. In *Lepile-*

TABLE 2
SEQUENCES OF DENTAL DEVELOPMENT AND ERUPTION IN CHEIROGALEINAE

Development	Initial Eruption	Completed Eruption
Cheirogaleus major, C. minor and *C. trichotis*		
(M1 I2I3 M2)P2 C M3 P4 P3	(M1 I2I3 M2) P2 C M3 P4 P3	(M1 I2I3 M2) P2 C M3 P4 P3
(M1 I2I3C M2) P2 M3 P4 P3	(M1 I2I3C M2) P2 M3 P4 P3	(M1 I2I3C M2) P2 M3 P4 P3
"Microcebus" coquereli		
M1 I2 M2 I3 C P2 M3 P4 P3	(same as development)	(same as development)
M1 I2I3C M2 P2 M3 P4 P3		
Microcebus murinus		
(M1 I2I3) M2 M3 C P2 P4 P3	(M1 I2 I3) M2 C P2 M3 P4 P3	(M1 I2I3) M2 C P2 M3 P4 P3
(M1 M2 I2I3C) P2 M3 P4 P3	M1 M2 I2I3C P2 M3 P4 P3	M1 M2 I2I3C P2 M3 P4 P3
Phaner furcifer		
M1 I2 M2 I3 C P2 P4 M3 P3	M1 I2 M2 ?I3 C P2 P4 M3 P3	M1 I2 M2 ?
M1 I2I3C M2 P2 P4 M3 P3	M1 I2I3C M2 P2 P4 M3 P3	M1 I2I3C M2 ?
Ancestral Morphotype (development and eruption)		
	M1 I2I3 M2 C⃗ P2 M3 P4 P3	
	M1 I2I3C M2 P2 M3 P4 P3	

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TABLE 3
SEQUENCES OF DENTAL DEVELOPMENT AND ERUPTION IN INDRIIDAE

Development	Initial Eruption	Completed Eruption
Avahi laniger		
I2 M1 I3 P4 M2 M3 P3 C M1 I3C P3 M2 M3 P2	I2 M1 I3 P4 M2 P3 C M3 M1 I3C P3 M2 P2 M3	I2I3 M1 P4 P3 M2 C M3 M1 I3C P3 P2 M2 M3
Propithecus verreauxi		
M1 I2 M2 I3 C P4 M3 P3 M1 I3C M2 P3 M3 P2	M1 I2 M2 I3 P4 P3 M3 C M1 I3C M2 P3 P2 M3	M1 I2 M2 I3 P4 M3 P3 C M1 I3C M2 P3 M3 P2
Propithecus diadema		
M1 I2 M2 M3 I3 P4 C P3 M1 I3C M2 M3 P3 P2	M1 I2 I3 M2 P4 P3 M3 C M1 I3C M2 P3 P2 M3	M1 I2I3 M2 P4 P3 M3 C M1 I3C M2 P3 P2 M3
Indri indri		
I2I3 M1 M2 C P4 M3 P3 I3C M1 M2 P3 M3 P2	I2I3 M1 ? I3C M1 ?	(see text)
Archaeolemur majori and *Hadropithecus stenognathus*		M1 M2 I3I2 M3 P4 P3 P2 C M1 M2 I3C M3 P4 P3 P2
Ancestral Morphotype (development and eruption)	(M1 I2I3) M2 C P4 M3 P3 P2 (M1 I3C) M2 P4 M3 P3 P2	
Daubentonia madagascariensis (development and eruption)	M1 M2 P4 M3 M1 M2 M3	

mur, *Microcebus* (the only cheirogaleines examined), lorises, and galagines, the order is $dp_2^2 \rightarrow dp_4^4 \rightarrow dp_3^3$. In some *L. rubriventer* this is the sequence displayed in the lower jaw, whereas the upper shows the general *Lemur* condition. In the upper jaw of *Propithecus* and *Indri* the posterior deciduous premolar erupts before the anterior one.

PHYLOGENETIC RELATIONSHIPS

Recent surveys of prosimian relationships, none of which has treated the question in much detail, have generally focused on temporal arterial circulation as a decisive factor in deciphering the phylogeny of the lower primates. It is generally agreed that "lemurine type" circulation, in which the stapedial artery is large and the anterior carotid is wanting, is primitive for Prosimii as a whole (e.g. Clark, 1971; Szalay and Katz, 1973), and this is certainly reasonable on grounds of communality of possession. Equally, the condition shared by the cheirogaleines and lorisids, in which an anterior carotid is present, has plausibly been viewed as a homologous derived character. But the conclusion drawn from this, that the cheirogaleines form a sister-group of the lorisids, whereas the remaining Malagasy primates form a homogeneous whole, at least with respect to the former, demands thorough examination. For communality of possession of a primitive character, in this case a state of carotid circulation, reveals nothing more than that such a character was present in the common ancestor of the group as a whole. It tells us nothing about phylogenetic relationships within that group. In discussing lemur relationships, then, we must turn to the consideration of other characters.

The results of such an analysis, based on the craniodental characters we have been discussing, are summarized in the cladogram given in figure 23. We shall discuss the derivation of this theory of relationships, where possible, by outlining our views as to the ancestral morphotype of each of the sister-groups shown in the figure.

We consider that the common ancestor of the indriines, palaeopropithecines, archaeolemurines, and *Daubentonia* (for want, at this stage, of a better term, "*Indri*-group") possessed a relatively globular braincase, with a short facial skeleton tucked somewhat beneath it. The orbits were widely separated and fairly well frontated; in the medial orbital wall the frontal was in broad contact with the maxilla. This latter bone was robust

and relatively deep. The corpus of the mandible was deep and laterally narrow; the unfused symphysis was long and oblique, with a well-marked genial fossa, and the gonial angle was expanded and well rounded-out. A large digastric was present, reflecting itself in an excavated attachment area on the medial aspect of the horizontal ramus, and in the presence of a salient paroccipital process. The considerably raised condyle possessed an extended, transversely convex articular surface, and reposed in a deep glenoid fossa. The nasal area was high and relatively broad. An inflated bulla was present; the tympanic ring and carotid circulation were as in the indriines. The dental comb possessed but two teeth, bilaterally; these were perhaps less slender and procumbent than those of the indriines. Three premolars were present in the upper and lower jaws. The molar teeth were not dissimilar to those of *Propithecus*; M^1 and, more so, M^2 were squarish, with a well-marked cusp at each corner, and more buccal elaboration than seen in *Indri*; M^3 was considerably reduced. The lower molars possessed four main cusps, the lingual pair more salient than the buccal; a small but distinct paraconid was present in addition, whereas M_3 also possessed a differentiated, if small, hypoconulid. In both their development and their eruption, initial and complete, the premolars appeared in the sequence $P_4^4 \rightarrow P_3^3 \rightarrow P_2^2$, and the upper canine appeared centrally in the total sequence. Three deciduous, as well as three permanent, premolars were present. dp_4 was a four-cusped molariform tooth, but was triangular in outline because the anterior cusp pair was more closely approximated than the posterior.

The hypothetical morphotype of the common ancestor of the other lemurs and the lorisids ("lemur/loris group"), taken together, differs strongly from that just described for the *Indri*-group in almost all characters beyond the simple number of nonincisor teeth and the condition of the ear region. This ancestor possessed a rela-
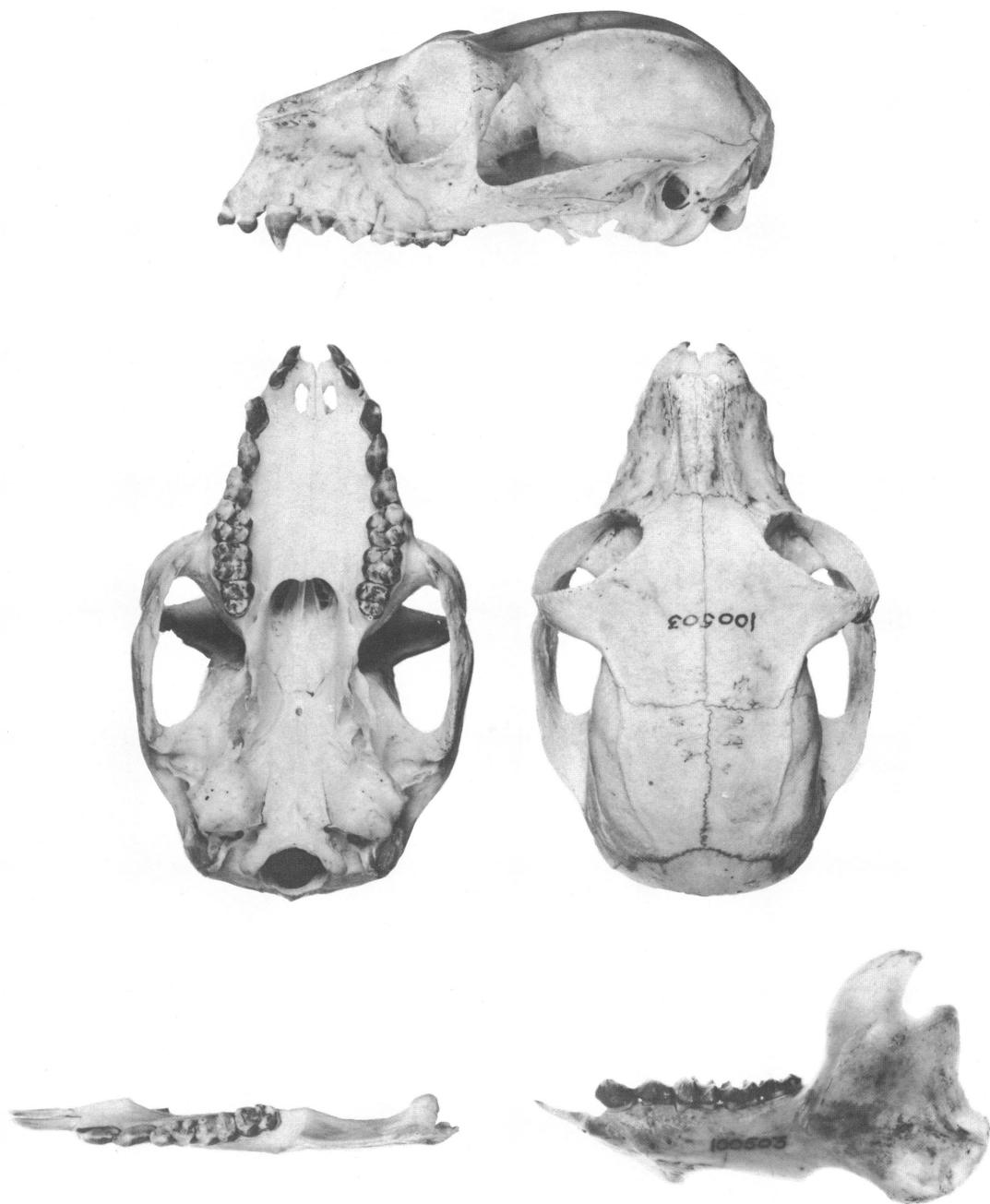
FIG. 5. Cranium and mandible of *Indri indri* (AMNH 100503). ×¾.
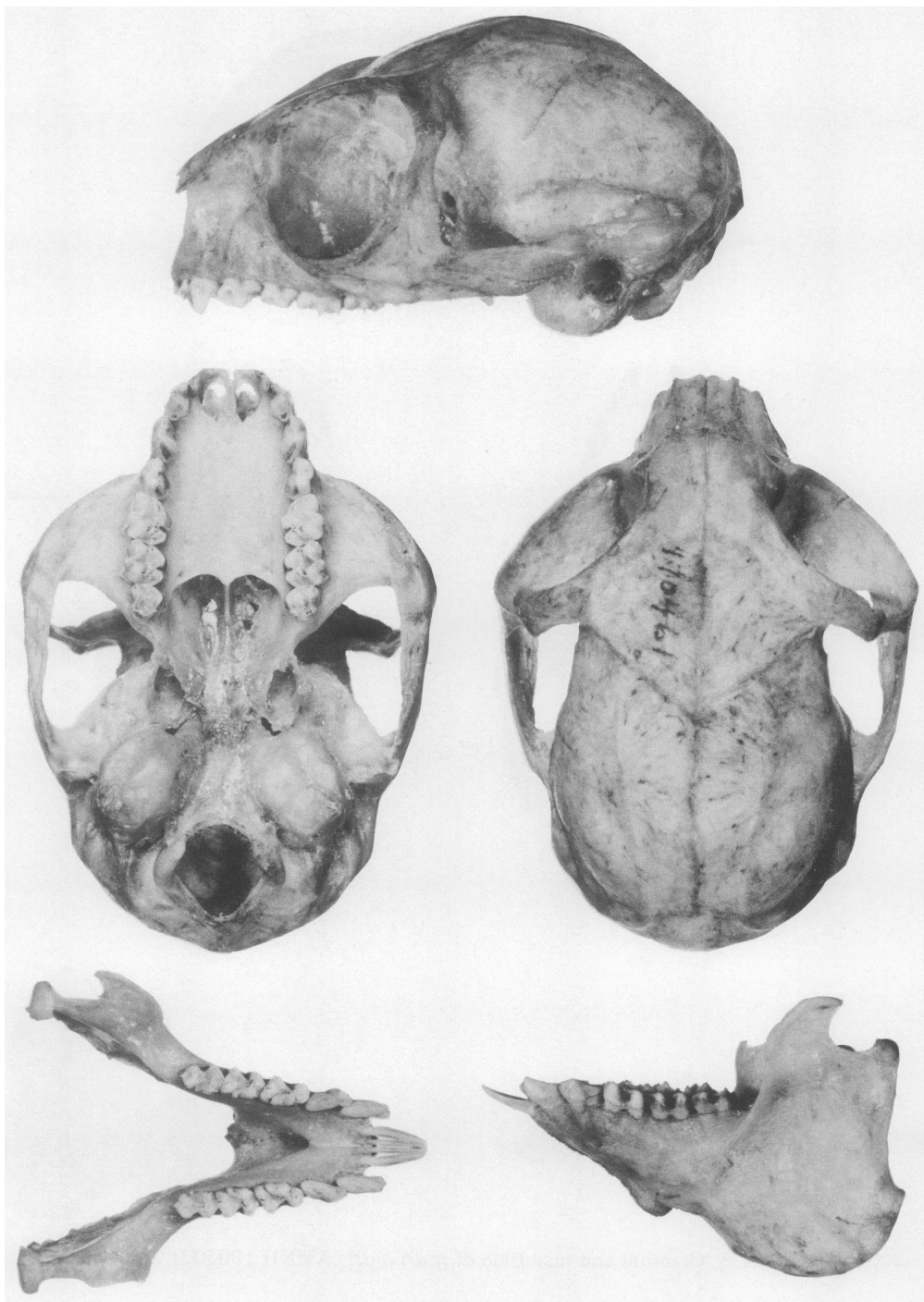
FIG. 6. Cranium and mandible of *Avahi laniger* (AMNH 170461). ×1½.
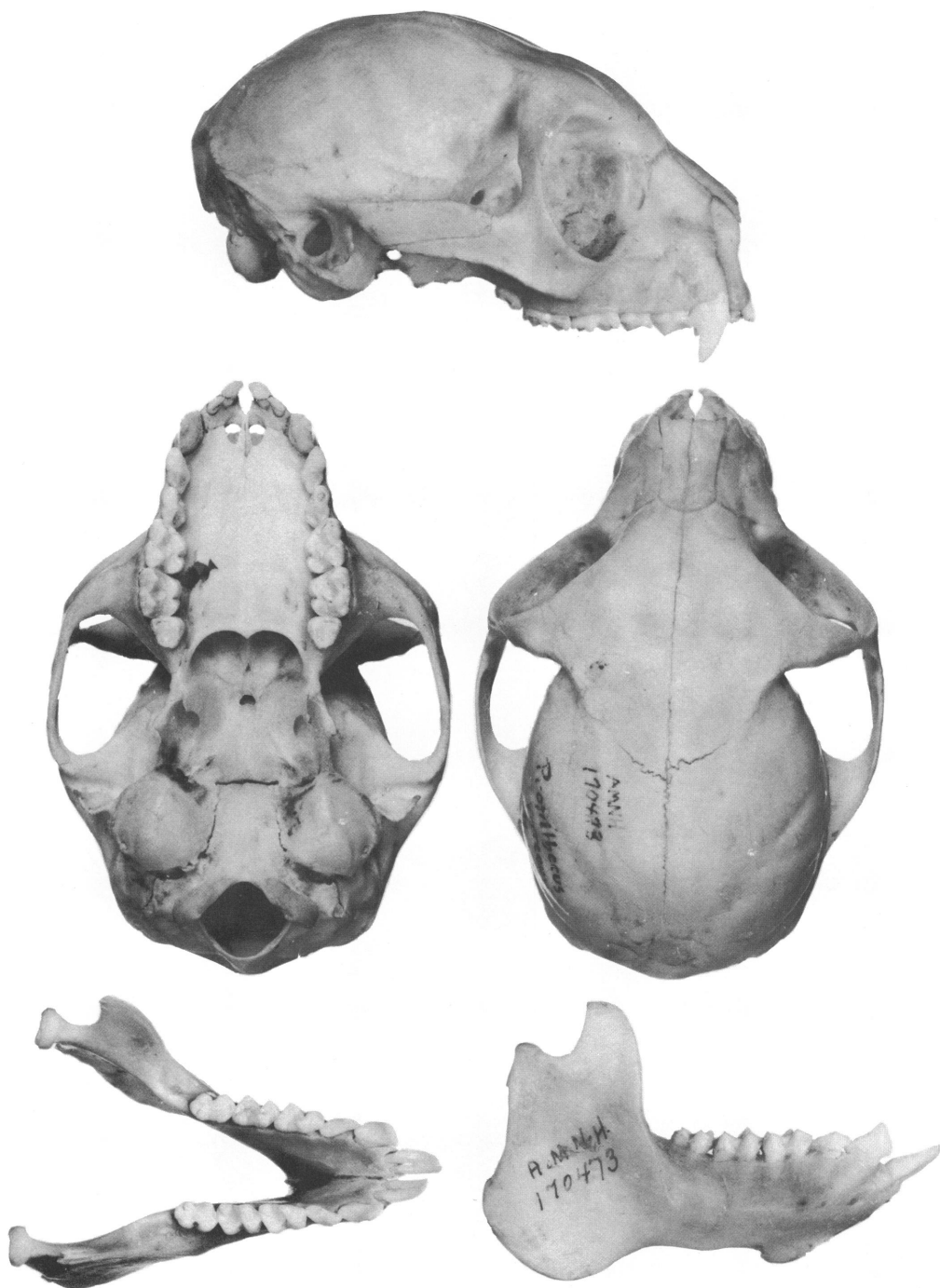
FIG. 7. Cranium and mandible of *Propithecus verreauxi* (AMNH 170473). Approximately ×1.

FIG. 8. Cranium of *Mesopropithecus globiceps* (Académie Malgache specimen). Approximately ×1.

FIG. 9. Cranium of *Archaeolemur majori* (Académie Malgache specimen). Approximately ×2/3.

FIG. 10. Cranium and mandible of *Hadropithecus stenognathus* (Académie Malgache specimen). *Above* ×1. *Below* ×¾.

FIG. 11. Cranium of *Palaeopropithecus ingens* (= *P. maximus*) (Académie Malgache specimen). Slightly more than ×½.

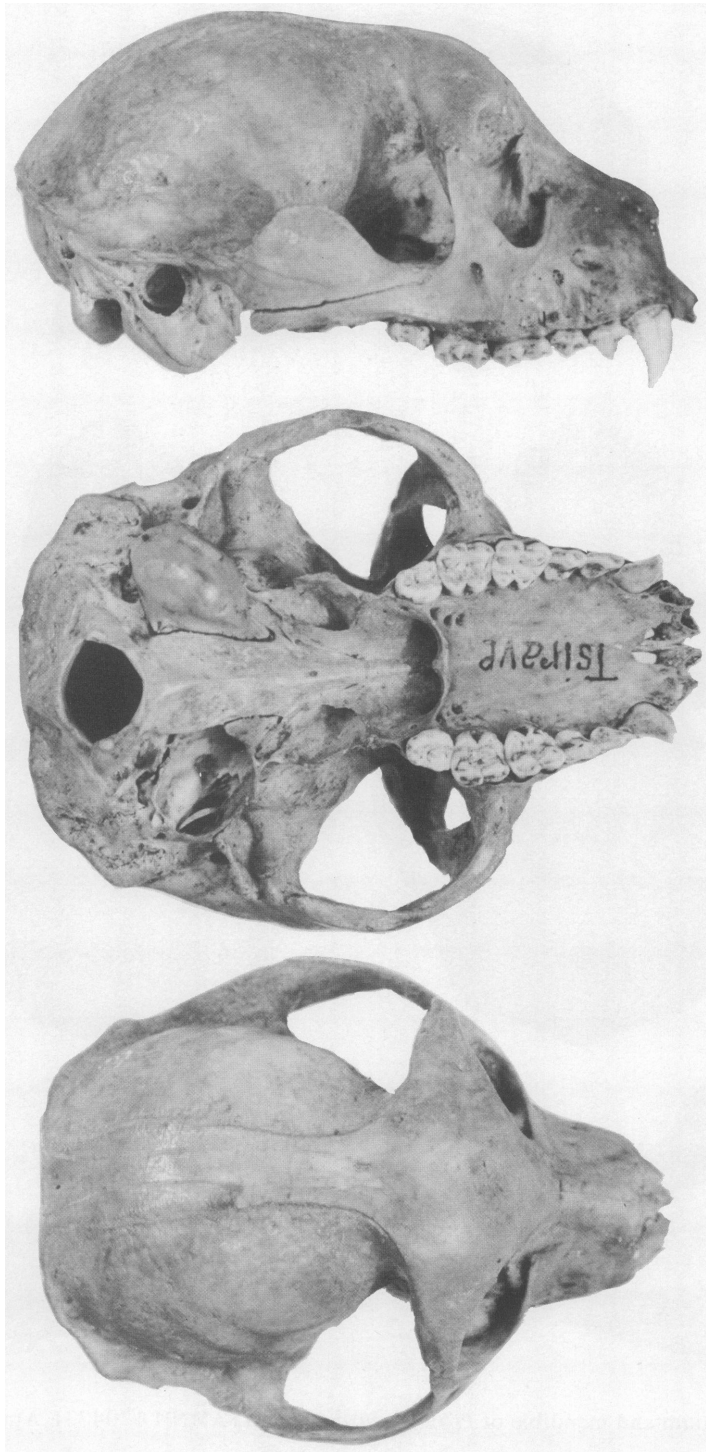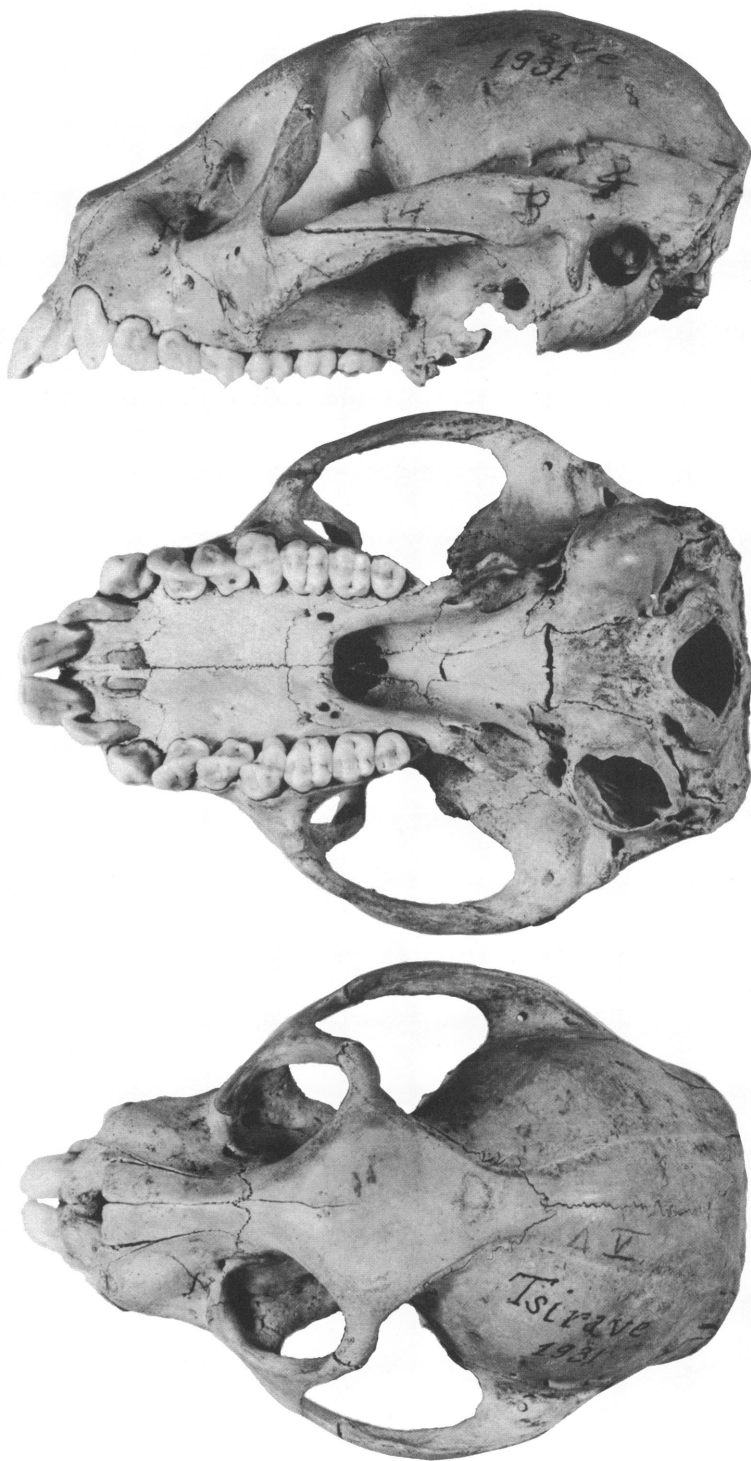tively (not extremely) long facial skeleton, situated anterior to, rather than beneath, the less inflated neurocranium. The horizontal ramus of the mandible was shallow and slender, its ovoid symphysis unfused. The condyles, wide transversely but restricted anterposteriorly and lacking transverse convexity, were raised above the level of the tooth row, but not to a very considerable extent; the glenoid fossa was not excavated. The gracile postglenoid process was not confluent with the bulla. The mandibular angle

was hooked, rather than inflated, with very little ventral extension. The nasal region lacked a high profile. The auditory bulla was well inflated, and the tympanic ring lay inside it, angled medially. The carotid foramen was lateral; a large stapedial artery was present, and the anterior carotid was lacking. The paroccipital process was very little pronounced, and the orbits were moderately frontated and convergent. The premaxillary and nasal bones did not project anteriorly beyond the alveolar margin; the posterior palatine foramen
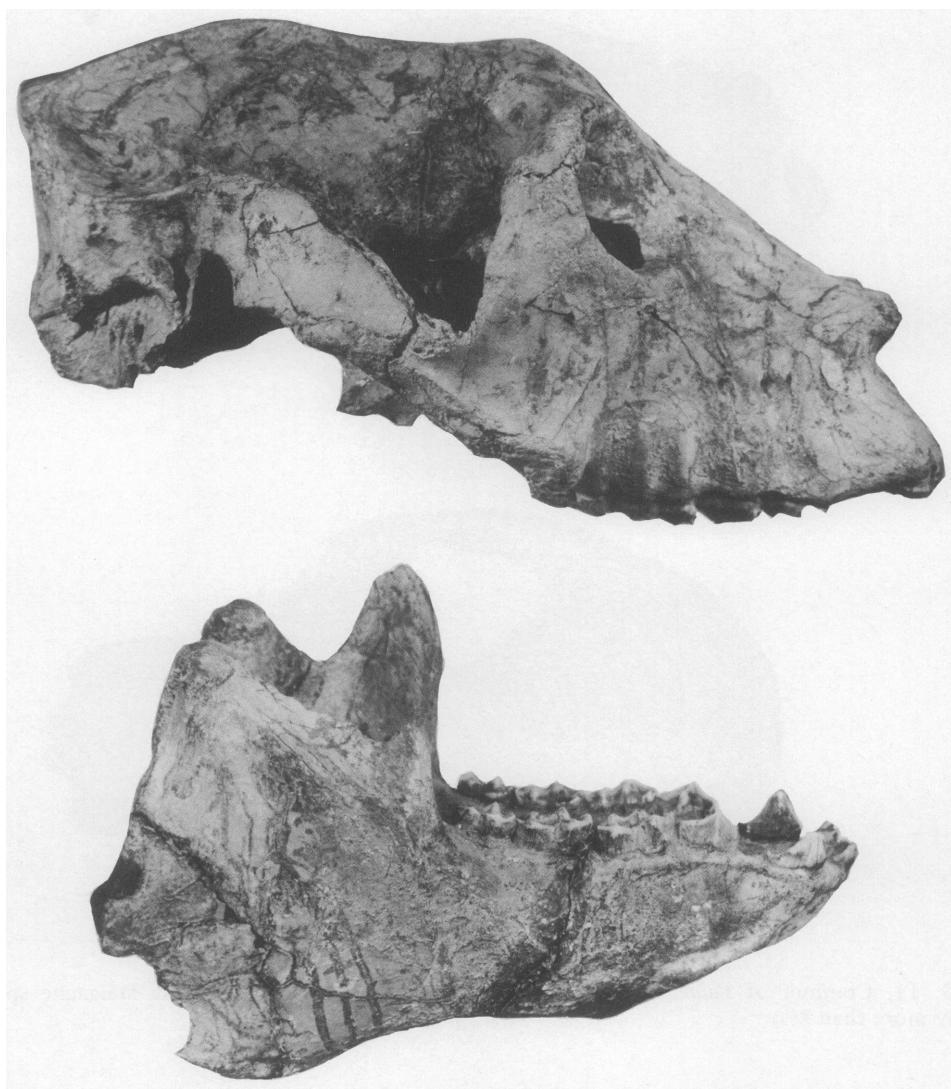
FIG. 12. *Archaeoindris fontoynonti* (Académie Malgache specimens). Slightly more than x½.

was formed as in *Microcebus*. The upper incisor teeth were probably high-crowned and slender, and the canine quite long and robust. The dental comb possessed six stout teeth, procumbent but not pronouncedly so. Both upper and lower anterior premolars were robust, somewhat canini-form teeth, noticeably more salient than those posterior to them. P^4 was probably bicuspid, the buccal cusp exceeding the lingual in size. M^1 and M^2 were subequal in size, bearing a small entoconid and a paraconid shelf. A hypoconulid was present in the small M_3. The deciduous teeth

FIG. 13. *Archaeoindris fontoynonti* (Académie Malgache specimens, as in fig. 12). Slightly more than ×½.
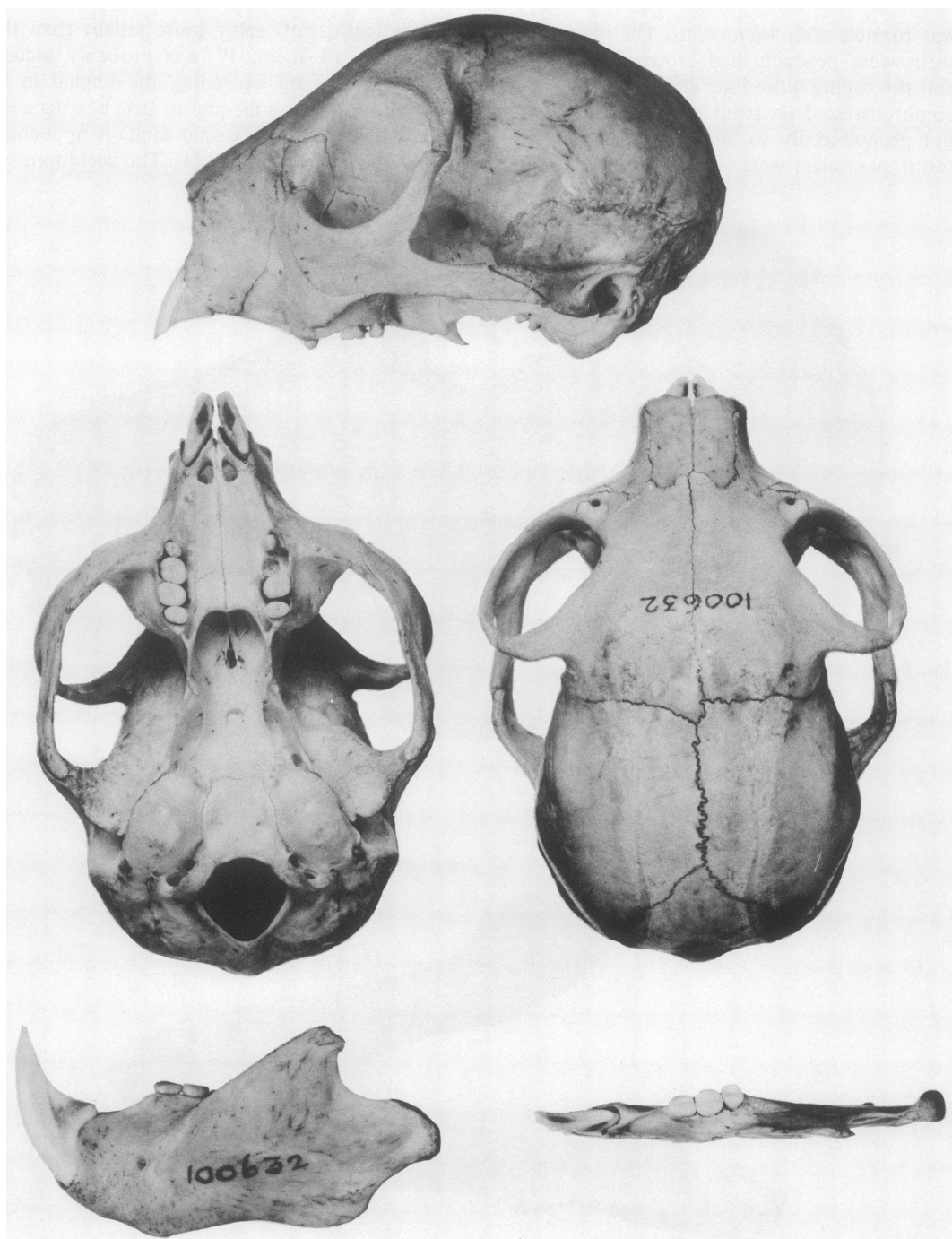
FIG. 14. Cranium and mandible of *Daubentonia madagascariensis* (AMNH 100632). Approximately ×1.

FIG. 15. Cranium and mandible of *Lemur fulvus* (AMNH 170770). x¾.
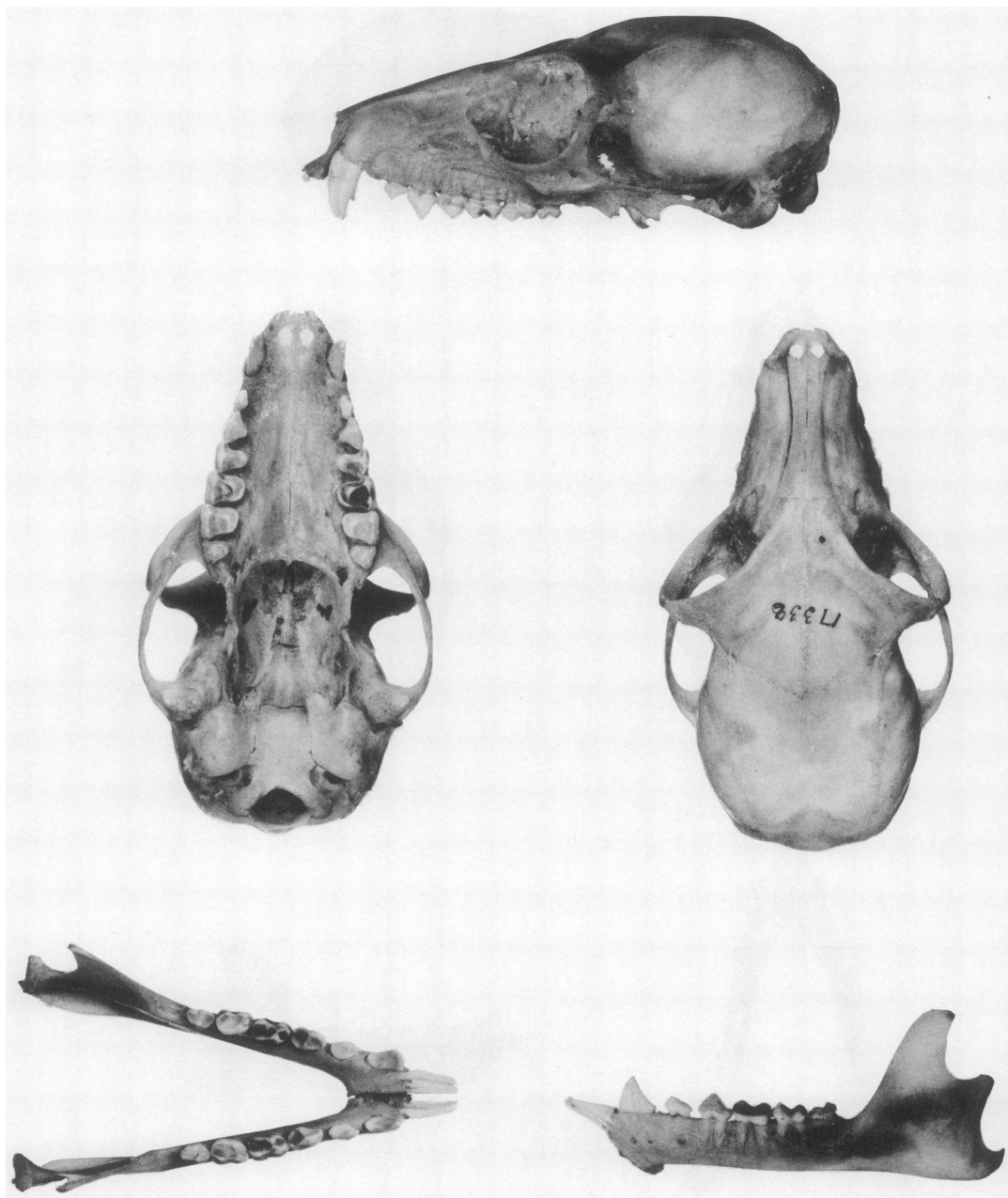
FIG. 16. Cranium and mandible of *Varecia variegatus* (AMNH 17338). ×¾.

FIG. 17. Cranium and mandible of *Hapalemur griseus* (AMNH 100534). Approximately × 1.
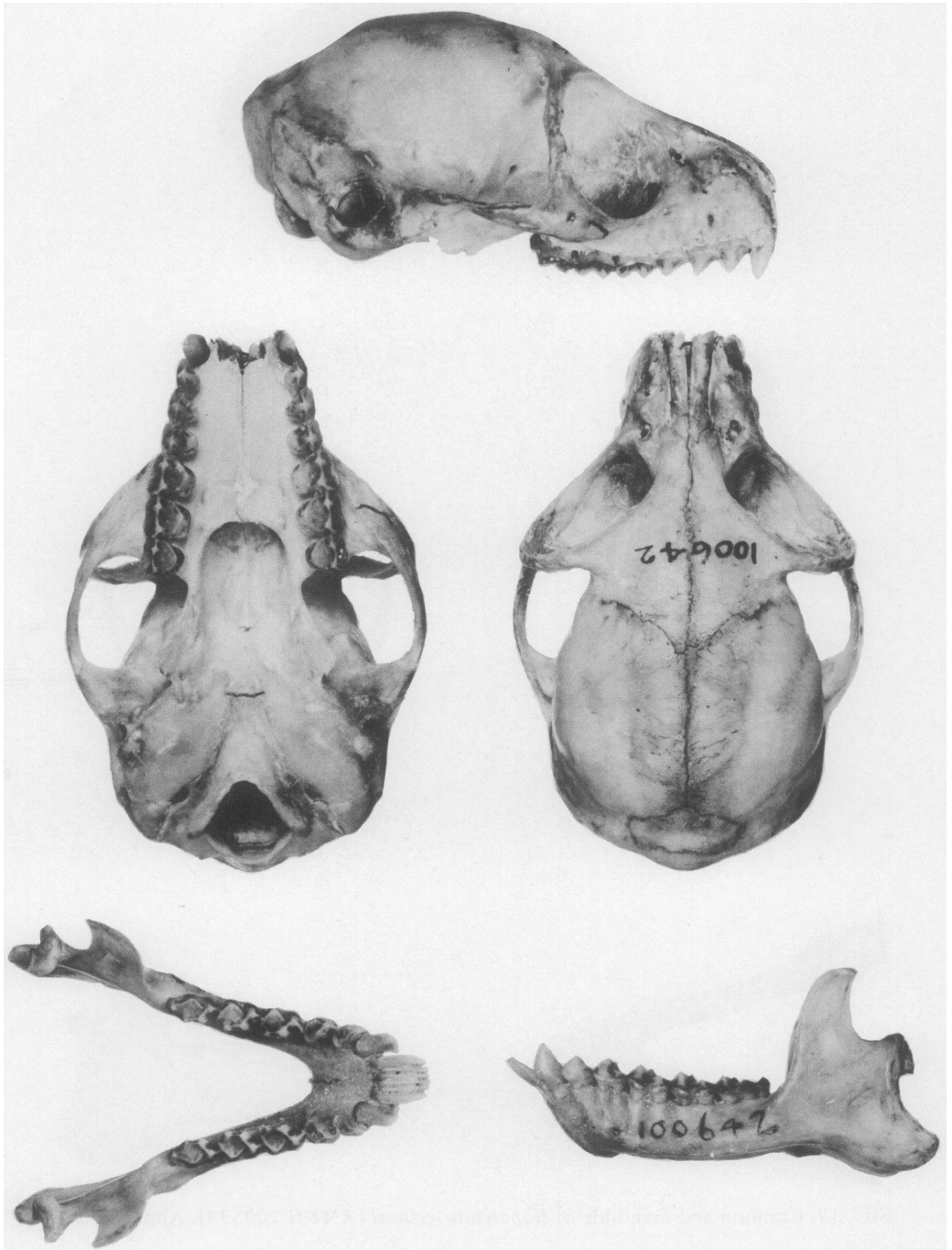
FIG. 18. Cranium and mandible of *Lepilemur mustelinus* (AMNH 100642). ×1½.

FIG. 19. Cranium and mandible of *Megaladapis madagascariensis* (Académie Malgache specimen). Slightly more than ×½.
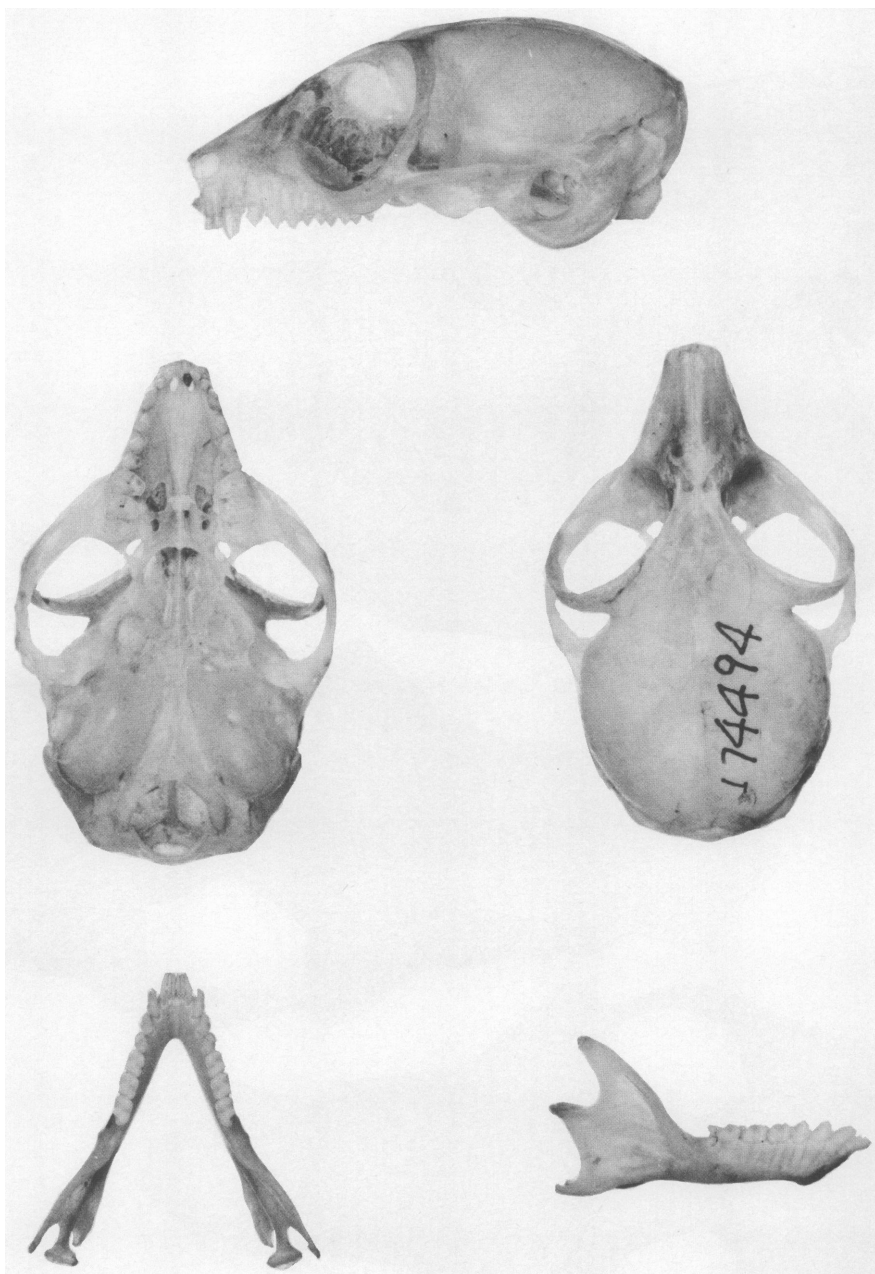
FIG. 20. Cranium and mandible of *Microcebus murinus* (AMNH 174494). ×2.

FIG. 21. Cranium and mandible of *Cheirogaleus major* (YPM 301, a young individual). ×1½.
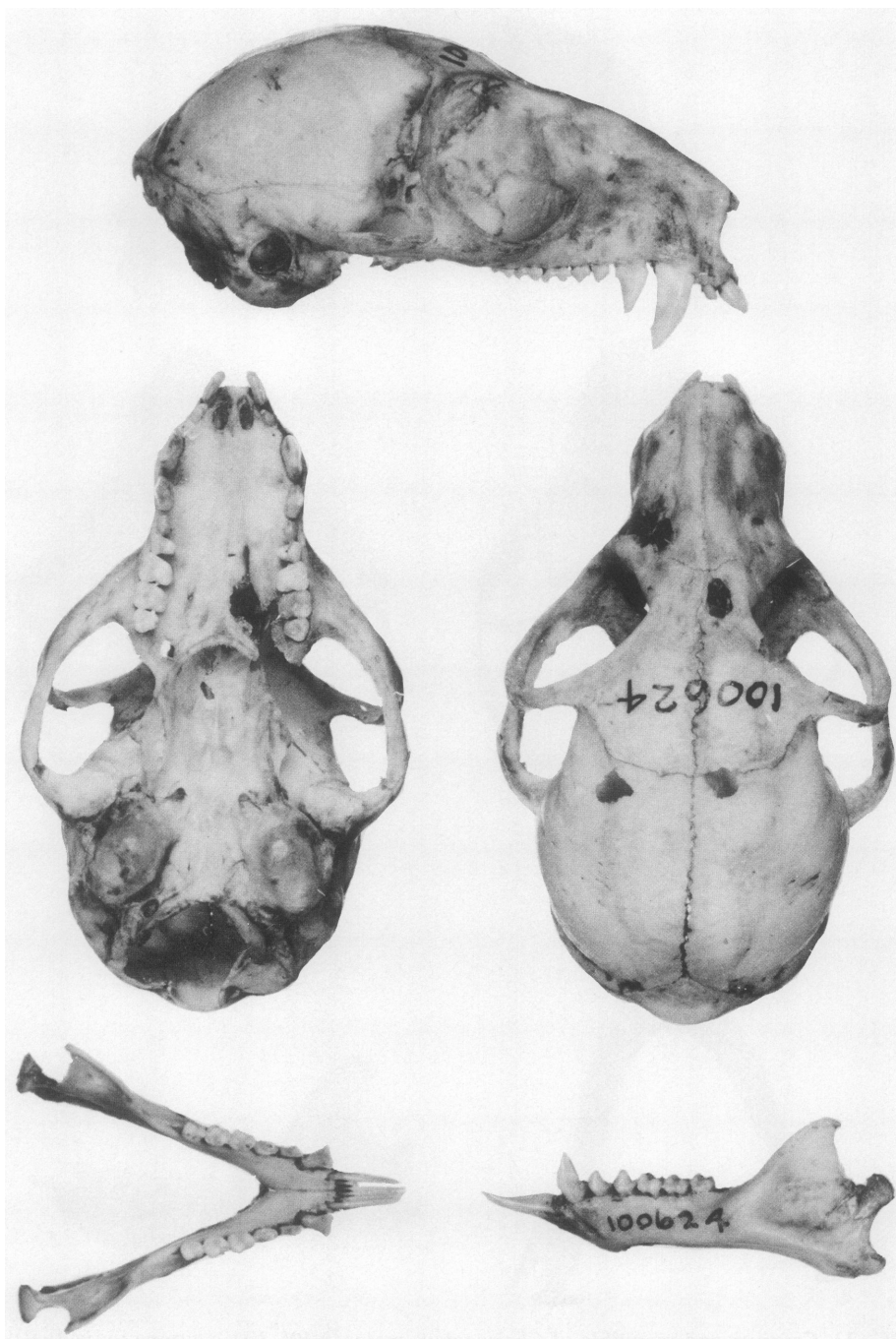
FIG. 22. Cranium and mandible of *Phaner furcifer* (AMNH 100624). ×1½.
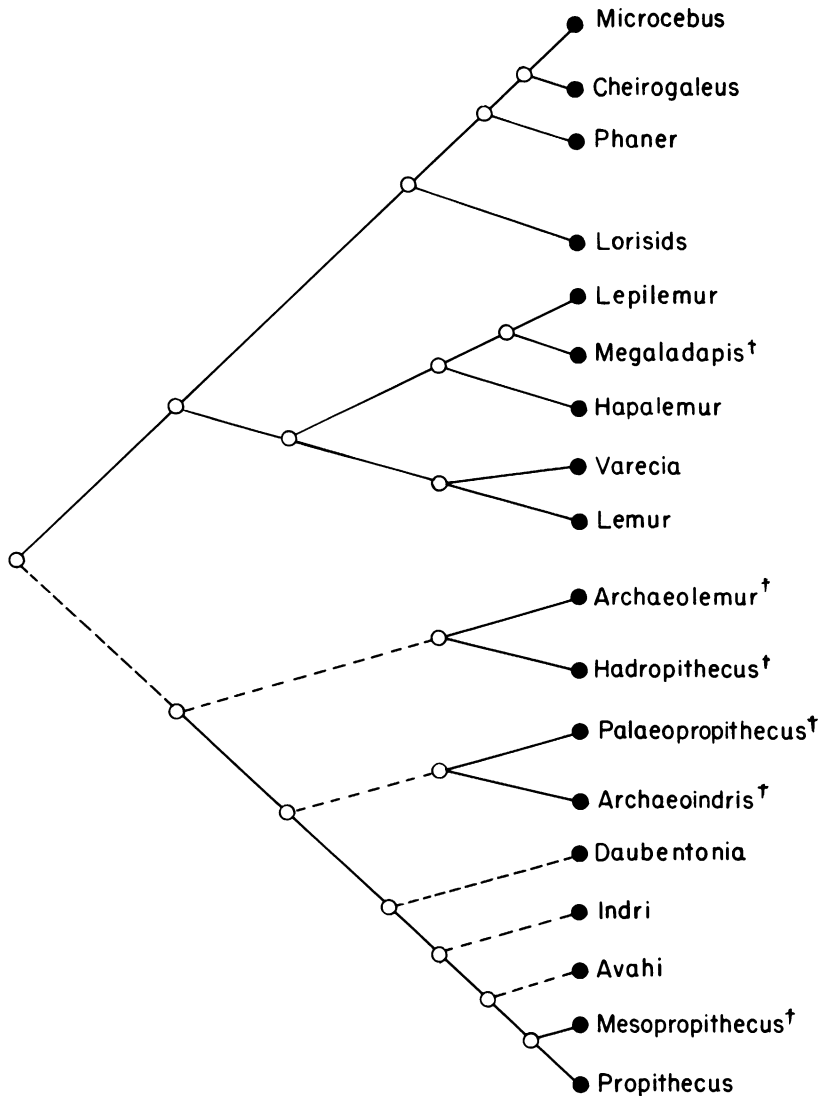
FIG. 23. Tentative theory of relationships among the Malagasy lemurs. Daggers denote extinct taxa.

resembled their permanent successors, except in the case of dp_4^4, which were molariform. The teeth of the dental comb were the first to appear in both the deciduous and permanent dentitions, although canine eruption was delayed relative to that of the incisors. Development and eruption of the upper canine were closely associated with those of P_2^2, and both permanent and deciduous premolars developed and erupted in the sequence $P_2^2 \rightarrow P_4^4 \rightarrow P_3^3$. The last three teeth of the permanent set to develop and erupt were $M_3^3 \rightarrow P_4^4 \rightarrow P_3^3$.

The common ancestor of the cheirogaleines and lorisids possessed an inflated bulla enclosing a free tympanic ring. An anterior carotid foramen was present, reflecting the presence of an anterior carotid artery. The promontory artery was larger than the stapedial branch; the internal carotid penetrated the bulla posteromedially

rather than posterolaterally. The postglenoid process was fused medially to the bulla; in the nasal fossa the large first endoturbinal descended to overlap the maxilloturbinal. The dental comb was probably more procumbent and less robust than that of the common ancestor of the lemur/loris group as a whole. P_2 was inclined forward. The hypocone on M^1 and M^2 was well differentiated and situated posterolingually; it was accentuated by waisting of the posterior margin of the tooth. The paracone was conical, while the metacone was compressed about an oblique axis. A distinct entoconid was present in the lower molars, and the paraconid shelf was reduced.

It should probably be noted that this hypothetical common ancestor is likely to have been remote in time; thus, although attention has recently been drawn by Charles-Dominique and Martin (1970) to the similarities between *Microcebus murinus* and *Galago demidovii*, their differences are equally striking, despite the fact that the two taxa share similarities in size and lifestyle.

As a group, the cheirogaleines are distinguished from the lorisids largely by the retention of the primitive state in a variety of characteristics in which the lorisid common ancestor was derived. Such derived states include a somewhat higher vaulting of the neurocranium, mastoid inflation posterior to the bulla, loss of the stapedial artery, reduction of the posterior palatine foramen, loss of the prenasopalatine lamina in the medial orbital wall, fusion of the tympanic ring to the lateral bulla wall, some filling-out of the mandibular angle, obliquity of the mesiodistal axis of the upper canine, and the molarization of P^4. Derived character states in the ancestral cheirogaleine include the lowering of cusp relief in the molar teeth, and the enlargement of the occlusal surfaces of the upper incisors, particularly I^2. The tooth comb was more gracile and procumbent, and M_1^1 were the first teeth of the permanent sequence to erupt (a condition possibly commonly derived in the galagines).

Within Cheirogaleinae, *Phaner* is distinct from the common ancestor of *Microcebus* and *Cheirogaleus* (as indeed from both modern genera) in possessing the following derived character states: stapedial artery lacking; mandibular condyles

compressed laterally; hypoconulid absent from M_3; mandibular angle less hooked; cranial roof somewhat vaulted; dental comb more slender and procumbent; P_2 more vertical; I^2 enlarged and forwardly projecting; last permanent teeth to develop and erupt $P_4^4 \rightarrow M_3^3 \rightarrow P_3^3$.

The common ancestor of Lemurinae and *Megaladapis* remained quite close to that of the lemur/loris group. The dental comb was, however, more gracile and procumbent; both upper incisors were reduced in height but broadened mesiodistally; M_1^1 were possibly the earliest teeth of the permanent series in both development and eruption; $\underline{C}$-P_2^2 developed as a unit, but the eruption of $\underline{C}$ was delayed; M_2^2 developed after this unit, but erupted before the canine. The protocone of the upper molars was large and somewhat anteriorly placed; the posterior palatine foramen bounded the entrance of a short, bony canal. The lateral pterygoid lamina was fused posteriorly to the bulla.

Somewhat more change is evident in the later evolutionary stages of this group. The common ancestor of *Lemur* and *Varecia* possessed an elongate facial skeleton, parallel temporal lines, and ventrally-protruding medial pterygoid laminae. P^2 was small; P^3 was the most salient upper premolar. The lingual moieties of the upper molars were shifted anteriorly; in P^4 a small internal cusp was closely approximated to the protoconid, and large anterior and posterior foveae were present. M^3 lacked a hypoconulid. The upper deciduous premolars erupted in the sequence $dp^2 \rightarrow dp^3 \rightarrow dp^4$.

The ancestral morphotype of *Hapalemur*, *Lepilemur*, and *Megaladapis* can be characterized as possessing somewhat downward curving nasal bones, and a facial skeleton somewhat longer than that found in either of the living genera. Slight mastoid inflation was present, and the temporal lines converged posteriorly. The postglenoid process was fused medially to the bulla, and was quite long dorsoventrally. The premaxilla was short anteroposteriorly; the small I^3 was masked from the side by the canine. In the upper molars, the paracone and metacone were connected by a ridge; the buccal margin of these teeth was quite pronounced. In the lower molars the trigonid basin opened internally. The mandibular angle probably protruded ventrally and was

slightly flexed medially. The premolars developed in the sequence $P_2^2 \rightarrow P_4^4 \rightarrow P_3^3$ (i.e., showed the primitive pattern), but erupted in the order $P_4^4 \rightarrow P_2^2 \rightarrow P_3^3$.

The common ancestor of *Lepilemur* and *Megaladapis* exhibited a peculiar condition of the temporomandibular joint wherein a secondary articular surface ran perpendicularly down from the posterior aspect of the medial moiety of the condyle. The stapedial artery was greatly reduced. No upper incisors were present in the permanent dentition. The upper molars were characterized by a posterointernal cingulum, lingual buttressing of the metacone, and the presence of a parastyle. On all lower molars a long, well-defined paracristid and elongated anterior fovea was present, but no metastylid. M_3 possessed an elongated heel supporting a very substantial hypoconulid. M_1^1 and M_2^2 were the earliest permanent teeth both to develop and to erupt.

Relationships within the *Indri*-group are more difficult to discuss within the context of ancestral morphotypes. This is largely because, however these relationships are viewed, the common ancestor of each sister-group within this array of related forms remained remarkably primitive in almost all aspects of craniodental morphology. In other words, hardly any of the derived character states to have arisen within the *Indri*-group are shared at any level beyond the generic.

The ancestral morphotype of the *Indri*-group, it will be recalled, is regarded here as possessing three deciduous premolars, replaced by three permanent teeth, the latter developing and erupting after M_3^3. In the indriines and palaeopropithecines one of the permanent premolars is lost. In both the indriines and *Daubentonia*, however, the deciduous dentition shows a highly derived condition, one which we consider unlikely to have evolved in parallel within each group. The indriines possess four deciduous premolar teeth, arranged as in figure 24. Conventional reasoning, under which tooth loss is generally regarded as derived, would suggest that four premolars represent the primitive condition. However, the recent work of Osborn (1973), on the mechanisms of dental development, supports the suggestion that this state is in fact derived within the *Indri*-group.
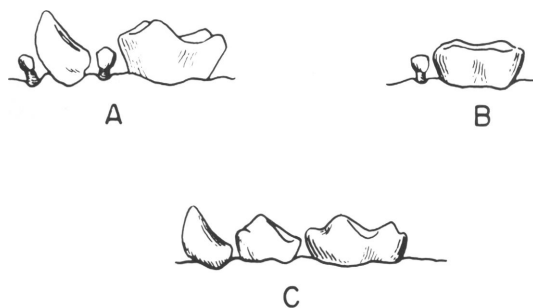

FIG. 24. Lower deciduous premolars. A. Indriines. B. *Daubentonia*. C. Primitive (prevalent) type with three deciduous premolars.

Tooth budding is initiated by neural crest cells migrating from the neural tube into the jaws. Deciduous premolar budding in mammals is initiated posteroanteriorly, its tempo governed by the rate at which the jaw is growing. In addition, the morphology of the deciduous premolars generally decreases in complexity from back to front; this is because the initiator of a tooth family is carried forward with the increase in jaw size, and stimulates the development of successively simpler teeth. In the lorisids, lemurids, and archaeolemurines, for example, one sees this morphological gradient in the deciduous premolars in the molariform dp_4, the caniniform dp_2, and the intermediate dp_3.

In the indriines, on the other hand, although dp_4 is molariform, it is not preceded by a merely slightly less complex tooth, but by a markedly reduced, almost rudimentary, dp_3 (fig. 24). dp_2, by comparison, is much more complex than dp_3 and, like dp_4, is preceded by a small, peglike tooth. This is not what one would expect to find if the neural crest cells were invading the developing lower jaw in a primitive single-wave fashion. However, it is what would occur if the first wave were rapidly followed by a second invasion of neural crest cells. The first wave would initiate a molariform dp_4; but the field of inhibition created by the encroaching second wave would cause dp_3 to be diminished in size. The fields of inhibition created by the follicular growth of dp_4 and dp_3 would, in turn, impede the morphogenesis of dp_2; the caniniformity of this tooth would

be further enhanced by its incorporation into the canine field (cf. Butler, 1939, 1963). By this time, interstitial growth would be minimal and the total inhibitory effect would demand a diminished dp_1. A mechanism of this type can obviously not be considered primitive when compared to the single-wave-initiated deciduous premolar gradient of other prosimians.

In *Daubentonia* the morphology of the two remaining deciduous premolars is extremely close to that of these teeth (dp_3 and dp_4) in the indriines (fig. 24). The development of these premolars is evidently initiated by the homologue of the first wave of neural crest cells in the indriines. The effects of the second wave, however, are cancelled by the field of inhibition created by the proximity of the root of the enlarged lower canine, and the appearance of the two anterior lower deciduous premolars is forestalled. We thus believe that the common ancestor of Indriinae and *Daubentonia* already possessed the indriine-type mechanism of lower deciduous premolar development, and that this shared character of the two taxa is derived with respect to all other members of the *Indri*-group. A similarly shared derived character lies in the eruption of P^4 before M^3_3.

In almost all cranial characteristics the archaeolemurines (*Archaeolemur majori* especially) are very close to Indriinae (particularly *Propithecus*). Yet in their dentition they are far more divergent from the latter, in both tooth number and morphology, than the palaeopropithecines. We suspect that the loss of a premolar in each quadrant of the dentition may have taken place independently, and through the operation of different mechanisms, in Indriinae and Palaeopropithecinae. However, in the absence of sufficient information on dental development and eruption in the latter, this cannot be demonstrated; we are left, then with an obviously derived character shared by both taxa.

The most striking departure in the palaeopropithecine skull from the indriine condition lies in the structure of the bony ear; however, the sharing between Indriinae and Archaeolemurinae of the same structure of this region is the sharing of a primitive character, and thus at this level is of no taxonomic value. Again, the significance of the reminiscence in form between dp_4 in *Archaeolemur*, *Daubentonia*, and Indriinae is impossible to assess in this context because this tooth is unknown in both *Palaeopropithecus* and *Archaeoindris*.

In details of cranial structure, despite disparities in size, the indriines remain an extraordinarily coherent unit. Nevertheless, *Propithecus*, *Mesopropithecus*, and *Avahi* retain the primitive short face and mandible, whereas the splanchnocranium and lower jaw of *Indri* are substantially longer. The corresponding elongation of the neurocranium in *Indri* is directly due to the functional demands on the masticatory musculature of the longer face. *Indri* also departs from the primitive condition in possessing less complex M^1 and M^2, with distinct reduction of buccal elaboration; in showing better cuspal differentiation on M^3_3; possibly in developing and erupting all the anterior teeth before M^1_1; in having mesiodistally long, relatively low-crowned lateral upper incisors; and (probably) in possessing a fifth endoturbinal. *Avahi* is distinguished from the primitive pattern largely in those features related to the increase in size of its orbits. In addition, however, its nasals do not contact the premaxillae, but jut forward over the nasal aperture; the carotid foramen is less laterally placed; the upper incisors are high-crowned but thin, I^3 exceeding I^2 in size; the canine is the last tooth to develop; I^2 develops and erupts before M^1_1; and lateral mastoid inflation is present. *Propithecus*, as far as we have been able to determine, remains very close to the primitive conformation in almost all aspects of cranial and dental morphology.

As *Indri* and *Avahi* are divergent in distinct ways from a common ancestor morphologically reminiscent of *Propithecus*, we have been unable to establish unequivocal sister-groups within Indriinae, except in the case of *Propithecus* and *Mesopropithecus*.

It will be noted that we have made no attempt to characterize the morphotype representing the common ancestor of the lemurs as a whole; moreover, we have left as uncertain the relationship shown in figure 23 between the *Indri*-group and the other lemurs. This is because the two groups are not directly comparable in most of the characters on which we have based our analysis. We assume, largely on the basis of the structure of the ear region, and of the mutual possession of a dental comb, that all the lemurs are members of a single radiation (although, even then, we cannot demonstrate conclusively that the dental comb, containing as it does different numbers of teeth, is derived in both groups from a single common ancestral form). But if, as com-

parisons outside the non-*Tarsius* prosimian fauna might suggest, the morphotype of the lemur-loris group most closely approximates the ancestral form, particularly in the dentition, then the consequently highly derived nature of the *Indri*-group sets it so far apart that it may be derived from almost any form retaining the primitive conformation of the temporal region. In terms of particular characteristics, we point out in defense of our theory of relationships that the *Indri*-group is distinguished from the entire lemur-loris group in terms of dental development and eruption. Specifically, we suggest that the ancestral non-*Tarsius* prosimian morphotype was characterized by $M_{\overline{2}}^2$ which developed and erupted prior to the $\underline{C}$-$P_{\overline{2}}^2$ functional unit, and by premolars which developed and erupted in the order $P_{\overline{2}}^2 \rightarrow P_{\overline{4}}^4 \rightarrow P_{\overline{3}}^3$. The primitiveness of the $P_{\overline{2}}^2 \rightarrow P_{\overline{4}}^4 \rightarrow P_{\overline{3}}^3$ sequence is strongly suggested not only by comparisons within the primates, but by the data presented by Slaughter, Pine, and Pine (1974) on postcanine eruption sequences in insectivores and

carnivores. In the ancestor of the lemur-loris group there was a shift such that the $\underline{C}$-$P_{\overline{2}}^2$ unit developed and erupted prior to $M_{\overline{2}}^2$. In the ancestor of the *Indri*-group, on the other hand, the co-ordinated appearance of $\underline{C}$ and $P_{\overline{2}}^2$ was lost, and the premolars developed and erupted in a posteroanterior sequence.

The possibility does of course exist that the *Indri*-group and the other Malagasy prosimians do not represent offshoots of the same primary radiation; although this seems unlikely, it is a proposition that deserves serious consideration. We have hypothesized the relationships shown in figure 23 largely because of the considerations of dental development and eruption given above, and because of our assumption of a single radiation. The question is, however, one that will not readily be solved on the basis of the information available to us. But the sheer extent and specialization of the *Indri*-group radiation appears to argue against a late derivation.

PROVISIONAL CLASSIFICATION OF THE MALAGASY LEMURS

In classifying the lemurs we start from the premise that a classification is not a phylogeny. A classification may be constructed to reflect a view of phylogeny; but equally, according to the purposes of the classifier, it may reflect purely patristic affinities. In our view, a classification should convey the optimum synthesis of information, and in most cases this is best achieved through combining both phyletic and phenetic considerations. It is this which we have attempted to do in deriving the provisional classi-

fication offered here. We have taken into account in this procedure not only the craniodental information presented in the present article, but also data available in the literature, or from our own observations, pertaining to protein biochemistry, cytogenetics, postcranial anatomy, external characteristics, and the soft tissues of the head. It must be stressed that our classification is provisional, and that a great deal of advance on all the fronts we have just mentioned will be required before a definitive synthesis can be obtained.

ORDER PRIMATES LINNAEUS, 1758

SUBORDER PROSIMII ILLIGER, 1811

Infraorder Lemuriformes Gregory, 1915
Superfamily Lemuroidea Gill, 1872
Family Lemuridae Gray, 1821
Subfamily Lemurinae Mivart, 1864
Lemur Linnaeus, 1758
L. catta Linnaeus, 1758
L. mongoz Linnaeus, 1766
L. macaco Linnaeus, 1766
L. fulvus (E. Geoffroy, 1812)
L. rubriventer (I. Geoffroy, 1850)
Varecia Gray, 1863
V. variegatus (Kerr, 1792)
† *V. insignis* (Filhol, 1895)

Subfamily Lepilemurinae Rumpler and Rakotosamimanana, 1972
  Lepilemur I. Geoffroy, 1851
    L. mustelinus I. Geoffroy, 1851
    L. ruficaudatus A. Grandidier, 1867
  Hapalemur I. Geoffroy, 1851
    H. griseus (Link, 1795)
  Prolemur Gray, 1871
    P. simus Gray, 1871
†Subfamily Megaladapinae Major, 1894
  †*Megaladapis* Major, 1894
    †*M. madagascariensis* Major, 1894
    †*M. edwardsi* (G. Grandidier, 1899)
    †*M. grandidieri* Standing, 1903
Infraorder Lorisiformes Gregory, 1915
  Family Cheirogaleidae Gregory, 1915
    Tribe Cheirogaleini, New tribe
      Cheirogaleus E. Geoffroy, 1812
        C. major E. Geoffroy, 1812
        C. medius E. Geoffroy, 1812
        C. coquereli (A. Grandidier, 1866)
      Allocebus Petter, 1967
        A. trichotis (Günther, 1875)
      Microcebus I. Geoffroy, 1828
        M. murinus (Miller, 1777)
    Tribe Phanerini, New tribe
      Phaner Gray, 1870
        P. furcifer (Blainville, 1841)
Infraorder Indriiformes, new rank
  Family Indriidae Burnett, 1828
    Subfamily Indriinae Burnett, 1828
      Indri E. Geoffroy and Cuvier, 1795
        I. indri (Gmelin, 1788)
      Avahi (Jourdan, 1834)
        A. laniger (Gmelin, 1788)
      Propithecus Bennett, 1832
        P. diadema Bennett, 1832
        P. verreauxi A. Grandidier, 1867
      †*Mesopropithecus* Standing, 1905
        †*M. pithecoides* Standing, 1905
        †*M. globiceps* (Lamberton, 1936)
    †Subfamily Palaeopropithecinae Tattersall, 1973
      †*Palaeopropithecus* G. Grandidier, 1899
        †*P. ingens* G. Grandidier, 1899
      †*Archaeoindris* Standing, 1908
        †*A. fontoynonti* Standing, 1908
    †Subfamily Archaeolemurinae Standing, 1908
      †*Archaeolemur* Filhol, 1895
        †*A. majori* Filhol, 1895
        †*A. edwardsi* (Filhol, 1895)
      †*Hadropithecus* Lorenz von Liburnau, 1899
        †*H. stenognathus* Lorenz von Liburnau, 1899
  Family Daubentoniidae Gray, 1870
    Daubentonia E. Geoffroy, 1795
      D. madagascariensis (Gmelin, 1788)
      †*D. robusta* Lamberton, 1934

†Extinct taxon.

The erection of higher taxa is essentially an arbitrary procedure. We have chosen to separate Indriiformes, Lorisiformes, and Lemuriformes at the infraordinal level primarily on the basis of what we take to be their long separate evolutionary histories. If, in terms of level of organization, these generally conservative groups do not show the magnitudes of difference seen, for instance, between the infraorders of Anthropoidea, they nonetheless represent the present endpoints of much more extended periods of independent evolution. In this scheme it is their common classification within Prosimii which bespeaks their position in terms of grade, as opposed to clade. For this reason we would also place *Tarsius* within Prosimii, whatever its exact phylogenetic affinities may eventually be discovered to be; the inclusion of this form with the higher primates in the suborder Haplorhini seems to us to vitiate any attempt at a rational or meaningful definition of the characteristics of the suborder.

ZOOGEOGRAPHICAL CONSIDERATIONS

Although there can no longer be any doubt that Madagascar was once integral with the African continent, considerable division of opinion still exists as to exactly where the two land masses were adjoined. Walker (1972), for instance, has strongly advocated a derivation of the island from a portion of the African coast immediately to its west. If this were indeed so, and Madagascar drifted directly eastward to its present position, then an effective isolation of the island from faunal invasions from the parent continent could be inferred from a relatively early stage in the period of drift. It seems to us unlikely, however, that this picture is in fact the correct one. The Paleozoic and Mesozoic stratigraphies of Antarctica agree far more closely with those of southern Africa than do those of Madagascar; thus, for instance, the upper Carboniferous Dwyka tillites are represented in both South Africa and Antarctica but are lacking in Madagascar, as in East Africa. Again, the upper Triassic Stormberg volcanics of South Africa are represented in Antarctica by the Kirkpatrick Basalt, but are absent from Madagascar and East Africa. The absence of Carboniferous tillites in Madagascar is of special significance, as the island's paleoposition must therefore of necessity have been to the north of the northernmost extent of the Carboniferous glaciation that covered Antarctica and southern Africa.

A much more plausible derivation of Madagascar is from the area of the East African coast, as, for instance, advocated by DuToit (1957) and Smith and Hallam (1970). A variety of positive factors point to this conclusion, among them being the observation that the Malagasy Karroo deposits exhibit characteristics intermediate between those of Tanzania and southern India, although differing considerably from those of southern Africa (Smith and Hallam, 1970).

Africa, Madagascar, the Mascareigne Plateau, and India remained a cohesive unit until the Upper Cretaceous. This does not pin down the separation very precisely, of course, because the Upper Cretaceous represents a rather long time span (*ca.* 100-64 m.y.), but as the earliest magnetic anomaly between India and the Seychelles (An 28) occurs in the Maestrichtian (very late Cretaceous, *ca.* 68 m.y.), it seems reasonable to conclude that separation was a relatively late event.

Active drift of Madagascar thus probably began in Maestrichtian times and persisted through most of the Eocene, ceasing by the end of that epoch. As the southerly direction of drift was roughly parallel to the African coastline, the two land masses must have remained in relatively close proximity for most of that time; rafting of prosimians to Madagascar from Africa would thus have remained a plausible proposition until relatively late in the period of drift, proportionally increasing the likelihood of multiple invasions of the island.

There has been a recent ground swell of opinion that the Malagasy prosimians reached the island from Asia, probably via India, rather than from Africa. This conclusion, based primarily on the observation that the Paleogene faunas of Eurasia contain forms obviously related to some lemurs, seems implausible on a variety of grounds. During the time period in question, for instance, India was isolated in the middle of what is now the Indian Ocean, although closer to Africa than to Asia; the presence of an apparent

adapid survivor in the Indian Miocene (Tattersall, 1969) is of no significance in this context because by that time physical contact had been established between India and Asia, and faunal interchange would have been possible.

Perhaps the most persuasive argument against an Asian derivation of the Malagasy prosimians, however, is that the Paleogene fauna of Eurasia contains no primates that may plausibly be regarded as representing sister-groups of any of the Recent Malagasy forms beyond Lemuridae. If the phylogenetic differentiations of the various higher taxa represented on Madagascar are as ancient as, on the basis of what is known of Paleogene primate diversity, we may reasonably suppose them to have been, then we should expect to find sister-groups in the parent fossil fauna. And the Holarctic primate fauna of the early Tertiary, despite the fact that it is reasonably well sampled, has yielded nothing, for instance, which may convincingly be viewed as related to the indriiforms. It would seem, then, far more reasonable to suggest that the presently unknown African early Tertiary primate fauna may have contained such forms, and that these ultimately gave rise to the primate fauna of Madagascar. Adapids were particularly ubiquitous in the early Tertiary of Eurasia, and there is no reason to suppose that they were not present in Africa during this time. Further, if, as may be the case, Adapidae (through less specialized representatives than any now known) forms the sister-group of Lepilemurinae and Megaladapinae (Schwartz, 1974b, In press), rather than of Lemuridae as a whole, we lack in Eurasia a sister-group even of Lemurinae.

The geographical origin of Cheirogaleidae is open to a variety of interpretations. The possibility exists of the differentiation of Lemuriformes and Lorisiformes on Madagascar, with subsequent invasion of the mainland by an offshoot of the ancestral cheirogaleid stock. The point has been made that the Oligocene primate fauna of Africa lacks prosimians, whereas the African Miocene forms are close to those existing today, and might plausibly be regarded as immigrants. It should be borne in mind, however, that Oligocene primates are known only from a very limited, peripheral area of northeast Africa, and that Miocene African prosimians are likewise represented in a circumscribed area, far to the south. We consider the possibility of a prosimian invasion of Africa from Madagascar, especially one as late as the early Miocene, to be extremely remote, particularly if the adapids are indeed phyletically closer to Lepilemurinae than to Lemurinae.

The most parsimonious hypothesis, then, appears to be that the last common ancestor of all the lemurs was a member of the African middle, or even early, Paleocene primate fauna, and that the split between Lemuriformes and Lorisiformes occurred not much later than this initial dichotomy. The ancestors of the three major Malagasy groups arrived from the mainland separately, at any time between the early Paleocene and the beginning of the middle Eocene, and probably by rafting. The order of their arrival was not, of course, necessarily related to their order of origin. We realize that this reconstruction implies that the African early Tertiary primate fauna will, when found, be seen to be of very different aspect from those known at present from North America and Eurasia. But it is difficult to interpret the comparative evidence otherwise.

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