

EVOLUTIONARY
RELATIONSHIPS OF
LIVING LEMURS AND LORISES
(MAMMALIA, PRIMATES) AND
THEIR POTENTIAL
AFFINITIES WITH EUROPEAN
EOCENE ADAPIDAE

JEFFREY H. SCHWARTZ AND IAN TATTERSALL

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JEFFREY H. SCHWARTZ

*Research Associate, Department of Anthropology
American Museum of Natural History
Associate Professor, Department of Anthropology
University of Pittsburgh*

IAN TATTERSALL

*Curator, Department of Anthropology
American Museum of Natural History*

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ABSTRACT

We comprehensively describe and illustrate the dentitions of all extant lemurs and lorises (family Lemnidae: *Lemur*, *Varecia*, *Hapalemur*; family Megaladapidae: *Lepilemur*; family Indriidae: *Indri*, *Propithecus*, *Avahi*; family Daubentoniidae: *Daubentonia*; family Cheirogaleidae: *Cheirogaleus*, *Microcebus*, *Mirza*, *Phaner*, *Allocebus*; family Lorisidae: *Loris*, *Nycticebus*, *Perodicticus*, *Arctocebus*; family Galagidae: *Galago*, *Euoticus*), providing, where necessary, descriptions of more than one species per genus. We use character sets derived from these descriptions as the basis for reconstructing evolutionary relationships among these genera, using a standard cladistic approach. These relationships are summarized in the cladogram given in figure 34. Potential affinities between the surviving "lower" primates and those of the Eocene are examined, and the Eocene family Adapidae is redefined to exclude those many fossil forms normally classified within it which do not

share at least some of the dental apomorphies of *Adapis*. As thus restricted, Adapidae consists of *Adapis* (*A. parisiensis*, *A. sudrei*), *Leptadapis* (*L. magnus*, *L. stintoni*), *Paradapis* (*P. ruetimeyeri*), *Alsatia* (*A. dunaifi*), and *Simonsia* (*S. lynnae*). Comparison of adapid last deciduous premolars (upper and lower) with the anterior molars of indriids shows a striking morphological correspondence between these teeth and suggests a phylogenetic relationship between these two families, with which *Lepilemur* also appears affined. Similarly, certain dental characters of the cheirogaleid + lorisid + galagid group are also possessed by certain Eocene non-adapid (*sensu stricto*) forms, e.g., *Anchomomys gaillardi* and *Periconodon helveticus*; a larger clade subsuming all of these forms as a distinct subclade may also embrace *Tarsius* and at least some of the numerous fossil "tarsoids."

INTRODUCTION

Where fossil records are sparse, explicit phylogenetic hypotheses tend to be few. This generalization, while possibly rendered facile by certain trends in systematics over the last couple of decades or so, is fully exemplified by the "lower" primates of Asia, Africa, and Madagascar: the lorises, bushbabies, and lemurs. All of these are classified together in the primate suborder Strepsirhini, or, if one throws the enigmatic tarsier in with them, the suborder Prosimii. Although they are represented by numerous genera and species of a wide-range of sizes, habitats, and adaptations, these primates tended to be looked upon implicitly as a rather homogeneous array of "primitive" forms. Since Gregory's review of 1915, the strepsirhines have been divided systematically along geographical lines, the "mainland" lorises and bushbabies of Asia and Africa being separated at the superfamilial level or thereabouts from the lemurs of Madagascar. Each group has been seen as an independent "survivor" from the Eocene: conventional wisdom has it that the lorises/bushbabies retreated into specialized nocturnal niches that took them out of competition

with the monkeys and apes, while the lemurs diversified in the splendid isolation of their own microcontinent. And there, pretty much, the matter has tended to rest.

Almost certainly, the reason why the question of the phylogenetic relationships of the strepsirhines has traditionally been relegated to its pale reflection in their classification is that there exists virtually no post-Eocene fossil record of the group. Both the few Miocene lorisoids known, and the subrecent extinct lemurs of Madagascar, are closely related to extant forms and in no way can be considered as ancestral to or even as "close to" the ancestry of any living strepsirhine. Moreover, although the primates of the Eocene (and even those of the Paleocene) have traditionally been classified within the Prosimii, many of them within the superfamily Lemuroidea, the 50-odd million years that separate the primates of the Early Tertiary from the lower primates of today seem to have discouraged most primate systematists from doing anything other than to conclude that the early prosimians, or at least those usually classified within the family Adapidae, were in some very general

way "ancestral" to the lower primates of today. We return to the question of the content and the affinities of the Adapidae in the last part of this contribution.

Very rarely, a particular Eocene primate has been proposed as putatively ancestral to living strepsirhines. For example, Gregory (1915) suggested that the Eocene *Pronycticebus* might lie somewhere near the common ancestry of lemurs and lorises, while Simons (1962) narrowed this potential ancestry down to that of the lorisoids alone. More commonly, paleontologists have simply pointed to characters in which extant strepsirhines, e.g., *Lepilemur* (Gregory, 1920), or *Hapalemur* (Gingerich, 1975), show similarities to one or more Eocene forms. But in such cases the assumption has always been that the Malagasy genus in question has simply remained "primitive." The question of potential relationships between particular Eocene primates and extant strepsirhines is taken up at the end of this contribution. But whatever conclusions may be reached in this regard, it remains true that at the present state of our knowledge the fossil record is unable to contribute anything of substance to our understanding of the evolutionary relationships among the many extant genera of strepsirhine primates.

The comparative study of the surviving strepsirhines thus provides the only available avenue for exploring these relationships, and several studies of this kind have been made over the past 10 years. Most of these have focused on the problem posed by the cheirogaleid lemurs. In 1970, Charles-Dominique and Martin called attention to a suite of similarities, mostly behavioral, between the cheirogaleids and the lorisoids, and particularly between *Microcebus* and *Galago demidovii*. These authors concluded that such similarities were best explained as common ancestral retentions, but before long Szalay and Katz (1973) proposed that many of the characters shared between cheirogaleids and lorisoids are in fact derived; that, in other words, these two groups are more closely related to each other than the cheirogaleids are to the other Malagasy lemurs. Cartmill (1975), in a detailed consideration of carotid circulation, auditory bulla construction, and the

architecture of the medial orbital wall, found that the morphology of these regions suggested that the lorisoids were probably derived from a "cheirogaleid near *Allocebus*." He was reluctant, however, to transfer Cheirogaleidae to Lorisiformes.

In the first detailed comparison of the dentitions and cranial anatomy of all the Malagasy strepsirhines (Tattersall and Schwartz, 1974, 1975), we concluded that the cheirogaleids are indeed most closely allied to the lorisoids, but we found it extremely difficult to be certain of the interrelationships among the remaining Malagasy forms. Over the past several years we have continued this investigation, and have broadened it to include detailed consideration of the lorisids and galagids; in this contribution we report our findings. Since we believed it important to incorporate as far as possible all known strepsirhines, living and fossil, into the study, we have paid most attention to the dentition, which represents the only anatomical region that is comparable throughout the spectrum of primates involved. Traditionally, the teeth of fossil lower primates have been described and studied in much greater detail than those of the extant forms; and in the absence of adequate previous descriptions we have found it necessary to provide detailed accounts of the dentitions of the living strepsirhines in the first section of this report, both to achieve a comparable level of dental detail with the fossils and to accumulate an adequate number of dental characters to permit the analysis of phylogenetic relationships.

Since in most strepsirhines there is relatively little dental variation among species belonging to the same genus, our descriptions and comparisons are largely at the level of the genus. Only in those rare cases where there is a substantial difference in dental morphology between congeneric species do we provide descriptions of individual species, or brief supplements covering intrageneric dental variation. In the lower-level systematics of the Malagasy primates we follow the generic and specific nomenclatures adopted by Tattersall (1982); in the case of the Afro-Asian forms we follow the nomenclature of Napier and Napier (1967), with the exception that we regard *Euoticus* as a full genus, rather than

as a subgenus of *Galago*. We recognize that, especially in the wake of our morphological findings and the as yet unpublished studies of Olson (1979), the nomenclature of the galagids clearly requires revision; but this is outside the scope of this contribution and in any event the generic or specific nomenclature involved does not affect our conclusions as to evolutionary relationships.

In the entire assemblage of living forms under discussion we recognize seven families: Cheirogaleidae (*Cheirogaleus*, *Microcebus*, *Mirza*, *Phaner*, *Allocebus*); Lorisidae (*Loris*, *Arctocebus*, *Perodicticus*, *Nycticebus*); Galagidae (*Galago*, *Euoticus*); Lemuridae (*Lemur*, *Varecia*, *Haplemur*); Indriidae (*Indri*, *Propithecus*, *Avahi*); Daubentonidae (*Daubentonia*); and Megaladapidae (*Lepilemur*). In case the reader finds this last familial name surprising, we should note that both *Lepilemur* and the giant extinct lemur *Megaladapis* should clearly be placed in the same family, and that the earliest name for a family-group taxon based on one of these forms is not *Lepilemurinae* Rumpler and Rakotosamimanana, 1972, but is, rather, *Megaladapinae* Major, 1894. Hence our use here of the name *Megaladapidae* for the family embracing both genera; and we must admit to finding it rather gratifying that *Megaladapidae* is not (yet) extinct.

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DENTAL MORPHOLOGY OF THE LIVING STREPSIRHINE PRIMATES

As we have noted, the dentition of none of the extant strepsirhines has been adequately described, even though the dentition is the system that permits the closest comparison of these "primitive" forms with putative fossil relatives. In the following account we attempt to correct this situation by describing in detail the dentitions of all living strepsirhine genera. This in turn sets the scene for comparisons with the fossil forms considered later in this contribution, as well as providing a basis for our discussion of the phylogenetic relationships among the living lemurs, lorises, and bushbabies. We provide discussion of intrageneric variation in dental morphology only where it is substantial enough to warrant comment; among most lemur genera this is not the case, whereas it clearly is in *Galago*, probably reflecting the fact that this genus requires extensive systematic reappraisal. The Contents lists the order in which the genera and species are described, and figure 1 illustrates the terminology used in the descriptions.

FAMILY LEMURIDAE

GENUS *LEMUR*

Within the genus *Lemur* there exists considerable variation among species and subspecies in the size and detailed morphology of the dentition; morphological variation is particularly marked in the upper jaw. *Lemur catta* is strikingly distinct from the other species conventionally assigned to its genus (but which may prove in fact to merit generic distinction) and we describe it separately here. We use *Lemur fulvus* as our "exemplar" for the other species, and note below some of the dental variations that occur within the group.

The other species of *Lemur* differ from *Lemur catta* in a variety of characteristics that they share among themselves. Among the most striking of these are the following: smaller M_3^3 ; distinct protostyle development on M^{1-2} ; lower premolars typically smaller; posterior lower premolars with a more developed anterior basin; trigonids and talonids on M_{1-3} enclosed by more continuous crests.

Within the non-*Lemur catta* group morphological differences are found primarily in the degree to which M^{1-2} protostyles and hypocone regions are developed; the degree to

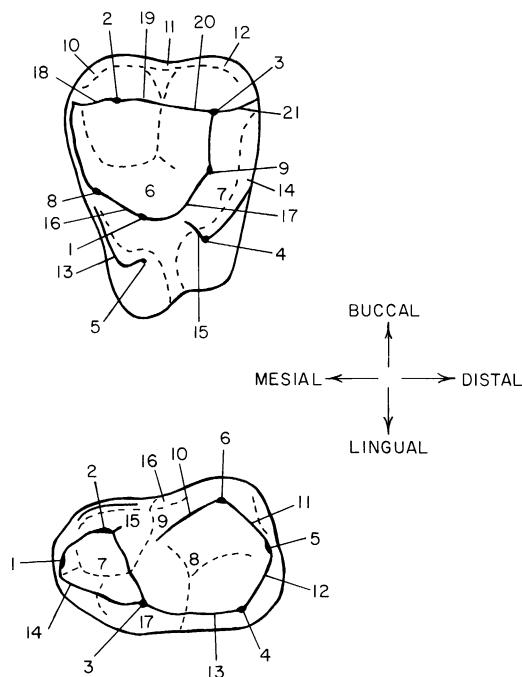


FIG. 1. Diagram to illustrate dental nomenclature employed in this publication. Above is first upper left molar, and below is first lower right molar, of "*Periconodon*" *pygmaeus*, *sensu* Szalay and Delson (1979). Upper molar: 1, protocone; 2, paracone; 3, metacone; 4, hypocone; 5, pericone; 6, trigon basin; 7, talon basin; 8, paraconule; 9, metaconule; 10, parastylar region; 11, mesostylar region; 12, metastylar region; 13, precingulum; 14, postcingulum; 15, prehypocone crista (or protocone fold if crista contacts the protocone apex); 16, preprotocrista; 17, postprotocrista; 18, preparamacrista; 19, postparamacrista; 20, premetacrista (19 + 20: centrocrista); 21, postmetacrista. Lower molar: 1, paraconid; 2, protoconid; 3, metaconid; 4, entoconid; 5, hypoconulid; 6, hypoconid; 7, trigonid basin; 8, talonid basin; 9, hypoflexid notch; 10, cristid obliqua; 11, hypocristid; 12, postentocristid; 13, postmetacristid; 14, paracristid; 15, protostylid region; 16, buccal cingulid; 17, metastylid region. Modified after Szalay and Delson (1979).

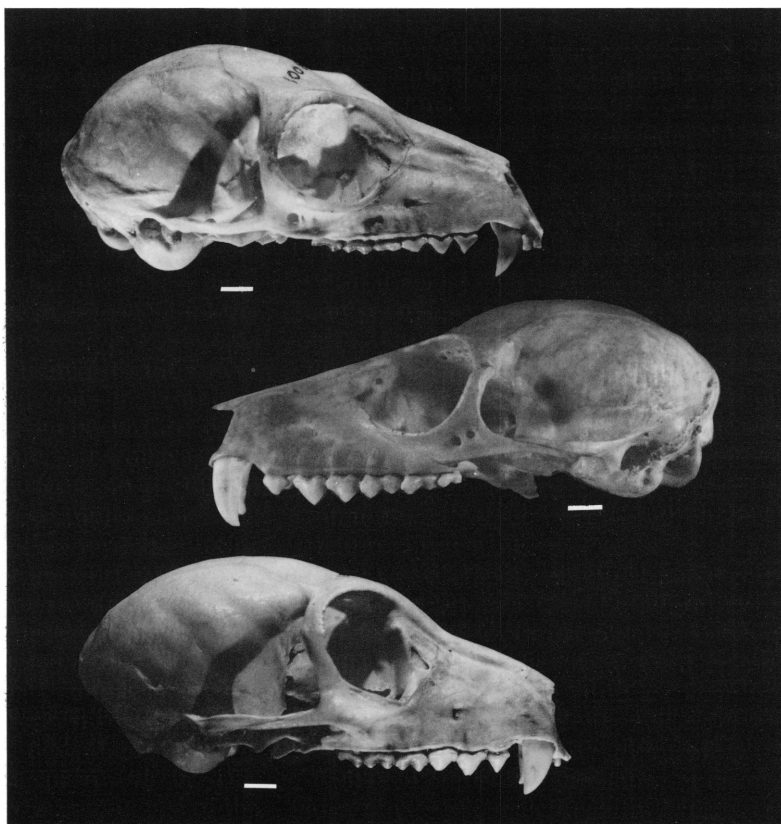


FIG. 2. Crania in lateral view of *Lemur* and *Varecia*. Top: *Lemur catta* (AMNH 100825); middle: *Varecia variegata variegata* (AMNH 77792); bottom: *Lemur fulvus rufus* (AMNH 100569). All scales represent 5 mm.

which the lower and, especially, the upper M_3 s are reduced; the extent of the reduction in size of the upper anterior and lower middle premolars; and the amount of lingual filling-out of the upper posterior premolars.

LEMUR CATTa

UPPER DENTITION (Figs. 2, 3, 4)

The upper incisors are rather diminutive teeth with low, spatulate, mesially distended crowns. The lateral incisor is about two-thirds the size of the central incisor and is noticeably separated from it. The central incisors are broadly separated from each other by a marked anterior extension of the palatine fenestrae.

The upper canine is an extremely tall, laterally compressed, dagger-like tooth that is moderately recurved posteriorly and which

flares slightly outward (i.e., buccally) at its tip. The tooth sits in a bony depression.

The anterior premolar lies somewhat behind the canine and is slightly separated from the middle premolar. The anterior premolar is not greatly lower than the other premolars and rises slightly higher than the molars; it is rather compressed buccolingually and its paracone bears sharp edges that terminate inferiorly in small but distinct styles; the anterior edge is gently convex whereas the posterior edge is slightly concave. In buccal view, the crown approximates an equilateral triangle.

The middle premolar is approximately two-thirds longer, but is more than twice as wide as the anterior premolar. Like its anterior neighbor, the middle premolar bears a large, compressed paracone with very sharp edges that terminate inferiorly in small but dis-

tinctly raised styles. In buccal outline the tooth approximates an equilateral triangle with a straight anterior edge and a slightly convex distal edge. The width of the crown is augmented by a low, inferiorly sloping, somewhat distally oriented, lingual distension. The slope and linguodistal orientation of this distension are enhanced by a rounded crest that borders a larger, shallow, posteriorly descending depression which may be bounded basally by a very thin postcingulum. A small, barely excavated anterior depression is bordered inferiorly by a very low lingual cingulum.

The posterior premolar is almost as long and wide as M^1 . The large, compressed paracone bears equally long and compressed edges that terminate inferiorly in raised styles that bulge a bit buccally. From these styles fairly thick pre- and postprotocristae converge centrally on the apex of a moderately developed protocone. The sides of the protocone are relatively long and are swollen inferiorly by a rounded band of cingulum that surrounds the cusp externally.

The upper molars possess a moderately low, but very broad, protocone incorporated into broadly divergent protocristae that bypass the buccal cusps to join the stylar regions. The paracone and metacone are quite compressed and are bounded on all sides by distinct crests. These cusps become more dramatically compressed and incorporated in the cresting system, and move markedly apart, from M^1 to M^3 ; the metacone also becomes relatively reduced in sequence so that on M^3 it looks like a large metastyle. M^3 retains a fairly triangular shape because there is minimal lingual development lingually. M^{1-2} bear an extremely thick, ledgelike cingulum that surrounds the protocone on its sides externally; it is most distended lingually and "straightens-up" that side of the tooth. On M^2 the distolingual corner of the tooth is squared-up; the mesiolingual corner of the tooth is more distended. On M^1 the cingular ledge is more rounded and is basically confined to the mesiodistal length of the protocone. M^2 is the largest molar, being bulkier and somewhat longer and wider than M^1 ; M^3 is a bit longer than M^1 but is markedly narrower buccolingually. The lingual plane of the molar series is thus offset obliquely.

LOWER DENTITION (Figs. 5, 6, 7)

The six lower anterior teeth are quite elongate and procumbent and the crowns curve gently upward toward their tips. The four central teeth are somewhat compressed laterally and bear thin distinct margocristids that lie inferiorly and delineate a central, rounded "keel." The lateralmost teeth of the six are more robust, broader and deeper, and flare laterally. They bear a ledgelike lateral and a thin medial margocristid; their crowns are somewhat skewed toward the midline.

The anterior premolar is not set too far behind the toothcomb but is quite well separated from the middle premolar. The anterior premolar is basically fairly tall, compressed, and bladelike. In buccal view, the crown forms a tall, broad-based triangle with a slightly convex anterior edge and a more concave posterior edge. The posterior edge terminates inferiorly in a small but bulky and rounded heel, whereas the anterior edge becomes a more acutely angled, pointed projection; the latter structure is also flexed somewhat lingually. Inferiorly and posterolingually, the crown is swollen and displays a narrow, shallow, vertical depression. This is a much fainter lingual depression anteriorly.

The middle premolar is approximately the height of the posterior premolar and both rise noticeably above the molars; it is, however, not quite two-thirds the height of the anterior premolar. The middle premolar is shorter mesiodistally than the anterior premolar but is subequal in width. The tooth bears a somewhat compressed, rather straight anterior edge that terminates inferiorly in a small but distinct stylid. The posterior edge is much longer with a gentler slope; this edge is crestlike, terminates posteriorly in an upwardly flexed, mesiodistally compressed and ledgelike heel, and forms the buccal border of a moderately excavated, distolingually opening, teardrop-shaped basin that descends from the apex of the protoconid. This basin is bordered lingually by a crest that descends from the apex of the protoconid. There is a short lingual cingulid that courses from the anterior stylid.

The posterior premolar is almost as long as, but a bit wider than, the anterior premolar. It bears a stout, straight, and crestlike



FIG. 3. Crania in ventral view of *Lemur* and *Varecia*. Top: *Lemur catta* (AMNH 100925); middle: *Varecia variegata variegata* (AMNH 77792); bottom: *Lemur fulvus rufus* (AMNH 100569). All scales represent 5 mm.

anterior edge that terminates in a moderately developed and broad stylid from which courses a low lingual cingulid that proceeds up to the apex of the small metaconid lying partway down the side of the protoconid; there is a sharp crest between these two cusps which, with the anterior edge and lingual cingulid, border a very shallow, steeply descending trigonid basin. The posterior edge of the tooth is also quite crestlike and terminates at a moderately enlarged, upwardly flexed, ledge-like heel; the edge is buccally emplaced. This edge borders a fairly deeply excavated, broadly teardrop-shaped basin that opens posterolingually. The compressed posterior border of the metaconid bounds this basin lingually.

On all molars the protoconid and metaconid are compressed and connected between

their apices by a sharp crest; the metaconid gets smaller, and is emplaced farther away from the protoconid, in the series M_{1-3} . On each molar, the metaconid is positioned only slightly posterior to the protoconid. A distinct paracristid courses down the face of the protoconid, turns, and proceeds posteriorly as a broad ledge to the base of the metaconid where it is broken by a crease before continuing as a thinner structure up the face of the metaconid. The subtended shallow trigonid basin is longest and broadest on M_1 and shortest and most distolingually oblique on M_3 . The cristid obliqua courses buccally, straight from the hypoconid to the metaconid, on M_1 , whereas it terminates lingual to the midline of that cusp on M_{2-3} ; this crest is most distinct and elevated on the posterior two molars. The moderately developed hy-

poconid and smaller entoconid are compressed and incorporated into the continuous cristid obliqua and hypocristid; these cusps are largest on M_2 and subequal in size on M_1 and M_3 . The talonid and its basin are oddly compressed so that the cristid obliqua and the postmetacristid are roughly parallel. On M_1 the talonid basin also opens or "empties" posterolingually via a moderately incised groove between the base of the entoconid and the terminus of the postmetacristid. The talonid basins of all molars are well excavated and those of M_{2-3} are enclosed by a continuous series of crests. The talonid basin of M_1 is subcircular, whereas that of M_3 is more ovoid. The postmetacristid of M_1 is thickened into a small metastylid about halfway down its length; M_2 bears an even more diminutive metastylid-like swelling and the postmetacristid of M_3 is unadorned. The protoconids of M_{1-3} are somewhat swollen buccally and bear a slip of cingulid inferiorly. M_1 is slightly shorter mesiodistally than M_2 , and M_3 is slightly shorter than M_1 . Because of the truncation of its distolingual corner, M_1 appears much narrower than M_2 , almost as narrow as M_3 . Although lacking such a structure, M_3 gives the impression of having a slight heel; this is due to the externally rounded entoconid being emplaced rather posteriorly and the hypoconid somewhat anteriorly.

LEMUR FULVUS (L. f. rufus)

UPPER DENTITION (Figs. 2, 3, 4)

The upper incisors are small and low-crowned, with slightly convex buccal surfaces and partially excavated lingual surfaces that bear a central pillar. The second incisor lies almost directly behind but slightly lateral to the central incisor; the latter is about two-thirds the size of the second incisor. The left and right incisor pairs are separated by the large anterior incisor pairs. The upper canine is large, trenchant and laterally compressed, and is noticeably recurved toward its tip. It is deeply emplaced in the maxilla, which is excavated lingual to this tooth to receive the tip of the lower anterior premolar.

The anterior upper premolar is the smallest and morphologically the simplest of the three, and is separated from the canine by the excavation noted earlier. The anterior premolar

is somewhat compressed laterally, and is dominated by the paracone which bears tiny styles at its base anteriorly and posteriorly; the anterior style is the more distinct of the two. A faint cingulum marks the lingual side of the tooth, which in lateral outline is roughly equilaterally triangular. The middle upper premolar also appears more or less this shape in buccal outline, but its anterior edge is more elongate and its stylar regions bulkier. In occlusal view the crown is also triangular due to the presence of a marked lingual swelling associated with a third root. A "preproto-crista" runs down the large paracone to terminate in a small stylelike structure on the end of the lingual swelling. Thin "pre-" and "postcingulae" traverse the sides of the tooth to become confluent around this distension, which faces somewhat posteriorly. The posterior upper premolar is rectangular in shape, being narrow mesiodistally and the widest tooth in the jaw buccolingually. Moderately developed anterior and posterior paracone styles make the buccal portion of the tooth a little longer than the lingual part. The well-developed protocone is nonetheless well filled-out and is squared-off at its corners, the anterior of which bears a distinct protostyle. A preprotocrista, incorporating a small paracnule, runs to the midline of the paracone, while a postprotocrista swings around the cusp to become confluent with the posterior buccal style. Faint "pre-" and "postprotocingulae" traverse the sides of the tooth; the former terminates at the protostyle, whereas the latter fades out along the lingual face of the tooth.

The upper molars are characterized by low, long protocones from which emanate arcuate protocristae that terminate at the midlines of their respective buccal cusps, and their trigon basins are truncated buccolingually. These molars bear distinct centrocrisae which become more accentuated as the paracone and metacone are increasingly squared in the series M^{1-3} . The preparacristae of all molars are relatively well developed; only M^{1-2} bear comparable postmetacristae. The anterolingual corner of each upper molar is distended. On both M^{1-2} there is a massive protostyle, more angular in the former and more narrowly elongate in the latter. M^1 bears a modest, stylelike hypocone, whereas on M^2 this

region is very poorly developed. M^2 is bulkier in all dimensions than is M^1 , whereas M^3 is only about the size of the trigon of M^2 .

LOWER DENTITION (Figs. 5, 6, 7)

The six anterior lower teeth are elongate and procumbent. The central four are fairly parallel-sided and bear thin margocristids on either side of a low, rounded central "keel." The lateral teeth are larger, deeper, and flare laterally; their broad, low central keels are bounded by quite well-developed margocristids. Inferiorly, the flared area is angular rather than smoothly rounded, and the occlusal surface of these teeth is turned somewhat inwardly.

The anterior premolar is the tallest of these teeth, standing about twice as high as its posterior neighbor. In buccal outline this former tooth is triangular, and the crown juts forward to overhang the root. Posteriorly, there is a moderately developed heel, and lingually there is a low, broad pillar that descends from the protoconid and subtends a broad and shallow anterior depression as well as a much narrower posterior one. The anterior lower premolar is separated from its anterior and posterior neighbors by noticeable diastemata. The middle lower premolar is the smallest of the three premolars in all dimensions. In buccal view its posterior edge is somewhat longer than the anterior, and descends to a small "heel." The posterior edge and a weak lingual crest that descends from the tip of the protoconid subtend a shallow, teardrop-shaped basin. The tooth is somewhat swollen posterolingually and is set slightly obliquely in the jaw. Only faint traces of lingual cingulid exist. The posterior premolar is about as long anteroposteriorly as the first molar, but is not as wide buccolingually. It is dominated by a stout, centrally placed protoconid to which a smaller metaconid is closely appressed. These two cusps are connected by a stout crest, which separates large anterior and posterior basins. The posterior basin is slightly deeper and more excavated than the anterior, and its inferior border bears a series of small cuspules. In buccal view a small stylid is seen anteriorly, and there is a trace of cingulid posteriorly.

M_{1-2} are subequal in all dimensions; M_3 is

much smaller. All molars are characterized by the continuity of the marginal cristids which incorporate rather diminutive cusps and completely enclose the talonid and trigonid basins. The cristid obliqua terminates at the midline of the protoconid in each molar, and the protoconid and metaconid are connected by a distinct crest. The paracristid descends anteriorly down the face of the protoconid, at the base of which it thickens markedly as it courses toward the metaconid. On M_1 , and less so on M_2 , this distinct paracristid courses up the face of the metaconid, but in M_3 it is much less well developed. The trigonid basin on all molars is narrow and fairly shallow, becoming more compressed from M_{1-3} . On M_{1-2} especially, the distolingual portion of the talonid is a bit distended, and a very tiny and peripheral entoconid in this region may be twinned, at least on M_2 . All lower molars bear fairly complete buccal cingulids, and show some pitting in the enamel of the basins.

GENUS *VARECIA*

VARECIA VARIEGATA

UPPER DENTITION (Figs. 2, 3, 4)

The upper incisors are relatively small with low, spatulate, and mesiodistally elongate crowns. The roots of the two central incisors are well separated, but the crowns of these teeth converge markedly through a long mesial extension that occupies more than half the width of the crown. The lateral incisors are much smaller, but are of similar morphology, and are positioned obliquely behind the central pair.

The anterior premolar is a low (even more so than M^1), relatively simple tooth, somewhat compressed buccolingually. In buccal outline the tooth is triangular, with subequal sides and a long base. The anterior and posterior edges are somewhat compressed, and distended inferiorly into moderate stylar processes. Shallow depressions subtend a thickened lingual paracone "pillar." Faint lingual cingulae may variably ring the crown.

The middle premolar is almost twice the height of the anterior premolar and is the tallest of the three. This tooth is dominated by a large, pointed paracone whose distended

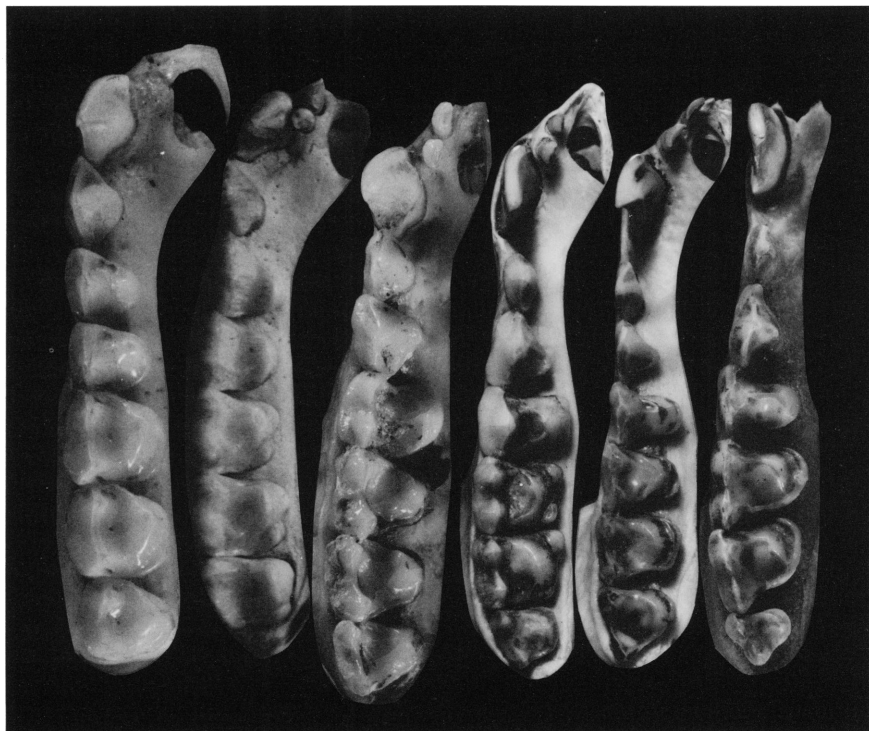


FIG. 4. Upper right dentitions in occlusal view of the lemurids and *Lepilemur*. From left to right: *Lepilemur mustelinus leucopus* (AMNH 170575); *Hapalemur simus* (BMNH 70.9.2.2); *Hapalemur griseus griseus* (AMNH 100534); *Lemur fulvus rufus* (AMNH 100569); *Lemur catta* (AMNH 100825); *Varecia variegata variegata* (AMNH 17792, incisors lost). Not to scale.

edges bear stout crests terminating in distinct stylar regions; the parastyle is quite developed, compressed and flexed linguallly. A thick postcingulum becomes confluent with a much thinner precingulum around the basally swollen lingual paracone "pillar." A raised crest descends the face of this "pillar," and borders a large but shallow posterior lingual depression.

The posterior premolar is almost as tall and as long mesiodistally as the middle premolar, but is much wider buccolingually and comparable to M^{1-2} in this respect. The paracone of the posterior premolar and its attendant edges, crests and stylar regions resemble those of the middle premolar. There is, however, a moderately developed protocone to whose apex runs the lingual paracone crest. This crest appears also to run faintly down the side of the protocone (as a weak protocone fold), to become confluent with the variably thick-

ened postcingulum that proceeds as far as the base of the lingual cusps; a thinner precingulum fades out well before reaching the protocone. The paracone-protocone crest bisects the crown into a large, broadly sloping moiety and a smaller anterior component. Since the protocone is narrower than the distended stylar regions, the posterior premolar is broadly T-shaped in occlusal view.

The molars are characterized by relatively small, subequal buccal cusps that are bound on all sides by stout crests; distended para- and metastylar regions; enlarged, low anteriorly displaced protocones; and large, shallow, posteriorly sloping trigon basins. The protocone looks more like a greatly thickened preprotocrista than a cusp.

At the base of the paracone there is a bifurcation with a thin crest running up the face of the cusp and a slightly more distinct crest coursing around to meet the parastylar

region. The absence of any postprotocone crest opens up and expands the trigon basin posteriorly, but this basin is truncated lingually by a thick protocone fold that courses to, and may join up with, the low, well-developed postcingulum; there may be a swelling of the enamel at this juncture. There may also be a thin precingulum on M^1 , but M^1 and especially M^2 bear a distended expanse of cingulum around the protocone anterolingually which becomes confluent with the postcingulum; this region is merely swollen a bit on M^3 . On M^1 , a distinct style protrudes from the cingulum at the midline of the tooth; a low, broad crest descends to this style from partway up the face of the protocone.

There is a distinct "obliqueness" to the lingual face of the molar series as a whole. M^3 is quite small, and is twisted such that its parastylar region overlaps the metastylar region of M^2 . The parastylar region of the much larger M^2 overlaps the metastylar region of M^1 and the lingual cingulum of the former tooth is most distended anteriorly. The slightly shorter M^1 is wider buccolingually due to the greater distension of its cingulum lingually.

LOWER DENTITION (Figs. 5, 6, 7)

The six lower anterior teeth are quite elongate and procumbent and their tips curve slightly upward. The central four teeth are narrow and laterally compressed; there are very thin, low-set margocristids on each side of the crown. The lateral tooth of the dental comb is much larger, and its crown flares laterally; a moderately thick lateral and a thin medial margocristid are separated from a central "keel" by narrow longitudinal depressions. The crown of the lateralmost tooth is tilted slightly toward the midline.

The anterior premolar is set slightly behind the toothcomb but is more markedly separated from the middle premolar; it is fairly tall, somewhat laterally compressed and elongate, and bladeliike. The anterior edge is rather straight and blunt, whereas the somewhat longer posterior edge is gently concave and compressed. The anterior edge terminates inferiorly in an angular corner that extends quite far from the root; the posterior

edge terminates in a less distended, more rounded "heel." A low lingual paracone "pillar" separates a narrow anterior from a broader posterior shallow depression.

The middle lower premolar is the smallest of the three in height and length; it is a bit wider buccolingually than the anterior premolar even though it is less than half as tall and is somewhat shorter mesiodistally. The middle premolar is dominated by a large protoconid which bears a short, stout anterior edge and a much longer, more compressed posterior edge; both edges terminate in distinct, pointed stylids with the posterior stylid being larger and more distended. Distinct cingulids run from these regions to become thinner as they join up around the swollen base of a thick lingual protoconid "pillar." This "pillar" is bounded by a small, moderately excavated anterior depression and by a much shallower depression that opens posterolingually.

The posterior premolar is about 25 percent taller than and about two-thirds the length and width of M_1 . In basic design this premolar is similar to the middle premolar, although the anterior and posterior stylids are relatively larger and more distinct and the depressions are more excavated. The lingual protoconid "pillar" is more compressed, more swollen basally, and bears a small metaconid inferiorly.

The lower molars are similar in that the large protoconid and larger hypoconid are compressed and elongate, and connected by a tall cristid obliqua; the talonid basins are long, moderately excavated, and "empty" posterolingually beyond a small, low, compressed entoconid that is incorporated into a long, stout postmetacristid. The protoconid and metaconid are quite closely positioned on M_1 and farthest apart (with the metaconid quite posterior to the protoconid) on M_3 ; the crest connecting these cusps is thickest and highest on M_1 and the weakest and lowest on M_3 . On M_1 , a stout paracristid courses anteriorly from the protoconid but arcs lingually as it proceeds inferiorly, posterolingually, and up the face of the metaconid; it borders a tall but shallow trigonid basin. On M_{2-3} , this crest proceeds a short distance anteriorly then "kinks" severely and courses in-



FIG. 5. Lower jaws in lateral view of lemurids and *Lepilemur*. Descending from top: *Lemur fulvus rufus* (AMNH 100569); *Varecia variegata variegata* (AMNH 77792); *Lemur catta* (AMNH 100825); *Lepilemur mustelinus leucopus* (AMNH 170575); *Hapalemur simus* (BMNH 70.9.2.2); *Hapalemur griseus griseus* (AMNH 100534). All scales represent 5 mm.

feriorly and quite posterolingually until it joins the metaconid. M^{1-2} bear a short, stout, truncated hypocristid emanating from the hypoconid, but M_3 possesses a small "heel." M_2 is slightly shorter than M_1 , but is wider buccolingually; M_3 is about one-third smaller.

GENUS *HAPALEMUR*

Hapalemur contains the large monotypic species *H. simus* (now, and possibly always, extremely rare), and the smaller species *H. griseus*, within which we recognize three subspecies. Subspecific dental differences in *H.*

griseus are too small to warrant separate description of the subspecies here, but those between the larger and smaller species are significant.

HAPALEMUR GRISEUS

HAPALEMUR GRISEUS GRISEUS
(AMNH 100534)

UPPER DENTITION (Figs. 4, 8, 9)

The right and left central incisors are widely separated with the lateral incisors emplaced immediately behind so that they are hidden from the front by the central incisors. The central teeth are only slightly larger than the lateral. Both incisors are extremely low-crowned with a gently arcing occlusal edge and a somewhat concave lingual face.

The upper canine is stout, trenchant, and laterally compressed, rising moderately above the anteriormost premolar and greatly above the posterior cheek teeth. This tooth arcs backward and possesses a strong, broad, longitudinal, lingual pillar that separates a narrow, shallow vertical, anterior depression from a broader, shallow posterior depression that opens lingually. There is but a minute basal heel internally. The tooth sits in a relatively deep lingual maxillary depression.

Each of the three premolars is three-rooted. The anteriormost of the set is taller than the middle premolar, which is in turn somewhat taller than the last premolar. All three emphasize buccal shearing crests. The anterior premolar is dominated by a paracone bearing a strong, broad lingual pillar that separates a very narrow and shallow anterior depression from a much broader posterior one. These depressions are bounded inferiorly by weak lingual cingula that meet at the base of the basally swollen paracone and form a short, flattened, vertically ascending "style" (reminiscent of *Lepilemur*). This tooth is triangular in buccal outline.

The middle premolar is squatter and bulkier than the anteriormost premolar. It is broader buccally and is more distended over the lingual root; the shallow anterior and posterior lingual depressions are broader and there is a small metacone which is incorporated into the crest that emanates buccally

from the paracone. The anterolingual basal cingulum is moderately developed but terminates farther up and more anteriorly on the lingual paracone pillar than it does on the anterior premolar. The weak posterior lingual basal cingulum becomes stronger as it courses up the base of this pillar, resembling here a protocone fold. Buccally, the middle premolar bears poorly defined metacone and paracone pillars; the latter borders a narrow anterior groove.

The posterior premolar is molariform, and although shorter buccally than the molars it is the broadest cheek tooth buccolingually and approximately of equal height with the molars. The subequal and closely approximated paracone and metacone are distinctly compressed and bear strong, but truncated, prepara-, postmeta-, and centrocristae. A sharp preprotocrista, moderately developed, courses anteriorly and meets a strong precingulum. Whereas the mesial side of this tooth is waisted below the paracone, it is convex distally; thus the low, flat postcingulum curves around, subtending a broad, shallow talon basin, before running distally up the face of the protocone. The postprotocrista terminates in multiple, small, globular "metacornules"; this effectively opens the trigon basin distally into the talon basin.

All molars are characterized by markedly compressed and widely separated paracones and metacones. Each bears a strong centrocrista and equally strong but very short preproto- and postmetacristae, as well as a distinct postcingulum that courses from the metastylar region to fade out at the base of the protocone. The ridgelike preprotocrista arcs around the paracone and joins the parastylar region. The lack of a postprotocrista, in conjunction with a de-emphasis of the distal face of the protocone, causes the trigon basin to open distally. In addition, each molar possesses a broad, somewhat low lingual paracone pillar that captures a narrow groove between it and the preprotocrista and bears a weak precingulum that fades out near the base of the protocone. The first two molars are subequal in size, bear a small globular mesostyle, and are trapezoidal in shape, having somewhat broader lingual faces than the more triangular M³.

LOWER DENTITION

The six teeth that comprise the toothcomb are elongate, quite slender, slightly recurved lingually at the tips, and markedly horizontally inclined. The central four teeth are extremely compressed laterally and parallel-sided, and bear faint lateral margocristids that are overshadowed by a dominant central keel. The lateral teeth are more robust and deeper with a noticeable lateral flare that bears a distinct margocristid; the crowns are rotated somewhat inwardly so that the distal margocristid is facing upward and the broad central keel faces medially.

The anterior two premolars are characterized by having highly crenulated enamel, especially in the posterior depressions, and by an inward, lingual arcing of the strong paracristid, the tip of the protoconid and the heel of the tooth. In both teeth, the posterior moiety is noticeably distended. The anteriormost premolar is somewhat compressed laterally and is dominated by a very tall protoconid. A low but distally ridgelike lingual protoconid pillar distinguishes a moderately broad, shallow depression anteriorly, and a larger, teardrop-shaped posterior basin that appears "filled-in" by enamel wrinkling; this posterior basin is bounded buccally by a distinct ridgelike crest that courses down from the protoconid. In buccal view, the anterior premolar looks roughly triangular, with its long distal slope somewhat concave and its more vertical anterior slope slightly convex.

The middle premolar, although higher-crowned than the posterior cheek teeth, is noticeably shorter than its anterior neighbor. Otherwise, this tooth is basically similar to the anterior premolar in its cresting and in the configuration of the anterior and posterior depressions. The posterior premolar is molariform and its height is equal to that of the molars. This tooth is dominated by strong, broad shearing crests that effectively embody the somewhat compressed cusps. The protoconid is slightly larger than the metaconid; the two cusps are closely appressed to each other and the metaconid bears a small, sometimes globular metastylid. The strong, somewhat buccally emplaced paracristid courses quite anteriorly until it arcs inwardly to ter-

minate as a compressed wall; this creates a very large, deep, and lingually opened trigonid basin. In contrast, the relatively larger talonid basin is enclosed by a complete arcuate crest that in its buccodistal aspect bears merely a swelling of a hypoconid, and in its mesiodistal region but a hint (at best) of an entoconid.

All three molars develop some buccal cingulids anteriorly and are characterized by having strong, rather straight, and buccally emplaced cristids obliquae that terminate at the bases of the protoconids. Each also has a strong, straight, disto-obliquely oriented hypocristid that courses from a flattened hypoconid to the entoconid as well as a stout, severely truncated, and buccally emplaced paracristid that "kinks" near the base of the protoconid to run as a diminishing ledge to the base of the metaconid. The paracristid thus encloses a truncated and steep trigonid basin, slightly open lingually. In addition, a strong crest connects the protoconid and metaconid from tip to tip. The trigonid on M_1 is more compressed than it is on the last two molars, and the first molar bears a large, distinct metastylid. What appears as a talonid heel on M_3 is, in fact, a large, distolingually distended entoconid.

HAPALEMUR SIMUS

UPPER DENTITION (Figs. 4, 8, 9)

The upper incisors are tiny and low-crowned. The crown of the central incisor is approximately 50 percent larger than that of the lateral incisor. Both teeth are similar in having a wrinkled, pitted, and flattish surface complemented by a bulging and inflated one. In the widely separated central incisors, the "flat" surfaces face toward the midline, whereas in the lateral incisors these surfaces face directly posteriorly. The lateral incisors are emplaced almost directly behind but slightly lateral to the central incisors; the roots of the central and lateral incisors are not separated by a bony alveolar septum.

The upper canine is a very stout tooth that is relatively broad at its base and shows little lateral compression. It is somewhat anteriorly rotated in the jaw, so that its mesial edge overlaps the lateral incisor. Its anterior

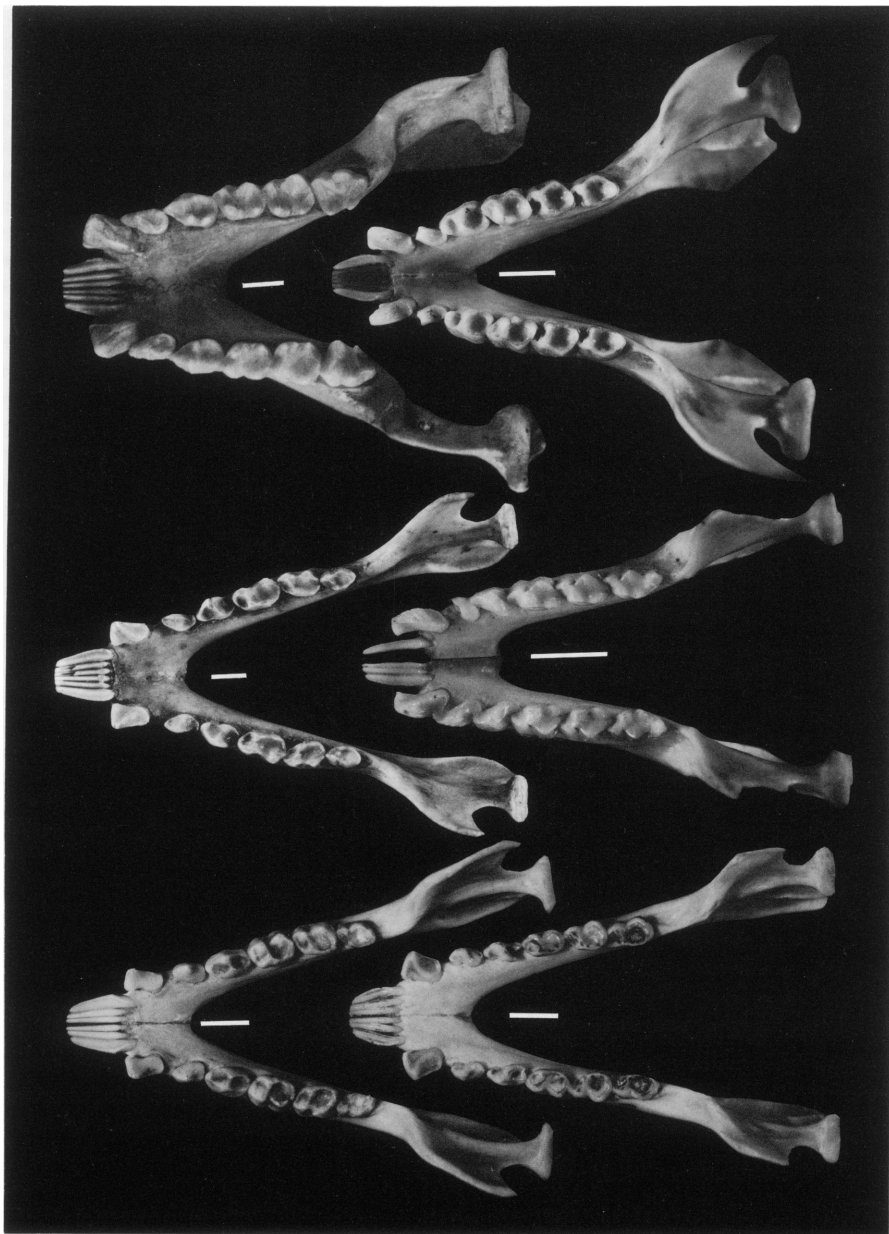


FIG. 6. Lower jaws in occlusal view of lemurids and *Lepilemur*. Clockwise from top left: *Hapalemur simus* (BMNH 70.9.2.2); *Hapalemur griseus griseus* (AMNH 100534); *Lepilemur mustelinus leucopus* (AMNH 170575); *Lemur catta* (AMNH 100825); *Lemur fulvus rufus* (AMNH 100569); *Varecia variegata variegata* (AMNH 77792). All scales represent 5 mm.

edge is gently convex and bears a thickened and raised crest, while the slightly convex posterior edge is sharply compressed; a broad, low lingual "pillar" bears on its anterior aspect a thickened crest which subtends a nar-

row vertical anterior depression. The effective height of the crown is reduced because the tooth is recessed somewhat into the alveolar bone.

The anteriormost premolar is the simplest

and the tallest of the three, its paracone almost attaining the height of the canine; a small diastema between the canine and this neighboring tooth is in part created by the slight anterior and outward skewing in the jaw of the anterior premolar. In buccal outline the premolar resembles an equilateral triangle adorned at its anteroinferior corner by a small, shelflike style which, in turn, is excavated by a small pit. Only the posterior half of the crown bears any cingulum buccally; the lingual cingulum is faint and discontinuous. A thickened, raised vertical lingual crest delineates shallow, rugosely enameled anterior and posterior foveae. In cross-section, the crown is essentially ovoid.

The middle premolar stands only about half the height of its anterior neighbor, but it is somewhat longer anteroposteriorly and is noticeably wider, with a well-developed and posteriorly rounded protocone region. The parastylar region is noticeably elongate anteriorly and is the confluence of a stout preprotocrista and a thickened preparacrista. These two crests, together with a vertical crest or ridge down the lingual face of the somewhat rounded paracone, subtend a shallow lingual anterior depression. The posterior depression is effectively a broad, "scooped-out" talon basin. A tiny metacone is emplaced just to the side of and a bit below the paracone; it is incorporated into the thick, almost denticulate postparacrista. The metastylar region is met by a ledge that is probably the postcingulum. Buccal cingulum development is weak.

The posterior premolar is little longer or wider than the middle premolar, but its sides, especially mesially, are much more filled-in; the protocone region is hence also fuller and broader. Although extensive and deep enamel crenulation pervades the occlusal surface, the trigon basin is essentially open, being subtended only by low pre- and postcingula (?) that emanate from the protocone and course to the stylar regions. The two buccal cusps rise surprisingly little above the level of their stout cristae; even more unusual is that the metacone is quite a bit larger, especially in bulk, than the paracone. These two cusps bear buccal pillars, of which the metacone pillar is much more distinct. There is a weak if fairly continuous buccal cingulum. (Note: an

alternative possibility is that the "metacone" is really a somewhat posteriorly displaced paracone and the "paracone" a displaced parastyle.)

The following features are both distinctive of and common to the upper molars: a compressed and anteroposteriorly elongate protocone, which forms a "corner" with the preprotocrista; an elevated, stout, and bold postprotocrista on M^{1-2} , that terminates on a large, almost pyramidal metaconule; a thickened postcingulum that swells into a long, ledgelike hypocone that is flexed partly around and below the thick protocone fold, from which it is separated by a deep groove or fissure; a protocone fold that angles off the protocone and courses back to the postcingulum; a very steep lingual protocone face; a preprotocrista that courses around the conical paracone to the parastylar region; broadly separated paracone and metacone, especially on M^3 , which are connected by a distinct centrocrista. The metacones of M^{1-2} are conical and just a bit smaller than the paracones; the metacone of M^3 barely emerges from the buccal crest. Molar paracones and metacones are swollen buccally as vertical "pillars" and there are small but distinct para- and metastyles. M^{1-2} have a low, long shelf in the region of a protostyle. M^2 is larger overall than the first and third molars which, even though M^3 has some cusps less developed, are subequal in size. All upper teeth show very rugose and crenulated enamel.

LOWER DENTITION (Figs. 5, 6, 7)

The lower anterior teeth are somewhat slender, elongate, and procumbent and appear relatively small and curiously gracile and fragile when compared with the bulk of the rest of the dentition. The four central teeth are quite compressed laterally and bear faint mesial and lateral cristids below the rounded central keel. The lateralmost teeth of the six are more robust, deeper, and flare somewhat laterally; the lateral margocristid is markedly thick, especially on the inferior half of the crown.

The anteriormost premolar is a stout tooth with a somewhat convex anterior edge and a longer, convex posterior edge; there are small but distinct stylids anteriorly and posteriorly.

The tip of the tooth arcs gently toward the midline and thus the lingual face of the crown is gently concave. A thickened elevated "crest" courses from the apex of the protoconid downward and slightly posteriorly; this "crest" subtends a posterior depression that is partly obscured by the heavily wrinkled enamel. This tooth stands almost twice as tall as the other cheek teeth.

The middle premolar is a low, anteroposteriorly elongate tooth that is compressed and distended anterior to the low protoconid; posterior to this cusp, the crown expands into an enclosed talonid basin. The cristid obliqua and another crest descend from the protoconid; on the latter crest is a low "metaconid." The thick, straight paracristid swells into a stylid ("paraconid") at its end. A rugose and fairly continuous lingual cingulid courses to meet this anterior "stylid."

The posterior premolar is larger in all dimensions than the middle premolar but shares the same general morphology. The metaconid is larger than the protoconid and is set lingually apart from it, thus creating a definite trigonid basin. The talonid is deeper and more expanded and is bordered by a long, localized thickening that corresponds to an entoconid. The cristid obliqua, which forms a notch posteriorly with the entoconid, bears a small "hypoconid" posterior to the protoconid. The parastylar ("paraconid") region is much more robust, but is still met by a buccal cingulid.

The lower molars are characterized by having very compressed trigonids with paracristids that parallel the protoconid-metaconid crest; enlarged and buccally swollen hypoconids; distinct, conical entoconids that contribute to a deep lingual "notch"; and cristids obliquae which are increasingly displaced buccally in sequence from M_{1-3} . In the series M_{1-3} , the protoconid and metaconid become increasingly separated from each other, as do the entoconid and an increasingly enlarging but flattened hypoconulid region. The entoconid and "hypoconulid" are connected by a rugose "crest" that, from M_{1-3} , broadens increasingly into a posterolingually deflected wrinkled surface. M_1 is the narrowest and shortest molar; M_3 is the broadest and stoutest. As in the upper dentition, all lower teeth bear rugose and wrinkled enamel.

FAMILY MEGALADAPIDAE

GENUS *LEPILEMUR*

Lepilemur is a substantially polymorphic genus whose systematics are poorly understood, and within which is found very considerable variation in dental size and morphology. Such marked differences may exist not only between populations from different parts of Madagascar, but also within the same local population. The individual (AMNH 170575) whose dentition we describe and illustrate below is representative of one end of the spectrum of variation found within its population, but other individuals from the same site (Amboasary) are much more "typical" of the dentitions of other *Lepilemur* from elsewhere in Madagascar. The morphological differences between the ends of the spectrum of dental variation in the Amboasary population of *Lepilemur mustelinus leucopus* reside primarily in the acuteness of the cusps and crests of both upper and lower molars, the obliqueness or "fullness" of the upper molar protocones anterolingually, the angularity or roundedness of the upper molar hypocone region, the depth of the lower molar hypoflexid notch, the narrowness buccolingually of the lower molars, and the degree of lingual (protocone) expansion in the middle upper premolar. The specimen described differs from some other Amboasary individuals and from more "typical" *Lepilemur* from elsewhere in the island in showing more acute molar cusps and crests, less rounded-off protocone and hypocone regions, more acute hypoflexid notch, narrower lower molars, and less lingually filled-out upper premolars.

LEPILEMUR MUSTELINUS

UPPER DENTITION (Figs. 4, 8, 9)

The upper incisors are represented only in the deciduous dentition, and then only by one pair of teeth (e.g., Schwartz, 1974).

The upper canine is a trenchant tooth, laterally compressed and moderately recurved posteriorly, that bears a minute, compressed swelling posteroinferiorly. There is a broad, low, central pillar that parallels the curve of the tooth and separates shallow anterior and posterior longitudinal depressions. This tooth

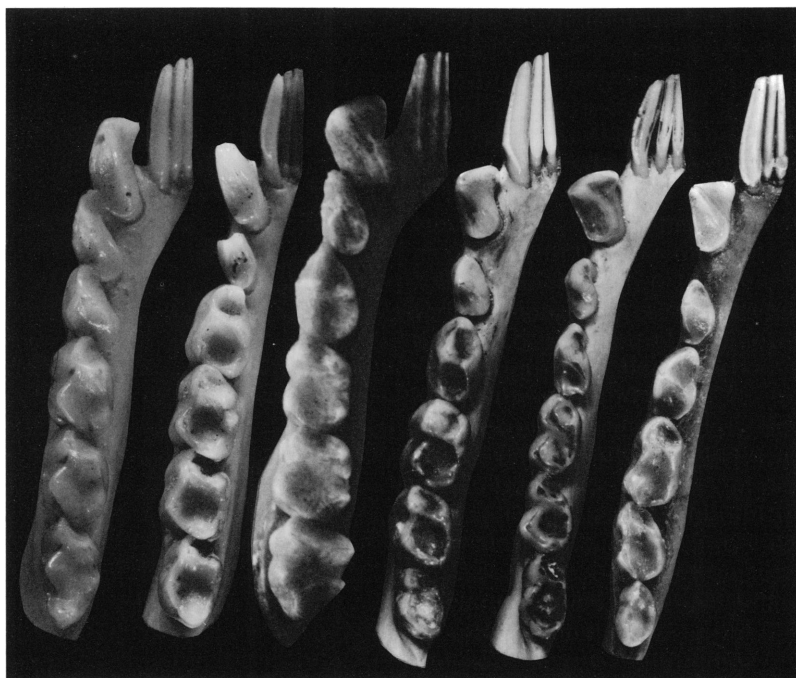


FIG. 7. Lower left dentitions of lemurids and *Lepilemur*. From left to right: *Lepilemur mustelinus leucopus* (AMNH 170575); *Hapalemur griseus griseus* (AMNH 100534); *Hapalemur simus* (BMNH 70.9.2.2); *Lemur fulvus rufus* (AMNH 100569); *Lemur catta* (AMNH 100825); *Varecia variegata variegata* (AMNH 77792). Not to scale.

is approximately twice the height of the cheek teeth.

All three of the premolars are three-rooted and are characterized by marked buccal cusp compression and strong buccal cresting. The anteriormost premolar is noticeably taller than the other two, which are subequal in height. All three premolars are triangular in buccal outline and bear small but distinct para- and metastyles. The paracone is the dominant, if not the only, distinct cusp of the anterior premolar; there is a lingual swelling above the root that bears anteriorly a minute "protocone" or "protostyle" which is barely distinguishable from the thin, anterolingual cingulum. This cingulum and a broad and strong lingual protocone pillar bound a shallow lingual depression.

The middle premolar bears a moderate protocone, slightly anterior to, but merged with, the base of the paracone; a distinct preprotocrista and a broad lingual paracone pillar subtend a somewhat excavated depres-

sion. A weak postcingulum originates at the metastylar region and fades out at the base of the protocone, bordering inferiorly a steep but shallow depression. The posterior premolar is basically similar to the middle of the set but its mesial, distal, and lingual faces are straighter (=more filled-out), the protocone is somewhat larger and farther away from the paracone, and the anterolingual depression is noticeably smaller.

All molars possess a broad lingual root and are characterized by marked buccal cusp compression, very strong and continuous buccal cresting, and by broad trigons with shallow trigon basins. The three molars also bear distended and compressed metastyles; extraordinarily lowered postprotocristae that "open" the trigon basin distally; distinct, slightly ledgelike postcingula that course from the metastyle to the base of the protocone; and weak, crenulated cingula around the anterolingual base of the protocone. The preprotocristae are strong and broad, and swing

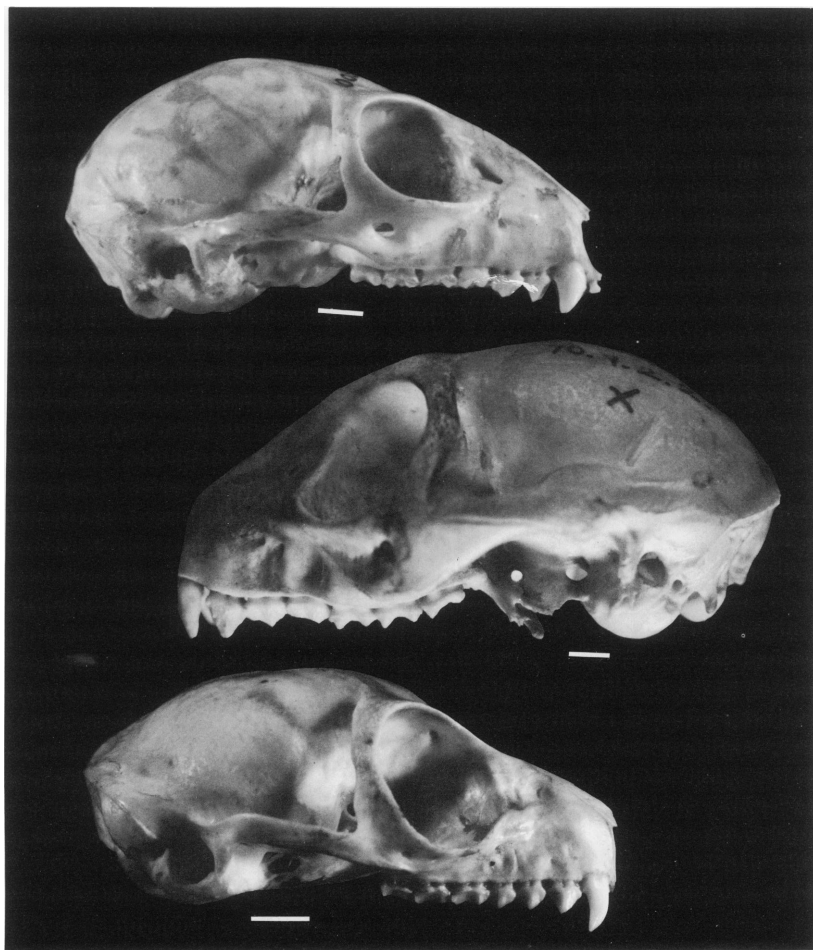


FIG. 8. Crania of *Hapalemur* and *Lepilemur* in lateral view. Top: *Hapalemur griseus griseus* (AMNH 100534); middle: *Hapalemur simus* (BMNH 70.9.2.2); bottom: *Lepilemur mustelinus leucopus* (AMNH 170575). All scales represent 5 mm.

anteriorly around the paracone to join the parastylar regions; and both lingually and buccally the paracones show short but distinct pillars. The lingual pillar, together with the preprotocrista, subtends a small, but moderately deep, depression. Although the molars are subequal in length and breadth, with M^2 only slightly larger than M^1 , M^3 is decidedly triangular, whereas the first two molars are filled-out in the talon region.

LOWER DENTITION

The six anterior teeth that make up the toothcomb are elongate, slender, moderately

procumbent, and curve somewhat lingually toward their tips. The four central teeth are laterally quite compressed and bear almost imperceptible margocristids laterally and inferiorly. In effect, the entire lingual face of the tooth is distended to form a keel. The lateral teeth are larger and deeper than the central teeth and flare laterally to some extent. A very shallow depression separates a weak distal margocristid from the longitudinal keel of the tooth.

Although the anteriormost premolar is single-rooted and the posterior two are double-rooted, all are characterized by a marked lingual incurving of the strong paracristid and



FIG. 9. Crania of *Hapalemur* and *Lepilemur* in ventral view. Top: *Hapalemur griseus griseus* (AMNH 100534); middle: *Hapalemur simus* (BMNH 70.9.2.2); bottom: *Lepilemur mustelinus leucopus* (AMNH 170575). All scales represent 5 mm.

the tip of the protoconid. Each also bears a shallow anterolingual depression and an elongate talonid that houses a relatively excavated, narrow basin that originates at the protoconid, opens lingually, and is bounded buccally and lingually by marked ridges or crests. The anteriormost premolar stands approximately two-thirds higher than the other two, which are only slightly higher-crowned than the molars. The posterior two premolars bear minute metaconids that are slightly posterior to the protoconid and are incorporated

in the strong lingual crest that emanates from that cusp. Only the posterior premolar develops a buccal cingulid which, however, is quite weak.

All three molars are characterized by distinct and complete buccal cingulids; by strong, short, anteriorly directed paracristids that lingually open broad but shallow trigonid basins; by talonids that open lingually from behind a very long crestlike wall that extends far posteriorly from the metaconid and ends in a compressed cusplike structure; and by

markedly compressed cusps that are confluent with strong cristids. On each the metaconid is positioned relatively close to but slightly behind the protoconid; and from the large hypoconid there emanates a strong hypocristid posteriorly and, anteriorly, an equally strong cristid obliqua that terminates on the lingual side of the protoconid. On M_{1-2} , the terminus of the hypocristid forms the buccal border of the posterolingually opening talonid basin. On M_3 , the hypocristid terminates centrally, at the base of the somewhat flattened and compressed talonid heel which forms the buccal border of the lingually opening basin.

Although the cusplike structure at the end of the long crestlike wall that extends posteriorly from the metaconid has been commonly identified as an entoconid (giving *Lepilemur* a broad "entoconid notch"), our comparisons with other strepsirhines, fossil and extant, lead us to favor the identification of this "cusp" as a metastylid, as for example in extant indriids and some *Copelemur*.

FAMILY INDRIIDAE

The living indriids dentally are a relatively homogeneous group. *Indri* and *Avahi* are monotypic (although *A. laniger* contains two subspecies), whereas the two species of *Propithecus* (and the numerous subspecies of each) are sufficiently similar dentally to justify the description of one species alone.

GENUS *INDRI*

INDRI INDRI

UPPER DENTITION (Figs. 10, 11, 12)

The central incisor is slightly smaller in all dimensions than the lateral; the two central incisors are broadly separated by the shelflike premaxillary bone anterior to the large palatine fenestrae. These teeth are also angled forward in the jaw and their tips converge medially. Both the central and lateral incisor are somewhat compressed laterally, with the apex of the crown of the central incisor anteriorly displaced and that of the lateral more centrally positioned; the anterior and posterior occlusal edges bear strong crests and there are traces of buccal cingula. The lateral incisor is rooted just posterior to, and in line

with, the central incisor. The long axis of the incisor "row" is outwardly divergent.

The upper canine is a stout, laterally compressed, and pointed tooth; it is separated from the lateral incisor by a broad diastema. The base of the canine is fairly long mesiodistally (it is almost as long as the anterior premolar), and is distended farther by a distinct, slightly inwardly deflected heel that bears a stout, short crest posteriorly. The sharp, somewhat concave posterior edge of the tooth arcs inferiorly to become confluent with this heel and both structures subtend a broad but shallow vertical lingual depression. The crown sits on a long, stout and compressed root, but does not rise significantly higher than the molars.

The anterior of the two premolars is subequal in height with its posterior neighbor, but is much longer mesiodistally and somewhat narrower buccolingually. The effective height of the former tooth is diminished because it sits more deeply in the maxillary bone. The anterior premolar is slightly skewed in the jaw, with its distended and somewhat buccally flared parastylar region overlapping the heel of the canine externally. The long anterior edge, and slightly shorter posterior edge, of the anterior premolar bear stout crests from the inferiormost extents of which descend inwardly arcing short lingual cingula that subtend moderately developed and excavated foveae. The base of the dominant paracone is only modestly swollen lingually and inferiorly. In its entirety, the tooth is somewhat "bladelike."

The base of the dominating paracone of the posterior premolar is more swollen lingually and squared-up distolingually; the para- and posterior stylar regions of this tooth are more swollen and bulkier and bear columnar styles. The alate nature of this tooth is thus not as striking as in the anterior premolar. The somewhat anteriorly distended and buccally recurved parastylar region does, however, overlap the anterior premolar posteriorly. The subequal anterior and posterior edges of the posterior premolar bear stout crests that converge upon the styles; from these confluences descend stout pre- and postcingulae that subtend a broad, shallow lingual depression, but which fade out near the base of the paracone.



FIG. 10. Crania of indriids and *Daubentonia* in lateral view. Clockwise from top left: *Propithecus verreauxi coquereli* (AMNH 100542); *Indri indri* (AMNH 100503); *Daubentonia madagascariensis* (AMNH 41334); *Avahi laniger laniger* (AMNH 100635). All scales represent 5 mm.

M² is the squarest and most bilophodont-looking of the molars. Distinct and somewhat compressed crests run between the anterior and posterior pairs of subequal cusps, but the anterior crest (the preprotocrista?) originates mesial to the apex of its buccal cusp (paracone) and fades out inferiorly on its lingual cusp (paracone); the anterior crest, with the thick precingulum, forms a thin, deep anterior groove, whereas the posterior crest borders upon a broad, somewhat shallow talon basin that is meagerly subtended by a low, flat postcingulum.

Although the posterior half of M¹ is rather similar to M², the anterior moiety of the former tooth is distinctly different: the protocone is the smallest of the four cusps and the anteriorly distended, buccally swollen paracone is the largest; a large, bulbous parastyle dominates the oblique mesial edge of the tooth and a preprotocrista is present as a short, very thick structure that connects the conule with the parastylar region.

In contrast again with M², the buccolingually narrow M³ lacks a posterior pair of

cusps, bearing instead a rounded heel that is bounded by a thick postcingulum that swells centrally into a small cusplike structure; this incorporates a low, much-reduced hypocone near the base of the protocone. The protocone of M³ is larger than that on M² but the paracone is much smaller.

The lingual cusps of all molars appear broad and flattened on their internal surfaces, whereas the taller buccal cusps are somewhat compressed (they are crescentic or subcrescentic in outline and bear stout crests on their occlusal edges). No molar bears a cingulum buccally or lingually but M¹⁻² do possess styles. On M¹ the para- and mesostyle are quite large, whereas on M² they are only moderately developed; in both molars the metastyles are puny. Size notwithstanding, however, the parastyle and especially the mesostyle of each molar are similar in that, as extensions respectively of the prepara- and premetacrista, they appear to roll buccally and then distally back toward the tooth, thus creating and capturing a small pit or fovea. The mesostyle thus does not sit between the

paracone and metacone, but is associated with the metacone as the parastyle is with the paracone. The first molar is only slightly wider buccolingually than the second molar, but because of distension in its parastylar region, is noticeably longer than the latter tooth. M^3 is markedly narrower than M^2 , but its expanded talon makes it longer mesiodistally.

LOWER DENTITION (Figs. 13, 14, 15)

The four lower anterior teeth are rather elongate, procumbent teeth that bear pronounced lingual "keels" and whose crowns curve gently upward. The central pair are somewhat laterally compressed and bear narrow, ledgelike margocristids inferior to the centrally emplaced "keel." The lateral anterior tooth is much broader, deeper, and more robust and is laterally flared; this tooth bears thin margocristids, as well.

The two premolars resemble each other in that they are laterally compressed, rather elongate, and anteriorly distended; the posterior can especially be described as somewhat bladelike. The anterior premolar is quite broadly separated from the toothcomb by a diastema and is further distinguished by its tall, pointed dominating protoconid. This tooth is the more markedly compressed laterally of the two premolars and bears a sharp anterior and a longer, but equally sharp, posterior edge; the tip of this tooth is curved inward slightly, as are the anterior and posterior extents of the crown, thus creating a broad, shallow lingual concavity that is interrupted by a low, vertical protoconid "pillar." There is a slight thickening (a small "heel"?) of the posterior edge about three-quarters down its length.

The bulkier-looking posterior premolar is a bit longer than the anterior premolar but only about two-thirds as high, being subequal in height with the molars; it overlaps the distal end of the anterior premolar. Both lingually and buccally, the squat posterior premolar is swollen at its base; there is a faint lingual cingulid that proceeds partway around the crown after descending from a flattened, ledgelike and buccally canted anterior distension. The short anterior and longer posterior edges are thick and swollen or corrugated in places; about three-quarters down its length,

the posterior edge thickens into a minute cusplike structure. Below this, and extending posterior to it, is a swollen low "heel." The anteriorly elongate trigonid of M_1 overrides this "heel" and the paraconid of the molar abuts upon the minute "cusp."

Mirroring the upper dentition, M_2 is the most bilophodont of the lower molars; it is also the most rectangular of the three molars. Distinct crests course between the apices of the paired and opposing buccal and lingual cusps; the anterior crest is the more distinctly raised of the two and is further set off by a thin groove that parallels its course posteriorly. M_2 is distended somewhat anteriorly; a faint, arcuate paracristid descends the face of the protoconid, thickens into a broad and somewhat creased shelf, and weakly ascends the face of the metaconid. The fairly deep trigonid basin thus subtended is narrower buccolingually than a posterior basin that is bounded by the arcuate hypocristid. This crest runs posteriorly down the face of the hypoconid, arcs, and proceeds up the distal face of the entoconid; it thickens centrally and may be creased such that a small, flat hypoconulid appears near the entoconid. The cristid obliqua courses buccally between the hypoconid and protoconid, kinking inward centrally to create a small hypoflexid notch.

M_3 resembles M_2 more than does M_1 ; distinct crests course between the protoconid and metaconid and between the hypoconid and entoconid, but the hypoconid is somewhat posteriorly shifted and does not lie opposite the entoconid. In contradistinction to M_2 , the protoconid and metaconid are farther apart than are the hypoconid and entoconid. The trigonid basin in M_3 is shorter and shallower but broader buccolingually than in M_2 . M_3 also bears a large, flat, distolingually emplaced hypoconulid that drastically reduces the talonid basin to a crease below the posterior crest; the entoconid, however, is quite reduced in size. M_3 is only slightly wider buccolingually than M_2 , but is noticeably longer. The cristid obliqua arcs quickly to the posteriorly shifted hypoflexid notch and then courses straight to the protoconid.

M_1 is subequal in width to M_3 , but is markedly longer. This is due to an elongate, narrow trigonid in which a stout paracristid extends straight forward and terminates inferiorly on

the protoconid as a thickened, lingually curling paraconid. The metaconid is equal in height with, but much less bulky than, the protoconid; the buccal cusp is situated farther posteriorly but the two are quite fused at their bases and are connected by a short, stout crest. The entoconid is slightly posterior to the larger hypoconid but these two cusps are connected by a thin, raised crest. A narrow but well-excavated talonid basin is subtended by this crest anteriorly and superiorly; posteriorly it is bounded by a thick hypocristid that descends the side of the stout hypoconid and terminates internally at the base of the entoconid, from which it may be separated by a groove; there may also be a swelling near the groove. The cristid obliqua is long and somewhat arcuate and courses to the protoconid, thus creating a deep hypoflexid notch, anteriorly emplaced.

The lingual cusps on all molars are quite compressed laterally and bear sharp edges (especially posteriorly); except for the trigonid cusps of M_1 , they are much taller than the buccal cusps.

GENUS *PROPITHECUS*

PROPITHECUS VERREAUXI

UPPER DENTITION (Figs. 10, 11, 12)

The incisors are low-crowned and spatulate, concave lingually. The central incisor is much larger than the lateral; although the right and left central incisors are noticeably separate at their bases, the tips of their crowns meet at the midline of the jaw. The apex of the central incisor crown is medial, thereby creating a long distal slope; the crown of the lateral incisor essentially furnishes a straight edge occlusally.

The upper canine is laterally compressed and is very dagger-like. The distal edge of this tooth is further compressed and slightly distended and is thus very bladelike. This tooth stands approximately twice the height of the cheek teeth.

The two premolars are characterized by their buccal compression and possession of marked pre- and postparacristae. Each bears a moderately developed buccal pillar on the centrally emplaced paracone as well as a central paracone pillar lingually that separates

an anterior from a posterior basin; the latter basin is the deeper, broader and more distended of the two. In addition, both premolars bear para- and metastylar swellings; these are larger in the posterior premolar, which also possesses a complete, ridgelike, lingual cingulum.

The first and second molars are quadrate; M^1 is slightly longer mesiodistally than M^2 . Both teeth are characterized by buccal cusp compression and an accentuation of all four buccal cristae. Each develops distinct paracone and metacone pillars lingually as well as buccally and each bears marked para- and mesostyles but more moderate metastyles; a broad, ledgelike postcingulum is continuous from the metastyle to the apex of the hypocone, thereby producing a large talon basin. The preprotocrista is also broad and ledgelike and swings medially around the paracone to meet the parastyle; the postprotocrista is reduced to small raised areas on either side of a compressed, moderately developed metaconule. There is a very weak paraconule (which may not even be present on M^1) and the rather internally emplaced protocone produces a noticeable protocone slope lingually as well as a rather squat trigon. Both M^{1-2} possess a strong, angular protocone-fold that connects the protocone and hypocone.

The third molar is distinguished by being rather trapezoidal, dominated by the large but low paracones and protocones, which are connected medially by a relatively strong, ledgelike precingulum (?) or preprotocrista (?). Distally, there is a smaller lower metacone, which is bounded by a relatively strong, ledgelike postcingulum running from the parastylar region to the apex of the protocone. M^3 also bears a moderately developed and low metaconule, distorted distally; the mesostyle hypocone regions are only slightly distended.

LOWER DENTITION (Figs. 13, 14, 15)

The four teeth of the toothcomb are only moderately slender, elongate and procumbent. The central two teeth are markedly laterally compressed, are parallel-sided, and bear a strong central keel that is bounded lingually and inferiorly by a thin margocristid. The lateral teeth are larger and deeper, with a



FIG. 11. Crania of indriids and *Daubentonia* in ventral view. Descending from top: *Indri indri* (AMNH 100503); *Propithecus verreauxi coquereli* (AMNH 100542); *Avahi laniger laniger* (AMNH 100635); *Daubentonia madagascariensis* (AMNH 41134). All scales represent 5 mm.

marked lateral flare that displaces the distal margocristid away from the longitudinal lingual keel; there is only a thin margocristid medially.

The two premolars are large, laterally compressed, somewhat recurved inwardly, and single-rooted. The anterior of the two is basically a high-crowned, subtriangular, blade-like tooth, whose distal edge is longer than its mesial edge. A low lingual protoconid pillar separates a very shallow anterior depression from a larger posterior one. There is also some swelling of this tooth inferiorly,

both anteriorly and posteriorly. This tooth is approximately two-thirds taller than the other cheek teeth.

The posterior premolar is a low-crowned, elongate tooth, dominated by an inwardly curving posterior distension bearing a deep, narrow, lingually opening basin that emanates from the protoconid and is bounded on both sides by a crest; the buccal crest originates at the protoconid and the other from a minuscule metaconid that is situated posterolingual to the protoconid. The metaconid and the strong, anteriorly directed and



FIG. 12. Upper left dentitions of indriids and *Daubentonia* in occlusal view. From left to right: *Indri indri* (AMNH 100503); *Propithecus verreauxi coquereli* (AMNH 100542); *Avahi laniger laniger* (AMNH 100635); *Daubentonia madagascariensis* (AMNH 41334). Not to scale.

slightly incurved paracristid lingually border a shallow depression and there is a weak and truncated lingual protoconid pillar.

The molars are relatively elongate teeth characterized by marked cresting. The compressed metaconid is the dominant cusp and increases in height from M_{1-3} . There is a long distal metaconid edge that terminates in a deep lingual notch that it makes with the tall and somewhat isolated entoconid; this posterior metaconid edge bears a small, compressed metastylid on M_1 , which is diminished on M_2 and almost imperceptible on M_3 . The protoconids, hypoconids, and entocoids of the molars bear low internal pillars, whereas, from M_{1-3} the protoconid and

metaconid become increasingly separated and the protoconid shifts from posterior to, to opposite, the metaconid. On M_{1-2} , the cristid obliqua terminates at the midline of a strong protoconid-metaconid crest but flexes outward to join the protoconid on M_3 . A strong anteriorly directed paracristid and the protoconid-metaconid crest subtend a relatively large and moderately deep, lingually open trigonid on M_1 ; on M_{2-3} , however, the paracristid increasingly terminates closer to and farther below the metaconid, thus compressing and lowering this basin. The lowering of the trigonid basin is also accomplished by a decrease in height of the protoconid from M_{1-3} . On M_{1-2} a strong but low hypocristid ter-

minates at the base of the entoconid, creating a small notch. M_3 is further distinguished from the first two molars in that its talonid is smaller and laterally truncated. The third molar also shows a low hypoconulid that receives a strong hypocristid; the hypoconulid lies close to the entoconid, producing a notch.

GENUS *AVAHI*

AVAHI LANIGER

UPPER DENTITION (Figs. 10, 11, 12)

The upper incisors are tall but tiny teeth, both compressed buccolingually; the central, in particular, is of highly limited mesiodistal extent. In the lateral incisor, which is distinctly the larger of the two, there is a hint of a central lingual pillar bounded fore and aft by faint depressions. The central incisors are widely spaced from the midline but are closely approximated to the laterals, which in turn lie close to the teeth behind them.

The upper canine is about as tall as it is mesiodistally long, is rather laterally compressed, and bears very sharp anterior and posterior edges; the crown, which rises about two-thirds higher than the anterior premolar, is borne on a long root that is also compressed laterally. The anterior edge of the tooth terminates inferiorly in a moderate, somewhat angular anterior extension and the longer, more vertical posterior edge joins a narrow, vertically oriented heel that is somewhat canted lingually. The heel and posterior edge subtend a moderately excavated lingual depression that is bounded anteriorly by a stout, vertical paracone "pillar"; this "pillar" forms the distal wall of a smaller and shallower anterior depression. The buccal face of the paracone is also swollen as a vertical "pillar." In sum, this tooth is characteristically premolariform rather than caniniform.

The anterior premolar is slightly taller and somewhat narrower buccolingually, but is noticeably longer than the posterior premolar. The anterior premolar is much longer than it is tall, being especially distended anteriorly; the angular anterior extension abuts upon and slightly overrides the heel of the canine. The anterior edge and the much shorter and more vertical posterior one are rather compressed, thereby contributing, with

the general lateral compression of the crown, to the tooth's somewhat bladelike appearance; both edges may be thickened a bit in places, and the posterior edge is distended as a small heel. Inferiorly, the posterior edge curves inward and, with a broad, fairly stout, vertical paracone pillar that barely swells the base of the cusp, subtends a moderately excavated lingual depression; there is a shallower depression anterior to the lingual pillar. Whereas the lingual surface of the tooth presents an overall gestalt of concavity, the buccal face is gently convex, and somewhat distended by a low, broad, vertical paracone pillar.

The mesiodistally shorter but buccolingually broader posterior premolar is subequal in height with the molars. As in the anterior premolar the anterior edge of this tooth is the longer of the two compressed edges, but the terminal distension is bulkier and swollen buccally; buccally, this extension overlaps the heel of the anterior premolar. The posterior edge of the posterior premolar is much shorter and it arcs more severely downward to proceed as a lingual cingulum to the base of the low paracone pillar; the distal edge of this pillar is compressed into a distinct crest which, with the posterior lingual cingulum, completely surrounds a moderately deep depression. There is a relatively straight, posterolingually oblique lingual cingulum that proceeds from the anterior distension to fade out at the base of the paracone and which subtends a rather broad but shallow depression. A rounded swelling that is like neither a crest nor a cingulum encompasses the paracone inferiorly, thereby adding to the general concave nature of the lingual surface of the posterior premolar. Buccally, there is a moderately swollen paracone pillar that, with the buccal anterior styler region swelling, subtends a shallow vertical depression behind. This buccal pillar presents an edgelike appearance and arcs out to thicken as a distinct, raised distal style.

The upper molars are characterized by noticeably compressed cusps that bear, and are connected by, prominent crests; this is especially marked in the buccal structures. The metacone of M^3 is quite reduced, is shifted posterocentrally, and is incorporated as an outward "kink" of the pre- and postmeta-

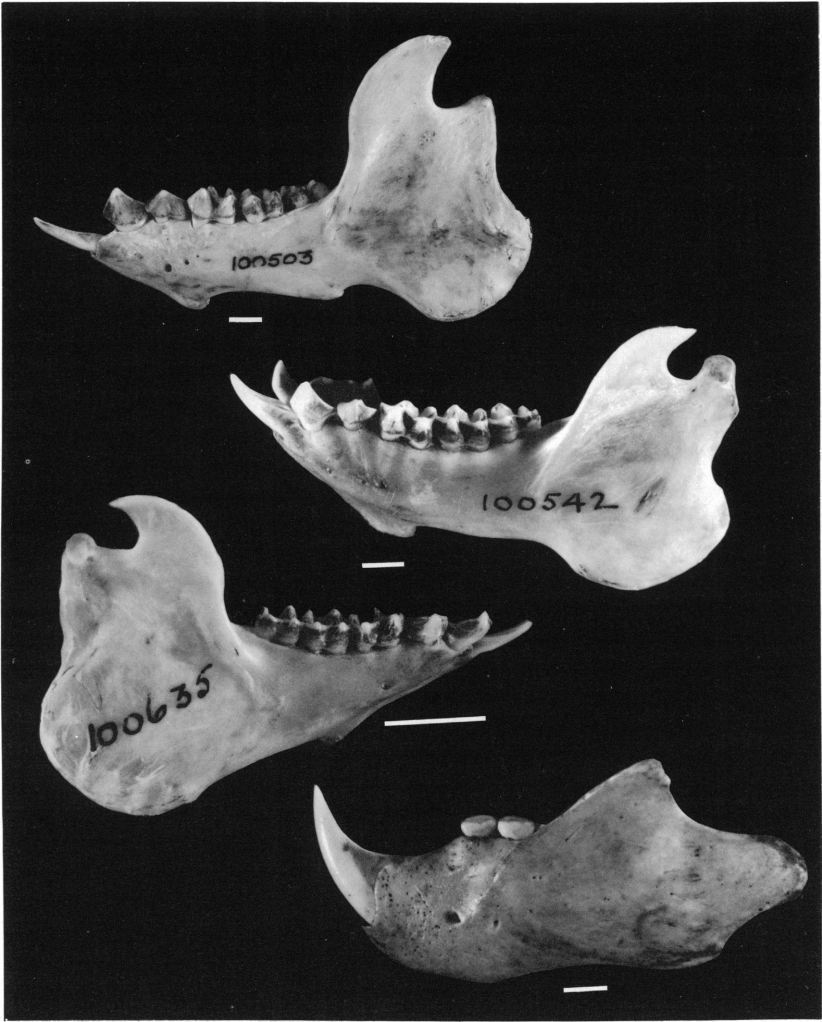


FIG. 13. Lower jaws of indriids and *Daubentonia* in lateral view. Descending from top: *Indri indri* (AMNH 100503); *Propithecus verreauxi coquereli* (AMNH 100542); *Avahi laniger laniger* (AMNH 100635); *Daubentonia madagascariensis* (AMNH 41334). All scales represent 5 mm.

cristal system; but the paracone is just as acutely crescentic in outline as are the paracones and metacones of M^{1-2} . On the first two molars, the metacone is smaller than the paracone and the pre- and postmetacristae are more severely arced buccally into a V-shape. A broad, low preprotocrista courses anteriorly past the paracone to join the confluence of the parastyle and preparacrista, but, on M^{1-2} , this protocone crest is distended more mesially by a long, raised, pitted and grooved paraconule. A crest, which represents the compressed distal border of a short

lingual paracone pillar, terminates at the inner extent of the paraconule of M^{1-2} , whereas on M^3 , the unimpeded crest traverses centrally across the broad trigon basin to the apex of the large protocone. The postprotocrista, which incorporates a small, compressed metaconule, courses quite divergently from the protocone and up to the apex of the metacone; on M^3 this crest, with a much-reduced metaconule, forms the posterior border of the crown, whereas on M^{1-2} it goes beyond the midline of the metacone before “kinking” and proceeding up the cusp. On

M^{1-2} there may appear to be twinned metaconules and double postprotocristae, but these are most probably pseudostructures resulting from the extensive crenulation, pitting and grooving that characterize the enamel of these teeth; the enamel of M^3 is much smoother.

M^{1-2} are quadricusate with all four cusps well developed, whereas on M^3 only the paracone and protocone are large. The hypocone is so enlarged on M^{1-2} that there is a deep notch between it and the protocone, and the crestlike anterior edge of the hypocone joins the postprotocrista just lingual to the metaconule. On M^3 , however, one finds only a short, thick crest that juts out posteriorly from the small, flat metaconule and which is also delineated by a pit or groove on its buccal side. Of the well-developed molar cusps, the buccal ones are displaced somewhat anterior to the lingual ones; the buccal cusps, especially the paracones, bear stout external pillars. All molars develop parastyles which fold back upon the preparacrista; this development is most marked on M^1 , and least on M^3 . The mesostyles are, however, the dominant buccal adornment, to the extent that the structure rivals the true cusps in size; on M^{1-2} , the mesostyle begins at the confluence of the postparacrista and premetacrista and then folds toward the metacone, whereas on M^3 this style is smoothly incorporated into the cresting system. M^{1-2} also bear a fairly prominent metastyle whose base is melded with that of the mesostyle, thus forming a V-shaped notch buccally; a thick, shelflike postcingulum descends from the style and subtends a narrow talon basin as it courses to the apex of the hypocone. M^3 lacks a metastyle and postcingulum. M^1 is slightly longer and wider than M^2 , which is markedly larger than M^3 in both dimensions.

LOWER DENTITION (Figs. 13, 14, 15)

The lower four anterior teeth are quite elongate, slender, and procumbent with crowns that curve gently upward; all bear stout longitudinal keels on either side of which are distinct, ledgelike margocristids. The central two teeth are markedly compressed laterally and more or less parallel-sided, whereas the lateral teeth are larger, deeper, and are gently flared laterally.

The anterior premolar bears a strikingly elongate crown whose protoconid is displaced anteriorly such that there is an extremely long posterior edge but not much of an anterior one. The latter edge is arcuate, descends quickly, and flexes inward and is quite sharply compressed; the posterior edge is thicker and straighter and turns a bit lingually near its posterobasal terminus at which point it angles sharply and, as a low cingulid, courses to become confluent with the anterior edge. This "system" encloses a very shallow lingual concavity that is intruded upon by a modest protoconid pillar; the buccal face of the tooth is somewhat convex. Although the root of the anterior premolar is noticeably separated from the toothcomb, the crown of the tooth extends for a third of the length of the procumbent teeth.

Almost as tall as the molars and thus less than two-thirds the height of the anterior premolar, the posterior premolar is also a rather elongate tooth. The protoconid is situated relatively far forward on the crown; but it is low, compressed lingually, and incorporated into a stout, lingually opening, broadly V-shaped cresting system. The anterior crest arcs anteriorly and lingually before veering sharply downward and then distally to proceed as a weakening buccal cingulid that subtends the long trigonid basin inferiorly. The somewhat longer posterior crest forms a steep wall to the trigonid basin as well as to the narrowly elongate, teardrop-shaped talonid basin; the posterior crest fades out rapidly around the base of the basin, which thus "empties" posterolingually. The talonid basin is bound buccally by a stout but only moderately tall cristid obliqua that diverges from the posterior crest just behind and below the tip of the protoconid. The buccally swollen protoconid emphasizes the narrowness and elongation of the tooth posteriorly.

M_1 is distinguished from the posterior two molars by being elongate, rather than somewhat "squared-up" anteriorly and posteriorly, and by having a fully developed trigonid. All three molars, however, are characterized by deeply wrinkled enamel, especially on either side of the metaconid; on M_{2-3} this creates a pitted trough that parallels the protocristids posteriorly. All three molars also bear a distinct but low metastylid (largest on

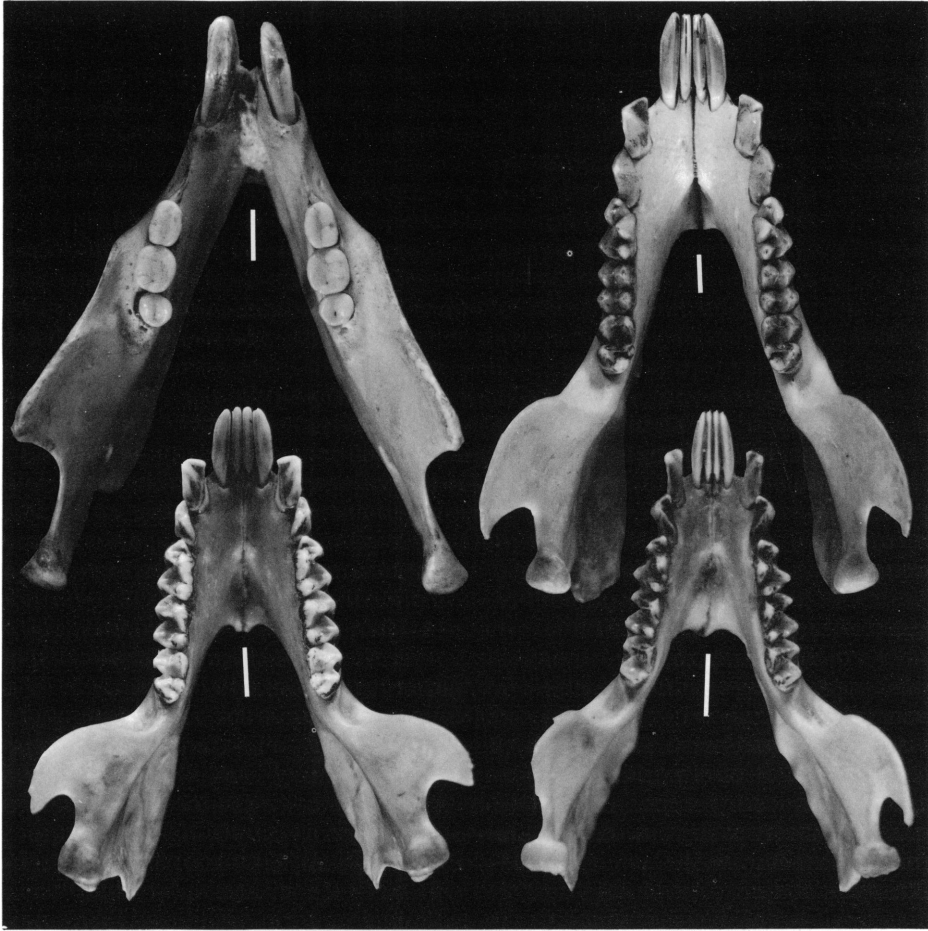


FIG. 14. Lower jaws of indriids and *Daubentonia* in occlusal view. Clockwise from top left: *Daubentonia madagascariensis* (AMNH 41334); *Indri indri* (AMNH 100503); *Avahi laniger laniger* (AMNH 100635); *Propithecus verreauxi coquereli* (AMNH 100542). All scales represent 5 mm.

M₁ and smallest on M₃) that is the terminus of thick, lingually deflected postmetacristids. A deep lingual notch is formed by the meta-stylid anteriorly and a tall, subconical entoconid posteriorly; the entoconid is delineated further by a groove between it and the well-developed hypocristid that terminates partly behind the cusp.

The three trigonid cusps of M₁ are fairly widely emplaced and create a large, moderately excavated trigonid basin that opens lingually; the protoconid and paraconid are incorporated into the tall, thick paracristid, whereas the larger metaconid remains distinct, being connected to the protoconid by

a thinner and markedly lower crest. The edge of the broad, slightly anteriorly arcuate paraconid shelf on M₂₋₃ is flexed upward, thus creating a moderately deep, buccolingually elongate trigonid basin; the protoconid and larger metaconid remain distinct. The long, variably "beaded" M₁ cristid obliqua courses rather directly from the large hypoconid to the protocristid centrally. On M₂₋₃, however, just before reaching the protocristid the shorter crest "kinks" outward to terminate at the apex of the protoconid. Although the protoconids of all molars are somewhat swollen buccally, the hypoflexid notches are more pronounced on M₂₋₃. The talonid basins of

M_{1-3} are fairly deep and are formed primarily by the broad, flattened face of the hypoconid. M_1 is longer mesiodistally and narrower anteriorly than M_2 but both possess equally broad talonids. M_{2-3} are equally broad anteriorly, but the talonid of M_3 is somewhat narrower and shorter.

FAMILY DAUBENTONIIDAE

Both the family Daubentoniidae and the genus *Daubentonia* are monotypic, at least as far as the surviving Malagasy fauna is concerned. The species *Daubentonia madagascariensis* is highly autapomorphic in its dentition.

GENUS DAUBENTONIA

DAUBENTONIA MADAGASCARIENSIS

UPPER DENTITION (Figs. 10, 11, 12)

The upper anterior tooth is quite robust, deep buccolingually, and compressed mediolaterally. It is continually growing (replacing itself as it is worn away); its long axis describes an arc from its center of growth over the molars posteriorly to its emergence palatally through the premaxilla. The tips of the single pair of anterior teeth meet at the midline of the jaw; each anterior tooth is separated from the cheekteeth by a long diastema.

There is only one upper premolar in the adult. It is a small, squatly oblong, peglike tooth whose otherwise smooth occlusal surface is indented by a pit from which radiate two or three faint grooves. The pit is situated a bit anterior of center and one or two closely approximated grooves course lingually and slightly posteriorly. Another groove courses rather directly buccally.

In overall gestalt, the upper molars are similar to the premolar: they are basically rounded, puffy teeth with little occlusal morphology; each bears a small, deep pit that is emplaced somewhat centrally. On M^{1-2} there is a faint groove that emanates from the pit and courses buccally; this groove delineates a large paracone from a smaller metacone that occupies the buccodistal aspect of the crown. Faint grooves on the paracone, in conjunction with the groove just mentioned, appear to delineate a broad mesostylar region. A pit on the metacone seems to point to a

blurry metastyle. The inner extents of the paracone and metacone are demarcated by grooves that radiate laterally and somewhat upward from the pit. These grooves, in turn, form the upper boundaries of large, broad, flat, wedge-shaped para- and metaconules that are delineated below by other grooves radiating from the pit; these conules are also present and similarly marked-off on M^3 . The conules are quite laterally emplaced and the paraconule of M^1 even distends the tooth a bit mesially. On all molars a shallow, wedge-shaped depression or trigon basin courses posterolingually until it is blocked by a large, swollen hypocone region. This basin also, of course, delineates a large protocone from whose blunted apex emanates, especially on M^1 , a weak postprotocrista. On all molars, the buccal cusps are taller and more distinct than the lingual cusps; the former are highest on M^3 . On this tooth the large buccal mass is flanked by the grooves that delineate the para- and metaconules; it is divided into three components by a small groove anteriorly and a pit posteriorly. It is difficult to identify these units with certainty: they could be a parastyle, paracone, and mesostyle; a parastyle, paracone, and metacone; or a paracone, mesostyle, and metacone.

The anterior edge of M^1 is truncated buccolingually causing the lingual face of the tooth to be long and oblique. The metaconule of M^2 distends the tooth distally with the result that the buccal face appears a bit shorter than the lingual aspect; nevertheless, buccolingual width is the greater dimension. M^3 , the smallest molar, carries the shortening of the buccal face and metaconular distension still farther. Although M^1 is somewhat longer mesiodistally than M^2 , the latter stands out because of its width.

LOWER DENTITION (Figs. 13, 14, 15)

There is a single pair of robust, compressed, continually growing anterior lower teeth. As in the upper anterior teeth, the long axis of these teeth follows an arc and the center of growth lies next to the molar region.

The cheek teeth are represented only by the molars. M_1 is thinly rectangular, M_2 is wider and somewhat longer mesiodistally, and the rather small M_3 is subcircular in shape.



FIG. 15. Left lower dentitions in occlusal view of indriids and *Daubentonina*. From left to right: *Indri indri* (AMNH 100503); *Propithecus verreauxi coquereli* (AMNH 100542); *Avahi laniger laniger* (AMNH 100635); *Daubentonia madagascariensis* (AMNH 41334). Not to scale.

The crowns are bisected by a shallow groove or basin that separates the lingual from the buccal cusps. Toward the distal extent of this groove there is a small pit which lies, on M_{2-3} , at the bases of the apices of the wedge-shaped hypoconid and entoconid; a groove emanating from this pit separates these cusps. On M_3 , the entoconid is more centrally emplaced. The molar crowns are raised lingually in long lophlike structures, which may reflect the presence of a postmetacristid; grooves on M_2 may indicate the existence of a metastylid.

Especially on M_{1-2} , there occur grooves and/or pits that delineate a small trigonid "basin" and the metaconid. A protoconid is most discernible on M_2 ; the protoconid regions of all

molars are lower and perhaps smaller than the metaconid regions. The trigonid of M_1 is the most anteriorly distended and one can recognize a thick paracristid that extends forward.

FAMILY CHEIROGALEIDAE

This family embraces five genera among which substantial variety in dental morphology is encountered.

GENUS CHEIROGALEUS

There is sufficient difference in the dental morphology of the two species of *Cheirogaleus*, one substantially larger than the other,

to warrant separate description of their dentitions.

CHEIROGALEUS MAJOR

UPPER DENTITION (Figs. 16, 17, 18)

The upper central and lateral incisors lie close to each other; the lateral incisor is separated from the canine by a small diastema, whereas the central incisors are displaced by the large anterior palatine fenestrae separating them. Interestingly, the bone in which these teeth sit is distended downward, thus artificially increasing their height. Both incisors are fairly low-crowned, but the central incisor is at least twice as high and broad as the lateral. The apex of the crown of the central incisor is anteriorly displaced, creating a long, not very steep, posterior edge; there is a small, rounded "heel" posteriorly, and a much more prominent distension anteriorly decreases slightly the distance between the crowns of the two central incisors. A shallow excavation characterizes the lingual faces of these teeth, which bear weak but complete cingula. The small posterior "heel" of the central incisor extends partly over the lateral incisor; the crown of this tiny tooth is roughly circular, and is higher anterobuccally than distally.

The upper canine is stout and simple, emphasizing neither pointedness nor compressed edges. The tooth stands well over twice the height of the molars, yet is most strongly characterized by its unusual mesiodistal length; this results primarily from a distended, somewhat compressed posterior heel that subtends a lingually directed depression. There is a trace of lingual cingulum anteriorly. The otherwise fairly conical primary cusp, with its rounded tip, arcs a bit backward; this creates a curvature mirrored by the mesial and distal edges of the tooth.

The anteriormost premolar is about one-half the height of the canine and sits closer to this tooth than to the middle premolar, which is intimately associated with the posterior cheek teeth. In buccal outline it approaches an equilateral triangle. This tooth bears a small heel posteriorly that is met by a weak but complete lingual cingulum. The crown is moderately compressed laterally and bears relatively sharp anterior and posterior

edges. A broad lingual paracone "pillar" subtends shallow anterior and posterior depressions.

The middle premolar is approximately two-thirds the height of the anterior premolar, but is about 30 percent longer mesiodistally; in this dimension it is subequal with the posterior premolar, although its paracone rises distinctly higher. The middle premolar is subtriangular in both buccal and occlusal views. The longer and slightly convex anterior edge terminates in a small style that is confluent with the weak but complete lingual cingulum, whereas the shorter and less steep posterior edge merely thickens slightly; both edges, but especially the anterior one, are compressed. There is a stout and broad lingual paracone pillar that arcs a bit mesially as it descends the moderate lingual swelling of the crown; this pillar subtends anterior and posterior shallow depressions, the latter larger.

The posterior premolar, which is subequal in height and buccolingual width with M^1 , is similar to the molars in de-emphasizing cusp height and cusp and crest distinctiveness, as well as in having relatively smoothly contoured enamel. The large but virtually flattened protocone constitutes the lingual portion of the tooth, and accounts for about two-fifths of the width of the crown. Low and relatively broad pre- and postcingula descend from the styler regions to fade out before rounding this cusp. Although the apex of the paracone is discernible, the anterior and posterior edges of this cusp fan out horizontally, thus creating an elongate, lophlike "blade."

The upper molars are similar in general gestalt to the posterior premolar: the large, low, and flattened protocone is narrower than the buccal moiety of the tooth and is delineated superiorly by a shallow mesiodistal crease. The waisting in this region, however, is not as marked as it is in the premolar. Furthermore, the protocone occupies approximately one-half of the crown of the tooth, and the buccal cusps are not completely confluent with each other, thus maintaining some of their identity. M^{1-2} are subequal in size but M^1 flares a bit more buccally and its protocone is slightly broader, these attributes contributing to a bit more waisting; both teeth, however, bear low and relatively thick

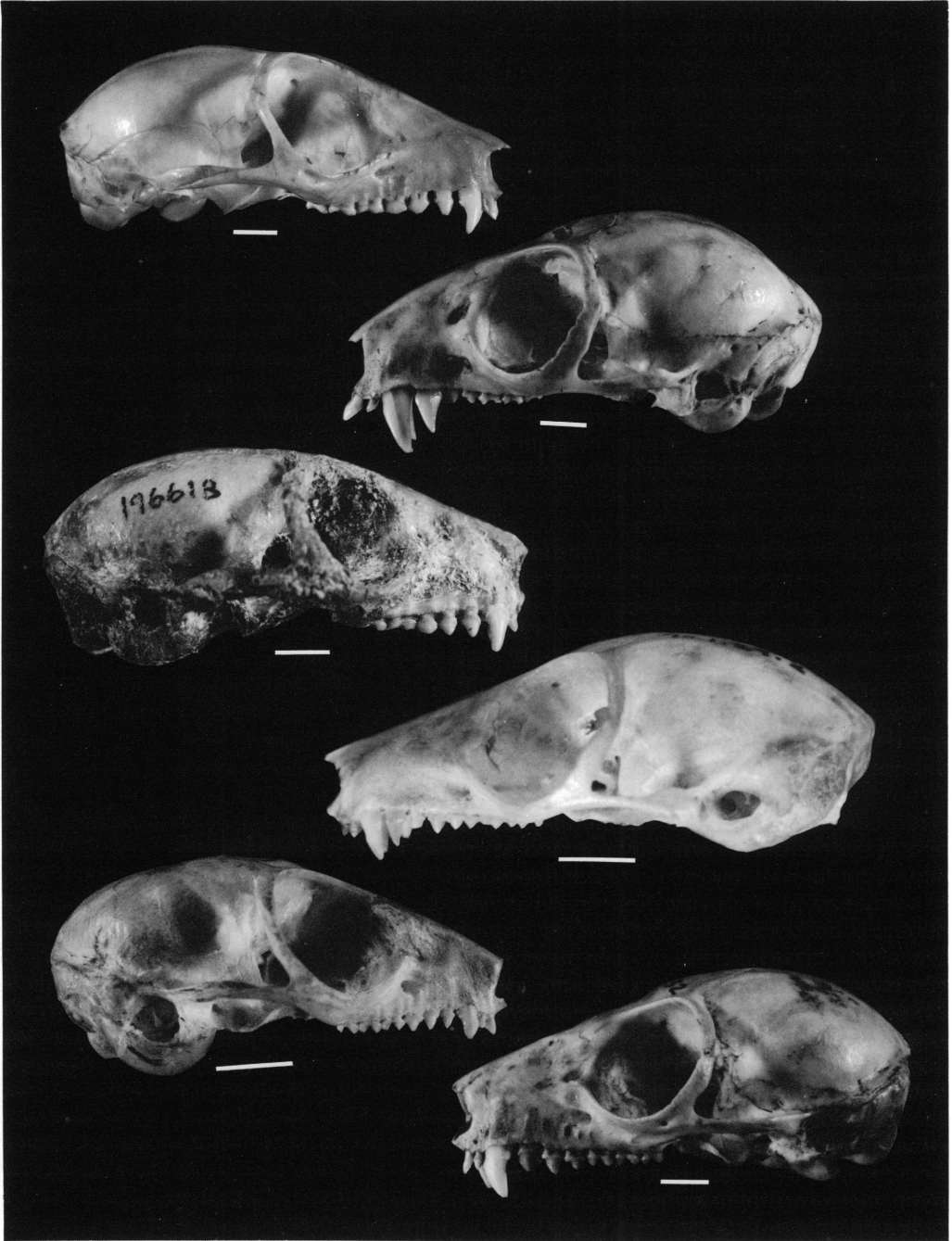


FIG. 16. Crania of cheirogaleids in lateral view. Descending from top: *Cheirogaleus major* (AMNH 100640); *Phaner furcifer* (AMNH 100829); *Cheirogaleus medius* (AMNH 196618); *Allocebus trichotis* (BMNH 75.1.29.20); *Microcebus murinus* (AMNH 174434); *Mirza coquereli* (AMNH 100832). All scales represent 5 mm.

pre- and postcingula that emanate from the styler regions and thicken even more as they

become confluent around the lingual face of the large protocone. M^3 is about three-fourths

the size of M^{1-2} and is relatively more triangular in occlusal outline due to the lack of cingula; the metacone of this tooth is also much smaller than the paracone.

LOWER DENTITION (Figs. 19, 20, 21)

The lower six anterior teeth are moderately elongate and procumbent, and arc upward slightly at their tips. The central two are the most elongate and laterally compressed. The teeth next to them are only slightly shorter and less compressed; their occlusal edges also curve inward. The most lateral of the procumbent teeth are distinctly shorter, deeper and more robust and flare laterally quite noticeably; these teeth bear a broad longitudinal central keel that is bounded by a distinct medial and a thicker lateral margocristid.

The anteriormost premolar is a moderately tall, robust, and thick-based tooth that is inclined a bit forward and whose tip arcs inward, thus creating a noticeably concave lingual face. The relatively short anterior edge is not as bladelike as the posterior edge, but thickens and, as a stout cingulum, descends steeply to surround a distolingual basal swelling and to terminate as a small, vertical, ledgelike heel. A broad lingual protoconid pillar follows the lingual concavity and backward curvature of the tooth, subtending anteriorly a small, shallow depression and posteriorly, a more elongate vertical depression. This tooth stands more than twice the height of the molars.

The middle premolar, approximately two-thirds the height of the anterior premolar, is essentially a smaller version of that tooth. Differences lie in the expectedly shorter protoconid, in a more compressed posterior edge, and in a slightly more distended posterior heel and posterior depression. This tooth is separated from its anterior and posterior neighbors by small diastemata.

The smoothly contoured posterior premolar, which stands two-thirds the height of the middle premolar and rises noticeably above the molars, carries the premolar morphocline farther. The protoconid is shorter and squatter (although it still tapers anteriorly), and the heel is much more distended.

On the continuous cresting system that encloses a moderately excavated and teardrop-shaped basin are two small thickenings that could loosely be identified as hypoconid and entoconid. This tooth and the middle premolar are subequal in length, but the former is much wider buccolingually. In these dimensions, the posterior premolar is approximately two-thirds the size of M_1 .

The extremely bunodont molars, like the posterior premolar, are smoothly contoured but, unlike any other teeth in this dentition, lack virtually all detail and delineation of individual features; one can therefore refer to structures only in a vague sense. The trigonids are distended anteriorly in the region of the protoconid and what would correspond to a narrow paraconid shelf angles acutely back to the low metaconid; this anterior extension diminishes from M_{1-3} . The protoconid and the smaller and somewhat posteriorly emplaced metaconid are solidly melded and are confluent with a thinner, lophlike cresting system that completely encircles the shallow talonid basin and terminates as the cristid obliqua quite buccally, blending in with the protoconid centrally. The protoconids of all molars are swollen buccally as are the hypoconids of M_{1-2} . M_1 is slightly longer than M_2 (because of the difference in anterior protocone extension) but both are subequal in buccolingual width. Although the trigonid of M_3 is almost as wide as it is on M_{1-2} , this tooth is much shorter than the M_{1-2} and tapers markedly to a small and very lingually displaced heel; the crest that continues buccally from this heel is much lower and less intrusive than the crest that courses to the heel from the metaconid.

CHEIROGALEUS MEDIUS

UPPER DENTITION (Figs. 16, 17, 18)

The lateral upper incisor is less than half the size of the central incisor but similar to it in that the slightly elongate crown is partially procumbent and oriented toward the midline of the jaw; both teeth have some swelling of the distal surface inferiorly. There is a reasonably large gap between the right and left central incisors; the lateral incisors



FIG. 17. Crania of cheirogaleids in ventral view. Descending from top: *Cheirogaleus major* (AMNH 100640); *Cheirogaleus medius* (AMNH 196618); *Phaner furcifer* (AMNH 100829); *Allocebus trichotis* (BMNH 75.1.29.20); *Mirza coquereli* (AMNH 100632); *Microcebus murinus* (AMNH 174434). All scales represent 5 mm.

are emplaced slightly posterior to and set off from the central teeth.

The canine rises at least three times higher than the molars, is gently curved backward, and is only moderately compressed laterally. This trenchant tooth is unadorned by surface detail.

There is a decrease in height anteroposteriorly through the upper premolar series, with the anteriormost premolar being approximately one-half the height of the canine and the last of the set noticeably higher than M^1 . All are triangular in buccal outline, with minute styler swellings, and are dominated by a buccally flattened and lingually convex paracone that is bounded internally by a thin basal cingulum. Among the three premolars there is an anteroposterior morphocline of lingual distension from the simple-sided anterior to the low protocone-like swelling of the ultimate premolar.

The molars bear complete but low buccal cingula; rather prominent pre- and postcingula that converge around the base of the protocone; widely separated paracones and metacones; large, broad protocones; broadly parabolic protocristae that are visible merely as low, rounded vestiges; and a preprotocrista that arcs anteriorly around the paracone. In addition, each presents an overall appearance of extreme bunodonty within which the paracone and metacone appear to rise as moderately tall cusps. M^{1-2} are subequal in size and both are approximately two-thirds larger than M^3 . The lingual face of M^1 is broadened by angular anterior and posterior cingular swellings; the lingual face of M^2 is broadly rounded. M^1 is rectangular, M^2 subrectangular, and M^3 basically triangular.

LOWER DENTITION (Figs. 19, 20, 21)

The six anterior teeth are slender, curved upward at their tips, and moderately procumbent. The central four are laterally compressed and parallel-sided, whereas the lateral two are much more robust and deeper with a marked lateral flare, and also bear distinct medial and lateral margocristids.

The anteriormost lower premolar stands more than twice the height of the molars, is somewhat conical, and bears a distinct and complete lingual cingulum that is thickened

distally into a short shelf; the crown of the tooth arcs inward at its tip. The gently concave distal slope of the tooth is longer than the convex mesial edge and the horizontal axis of the tooth is oriented obliquely to the main axis of the jaw.

The penultimate premolar is approximately two-thirds the height of the anterior premolar, but is almost as long as a result of the presence of a large, ledgelike distal cingulid; the tooth is otherwise similar to its anterior neighbor. The last premolar is distinguished by its relative molariformity. The occlusal surface of the tooth is smooth in its concavities and convexities, thereby creating cusp-crest continuity. A weak, shallow groove appears to delineate a merged protoconid and smaller metaconid. A rounded paracristid courses anteriorly down the face of the protoconid and angles acutely as a weak structure that courses to the base of the metaconid and merely traces the vestiges of a trigonid basin. The longer and slightly wider talonid is distinguished by a thick, lophlike "crest" that arcuately encloses a shallow basin. There is a distinct and complete buccal cingulid.

The molars are generally similar to the last premolar. They are very low crowned, with extremely compressed trigonids in which the rounded paracristid runs parallel to the oblique protoconid-metaconid axis due to the slight posterior displacement of the metaconid. The protoconid is quite melded with the metaconid, and there are also outward swellings lingually and especially buccally, a complete buccal cingulid, an enlarged hypoconid, and a completely enclosed, shallow talonid basin bordered by a buccal and straight cristid obliqua that terminates at the protoconid.

GENUS *ALLOCEBUS*

ALLOCEBUS TRICHOTIS

UPPER DENTITION (Figs. 16, 17)

The bone in which the central incisors are emplaced is greatly distended downward: the central incisors are separated broadly by the anterior palatine fenestrae. Although small, the upper central incisors are tusklike and convergent toward the midline. The lateral incisors sit behind the central incisors, from

which they are separated by a moderate diastema. The lateral incisors have short, subtriangular crowns.

The upper canine is a tall, laterally compressed, trenchant tooth whose large root makes a slight external impression on the maxilla. The anterior edge of the tooth is slightly convex, whereas the posterior edge is rather vertical and terminates in a small, compressed heel. Both edges are quite blade-like. Lingual to the base of this tooth is a fairly deep and elongate depression that accommodates the tip of the lower anterior premolar.

The anteriormost premolar is approximately four-fifths the height of the canine and is also trenchant. The premolar is not compressed laterally and bears small styles anteriorly and posteriorly. The mesial edge of the tooth is only slightly convex, whereas the longer posterior edge arcs more noticeably concavely. The crown of the anterior premolar is quite narrow, in contrast to the stout root that supports it; the root also makes a slight external impression on the maxilla.

The middle premolar is greatly reminiscent of the anterior one, although it is only half the height. The mesial and distal edges of the crown are subequal in length and the anterior one bears a relatively well-developed style. The pointed, almost conical crown sits on a large, trifurcating root. The posterior premolar is slightly lower, longer mesiodistally, and broader buccolingually than its predecessor, and bears a more noticeable posterior style. This tooth is almost completely ringed by cingulum that emanates buccally from the style to fade out; the middle premolar is similar in this feature. The root of the last premolar is also large and trifurcating.

The upper molars are dominated by the trigon, which bears relatively large and divergent buccal cusps adorned with pre- and postcristae, and of which the paracone is the larger. The protocone is broad but low, and from it emanates a thin postprotocrista that runs up the face of the metacone, and a thin preprotocrista that courses lingually around the base of the paracone to become confluent with the buccal cingulum. The preprotocrista bears a small, somewhat compressed conule near the base of the paracone. These two crests subtend a relatively broad and moderately

deep trigon basin. All molars bear a relatively well-developed postcingulum that is posteriorly quite shelflike on M^1 , less so on M^2 , and is least expanded on M^3 . On all three molars the postcingulum continues around the face of the protocone to become confluent with the thin precingulum. On M^1 , the postcingulum bears a large, somewhat flattened hypocone that "squares-up" the posterolingual corner of the tooth. On M^2 , this area is not as broad and is rounded; on M^3 , this region is barely distended. M^1 and especially M^2 bear a faint prehypocone crista that is most evident as it crosses between the bases of the protocone and hypocone. All three molars are subequal in mesiodistal length and M^2 is longer buccolingually than the others.

LOWER DENTITION (Figs. 19, 20)

The six lower anterior teeth are quite elongate, laterally compressed, and procumbent. The tips of all arc gently upward, and the lateral edge curves in toward the midline. The central four teeth are basically parallel-sided and bear a broad longitudinal "keel" subtended inferiorly on both sides by margocristids. The outermost tooth is more robust, deeper, and slightly laterally flared. The distal edge of this tooth is tilted upward, so that the crown slopes inward. The outermost tooth also bears a small central keel which is bounded by a thin lateral margocristid.

The anteriormost premolar is a tall, thin, pointed tooth that sits apart from the toothcomb. The anterior edge of this premolar is somewhat concave and distended inferiorly; the longer posterior edge is gently convex, terminating in a small, pointed heel. The lingual face of the tooth is moderately swollen, especially inferiorly, and is bounded by a thin cingulid that joins the small heel. A thin buccal cingulid also becomes confluent with the heel. The tip of the tooth is gently recurved.

The middle premolar is essentially a shorter version of the anterior; it is only about one-half the height of the latter but its base is almost as long. The trenchant, pointed, recurved crown of the middle premolar is bounded inferiorly by a thin buccal and lingual cingulids that become confluent posteriorly to create a slightly swollen, rather than elevated, heel. The middle premolar is situ-

ated quite close to the anterior premolar and is separated from the posterior of the set by a rather wide diastema; the mandibular bone appears somewhat "reabsorbed" in the diastema.

The posterior premolar is shorter yet again, but bears a large, somewhat vertical, pointed, and centrally emplaced heel; a thin crest runs down the posterior edge of the tall, compressed protoconid and then courses up the heel centrally. This crest delineates a small, lingually opening depression and a quite large buccal depression (reminiscent of a hypoflexid notch) that is subtended inferiorly by a swollen cingulid that becomes thinner as it proceeds anteriorly.

On all molars, the protoconid and metaconid dominate the trigonid. These cusps are quite confluent at their bases and form a wall facing upon the talonid. All molars bear buccal cingulids that are most prominent around the somewhat swollen base of the protoconid; the cingulid in this region is almost developed enough to be identified as a protostylid. A relatively straight cristid obliqua terminates centrally at the base of the protoconid on M_{1-3} and thus, with the basal swelling of this cusp, forms a very deep hypoflexid notch. On all molars the talonid cusps, especially the entoconid, are laterally compressed; on M_{1-2} a system of crests, weakest between the entoconid and hypoconid, surrounds the relatively long but shallow talonid basin.

M_3 bears a moderate heel that is displaced buccally. There is a broad but shallow "notch" between the heel and the hypoconid through which the talonid basin opens; there is a deeper but narrow talonid "notch" on M_2 whose homologue is even deeper and narrower on M_1 . On M_{1-3} a weak paracristid runs anteriorly down the face of the protoconid, then kinks sharply and runs as a thin shelf up the face of the metaconid; in addition a tall, compressed crest connects the metaconid and hypoconid.

GENUS *PHANER*

This genus is geographically split into a number of isolates which are all subsumed into the species *P. furcifer*, although the latter may ultimately prove to be divisible (see Tattersall, 1982). However, dental variations be-

tween the populations do not appear to warrant separate description here.

PHANER FURCIFER

UPPER DENTITION (Figs. 16, 17, 18)

The central incisor is at least three times larger than the lateral incisor. The root of the larger tooth is angled forward and the crown flexed even more so. In outline, the crown of the central incisor curves downward at its tip; the crown is laterally compressed to the extent that the occlusal surface is edgelike, rather than a flat surface. Although the roots of the right and left central incisors are widely separate, their crown tips converge upon the midline of the jaw. The lateral incisor is a small, conical tooth whose crown is of the same diameter as its root; the crown bears a narrow central groove or fovea lingually.

The upper canine is extremely elongate, trechant and laterally compressed, slightly recurved distally and lacking a posterior heel. The lingual surface of this tooth has minimal relief; there is only a very flat longitudinal pillar separating moderately broad, but extremely shallow, anterior and posterior depressions. The tooth sits in a fairly deep lingual maxillary depression and the contour of the long, single root is impressed upon the maxillary bone externally. This tooth rises at least four times the height of the molar row.

The anteriormost of the three premolars is approximately two-thirds the height of the upper canine and, like the canine, is markedly compressed laterally and bears a broad and relatively low lingual central pillar. In buccal view, this tooth is triangular, its mesial and distal edges being subequal in length; the former edge ends inferiorly in a minute swelling, whereas the distal edge, which is slightly concave, terminates in a puny, pointed heel. The posterior two premolars, although morphologically distinct, are equal in height with each other and with the molars. The middle premolar is somewhat compressed laterally; its mesial and distal edges, as well as its base, are of equal length. This tooth bears a distinct but moderately developed parastyle and a similarly sized posterior heel, as well as a complete lingual cingulum. The paracone of the posterior premolar is the dominant cusp; this tooth bears a large parastyle and a smaller



FIG. 18. Upper right dentitions of cheirogaleids (except *Allocebus*) in occlusal view. From left to right: *Mirza coquereli* (AMNH 100832); *Microcebus murinus* (AMNH 174434); *Phaner furcifer* (AMNH 100829); *Cheirogaleus medius* (AMNH 196618); *Cheirogaleus major* (AMNH 100640). Not to scale.

posterior style, connected by a weak cingular swelling buccally as well as by distinct pre- and postcingula that course to the base of the protocone that is approximately one-half the size of the paracone.

All three molars possess strong buccal cingula; conical, pointed and well-separated paracones, and metacones; and lower, but much broader and somewhat buccolingually compressed protocones. Each is also characterized by having broadly parabolic protocristae with the preprotocrista bearing a tiny paraconule and coursing around the paracone to meet the parastylar region; a distinct postcingulum that swells out toward its lingual terminus; and moderate waisting of its distal face. M^{1-2} are subequal in size and are relatively rectangular, with the distolingual corner of the tooth bearing a distinct hypocone as well as a distended cingulum that continues around the base of the protocone; the postprotocristae of each tooth encompass moderately developed metaconules. M^3 is

approximately two-thirds the size of its neighbor, is subtrapezoidal in shape, and possesses a weak postprotocrista lacking a metaconule.

LOWER DENTITION (Figs. 19, 20, 21)

The six lower anterior teeth are extraordinarily elongate, slender and procumbent; their tips curve markedly upward. This is the most exaggerated of strepsirhine toothcombs. The central four teeth are extremely compressed laterally and parallel-sided, bearing virtually imperceptible margocristids. The lateral teeth are also extremely compressed laterally but are noticeably deeper and more robust than the central teeth; the former are only slightly flared laterally and bear distinct, but very weak, lateral margocristids.

The three premolars are all triangular in outline and dominated by a laterally compressed and somewhat arcing protoconid. The anteriormost premolar is approximately twice

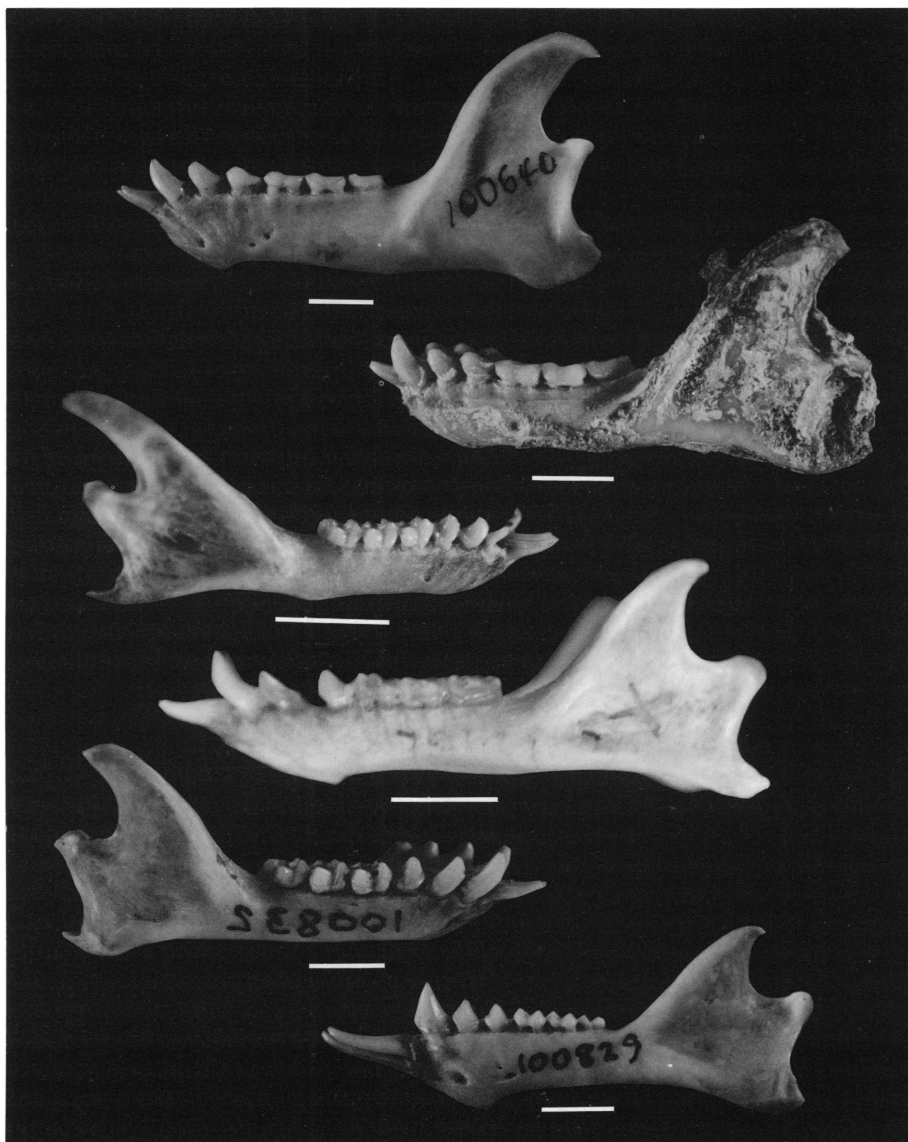


FIG. 19. Lower jaws of cheirogaleids in lateral view. Descending from top: *Cheirogaleus major* (AMNH 100640); *Cheirogaleus medius* (AMNH 196618); *Microcebus murinus* (AMNH 174434); *Allocebus trichotis* (BMNH 75.1.29.20); *Mirza coquereli* (AMNH 100832); *Phaner furcifer* (AMNH 100829). All scales represent 5 mm.

the height of the others, rising to more than twice the height of the molars. This tooth is by far the most compressed and least ornate premolar, bearing but a small posterior heel and a complete but weak lingual cingulid; its distal edge is slightly concave, approximately the same length as the base, and a bit longer than the mesial edge. The middle and pos-

terior premolars are about two-thirds the length of the anterior of the set and the middle premolar is slightly taller than the posterior one. Both of these premolars possess a moderately developed "heel" (centrally emplaced in the latter tooth and more buccally skewed in the middle premolar) and a complete, but weak, lingual cingulid; the last pre-

molar, however, also bears a distinct basal anterior swelling of cingulid and more prominent cingular development buccally.

The three molars are characterized by having thick buccal cingulids anteriorly (creating the impression of deep hypoflexid notches); very shallow trigonid basins that are enclosed by low paracristids that run approximately halfway down the face of the protoconid, to turn sharply and arc up the face of the metaconid; and moderately tall protoconids and metaconids that are melded at their bases and thus form high, steep walls facing the talonid basins. In addition, these teeth possess large, broad, buccally swollen hypoconids (especially on M_{1-2}) from which originate rather straight cristid obliquae that terminate at the base of the protoconid; and spacious talonid basins that are enclosed by arcuate cresting systems that incorporate low entoconids. M_{1-2} are subequal in size and have very large and broad talonids, whereas the relatively diminished M_3 talonid is even narrower than the tooth's anterior moiety.

GENUS *MICROCEBUS*

The two species of *Microcebus* differ somewhat in cranial detail, but are similar enough dentally for a description of one to stand for both.

MICROCEBUS MURINUS

UPPER DENTITION (Figs. 16, 17, 18)

The upper central incisors are fairly large (approximately two-thirds the height of the upper canine), slightly procumbent teeth that are widely separated by the anterior palatine fenestrae; they are also emplaced such that their anterior edges face a bit inward. In buccal view the tall, pointed apex of the central incisor is anteriorly displaced, the mesial face of the tooth is moderately distended, and a small pointed heel is present. In occlusal view, this tooth looks even more like a lower premolar: a distinct lingual cingulum turns downward from a point high on the anterior edge only to turn upward from the base of the heel to become confluent with this structure at its tip. From here emanates another cingulum that courses partway around the somewhat swollen buccal side of the crown;

the small heel sits at the base of the rounded distal edge of the tooth. The lateral incisor sits behind and slightly apart from the central incisor, but it is emplaced a bit more laterally than the larger tooth; the lateral incisor is less procumbent than the central incisor. In contrast to the central, the lateral incisor is minute; but the crown of this puny tooth is a miniature version of its larger neighbor. The bone in which the upper incisors sit is distended downward.

The emplacement of the upper canine continues the outward progression of the anterior teeth; the mesiodistal axis of this long, tall and pointed tooth is thus skewed relative to the long axis of the jaw. The short and convex anterior edge is stout, bladeliike, and noticeably distended; it thickens into a lingual cingulum that descends to the base of the narrow, pointed posterior heel that lies at the base of the long, sharp and concave distal edge of the tooth. From the heel there runs a thick, ledgeliike buccal cingulum that thins and fades out halfway around the crown. Internally, the crown bears a thick central pillar with depressions fore and aft of it. The upper canine is longer mesiodistally than the last premolar and stands more than three times higher than the molars.

The premolars are subequal in height and stand approximately half as tall as the canine. These three teeth are dominated by a large, sharply edged paracone and each is ringed by a complete and fairly well-developed basal cingulum bearing anterior and posterior styles. These cusps increase in size from front to back. The premolars also form an anteroposterior morphocline in the expansion of the lingual face of the crown: in occlusal view, the anteriormost premolar is relatively narrow buccolingually, the middle premolar is moderately swollen (especially distolingually), and the posterior premolar is definitely triangular, bearing at the base of its paracone a small but pointed protocone, somewhat anteriorly displaced. On the posterior premolar, what presents itself as a precingulum becomes confluent with the protocone, but the cingular ring is maintained by the convergence with this precingulum, buccal to the protocone, of a postcingulum that has swung around the base of this cusp (the disposition of this "precingulum" leads

one to suspect that, in fact, it is a preprotocrista). The posterior premolar is about the same size as the trigon of M^1 .

The upper molars develop fairly tall and separated paracones and metacones that bear stout crests on their sides; lingually there is a well-developed stylar shelf between these two cusps that is met by a thin buccal cingulum that emanates from a small parastyle. The relatively small metacone and postmetacrista of M^3 are angled outward, as are the larger metacone and longer postmetacrista of M^{1-2} ; on these two molars, the metacone and paracone are subequal in size and both bear long crests. The molar trigons are moderately long and broad. The protocone is relatively low, broad, and internally flattened and is only slightly displaced anteriorly. The protocristae, V-shaped but somewhat broadly divergent, subtend a rather deep trigon basin. The moderately stout preprotocrista arcs forward and around the paracone to become confluent with the parastyle; the much weaker postprotocrista, which may thicken at the base of the metacone on M^{1-2} , fades out as it courses centrally up the lingual face of this cusp. A relatively thick postcingulum runs from the metastylar region around the base of the protocone and, as a much thinner structure, converges upon the preprotocrista just buccal to the protocone. In the talon region of M^3 , the postcingulum is only slightly distended. On M^{1-2} , however, the postcingulum in this region thickens markedly to square-up the corner of the tooth and then continues as a straight, ledgelike structure around the lingual face of the protocone; on M^2 especially, the cingulum thickens antero-lingually into a protostyle that tends to square-up that corner of the tooth as well. The talon of M^{1-2} bears a moderately elevated, broad hypocone (relatively larger on M^2) that is situated below and behind the protocone, but which is connected to that cusp by a faint prehypocone crista; this crest is most easily observed as it crosses a narrow groove between the bases of the two cusps.

Because the lingual faces of the molars are relatively straight and squared-up, but are narrower mesiodistally than the buccal sides, these transverse teeth may be described as elongately trapezoidal in shape. M^3 bears the straightest anterior and distal sides; the posterior side is only minimally "waisted." The

lingual faces of M^{1-2} , however, are skewed slightly and are thus not quite parallel to the buccal side of the tooth; the anterior face is therefore somewhat longer and convexly arcuate, whereas the distal side of the tooth is moderately flexed (more deeply on M^1) into a shallow notch to the side of and lingual to the base of the metacone. Buccally the three molars are subequal in mesiodistal length; but lingually M^2 is longer than M^1 which, in turn, is longer than M^3 . M^2 is the widest molar; M^1 is only slightly wider buccolingually than M^3 .

LOWER DENTITION (Figs. 19, 20, 21)

The lower six anterior teeth are quite elongate and procumbent and arc gently upward at their tips. The central four are the most compressed laterally, but the central pair are slightly more compressed and longer than their neighbors. All four teeth bear strong, compressed longitudinal keels that are subtended inferiorly by thin, but distinct, margocristids; the tips of these teeth arc toward the midline, so that, as a unit, their tips are like the teeth of a fine saw. The most lateral of the six teeth are shorter, but are much deeper and robust and flare laterally; these teeth bear a low, broad, longitudinal keel that is quite medially emplaced. This keel is separated by a broad, shallow longitudinal groove from a moderately developed lateral margocristid; a thinner margocristid bounds the tooth medially.

All premolars are dominated by a stout, pointed protoconid. The root of the anteriormost premolar is distanced from the toothcomb, but the crown is distended anteriorly and inclined moderately forward such that buccally it slightly overlaps the heel of the lateral procumbent anterior tooth. Although the anterior lower premolar is fairly trenchant, it does not stand much more than one-third taller than the molars and is not much taller than the middle and posterior premolars. The anteriormost extension of the anterior premolar occurs three-fourths the way up the crown, thereby delineating a long, concave, posteriorly sloping edge inferiorly and, superiorly, a much shorter, more compressed, and strongly arcuate edge. The long, relatively sharp posterior edge mirrors the curvature of the longer anterior edge; it

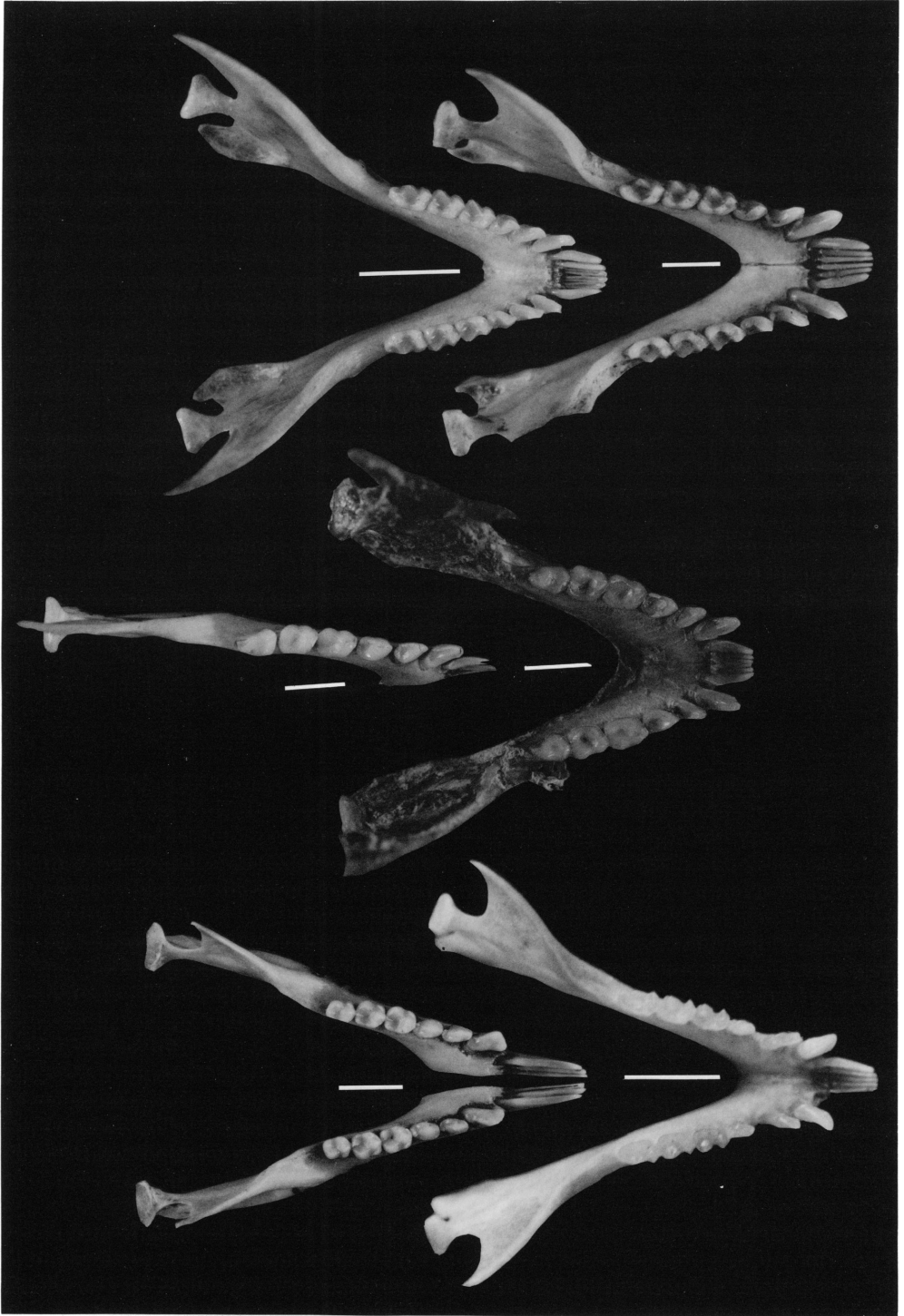


FIG. 20. Lower jaws of cheirogaleids in occlusal view. Clockwise from top right: *Mirza coquereli* (AMNH 100832); *Cheirogaleus medius* (AMNH 196618); *Allocebus trichotis* (BMNH 75.1.29.20); *Phaner furcifer* (AMNH 100829); *Cheirogaleus major* (AMNH 100640); *Microcebus murinus* (AMNH 174434). All scales represent 5 mm.

terminates at a slightly thickened and elevated heel that faces lingually and subtends inferiorly a shallow and teardrop-shaped posterior depression. This depression is bounded lingually and inferiorly by a low, broad protoconid pillar that courses from the tip of the tooth and basally swells the crown distolingually. A thin lingual cingulid proceeds steeply from the anterior extension down and around this swelling and then straight up to join the small heel, from which emanates a thin and slightly bumpy cingulid that encircles the tooth buccally, but which fades out anteriorly.

The middle premolar is a longer, stouter tooth, more compressed buccolingually than the anterior premolar. As in the latter, the middle premolar is noticeably distended anteriorly; but the anteriormost point occurs slightly lower on the crown, causing the anterior edge to be somewhat longer superiorly. The sharp posterior edge of this tooth terminates lingual to a centrally emplaced, moderately thickened and distended heel; the posterior edge converges distolingually upon the low, broad protoconid pillar and truncates a long, narrow, shallow posterolingual depression. A thin lingual cingulid proceeds steeply downward from the most anterior part of the tooth, thickens distolingually, and turns upward to join the posterior heel; from here there emanates a thick buccal cingulid that thins, to fade out, as it runs anteriorly.

The posterior premolar is stouter and slightly wider than the middle premolar, but is somewhat shorter mesiodistally. In fact, when compared with the middle premolar the posterior premolar appears compressed mesiodistally. Its thick buccal cingulid is thus U-shaped, and the very thick and quite lingually emplaced posterior heel is angled up and forward; the anterior extension is not greatly emphasized. The relatively thick paracristid proceeds anteriorly, and the sharply compressed posterior edge, incorporating a low metaconid swelling, descends to terminate lingually, creating a moderately developed notch between the compressed metaconid and the upturned heel. A thin lingual cingulid courses slightly downward from the modest anterior extension to fade out below this notch. From the heel a thick, ledge-like cingulid proceeds inferiorly, slightly an-

teriorly and rather buccally, to terminate at a narrow groove; on the other side of this there continues a thick buccal cingulid that thins as it courses around the base of, and partway up, the anterior face of the tooth. The posterior heel and the thicker region of cingulid subtend, inferiorly, a wide, posterobuccally oriented excavation that is opened by the cingulid groove. Depth is given to this excavation by a marked posterobuccal compression or truncation of the protoconid; this makes the tip and vertical axis of the cusp appear more lingually displaced than they actually are. The posterior premolar is slightly narrower than the trigonid of M_1 , but is distolingually much shorter than the latter tooth.

The molar protoconids and metaconids are broadly melded at their bases, and their tips, especially on M_{1-2} , are connected by a stout crest. The metaconid sits somewhat posterior to the protoconid; it is most intimately associated with the latter cusp on M_1 and is farthest away on M_3 ; these two cusps form a fairly steep wall that faces upon the talonid. A distinct paracristid proceeds down the face of the protoconid, kinks at its base, then runs posteriorly as a paraconid shelf that fades out as it travels up the face of the metaconid. The paracristid extends farthest anteriorly on M_1 , so the paraconid shelf subtends inferiorly an increasingly narrow trigonid basin from M_{1-3} . Moderate lingual swelling of the hypoconid and especially of the protoconid is greatly enhanced by a cingulid that descends from the point of flexion of the paracristid to thicken markedly around the protoconid; it thins out once more as it proceeds around the base of the hypoconid. The increased lingual expansion of the protoconid effectively deepens the hypoflexid notch. On M_{1-2} , the lingual cingulid continues around the hypoconid to converge upon the hypocristid just medial to the base of that cusp; on M_3 it courses past the hypoconid to thicken into a ledge-like structure bearing two minute swellings before thinning and swinging up to join the tip of the buccally compressed and displaced hypoconulid heel. The buccal cingulid of M_3 both broadens the narrow heel inferiorly and forms the border of a long basin in the broad "notch" between the hypoconulid and hypoconid; this is subtended superiorly by a

distinct concavely arcing crest that courses between the two cusps. The mesiodistally shorter M_{1-2} are fairly straight on their posterior sides and, at most, bear thin hypocristids that thicken slightly at their confluence with the distal continuation of the buccal cingulid.

The molars show stout and rather straight cristae obliquae; these emanate from a fairly well-developed hypoconid, and run just medial to the midline of the protoconid to fade out as they ascend the posterior face of that cusp. On M_3 the cristid obliqua courses a bit farther medially than on the anterior molars (thus creating a somewhat deeper hypoflexid notch on the tooth) before it arcs buccally to meet the protoconid just to the inside of the midline of that cusp. The talonid basin is thus subtended anteriorly by the metaconid and part of the protoconid. Curiously, the fairly deep talonid basin is overhung by the metaconid, which arcs backward at its tip; the cusp pulls with it the attendant premetaconid cristid as well as a thin postmetaconid cristid that passes to the entoconid, forming a broad notch lingually. On M_{1-2} the feebly incurved entoconid also overhangs the talonid basin; on M_3 the compressed entoconid is connected to the closely approximated hypoconulid by a short crest and all three structures arc inward slightly. Although the three molars increase only slightly in maximum buccolingual width from M_{1-3} , M_2 is noticeably longer than M_1 , and M_3 is markedly the longest of the set.

GENUS *MIRZA*

MIRZA COQUERELI

UPPER DENTITION (Figs. 16, 17, 18)

The upper incisors are small, the lateral incisors approximately half the size of the central pair. Both are similar in that the crown is slightly elongate and flexed upward, and the long axis of the tooth arcs gently toward the midline. The central incisors are noticeably separated from each other.

The canine is very tall, standing more than three times the height of the molars, and is triangular in outline, with a small heel posteriorly and the anterior edge emphasized inferiorly by a constriction at the neck; there is a weak lingual cingulum anteriorly. Although

the crown of the tooth is compressed or flattened buccally, its lingual face is convex.

The anteriormost of the three premolars is approximately one-half the height of the canine and although it is somewhat taller than its posterior neighbor, it sits deeper in the jaw so that the tip of its trenchant paracone is below that of the latter. From the middle to the last premolar and through the molar series there is a gradational decrease in crown height. All three premolars are dominated by a strong, pointed paracone that is flattened buccally, is lingually convex, and bears a robust, continuous buccal cingulum. On the anterior premolar the cingulum proceeds to encircle the base of the crown and is thickened posteriorly into a small heel. The cingulum of the middle premolar also rings the tooth but is more ledgelike and is distended not only posteriorly but anteriorly and centrolingually as well. The protocones of the last two premolars arc slightly backward. The more equilateral paracone of the posterior is bounded buccally by a stout cingulum that expands anteriorly into a large, ledgelike parastyle and posteriorly into a smaller distension. From the anterior and posterior stylar regions of this tooth, broad pre- and postcingula, respectively, descend toward a moderate and low protocone; the precingulum proceeds toward the apex of this cusp, and the postcingulum fades out at the base of the protocone. The three molars are similar in possessing relatively tall, distinctly separated paracones and metacones, and lower but very broad protocones from which emanate thin, fairly arcuate protocristae; the preprotocristae arc around the protocones to become confluent with the parastylar regions, which are also joined by weak preparacristae. Each also bears a complete, somewhat crenulated buccal cingulum as well as a distinct precingulum and a stronger posterior one that converge around the face of the protocone to form a broad ledge. M^{1-3} are approximately equal in breadth but M^1 is broader and squarer, whereas M^3 is subtrapezoidal in shape. The noticeable lingual dimension of the first molar is created by the widely separated and ledgelike cingular swellings of the protostylar region and the moderately developed hypocone; in contrast, these structures in M^2 converge at the base of the protocone.



FIG. 21. Lower left dentitions of cheirogaleids (except *Allocebus*) in occlusal view. From left to right: *Mirza coquereli* (AMNH 100832); *Microcebus murinus* (AMNH 174434); *Phaner furcifer* (AMNH 100829); *Cheirogaleus medius* (AMNH 196618); *Cheirogaleus major* (AMNH 100640). Not to scale.

LOWER DENTITION (Figs. 19, 20, 21)

The six anterior lower teeth are quite elongate, relatively slender, curve slightly upward at their tips, and are markedly procumbent. Among toothcombed strepsirhines, the toothcomb of *Mirza* compares most closely with that of *Phaner*. The central four teeth are very compressed laterally, are parallel-sided, and bear faint margocristids which are most noticeable at the base of the tooth. The lateral teeth are more robust and deeper than the central set and also flare noticeably lateralward. These teeth bear distinct lateral margocristids but traces of a medial margocristid are observable primarily toward the base of the tooth.

The anteriormost of the three premolars is trenchant and, although slightly forwardly inclined, stands more than twice the height of the molars. The buccal face of this tooth is somewhat convex, the crown gently arcing inward toward its tip. The strong protoconid bears a broad pillar lingually that forms a

groove toward its base with a relatively vertical, inwardly facing, posterior heel; from this extends buccally an incomplete cingulid and lingually a complete one that arcs to terminate halfway up the crown anteriorly. The distal edge of the anterior premolar is concave, whereas the much shorter mesial edge is gently convex. The horizontal axis of this tooth is oriented somewhat obliquely to the long axis of the jaw.

The shorter middle premolar is basically similar in outline and orientation to its anterior neighbor but differs in that the posterior heel protrudes more posteriorly and the buccal cingulid extends anteriorly to form a small stylid with the lingual cingulid. The posterior premolar is a very distinctive tooth characterized especially by its lingually offset protoconid that appears buccally excavated, especially posteriorly. A small, compressed cusp at the base of the protoconid is most likely a very lingually emplaced hypoconid which adds depth to the posterior aspect of the protoconid excavation. From the level of

this small cusp a faint lingual cingulid extends anteriorly to thicken and become ledgelike as it encloses the buccal excavation basally.

This pattern of buccal excavation is maintained in the molars, where the protoconid is shifted centrally, bringing an attendant cristid obliqua with it and creating a deep hypoflexid notch. This notch is further emphasized by the presence of a stout, continuous buccal cingulid. All molars also possess relatively tall protoconids and metaconids that are melded at their bases and form a steep wall facing the talonid basin; metaconids that are emplaced somewhat behind the protoconids; and very compressed trigonid and shallow talonid basins. In addition, each molar bears a weak paracristid that proceeds partway down the face of the protoconid, then angles sharply, and continues as a thin shelf to the base of the metaconid, and a slightly buccally displaced entoconid that is incorporated in an arcuate cresting system, from the metaconid to the hypoconid; this, together with the straighter cristid obliqua, encloses the talonid basin. The molars are subequal in length but M_3 narrows to a moderately developed, buccally situated heel, whereas the first two molars display relatively broad talonids.

FAMILY LORISIDAE

This family of four genera clearly requires some systematic reappraisal, but at present each genus is regarded as specifically monotypic. From two to 10 subspecies have been proposed for each of these species, but population variation in dental morphology appears to be sufficiently restricted to allow a single description to suffice for each, at least for present purposes.

GENUS *LORIS*

LORIS TARDIGRADUS

UPPER DENTITION (Figs. 22, 23, 24)

The upper incisors are thin, small, fairly high-crowned teeth, subequal in size and tilted palatally. The central and lateral teeth are tightly packed together; the lateral teeth lie close to the upper canine, whereas the central incisors are widely separated by the anterior palatine fenestrae. The crowns of the incisors

are flattened somewhat lingually and are very slightly distended mesially and distally.

The upper canine is tall, robust, trenchant, and somewhat laterally compressed; it bears distinct anterior and distal styles that are appressed basally to the pointed paracone. This tall, dominant cusp possesses a broad, vertical lingual pillar that subtends narrow anterior and posterior depressions. The crown stands quite vertically, its edges straight and steeply descending; but its height is diminished somewhat because the tooth sits deeply in the jaw. A fovea lingual to the root of this tooth accommodates the tip of the lower anterior premolar. The upper canine is still more than twice the height of the posterior cheek teeth; the impression of its robust root, which is longer than the crown is high, is boldly molded onto the maxillary bone externally, thus causing the snout to look somewhat puffy. The tooth is set obliquely in the jaw so that the lingual surface faces quite markedly posteriorly.

All premolars are dominated by a tall, pointed, conical paracone that is triangular in buccal outline and bears strong pre- and postcristae terminating in distinct, pointed styles; the anterior and posterior styles of the first two premolars are subequal in size, but the anterior and much more so the posterior style of the last premolar are larger in height as well as in basal expansion.

The anterior premolar stands approximately two-thirds the height of the canine and is about 25 percent taller than the posterior premolar; it is much higher than the middle premolar, which is the lowest of the set. The anterior premolar is also the longest mesiodistally and the least expanded lingually of the three teeth. What minor development there is lingually is caused by the lingual paracone pillar centrally and by the distolingual distension of the shallow posterior depression that the pillar subtends. The complete lingual cingulum, slightly corrugated in parts, is most developed and ledgelike as it leaves the styler regions and is weakest around the slight distolingual expansion.

The middle premolar is the smallest of the three in height and mesiodistal length; in width, however, even with the presence of a moderately developed protocone to which is appressed somewhat basally a small but



FIG. 22. Crania of lorids in lateral view. Descending from top: *Loris tardigradus* (AMNH 217303); *Nycticebus coucang bengalensis* (AMNH 87279); *Perodicticus potto* (AMNH 31252); *Arctocebus calabarensis calabarensis* (USNM 511930). All scales represent 5 mm.

distinct hypocone, this tooth is slightly larger than the anterior premolar. The compressed, pointed hypocone is incorporated into a postcingulum that emanates from the posterior style as a thickened band but fades out as it climbs the lingual face of the anteriorly emplaced protocone. The postcingulum borders a moderately developed talon basin that seems to flow from the steep sides of the paracone and the displaced protocone. A thickened, ledge-like precingulum emanates from the parastyle and becomes confluent with the

protocone. In occlusal view the tooth is noticeably waisted anteriorly and posteriorly; this waisting is created by lateral expansion buccally at the expense of the protocone and hypocone. The buccolingual axis of this tooth is skewed such that the poststyler region of the tooth sits in the area of waisting below the expanded parastylar region of the posterior premolar.

The posterior premolar is slightly shorter mesiodistally than the anterior premolar but its width is much greater than its length; the

tooth is about the size of the trigon of M^1 . In virtually all details the posterior premolar is similar to the middle premolar. The poststylar region is much more expanded than the enlarged parastylar region; the poststylar region is also skewed a bit buccally, as it is on M^1 . The waisting of the tooth occurs before its horizontal midline and appears as a moderately deep and narrow notch posteriorly due to the greater expansion of the postcingulum inferior to it; as it courses downward and inward from the poststylar region the postcingulum kinks severely distally and inferiorly to proceed, as a thickened structure, to the side of the relatively expansive talon basin and up to the hypocone. The apical part of the hypocone is separated from the protocone by a relatively deep notch. The thickened precingulum bears a moderately developed paraconule, which seems to indicate that what appears as a precingulum is instead a preprotocrista (as possibly in strepsirhine upper premolars in general).

The molars bear tall, pointed cusps, the tallest of which are the paracone and metacone, and the lowest the hypocone; all buccal cusp and protocone crests are distinct and there is also a thin prehypocone crista that is most easily observed as it courses between the bases of the hypocone and protocone. The molar trigons are quite transverse and the V-shaped protocristae, which subtend a well-excavated trigon basin, bear strong para- and metaconules. On each tooth, the protocone is noticeably displaced anteriorly, and thus the rather straight preprotocrista courses directly to the small, low parastyle, anterior to the paracone. The shorter postprotocrista, which fades out centrally at the base of the metacone, is further truncated by the large metaconule. From the small metastyle (which is subequal to the parastyle on M^{1-2} but smaller on M^3) emanates a stout postcingulum that fades out lingual and inferior to the metacone on M^{1-2} . On all molars, the posterior side of the tooth is markedly waisted in this region, but on M^3 the thick postcingulum continues arcuately around the exceedingly distolingually distended talon to fade out centrally on the hypocone.

The talon of M^{1-2} is also extraordinarily expanded, but its longer distal face is straighter than on M^3 ; distal and inferior to the ter-

minus of the metastyle-bearing postcingulum, another stout and slightly crenulated postcingulum arises to course around the lingual face of the hypocone, rise as a cuspule between the bases of the hypocone and protocone, and then fade out partway around the face of the protocone. In the sequence M^{1-3} the hypocone is removed farther from the protocone, hence the trough internal to the cingular cuspule is larger. In addition to showing this small depression, M^3 bears two other foveae: a narrow, crescentic talon basin between the buccal side of the hypocone and the postcingulum; and a deep, narrow pit just distal to the metacone, also internal to the postcingulum. In contrast, the posterior side of M^{1-2} is open between the unconnected postcingula. The trigon of M^1 is smaller than that of M^2 but the greater talon expansion of the former tooth makes the two molars subequal in overall size. The much smaller M^3 trigon, in which the metacone is somewhat reduced in size, bears a rounded and greatly distolingually expanded talon.

LOWER DENTITION (Figs. 25, 26, 27)

The lower six anterior teeth are dwarfed by the relative bulk of the other teeth. These six are rather slender and elongate and curve slightly upward at their tips; they are separated somewhat at their roots but the crowns converge. As a unit, these teeth are barely procumbent. The central four are quite compressed laterally; they bear a broad longitudinal keel bordered inferiorly by faint margocristids. The lateral teeth are a bit shorter, but much deeper, more robust, and moderately flared laterally.

The anteriormost premolar is an extremely tall, robust, and trenchant tooth that is inclined slightly forward; it is quite broad at its base but tapers at its inwardly curved tip to a fine point. The short, straight and anteriorly directed anterior edge is bladelike; inferiorly it thickens and emits a moderately developed lingual cingulum that descends steeply to course weakly around the inferiorly and distolingually swollen base of the crown before rising somewhat as a thicker structure. The steep, longer posterior edge is more rounded; a thick crest descends from the apex of the crown to fade out well before reaching the



FIG. 23. Crania of lorids in ventral view. Descending from top: *Loris tardigradus* (AMNH 217303); *Nycticebus coucang bengalensis* (AMNH 87279); *Perodicticus potto* (AMNH 3152); *Arctocebus calabarensis* (USNM 511930). All scales represent 5 mm.

distolingual swelling. The mesiodistal axis of this tooth is noticeably angled inward posteriorly and the tooth is situated such that, in side view, only the tips of the toothcomb teeth are visible in their entirety. The tooth stands approximately two-thirds higher than the middle and posterior premolars, which

are subequal in height and rise only slightly above the molars.

The long axis of the rather simple middle premolar is also skewed inward posteriorly; the tooth is inclined slightly forward. Especially in comparison with the anterior premolar, the middle one appears somewhat di-

minished; indeed, even though the crown bears a stout, pointed protoconid, its buccal side is fairly flat and there is only moderate development of a cingulid lingually and a heel posteriorly. A thin, ledgelike cingulid emanates from a flattened anterior styloid and courses down the lingual face of the tooth to fade out just before reaching the heel, allowing a relatively shallow, teardrop-shaped basin to open lingually; this basin is bounded externally by a thin cristid obliqua that runs from the small and buccally emplaced hypoconid up to the tip of the large protoconid. On its lingual side, it is bordered by a fainter, more rounded crest that runs centrally down the steep posterior face of the protoconid to fade out just prior to meeting the lingual cingulid. The small heel is flattened internally and separated from the hypoconid in front of it by a narrow groove.

In length the bulky posterior premolar is subequal to or slightly shorter than the middle premolar, but it is much wider, being especially swollen mesiolingually and distolingually. The tooth bears a well-developed metaconid that is broadly melded with the taller and stouter protoconid and is emplaced somewhat behind it; these two pointed cusps are further connected by a relatively broad paraconid shelf. The two cusps form a steep, flat wall that faces onto a moderately large and excavated talonid basin; this basin is wider than it is long, with the cristid obliqua emanating from the small, low, and buccally emplaced hypoconid and coursing centrally up the face of the protoconid. The talonid basin is enclosed by a thin, continuous cresting system that is opened lingually by a small notch between the base of the metaconid and a small but distinct entoconid.

The molars also develop a steep protoconid-metaconid wall facing the talonid as well as a thick paraconid shelf that runs from the base of the slightly taller and stouter protoconid up the face of the metaconid. However, this shelf subtends a slightly larger and well-excavated trigonid basin and is confluent with a paracristid (most prominent on M_1) that courses down the face of the protoconid. Furthermore, it is only the metaconid that faces onto the talonid basin; the protoconid lies on a deep hypoflexid notch because the straight

cristid obliqua runs medially, to terminate between the metaconid and protoconid. These cusps, although broadly melded at their bases, are widely divergent at their crest-connected tips. Even though the trigonid towers over the talonid, the entoconid and the lingually swollen but slightly smaller hypoconid are themselves quite salient and pointed. From the hypoconid of M_{1-2} runs a low, straight hypocristid that terminates behind the entoconid and bears two small, flattened hypoconulids. Thin, sharp crests descend the steep internal faces of the metaconid and entoconid and enhance the deep lingual notch created by these two cusps.

All molars, notably M_{2-3} , bear well-developed lingual cingulids; these descend posteriorly to fade out at the bases of the hypoconids. These cingulids thicken to form a floor to the deep hypoflexid notch and condense at the base of the protoconid to form proto-stylids that typically increase in size from M_{1-3} . Although subequal in width, buccolingually the molars increase in length from M_{1-3} . M_3 would, however, be much shorter than M_2 if it did not develop a fairly long hypoconulid; this cusp is centrally emplaced and flattened internally, and separated lingually from the entoconid by a narrow groove.

GENUS *NYCTICEBUS*

NYCTICEBUS COUCANG

UPPER DENTITION (Figs. 22, 23, 24)

There are geographic regional differences among *Nycticebus* in the number of successional incisors present in the adult (e.g., Hill, 1955; Schwartz, 1974). Some have four while others have two. In the latter cases, it is the lateral incisors that do not develop.

The central incisors are high-crowned teeth whose lower halves are thick and somewhat laterally compressed, whereas the upper parts are broader, being distended mesially and compressed buccolingually; the mesial distension accentuates the gentle inward arcing of the tooth. Lingually, a thin distal and a much thicker mesial cingulum border depressions: the posterior depression is low on the crown and is both shallower and broader than the anterior depression, which is higher up



FIG. 24. Upper right dentitions of lorises in occlusal view. From left to right: *Perodicticus potto* (AMNH 31252); *Nycticebus coucang bengalensis* (AMNH 87279); *Arctocebus calabarensis calabarensis* (USNM 511930); *Loris tardigradus* (AMNH 217307). Not to scale.

on the crown. The lateral incisors, although morphologically similar to the central incisors, are quite diminutive by comparison. The lateral incisors are crowded between the central incisors and the canines.

The upper canine is a very tall and robust tooth that is somewhat distended postero-inferiorly; the mesial and distal edges are compressed. The tip of the tooth flares slightly outward (i.e., buccally) but also arcs somewhat distally; a strong buccal pillar as well as the mesial edge arc backward while the distal edge is gently concave. Although this tooth is high-crowned, it does not rise markedly above the other teeth because it is set deeply in the jaw, being bordered lingually by a pit that accommodates the tip of the lower anterior premolar. The upper canine is set obliquely in the jaw and there is a small di-

astema separating it as from the anterior premolar. The stout root of this tooth extends almost as far as the nasomaxillary suture, making the snout of *Nycticebus* appear "puffy."

The anterior upper premolar differs from those posterior to it not only in lacking development lingually, but in being taller and much longer mesiodistally. The tooth is further set apart because its mesiodistal axis is not in line with the other cheek teeth but is skewed noticeably outward. The dominant paracone bears a stout lingual pillar that distends the base of the tooth; this pillar delineates a distinct, vertical depression anteriorly and a broader but shallower one distally. The paracone curves gently backward as does its anterior edge; the slightly longer distal edge is concave. Both edges bear small styles ba-

sally, the anterior one larger and somewhat farther up the crown.

The middle premolar is slightly taller, but is narrower both mesiodistally and buccolingually than the posterior premolar. Both bear small anterior and posterior styles. In the middle premolar a thin band of cingulum courses lingually between these two styles. The tooth is dominated by the paracone and is only moderately expanded lingually and distally into a posteriorly oriented, inferiorly sloping, ledgelike talon. It bears a small, pointed protocone that is anteriorly emplaced and close to the base of the paracone; the compressed external face of this diminutive cusp is incorporated into the band of cingulum. Centrally, there may also be a slight elevation of the lingual cingulum, sometimes distinctly pointed, that could be a minute hypocone. The mesial edge of the paracone is more compressed and bladelike than the distal edge; the sharpness of the anterior edge is emphasized further by a narrow vertical groove lingually.

The posterior premolar bears an anteriorly displaced protocone that is as large as that on M^1 , and a small but distinct hypocone at the base of the protocone; a lingual pit or groove further distinguishes these cusps. Both are confluent with the thick pre- and postcingula that emanate from the anterior and posterior styles. The postcingulum borders a broad but shallow talon basin, and may be wrinkled such that it appears to bear a small cuspule/style or two; the enamel of the talon basin is also somewhat crenulated. The anterior and posterior paracone styles of the posterior premolar are heavier lingually than are those of the middle premolar but as in the latter the anterior paracone edge is compressed and bears a vertical groove internally. The posterior premolar may also possess a small conule, somewhat anteriorly displaced, at the internal base of the paracone.

The cusps of the molars are somewhat low and puffy but also bear reasonably developed crests on their sides. On M^{1-2} a strong postprotocrista proceeds to the apex of the metacone, and on M^{1-3} the interior face of the protocone is strongly compressed, and in M^{1-2} quite crestlike; on these teeth this crest joins the broad precingulum at a swelling that truncates the preprotocrista, whereas the para-

cone of M^3 crista is subtended basally by a broad preprotocrista as the latter structure courses to the parastylar region. Because of the distinctiveness of the structures on M^3 (and especially since the molars are serial derivatives of the same stem cell mass), it is reasonable to conclude that the precingulum-like structure on M^{1-2} is, in fact, the continuation of the preprotocrista with which the paracone "crista" has become conjoined. These paracone "cristae" effectively truncate and narrow the otherwise V-shaped trigon basin.

M^1 is longer mesiodistally and more rectangular than M^2 but is narrower buccolingually. M^2 is more "waisted" distally, has a less squared-up mesial face, and has its hypocone distended lingual to rather than behind the protocone. Both M^{1-2} bear a broad postcingulum that emanates from the metastylar region and terminates at the base of the hypocone, in front of which the cingulum may bear a small cuspule/style. The hypocone on M^{1-2} is connected posteriorly to the protocone by a strong prehypocone crista that forms the wall of a relatively broad and deep lingually opening groove that separates the two cusps; a small but distinct style is either present in the groove or appressed to the hypocone; in the latter case, especially, there is a small pit between the style and the cusp. In addition, there is a distinct mesostyle on M^{1-2} which, on M^2 , is connected to the metastylar region; M^2 also bears traces of cingulum around the face of the protocone.

The third molar is smaller than M^{1-2} but the metacone and postprotocrista are markedly diminished, and the tooth lacks lingual development but for a buccal continuation of the broad precingulum into the parastylar region, partway around the paracone. A narrow, corrugated postcingulum originates below the paracone and fades out as it courses lingually around the protocone.

LOWER DENTITION (Figs. 25, 26, 27)

The lower six anterior teeth are moderately elongate and procumbent and recurve somewhat at their tips. The central four are quite compressed laterally and are dominated by a longitudinal central keel with faint margo-cristids on its sides. The outermost of the six

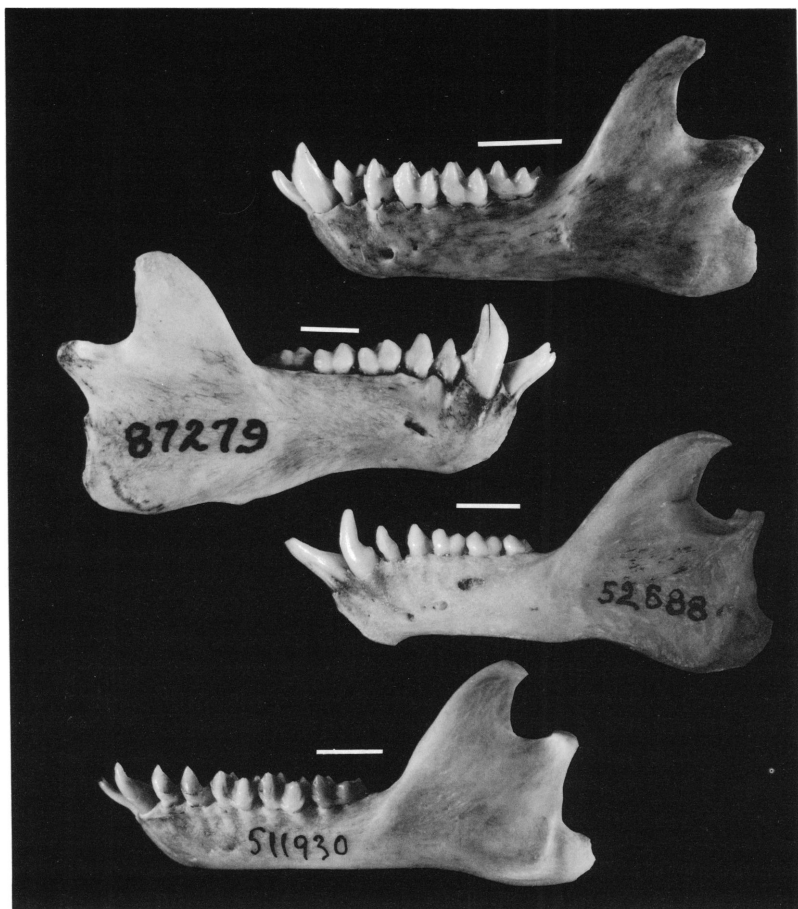


FIG. 25. Lower jaws of lorids in lateral view. Descending from top: *Loris tardigradus* (AMNH 217303); *Nycticebus coucang bengalensis* (AMNH 87279); *Perodicticus potto* (AMNH 52688); *Arctocebus calabarensis calabarensis* (USNM 511930). All scales represent 5 mm.

teeth are more robust, deeper, recurved inward more markedly, and are quite broadly flared laterally; they are also longer. These teeth bear a low longitudinal central keel and faint margocristids of which the medial is the more distinct. Their lingual faces are oriented inward such that the keel is directed medially and the lateral margocristid upward.

The anterior premolar is an extraordinarily trenchant and tall tooth, standing more than twice the height of the molars; it is also much longer mesiodistally than the middle and posterior premolars, approaching the molars in this dimension. The tip of this tooth arcs gently inward and backward; this curvature is followed by the broad, basally swollen lingual protoconid pillar. This pillar borders a

narrow, vertical groove anteriorly and forms the edge of the long, sloping heel. The concave distal edge of the tooth is only marginally compressed, whereas the shorter, convex anterior edge is markedly distended and bladeliike. Weak but distinct cingulids course from these edges to become confluent around the base of the tooth lingually. The mesio-distal axis of this tooth is oriented obliquely to the long axis of the jaw; this also characterizes the middle and posterior premolars, which appear to be more skewed because of the degree to which they are posterolingually distended.

The middle premolar is slightly smaller than the posterior premolar in all dimensions; both, however, emphasize the anterior

and posterior crestlike edges of the paraconid. In each tooth, a prominent crest diverges from the posterior edge about one-third the distance from the tip of the protoconid and proceeds inferiorly toward the distolingual distension. On the middle premolar, this posterointernal crest fades out before reaching the "heel"; this inverted Y-shaped cresting system creates and circumscribes a deep posterior fovea. In contrast, this crest on the last premolar "kinks" near the base of the protoconid and proceeds as a narrow ledge to the anterior extent of the tooth; this forms a shallow depression in the middle of which is a broad lingual protoconid "pillar." The posterior protoconid edge, which flows into a relatively broad and descending postcingulid, thus forms a somewhat compressed posterior basin that opens lingually. On the middle premolar, however, the posterior protoconid edge is confluent with a distinct cingulid that completely rings the base lingually, thereby effectively closing off the posterior fovea and subtending a broad protoconid pillar inferiorly.

The molars are characterized by having relatively low and puffy cusps (especially the protoconid anterobuccally and the entoconid distolingually) and buccal cingulid development (especially anteriorly). The metaconid is emplaced posterior to the protoconid; the relatively broad paracristid, which courses down the face of the protoconid and then kinks to run to the base of the metaconid, follows this oblique path, enclosing a narrow trigonid basin. M_{1-2} are subequal in size and bear fairly stout cristid obliquae that terminate centrally, below another stout crest that connects the protoconid and metaconid; these cusps are relatively close to each other and their bases are quite melded, whereas the cusps are widely separated on M_3 . The cristid obliquae of M_{1-2} are further emphasized by a moderately deep crease buccally that also enhances the hypoflexid notch. These two molars lack a discernible hypoconulid but the hypocristid is slightly distended and flexed inferiorly by a crease that runs the length of the talonid basin just internal to the entoconid.

The narrower M_3 bears a moderately developed and centrally emplaced heel that is not connected to either of the other talonid cusps; this elongate, triangular moiety is typ-

ically narrower than the trigonid. In contrast to the condition on M_{1-2} , the cristid obliqua of M_3 arcs to the protoconid; a faint buccal groove accents the shallower hypoflexid notch.

GENUS *PERODICTICUS*

PERODICTICUS POTTO

UPPER DENTITION (Figs. 22, 23, 24)

The upper incisors are moderately thick, slightly procumbent, somewhat elongate, high-crowned teeth whose height is effectively increased by an orad distension of the bone in which they sit. The lateral incisor is about two-thirds the height of the central incisor but the crowns of both teeth are similar in that they flare a bit (especially mesially) and bear thickened margocristae that circumscribe the lingual face of the rather conical tooth. The lateral incisors tilt only slightly toward the midline. The central incisors, although separated at their roots by the anterior extents of the palatine fenestrae, arc markedly toward the midline of the jaw at their tips.

The upper canine is a very stout, trenchant, pointed tooth of relatively simple structure. The slightly convex mesial edge bears a sharply descending crest that becomes enlarged as it proceeds inferiorly. The posterior edge of the tooth is slightly convex, compressed, and bladelike; this edge subtends a shallow, vertical lingual depression.

The premolars are quite a heteromorphic threesome. The anteriormost premolar is quite tall (almost two-thirds the height of the canine) and stout, especially basally. In buccal outline, this tooth is triangular with rather straight, compressed edges that terminate inferiorly as styler-like distensions; these edges subtend narrow, shallow, vertical lingual depressions that emphasize a stout paracone "pillar." The tooth arcs noticeably outward (buccally) at its tip, thereby creating concave buccal and convex lingual faces.

The middle premolar is taller than the molars and just over half the height of the anterior premolar. In buccal outline, the middle premolar is similar to the anterior premolar but more equilaterally triangular. On the middle premolar, however, broad lingual

cingula emanate from the anterior and posterior styles and become confluent around the thickened base of the paracone "pillar" at which juncture there is a small, V-shaped notch. This basically conical tooth is skewed in the jaw so that it is overlapped posterobuccally by the parastylar swelling of the posterior premolar.

The posterior premolar stands higher than the molars but is not quite as tall as the middle premolar. In buccal outline the posterior premolar is similar to the middle premolar but the base of the paracone is much longer mesiodistally; the paracone is also markedly bulbous buccally. The posterior premolar also bears a bulbous protocone that lies opposite, but is in all dimensions somewhat smaller than, the paracone; in occlusal view, the crown looks like a thick "T." Broad pre- and postcingula emanate from the buccal stylar regions and thin as they proceed up the side of the protocone to meet at the apex of the cusp. The posterior premolar is approximately two-thirds the buccolingual width of M^1 .

The upper molars are dominated by large, somewhat low, and extremely bulbous cusps. The protocone is the lowest of these; it is virtually flat but is almost as long and wide as the buccal cusps together. The paracone and metacone swell outward in all directions and are delineated by narrow creases or grooves, especially at their basal confluence; although these cusps are so rounded and swollen, there are traces of attendant crests, with the centrocrista the most discernible. All molars bear rounded parastyles with the largest borne by M^1 and the smallest by M^3 ; the parastyles with the largest borne by M^1 and the smallest by M^3 ; the parastyle is met by a fairly broad preprotocrista that courses around the paracone and which, on M^{1-2} , incorporates a broad and low paraconule. All molars show a thin postprotocrista that courses to the inside of the metacone, thus truncating the trigon basin; on M^{1-2} , this crest is variably thickened in the metaconular region.

The talon region of all molars is swollen and rounded, but on M^2 and especially M^3 , there is a diagonal crease that delineates a hypocone. From behind the apex of the protocone of M^{1-2} a thick, low crest, probably a

prehypocone crista, courses to cross the crease and meet the apex of the hypocone; at the juncture where this crest leaves the postprotocrista there is a pit whence a shallow groove proceeds obliquely and buccodistally.

On M^1 the metacone is a bit shorter mesiodistally but slightly wider buccolingually than the paracone; on M^2 both cusps are somewhat laterally compressed but the paracone is wider than, and not as long as, the metacone. On M^3 , however, the metacone is quite diminished and is twisted inward, thus giving a slant to the buccal side of the tooth. M^1 is longer mesiodistally but not as broad as M^2 ; M^3 is the smallest molar in all dimensions.

LOWER DENTITION (Figs. 25, 26, 27)

The central four teeth of the toothcomb are thin and laterally compressed whereas the lateral two teeth are thicker, deeper, and quite robust. The central teeth bear moderately developed margocristids that sit quite inferiorly on either side of a rounded longitudinal "keel." The lateralmost tooth flares slightly laterally and bears margocristids of the same size as those on the central teeth. These teeth are crowded together and are only minimally procumbent.

The anterior premolar is a tall, trenchant, and stout tooth; it is thickened inferiorly, especially buccolingually. The anterior and longer posterior edges are compressed and bladelike; from them descend thick cingulids that become confluent around the basal lingual swelling of the crown.

The middle premolar is about half the height of its anterior neighbor but remains morphologically quite similar to it, although the anterior and posterior "blades" are less pronounced. The middle premolar is about as wide buccolingually as the anterior premolar but, because it is short, appears compressed. The tooth also seems to be skewed in the jaw but this is an artifact of the more lingual displacement of the posterior region.

The posterior premolar is not quite as tall as the middle premolar but is almost twice the height of the molars. This premolar bears a rounded and bulbous protoconid at the base of which lies, posterolingually, a small,

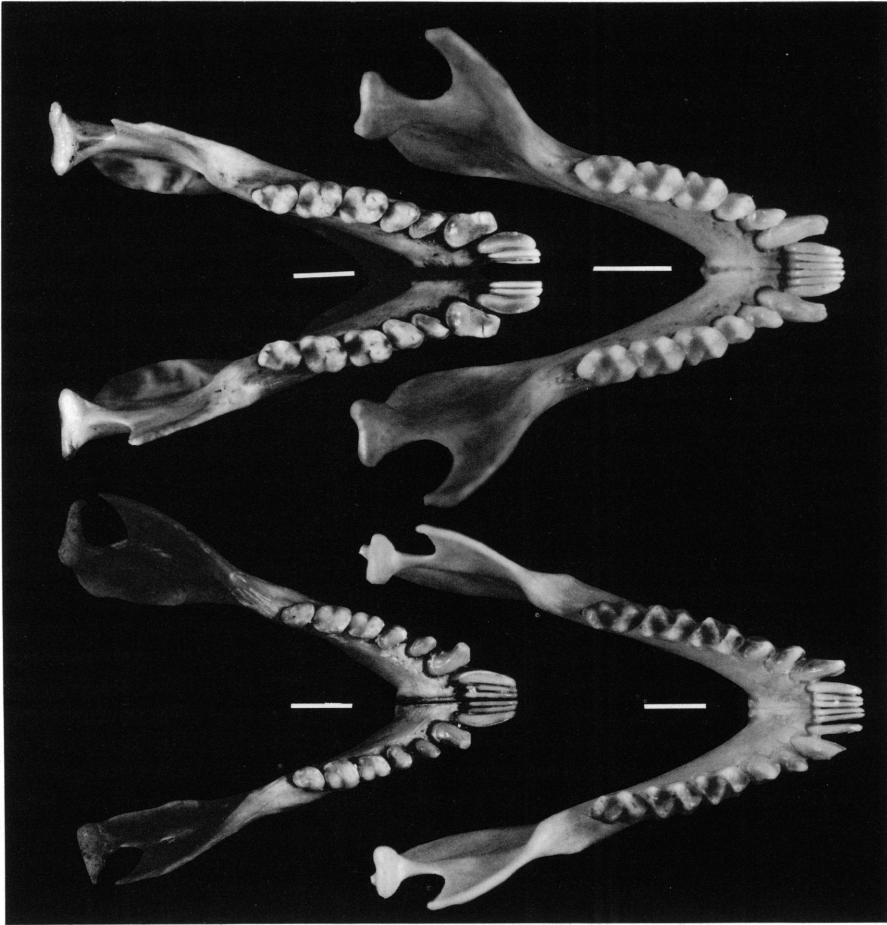


FIG. 26. Lower jaws of lorises in occlusal view. Clockwise from top left: *Loris tardigradus* (AMNH 217303); *Arctocebus calabarensis calabarensis* (USNM 511930); *Perodicticus potto* (AMNH 52688); *Nycticebus coucang bengalensis* (AMNH 87279). All scales represent 5 mm.

rounded metaconid. The distension of this region is augmented by thickening of the lingual cingulid. The buccolingual dimension of the tooth is further exaggerated by the noticeable swelling-out of the protoconid inferiorly.

The molars are characterized by low cusps that are swollen in all directions and delineated by grooves or creases. On M_{1-3} , the protoconid and metaconid are opposite each other and are connected, at least at their bases, by a thick, stout crest; these two cusps and the hypoconid are the largest molar cusps, the protoconid being the largest and most outwardly distended and swollen of the three. The entoconid is quite small and low by com-

parison and is emplaced near the base of the metaconid. The inner side of the entoconid is delineated by a fairly deep groove that also separates the cusp from what on M_1 is a low, flattened area but, on M_2 and especially on M_3 , is a more recognizable and developed hypoconulid. The deep groove is the deepest part of the moderately sized and excavated talonid basin; this basin is, however, truncated by the swollen buccal cusps as well as by the lower and centrally displaced cristid obliqua. An equally low paracristid descends the face of the protoconid but thickens after it kinks to proceed to the base of, and then up, the face of the metaconid.

M_1 is a bit smaller in length and width than

M₃ and much more so than M₂. The width of M₃ across the protoconid and metaconid is greater than across its talonid.

GENUS *ARCTOCEBUS*

ARCTOCEBUS CALABARENSIS

UPPER DENTITION (Figs. 22, 23, 24)

The upper central and lateral incisors are subequal in size; both are relatively high-crowned and somewhat spatulate with some distension medially. The four upper anterior teeth are not crowded together; in fact, the central two are widely separated by the large anterior palatine fenestrae and thus the gentle incurving of the crowns does little to approximate the teeth.

The upper canine is very simple and laterally compressed; it bears little adornment other than a small posterior heel and some faint cingular development, especially on the lingual face of the anterior edge. The tooth is not excessively tall and the crown gently arcs backward, creating a convex anterior edge and a concave distal one. Its mesiodistal axis is antero-obliquely oriented and the tooth is separated from the anteriormost premolar by a small diastema.

The anteriormost premolar is much taller than the other cheek teeth and somewhat triangular in occlusal outline, with a large paracone and some distension of the distolingual aspect of the tooth. A fairly robust lingual cingulum arcs downward from the anterior edge, and buccally a complete cingulum courses to, and becomes confluent with, a small but distinct posterior style.

On the middle premolar the paracone is quite large; the only other cusp is a small hypocone at its anterior base that is compressed and incorporated into the thin, ledge-like cingulum that completely encircles the tooth. In occlusal outline, the central premolar is squared-up distally by the expanded talon corner but is oblique anterolingually. The broad talon flows inferiorly from the large paracone. The longer and wider posterior premolar is generally similar to its anterior neighbor, but is more squared-up mesially (due to its somewhat larger protocone) and bears a slightly smaller hypocone near the base of the protocone. The distinct precin-

gulum effectively terminates at the protocone on the other side of which there also terminates a stout postcingulum that emanates from the parastyle and across which it is confluent with the buccal cingulum. The hypocone is incorporated into the postcingulum, and the broad talon basin is thus more enclosed than it is on the middle premolar.

The molar paracones and metacones are the highest and most distinct cusps; although connected by a thin centrocrista, they are widely separated. On M¹⁻³, a thin preparacrista kinks up to the parastylar region, whereas on M¹⁻² the metacone is oriented in the direction of the corner of the tooth and the postmetacrista thus courses more directly to the metastylar region. The metacone of M³ is much smaller than the paracone and the metastylar region of this tooth is diminished to a confluence of the buccal and posterior cingula. The molar protocones are rather low, ledge-like, and quite lingually and anteriorly emplaced; the talon basin is thus rather tapering and elongate, subtended mesially by distinct protocristae. The preprotocrista swings anteriorly (markedly on M¹ and somewhat so on M²); from the point of incorporation of a reasonably sized paraconule, it travels more directly to the parastylar region, where it joins the buccal cingulum. The slightly thinner postprotocrista, which lacks a conule, courses in shallow sinuosity to fade out internal to the base of the metacone.

The very broad and interno-obliquely oriented talon basin is more excavated on M¹⁻² than on M³; in the former teeth it is bounded by a low and compressed hypocone, whereas it is somewhat closed-off lingually on M³ by the continuation of the rounded, shelflike postcingulum. On M¹⁻², a very weak prehypocone crista courses down the internal face of the hypocone, across the troughlike talon basin, and up the protocone posteriorly; this structure does little to affect the topography of the talon basin, although it is in this region that the slight rise of the crest is most easily observed. No sign of a prehypocone crista is evident on M³.

All molars bear a broad buccal cingulum, most expanded in the parastylar region, that becomes confluent with a distinct postcingulum that flows into the hypocone on M¹⁻² and thickens as a talon shelf on M³. From

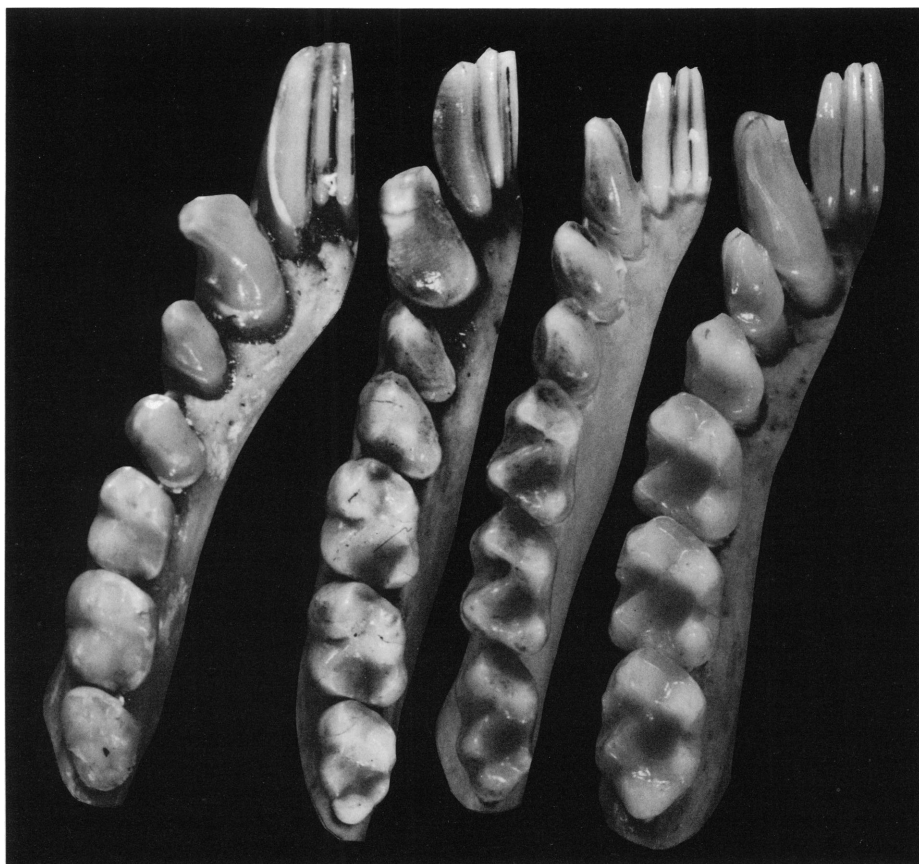


FIG. 27. Lower left dentitions of lorises in occlusal view. From left to right: *Perodicticus potto* (AMNH 52688); *Nycticebus coucang bengalensis* (AMNH 87279); *Arctocebus calabarensis calabarensis* (USNM 511930); *Loris tardigradus* (AMNH 217307). Not to scale.

either the hypocone or the talon shelf, a thinner cingulum traverses around the lingual face of the protocone to become confluent with the precingulum; the development around the protocone is quite clear on M^{1-2} and weaker on M^3 . In each case, however, the precingulum originates from the anteriorly displaced paraconule that is incorporated in the preprotocrista.

M^{1-2} are subequal in mesiodistal length but M^2 is slightly wider buccolingually and thus appears more transverse; the metacone and metastylar region of M^1 are noticeably distended outward. Due to the greater development of its parastylar region, the maximum width of M^3 approaches that of M^1 ; but the third molar is much shorter mesiodistally than M^{1-2} .

LOWER DENTITION (Figs. 25, 26, 27)

The six anterior teeth are fairly gracile and diminutive in comparison to the dentition as a whole; they are moderately procumbent and curve noticeably upward at their tips. The central four are quite compressed laterally and are dominated by a stout longitudinal central keel; margocristids are only hinted at. Interestingly, the central and lateral teeth of these four present themselves as pairs, united by the inward curvature of the tip of the lateral tooth and a mirror-image outward curvature of the tip of the central tooth; the central teeth are thus separated at their tips.

The distinction of paired central teeth is further emphasized by the dissociation of the tips of the lateral teeth due to their greater

arc ing inward; this also makes the lateral teeth appear to be shorter than the central four teeth. The former are also deeper, more robust, and moderately flared laterally. These teeth bear a broad longitudinal central keel and thin but distinct margocristids, the medial of which are quite low on the crown, thus creating a steep medial face on the tooth.

The anteriormost premolar, especially in contrast to the anterior teeth, is quite robust and trenchant. Even though it sits a bit low in the jaw and is inclined slightly forward, this tooth rises markedly above the height of the molars; there is a gradational decrease in crown height through the premolar series to the molars. The anteriormost premolar is a fairly simple tooth, bearing weak but complete buccal and lingual cingulids that become confluent around a slightly distolingually distended heel; the enlarged, pointed protoconid arcs noticeably backward at its tip, creating a marked convexity of the anterior face and a concomitant concavity of the posterior face. This general form of the protoconid is retained in the shorter and stouter middle and posterior premolars, but with an increasing emphasis anteriorly, especially in compression and cingulid development. The anteriormost premolar is isolated by a small diastema anteriorly as well as posteriorly.

The middle premolar has a small, compressed heel that bears a minute hypoconid emplaced just buccal to the midline, and which is joined to the protoconid by a weak but distinct cristid obliqua. There is also another crest lingually that descends from the tip of the protoconid and creates a shallow, teardrop-shaped and distolingually distended depression; the cristid obliqua, which bounds this depression, also delineates a shallower one buccally. Both depressions are subtended inferiorly by the most thickened parts of the continuous buccal and lingual cingulids.

The molars emphasize the somewhat pointed and widely separated cusps (whose height appears diminished because of filling-in and cresting between them) as well as the excavation of the talonid basin and the hypoflexid notch. The metaconid sits posterior to the protoconid; the two, quite melded and connected by a thick crest, form a steep wall

upon the middle of which abuts the stout, slightly buccally recurved cristid obliqua. This causes the large and buccally swollen protoconid to subtend the deep hypoflexid notch and the somewhat lingually deflected metaconid to be the apex of the talonid basin. The steep anterior face of the protoconid-metaconid "wall" is bounded inferiorly by a broad paraconid shelf; there is a weak paracristid that courses down the face of the protoconid and kinks inward to expand into a shelf that thins at the base of the metaconid. In parallel with the oblique metaconid-protoconid orientation, the entoconid is set posterior to the somewhat buccally swollen hypoconid. On M_1 , the fairly stout hypocristid curves slightly distally before arc ing around to join the hypoconid; on M_2 , however, a thickening of the hypocristid just distal and internal to the base of the entoconid prevents the confluence of cusp and crest.

The talonids of M_{1-2} are a bit wider buccolingually than the trigonids (although the deep hypoflexid notch of each makes it seem the other way around); in contrast, the elongate talonid of M_3 is slightly narrower than the trigonid. The hypoconid and entoconid of this tooth are not connected but are set off by small grooves from a fairly large, internally compressed, and centrally emplaced talonid heel.

FAMILY GALAGIDAE

For the purposes of our discussion here, we recognize two genera within the family Galagidae: the monotypic *Euoticus* and the polytypic *Galago*. The four species we provisionally recognize within the latter genus differ widely in size and in detailed morphology of dentition, and each is described independently. We have not been concerned with documenting potential variations in dental morphology between the numerous local populations that comprise each species.

GENUS *GALAGO*

GALAGO SENEGALENSIS

UPPER DENTITION (Figs. 28, 29, 30)

The upper central and lateral incisors are subequal in size, very thin and high-crowned. The distal edges of these teeth are slightly

concave and the mesial edges mirror them in their convexity.

The upper canine is a very trenchant tooth, virtually unadorned, that rises more than twice the height of the molars. Its tip is rather broad and rounded; the anterior edge descends rather steeply, terminating in a meager swelling near the neck. The somewhat longer posterior edge descends steeply, but in a gentle inward arc, and becomes rather bladelike as it joins a small, inwardly flexed heel bordering a shallow basal depression. There is a long, thin, shallow, vertical lingual depression anteriorly.

Each premolar is remarkably distinct. The anteriormost is more than one-half the height of the canine and rather closely approximated to it; it is somewhat separated from the middle premolar. The latter tooth is more intimately a part of the posterior cheek tooth row. The anterior premolar is dominated by a broad, stout, and laterally compressed paracone that is bounded anteriorly by a small style and posteriorly by a somewhat larger, spikelike heel. The long, sharp distal edge descends steeply toward the heel, whereas the shorter anterior edge arcs broadly to the style. Lingually, a thin cingulum descends from this style to form the inferior border of a moderately anterior depression.

The middle premolar is noticeably shorter than its anterior neighbor and is only slightly taller than the posterior premolar. In buccal outline, the edges and base of this tooth form an equilateral triangle; its sharp distal edge terminates in a distinct, spikelike style. The lingual surface is distended inferiorly over the inner root and bears a thin cingulum anteriorly; these developments cause the anterior part of the tooth to be more swollen, flowing posteriorly into a concave configuration. This tooth is the narrowest of the three premolars.

The last premolar is molariform, and although slightly less tall than the molars resembles them in having a very tall paracone and metacone (the former higher), a narrow trigon, and a broad and distally distended talon. This tooth differs from the molars, however, in that the buccal cusps are compressed, very bladelike, more closely approximated, and melded at their bases; the preprotocrista bears a compressed paraconule, is broader, and swings out more anteriorly as

it courses to the more distinct parastyle; the moderately tall protocone is relatively narrower; the postprotocrista is narrower and straighter and either almost fades out, or terminates in a minute metaconule, at the base of the metacone where it is met by a flat postcingulum; the hypocone is relatively smaller and is more or less in line lingually with the protocone to which it is connected by a very short, horizontal prehypocone crista, thereby distending slightly the distolingual face of the tooth; and the broad, shallow, distally distended talon basin is subtended by a markedly thickened postcingulum. This tooth is about as broad as the trigon of M^1 .

M^{1-2} are subequal in size and are characterized by having an extremely tall paracone and metacone (the former is the larger and taller of the two and is somewhat tilted buccally); very sharp buccal cristae; a distinct para- and metastyle; an excavated stylar shelf; and waisting of the distal edge below the metacone that further emphasizes the very distally and lingually distended talon that is also open distally. Each of these molars also bears a prominent, conical hypocone from which a prehypocone crista courses at least as far as the base of the protocone (more weakly on M^2 than M^1); a buccolingually compressed, somewhat narrow, anteriorly displaced protocone from which emanate strong pre- and postprotocristae, each of which incorporates a compressed conule; a preprotocrista that courses around the paracone to join the parastyle while the posterior crest fades out at the base of the metacone (from which emanates a stout, lingual metacone pillar); and a stout, but truncated, postcingulum that leaves the metastyle to fade out just beyond the base of the metacone. In occlusal view, the metacone of M^{1-2} looks like a skewed "T," formed laterally by the buccobliquely oriented pre- and postmetacristae, and lingually by the metacone pillar. M^1 differs somewhat from M^2 in that the two buccal cusps are further apart, the narrow trigon is not as elongate buccolingually, and the talon is longer.

M^3 is distinctly different from the other molars in that it is small and essentially triangular. As in the larger molars, however, the metacone is tall and the protocone is shifted anteriorly; but the distally emplaced meta-

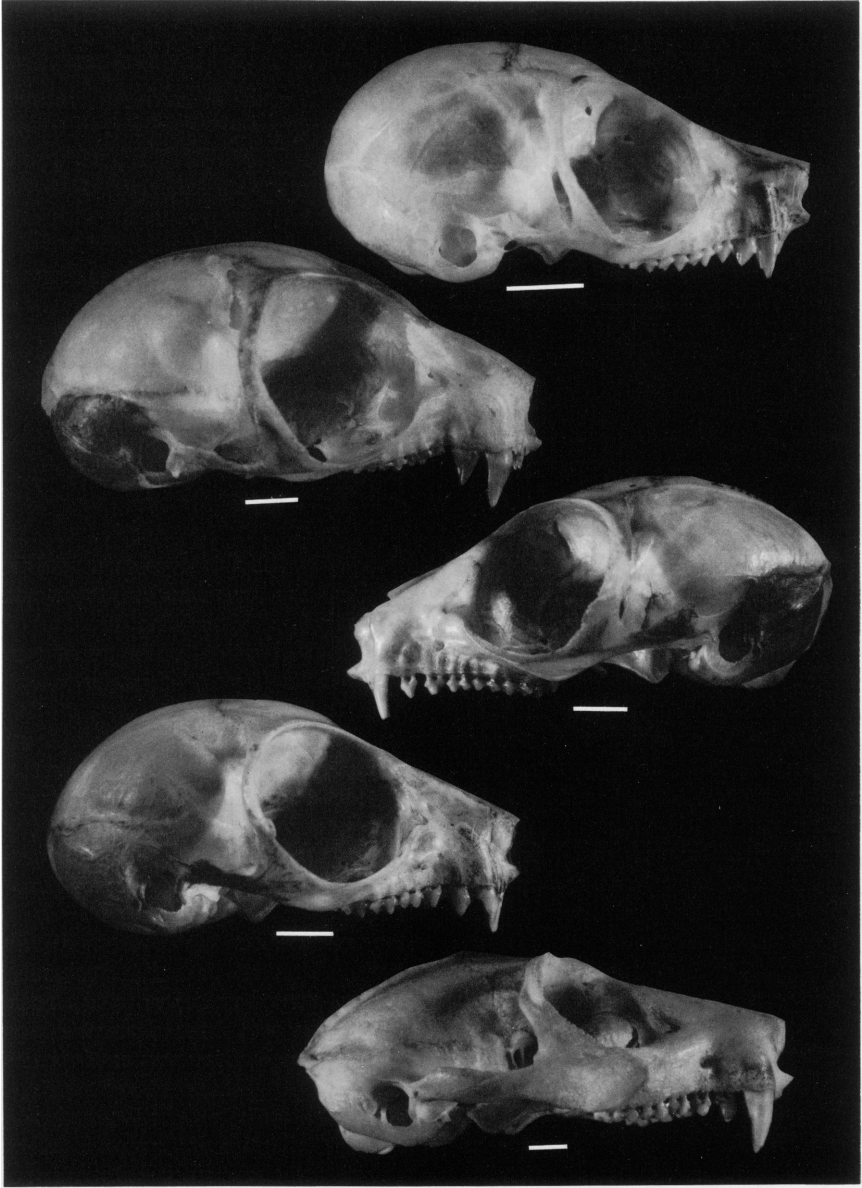


FIG. 28. Crania of galagids in lateral view. Descending from top: *Galago demidovii demidovii* (AMNH 241122); *Euoticus elegantulus* (AMNH 241126); *Galago alleni* (AMNH 24119); *Galago senegalensis* (AMNH 180100); *Galago crassicaudatus monteiri* (AMNH 80801). All scales represent 5 mm.

cone is situated centrally so that it forms the apex of a triangle whose base is a paracone-metacone axis. The protocone and metacone are connected by a stout crest, and an equally robust preprotocrista courses to join a parastyle.

LOWER DENTITION (Figs. 31, 32, 33)

The lower six anterior teeth are somewhat elongate and slender and arc upward slightly at their tips; they are not very procumbent. All have prominent longitudinal keels lin-

gually, and distinct margocristids. Of the central four teeth, the innermost two are parallel-sided, whereas the outer two are curved, toward the tip, giving an arcuate edge to the four-toothed "unit." The lateral two teeth are deeper and more robust, with some amount of lateral flaring.

The anteriormost lower premolar is a somewhat anteriorly inclined, fairly narrow tooth that is almost twice the height of the molars. Following the slight inward curvature of the rounded tip of the tooth, the buccal face is convex and the lingual face concave. The mesial edge of the tooth is compressed and short and drops rather steeply; at the terminus of this edge, approximately one-third down the crown, a weak lingual cingulum courses posteriorly to a moderately swollen heel that is met by the long, gently concave distal edge.

The middle premolar is noticeably lower and is quite narrow and elongate. The blade-like protoconid is displaced markedly forward, with a short, antero-obliquely oriented mesial edge and a long, sloping distal edge that broadens lingually into a small, ledgelike heel. This heel is oriented such that the very shallow posterior depression opens lingually.

The posterior premolar is lower yet, but still rises above M_1 . This tooth is relatively molariform and bears a moderately developed metaconid appressed posteriorly to the centrally emplaced protoconid, and a sharp, anteriorly directed paracristid that terminates inferiorly in a small, stylid-like "paraconid" from which a thin cingulid courses back to the base of the metaconid, thus subtending a very shallow trigonid basin. The base of the tall protoconid is noticeably swollen buccally. The melded protoconid and metaconid form a steep wall that faces a distinct but slightly truncated talonid bearing a relatively large and somewhat buccally displaced hypoconid as well as a smaller, posteriorly emplaced entoconid that forms a deep lingual notch with the base of the metaconid. A stout cristid obliqua courses inward to the midline of the protoconid-metaconid wall; the resultant hypoflexid notch is further emphasized by the buccal swelling of the protoconid.

All molars have very tall and somewhat separated protoconids and metaconids, the

latter cusp being set a bit more posteriorly; these cusps form a steep wall facing the talonid basin. A compressed paracristid descends the face of the protoconid and angles back at the base of this cusp toward the metaconid as a broad, horizontal ledge. A stout and rather straight cristid obliqua terminates at the lingual side of the protoconid base, forming a hypoflexid notch whose depth is augmented by the buccally swollen protoconid and hypoconid. An entoflexid notch is created by lingual swelling of the metaconid and entoconid; there is also a vertically deep notch between the rather tall entoconid and metaconid. The posterior wall of the talonid on M_{1-2} is formed by a rather straight entoconid-metaconid crest. The smaller M_3 , however, bears a moderately developed, somewhat compressed, and centrally emplaced heel.

GALAGO CRASSICAUDATUS

UPPER DENTITION (Figs. 28, 29, 30)

The upper incisors are tall, slender teeth, often not juxtaposed, and the central pair are widely separated by the anterior palatine fenestrae. Lingually, the narrow crown of both incisors is flattened or excavated, sometimes with a central keel separating lateral longitudinal depressions.

The upper canine is a very tall, stout, pointed and trenchant tooth that stands well over three times higher than the molars even though set deeply in the jaw; a deep but relatively narrow maxillary fovea, which accommodates the tip of the lower anterior premolar, rings the root of the tooth lingually. The massive canine root extends to the nasomaxillary suture and its contour is molded upon the maxillary bone externally, causing the snout to appear puffy. The tooth is quite pointed and bears a stout vertical pillar lingually that is compressed superiorly into the anterior edge of the tooth; from the apex of the tooth, this edge descends merely a short distance before coursing lingually and steeply downward as a thin cingulum that fades out centrally at the base of the pillar. The much better defined and more compressed distal edge descends rather steeply and is distended inferiorly into a relatively tall, lingually thickened and minutely pointed heel; the long



FIG. 29. Crania of galagids in ventral view. Descending from top: *Galago demidovii demidovii* (AMNH 241122); *Galago senegalensis* (AMNH 180100); *Euoticus elegantulus* (AMNH 241126); *Galago alleni* (AMNH 241119); *Galago crassicaudatus monteiri* (AMNH 80801). All scales represent 5 mm.

lingual face of the posterior moiety of the crown is modestly excavated into a depression that is bounded anteriorly by the vertical

pillar. This tooth is markedly skewed outward relative to the posterior cheek teeth.

The anterior premolar is approximately

one-half the height of the canine and is subequal to that tooth in length and width. The mesiodistal length of the premolar derives from a buccally compressed, elongate paracone that is bounded anteriorly and posteriorly by stout, slightly elevated, ledgelike styles of which the latter is borne upon a rather distended, broad heel. The anterior style is located on the crown at a position equal in height to and opposite the tall canine heel; the posterior style is markedly lower on the crown but sits high on the talon, which descends lingually and is thus flatly distended lingually over the broad and mesiodistally compressed posterior root. Whereas the anterior style is broadly incorporated into a somewhat corrugated cingulum that rings the crown lingually at the same level, the posterior style is better delineated as a cuspule and sits immediately buccal to the slightly thickened and raised posterior edge that runs somewhat buccally to the distal edge of the broad heel; the lingual cingulum terminates at this crestlike edge. Because of the position of the posterior edge, most of the heel is isolated and faces distolingually. The lingual face of the paracone is somewhat swollen centrally, to the width of the heel, so that the tooth tapers anteriorly. Even with its emphasized paracone and edges, the tooth appears somewhat coarse and bulky.

Although it is almost as wide buccolingually as the anterior premolar, the middle premolar, only slightly longer than it is wide, is much shorter, and stands only one-half as tall as the former. In buccal view, the middle premolar presents itself as an equilateral triangle bounded anteriorly and posteriorly by small but broad styles; the anterior style is emplaced slightly higher on the crown and both are met by a stout and somewhat compressed paracone edge. The anterior edge runs directly to the style, whereas the posterior edge curves gently lingually to terminate just internal to the slightly lingually displaced posterior style; the paracone edges subtend shallow lingual depressions that are widely separated by a broad paracone pillar. A thickened, perhaps roughened, cingulum gently descends posterolingually from the anterior style to incorporate a small, pointed protocone, which is emplaced just posterior to the midline of the paracone; it then descends more

steeply. The posterior cingulum lingually borders a distally rounded, steeply sloping, and moderately expanded talon which bears a low, thin crest that bisects it and is bordered by a shallow depression on either side. Superiorly, this crest joins a thickened cingulum that barely arcs as it courses from the protocone around the distal side of the paracone pillar; this cingulum borders superiorly the posteriorly opening talon.

The highly molariform posterior premolar is slightly narrower buccolingually than the trigon of M^1 , but is slightly longer than the molar due to its enormously posteriorly distended talon. Although M^{1-2} also bear massive talons, that of the premolar differs in that it is expanded only posteriorly into a long and broad heel which barely extends beyond the protocone lingually. The face of the talon is fairly straight lingually and somewhat rounded posteriorly, and its short buccal edge courses obliquely anterobuccally into a fairly deep, broadly V-shaped notch that lies lingual to the base of the metacone. The shallow talon basin is encompassed by a low, thick cingulum that emanates from a small meta-style and follows the posterior contour of the tooth to become slightly raised in the region of the very low and broad hypocone; it then continues up the side of the protocone to its bulbous apex. We are inclined to identify the latter part of this cingulum as a prehypocone crista because it does not course as directly or as lingually down the face of the protocone as does a protocone fold; it is directed a bit posteriorly as it descends from the protocone and has to kink slightly lingually to connect with the distended hypocone region.

The rather low, bulbous paracone is the dominant cusp of the posterior upper premolar; the other cusps are also bulbous but the metacone and protocone are much lower and smaller. A very stout preparacrista and a weaker postparacrista border the paracone; at the terminus of the former crest is a low, somewhat broad, bulbous parastyle. The low metaconid is melded with the protocone at its base and looks more like a large style than a cusp; nevertheless, it bears distinct cristae, the posterior of which extends into the metastylar region, flexing lingually as it does so. Moderately thickened but very tall cingula extend from the stylar regions and wrap

around the protocone and metacone buccally, converging at the midline of the melded cusps. The trigon basin is shallow and narrowly V-shaped; the very low preprotocrista courses directly to the parastyle, past the paracone, while the equally faint postprotocrista arcs somewhat as it proceeds to terminate at the midline of the two melded buccal cusps. The broad paracone and small protocone thus subtend the trigon basin. The "V," whose apex is formed at the protocone by the postprotocrista and the prehypocone crista, is bisected by a low, broad, and short crest that blends distally into the face of the talon basin. A weak, thin and irregular precingulum emanates from the parastylar region, thickens and increases in height around the face of the protocone, sometimes forming a flat and compressed stylelike structure between the base of the protocone and the hypocone. It then courses around the hypocone to become confluent with the postcingulum just behind the cusp. Without a doubt, the posterior premolar is a strange and unique tooth.

Although their cusps and other features are more normal in appearance, the molars are reminiscent of the posterior premolar, especially in possessing a large, dominant protocone and a much smaller and lower metacone. These two cusps are farther apart and only slightly melded at their bases; but, as in the premolar, they bear distinct cristae on their sides. These cristae, however, are much more compressed and distended in the molars; only on M^3 is the postmetacrista low and rounded, but then the whole metacone region of this tooth is distobuccally reduced and rounded. M^{1-2} bear tiny, anterior and posterior styles at the termini of the cristae, but these "styles" may only be slight distensions of the pre- and postcingulae. Because the metastylar region of M^2 overrides M^3 anterobuccally, it is difficult to determine with certainty, but it appears that the latter tooth also develops a "parastyle." There is a fairly deep flexure buccally between the paracone and metacone on M^{1-3} which, on M^{1-2} , is accentuated inferiorly by a noticeable ring of swelling that also distends the metacone-metastylar region buccally and posteriorly.

All molars bear expanded talons whose

elongate and shallow basins are higher lingually and open downward buccally, and whose long axes are anteroposteriorly oblique, parallel to those of the postprotocristae. Although the talon of M^3 is narrower buccolingually than those of M^{1-2} , it is as long; the margin of the talon of the small third molar arcs gently posterobuccally from the protocone and swings in rather sharply lingual to the base of the metacone where it is quickly met by the thick, low postcingulum that courses straight down the side of that cusp. The posterior margin of the talon of M^{1-2} is not only wider buccolingually but straighter; superiorly a "notch" is formed between the short buccal margin of the talon and the posteriorly projecting metacone. On M^2 , the notch is deep and more acute because the metacone and stylar region are flexed inward and downward (i.e., lingually). Both M^{1-2} develop a relatively large, pointed hypocone; this cusp is larger and more distended distolingually on M^1 , and a much stouter prehypocone crista courses between it and the protocone than on M^2 . In addition, the M^{1-2} hypocones develop a lingual swelling basally which subtends a groove that courses between the two lingual cusps from the prehypocone crista; on M^1 , this swelling is enlarged into a small horizontal ledge.

The molar trigons are somewhat transverse and the low, rounded protocristae subtend moderately excavated basins. On each molar, the preprotocrista snakes its way past the paracone to join the parastylar region; this crest thickens slightly near the base of the paracrista and, with the side of that cusp and its preparacrista, borders a narrow, vertical depression. The gently arcuate postprotocrista fades out as it ascends the base of the metacone. A thin and irregular precingulum emanates from the parastylar region and courses down the side of the tooth to fade out on the side of the protocone; the postcingulum is quite thickened as it departs from the metastylar region of the posterior notch. Only the talon of M^3 bears a slight cingulum on its lingual margin, but this tooth also lacks a hypocone. Were it not for the enormous posterior expansion of its talon, M^3 would be only two-thirds the size of M^{1-2} ; if the hypocone region of M^1 were not as expanded

and the metacone region of M^2 flexed downward, these two teeth would be subequal in size.

LOWER DENTITION (Figs. 31, 32, 33)

The lower six anterior teeth are fairly elongate, slender and procumbent teeth arcing gently upward at their tips; they appear somewhat dwarfed and gracile in comparison with the remaining teeth, which are bulky and stout. The central four anterior teeth are longer and slenderer than the lateralmost two of the six; lingually, these four teeth are compressed into a stout longitudinal keel, giving rise inferiorly to distinct ledgelike margocristids of which the lateral crest is slightly larger. The lateralmost teeth of the toothcomb are set apart not only by being somewhat shorter than those mesial to them, but in being deeper and more robust and in curving upward more prominently at their tips; these tips also cant a bit medially, so that they overlap the lateral margocristid of the mesially neighboring teeth. The crowns as a whole are moderately flared laterally and bear ledgelike margocristids inferiorly on either side of a stout, broad longitudinal keel.

The anterior premolar is a massive tooth that is both tall and long basally. The crown is dominated by a stout protoconid that arcs a bit backward and inward and whose gently convex anterior face is compressed and distended into a bladelike edge; this edge extends slightly more than halfway down the crown at which point internally there is a tiny, pointed cusp or stylid whence descends lingually a thin cingulid that fades out before reaching the heel of the tooth. The slightly concave posterior face of the tooth, compressed superiorly, is broadly rounded inferiorly and slopes steeply until expanding posteriorly into a gently rounded heel. Because the tooth is skewed inward slightly this sloping heel is directed lingually; distally there is a tiny, pointed cusp or stylid from which descends steeply a distinct cingulid that fades out at the heel. Although the anterior premolar is inclined forward slightly and is set deeply in the jaw, this tooth stands more than twice the height of the molars.

The middle and posterior premolars are

subequal in height and are half the height of the anterior premolar; these three teeth are subequal in mesiodistal length but the two posterior premolars are noticeably narrower. Even though it is much shorter, and its protoconid is thus stubbier, the middle premolar mirrors the anterior premolar in its general configuration: the tooth is set obliquely in the jaw and its stout protoconid arcs gently inward. The relatively short anterior face of the protoconid is compressed and bladelike and extends quite far anteriorly; from the angular anterior extension emanates a thin, ledgelike cingulid that courses lingually to terminate posterior to the midline of the protoconid. The much longer distal edge of the tooth is compressed and extends across the expanded, low heel.

The posterior premolar is a molariform tooth whose tapering trigonid is dominated by a tall but bulbous protoconid. A thick paracristid courses down the face of this cusp and kinks acutely inward to proceed as a thinner structure to the base of the metaconid; there may be a tiny paraconid at the point of flexure. The metaconid is fairly small and sits much lower than and somewhat posterior to the protoconid, to which it is almost entirely melded; a crest of variable development courses between the tips of these two cusps. Given this arrangement of cusps, the feeble paraconid "shelf" borders a steep but shallow trigonid.

Posteriorly, the melded protoconid and metaconid form a sheer wall that faces upon the low talon. A stout cresting system, forming right angles at the entoconid and hypoconid, encloses a truncated but moderately excavated talonid basin. The rather internal placement of these crests makes the crown appear to bulge inferiorly; the hypoflexid notch, however, remains shallow. The cristid obliqua courses directly from the bulbous hypoconid to the base of the protoconid centrally. The slightly smaller and lower entoconid sits posterior to the hypoconid, to which it is connected by a straight hypocristid; the entoconid and metaconid are connected by a stout crest that courses directly to and centrally up the face of the latter cusp. The trigonid of this tooth is slightly longer mesiodistally than the talonid and is also slightly

wider due to buccal expansion of the protoconid. The posterior premolar is subequal in length to but is somewhat narrower than M_1 .

The molars bear relatively stout, bulbous protoconids and slightly offset metaconids that are fairly far apart on M_{1-2} , but are more intimately associated on M_3 . A variably developed centrocristid connects the somewhat swollen protoconid with the smaller metaconid, and the two cusps form a broad, sheer wall that faces onto the talonid. A stout paracristid courses down the face of the protoconid, flexes acutely down, then gently climbs at least partway up the face of the metaconid. On M_1 the metaconid is twisted a bit inward and the terminal extent of the paraconid shelf closely follows this medial curvature. The paracristid extends farthest anteriorly, and its continuation inferiorly as a paraconid shelf is the thickest on M_1 ; hence from M_{1-3} there is a marked reduction in the size of the broad, narrow trigonid basin defined by these structures.

On all molars, a broad cristid obliqua runs rather directly from the hypoconid to the protoconid inferiorly and terminates just medial to the midline of the latter cusp; at the base of the protoconid the crest thickens somewhat, and especially on M_1 may even appear as a low conulid. From M_{1-3} the talonid becomes narrower due to a more medial shifting of the hypoconid; thus there is a concomitant shallowing of the hypoflexid notch (never very deep) from the first to the third molar. Even so, the hypoconid is moderately swollen buccally. On M_{1-2} , the entoconid is more compressed than the hypoconid, and on M_2 noticeably taller; on both molars a high-rising crest connects the entoconid with the metaconid centrally; the cusp and the crest are much lower on M_3 . When viewed from behind, the entoconid and hypoconid of M_{1-2} form a broad "U," the bottom of which is the only region where a (somewhat thickened) hypocristid is observable; the fairly well-excavated talonid basin of these molars is thus not entirely enclosed.

The subtriangular and tapering talonid basin of M_3 is also not completely encircled by crests. The moderately developed heel of this tooth, displaced linguallly, receives a stout crest only from the nearby entoconid; a weaker crest arcs linguallly from the hypoconid,

but the talonid basin remains open inferiorly and posterobuccally. There is a broad shallow notch between the hypoconid and the heel. The third molar is the smallest of the three: M_1 is somewhat longer mesiodistally and wider buccolingually (especially in the talonid) than M_2 , and M_3 is no more than two-thirds the size of M_2 in both dimensions.

GALAGO DEMIDOVII

UPPER DENTITION (Figs. 28, 29, 30)

Although small and thin, the upper incisors are high-crowned teeth whose height is effectively increased by a marked downward distension of the bone in which they sit; these teeth are inclined palatally somewhat so that, in buccal view, the lateral incisor is to a large extent hidden by the canine. The lateral incisor is isolated from neighboring teeth anteriorly and posteriorly by small diastemata, whereas the central incisors are widely separated from each other by the anteriorly encroaching anterior palatine fenestrae. The central and lateral incisors are subequal in size and bear occlusally rounded, linguallly flattened crowns that minimally flare laterally beyond the neck of the tooth.

The upper canine, although set deeply in the jaw, is a notably tall and dagger-like tooth. The bone is shallowly depressed lingual to the stout canine root, which impresses itself on the maxilla externally. This rather simple tooth is laterally compressed, especially on its steep, relatively straight edges, and basally bears only a minute posterior heel. A low, broad central lingual pillar delineates a long, shallow vertical depression; there is minimal cingular swelling basally. The mesiodistal axis of the upper canine is skewed outward a bit posteriorly: the tooth stands about two-thirds above the posterior cheek teeth and somewhat less than that above the anterior premolar.

The anterior premolar is buccolingually extremely compressed; it is noticeably longer mesiodistally than the middle premolar and is slightly shorter than the posterior of the set. Its gently convex, bladelike anterior edge and its longer and sharper posterior edge terminate in small styles that are connected by a well-developed lingual cingulum that bears a small protocone near the base of the para-



FIG. 30. Upper right dentitions of galagids in occlusal view. From left to right: *Euoticus elegantulus* (AMNH 241126); *Galago senegalensis* (AMNH 180100); *Galago demidovii demidovii* (AMNH 241122); *Galago alleni* (AMNH 241119); *Galago crassicaudatus monteiri* (AMNH 80801). Not to scale.

cone; this minuscule cusp is appressed to the anterior terminus of a pillar that flanks the somewhat anteriorly displaced paracone and thus forms a basal corner to a shallow anterior lingual depression. This pillar also subtends a larger and broader posterior depression. The tooth is set obliquely in the jaw such that its posterior end is slightly skewed inwardly.

The middle upper premolar is the shortest of the three but is much wider buccolingually than the anterior premolar. The gently convex and sharply compressed edges of the trenchant paracone are subequal in length and terminate in distinct styles that are connected by a well-developed and complete basal cingulum along the lingual side of the tooth; this is especially expanded distolingually. The posterior style is the larger of the two and is

noticeably distended buccally. As the lingual cingulum descends the lingual side of the tooth, it incorporates a small, anteriorly emplaced protocone before dropping steeply to circumscribe the distolingual expansion; it then ascends, as a postcingulum, to meet the metastylar region. As in the anterior premolar, a low paracone pillar meets the tiny protocone basally and anteriorly so that both subtend the shallow anterior depression. The posterior lingual depression is a broader, longer, and steeply descending structure that opens distolingually.

The posterior premolar is a fairly molari-form tooth; it is slightly smaller than M^1 in length and width and appears less stout, especially distally, due to its more weakly developed postprotocrista and hypocone and to its less expanded and squared-up talon. As

in the molars, however, this tooth develops tall, markedly compressed buccal cusps that bear stout crests on their sides, and a long trigon whose pointed protocone is anteriorly displaced such that the strong preprotocrista, with little arcing, courses past the paracone to become confluent with a small style at the base of the preparacrista. As it does on M^{1-2} especially, the preprotocrista of this tooth is thickened and raised to form a large, compressed paraconule lingual to the base of the paracone. In contrast to the situation on M^{1-2} , and especially on M^3 , the straighter postprotocrista of the posterior premolar courses more centrally, to the midline of the broadly melded paracone and metacone, before abruptly kinking distally to circumscribe the base of the metacone. Beyond this, the postprotocrista becomes confluent with the distended metastylar region; where it kinks, this crest may bear one or two small metaconules. The more central emplacement of the postprotocrista creates a narrower trigon basin on the premolar as well as a longer and more sloping wall that faces onto the talon basin. The buccal face of the posterior premolar is relatively straighter than that of M^{1-2} (as a result of there being markedly less invagination between the paracone and metacone); the waisting of the posterior side of the premolar below the metacone is less acute (because the posterior wall of the talon is not as straight); and a distinct postcingulum diverges from the postprotocrista just distal to the metaconular region to enclose the talon basin, coursing downward and gently outward and then thickening into a shelf before it thins to travel around and up the hypocone. This thickening of the postcingulum narrows the talon basin. Just as the paracone and metacone of the premolar are closely approximated, so also is the low, pointed hypocone closely appressed distally to the base of the protocone, to which it is connected by a well-developed prehypocone crista which may bear a pit or a small, narrow groove lingually.

M^1 is slightly longer and wider than M^2 , and both are noticeably larger than the very transverse, but narrow, M^3 ; the metacone and metastylar region of M^1 are more distally distended than on M^2 and the hypocone of M^1 is more distended lingually than on M^2 . The

tall, compressed and pointed paracones and metacones of M^{1-2} are widely separated and bear stout cristae on their sides, whereas the metacone, metastylar region and postmeta-crista of M^3 are greatly reduced. The talons of M^{1-2} bear stout, pointed hypocones and are markedly expanded with long, relatively straight distal edges, while the talon of M^3 is merely a broad, shelflike, arcuate cingulum on the distal side of the tooth. The "waisting" below the metacone on M^{1-2} is thus deeper and more acute, whereas it is shallower and more broadly concave on M^3 . On no molar, however, does a postcingulum course down to the talon from the postprotocrista; on M^{1-2} , the thin cingulum that subtends the shallow, buccolingually elongate talon basin originates at the buccalmost extent of the talon and either fades out on the base of the hypocone distally (M^1) or ascends the cusp (M^2). The hypocone of M^1 is larger than that of M^2 , but, on both teeth, the cusp is lower than the protocone to which it is melded at the base and to which it is connected by a very thin prehypocone crista; this crest is slightly stouter on M^1 , but on both molars it is easily observed as it courses between the bases of the hypocone and protocone. Lingually, a circular build-up forms the floor of a slightly mesially oriented, lingually broadening groove that flows from the prehypocone crista between the bases of the protocone and hypocone. Another, stouter, crest is also associated with the hypocone; it goes straight back (i.e., buccally) from the cusp to abut inferiorly upon the wall of the postprotocrista. This hypocone crest both subtends and truncates the talon basin superiorly; it also creates a small depression, bounded lingually by the hypocone, against the wall of the postprotocrista.

As on the posterior premolar, the stout molar preprotocristae course directly past the paracone to a small style at the base of the preparacrista; the protocone is displaced somewhat anteriorly. A flattened paraconule, incorporated into the preprotocrista, is quite large on M^{1-2} ; but even though the paraconule on M^3 is absolutely slightly smaller, it is a proportionately larger feature of this narrow tooth. Only on M^{1-2} does the postprotocrista bear a conule; this metaconule is emplaced directly in front of the metacone and is slightly larger on M^1 than on M^2 . On M^3 this crest

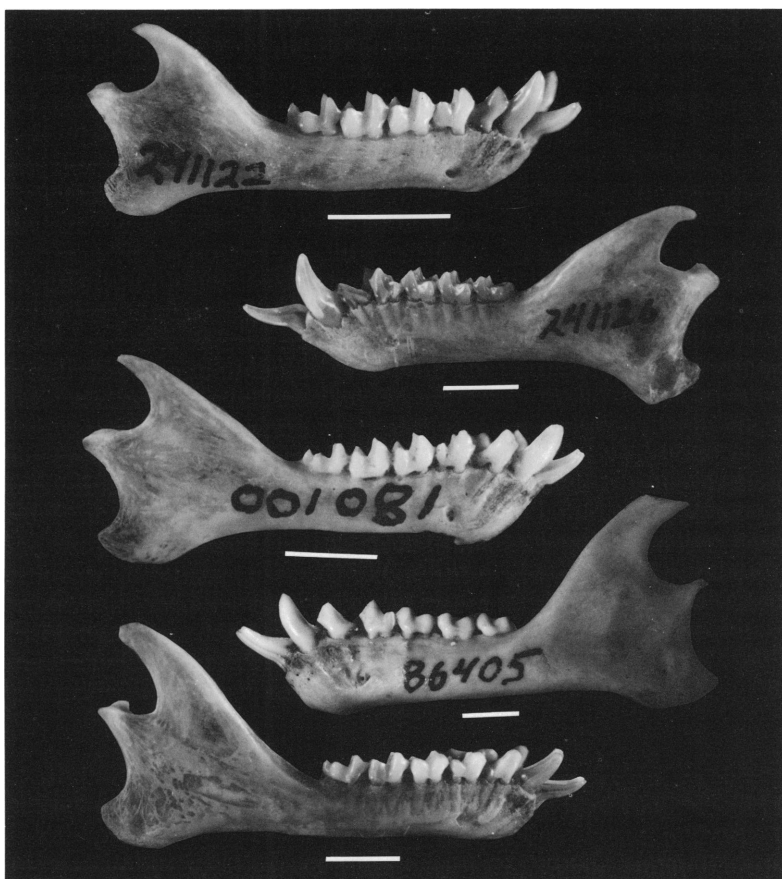


FIG. 31. Lower jaws of galagids in lateral view. Descending from top: *Galago demidovii demidovii* (AMNH 241122); *Euoticus elegantulus* (AMNH 241126); *Galago senegalensis* (AMNH 180100; reversed); *Galago crassicaudatus monteiri* (AMNH 86405); *Galago alleni* (AMNH 241119). All scales represent 5 mm.

courses directly to the apex of the metacone, subtending, with the preprotocrista, an elongate, narrowly V-shaped and well-excavated trigon basin. However, as the postprotocristae of M^{1-2} leave the metaconule, they round the metacone to become confluent with the terminus of the postmetacrista.

LOWER DENTITION (Figs. 31, 32, 33)

The lower six anterior teeth are moderately elongate and procumbent; they curve gently upward at their tips. The central four bear markedly compressed and ridgelike central longitudinal keels that are bounded inferiorly by very broad and ledgelike margocristids. These four teeth are longer than the lateralmost two of the six and appear to segregate

naturally into right and left pairs: the sides of the tips of the teeth of each "pair" curve inward so that each looks like a long single tooth with a centrally emplaced apex. The lateral teeth are deeper and more robust and flare laterally. Each bears a stout, compressed longitudinal keel on either side of which is a moderate depression that is bounded externally by a thin margocristid; the mesial margocristid is a bit thicker than the lateral crest. The crown of the tooth appears to be turned inward such that the keel faces fairly medially and the lateral margocristid rather occlusally. The teeth of this toothcomb strike one as being disproportionately small and especially gracile in comparison to the rest of the dentition.

The anteriormost lower premolar is a tall,

simple tooth, somewhat bladelike. It is emplaced close to the toothcomb and is inclined slightly forward; thus, in buccal view, it hides the posterior part of the lateral anterior tooth. The crown of this premolar is somewhat broadened distolingually and bears a thin cingulum that courses around this distension; this proceeds lingually to travel partway up the anterior edge of the tooth. This edge is somewhat convex in lateral view, whereas the longer posterior edge is relatively straight. The tip of the crown curves inward slightly and the whole tooth is skewed in the jaw. Even forwardly inclined as it is, this tooth stands almost twice as tall as the other cheek teeth.

The middle premolar is a stouter version of the anterior premolar: it is longer medio-distally and more inferiorly swollen distolingually, but the emphasis and character of its protoconid and its orientation in the jaw are the same. The very short, convex anterior edge is a quite bladelike. The longer, gently concave and equally bladelike posterior edge subtends superiorly a shallow lingual depression that broadens and opens inferiorly; this depression is bounded anteriorly by a short, swollen crest that diverges from the weak basal cingulid and ascends partway up the lingual face of the protoconid. Almost like a glove, on the buccal side the anterior portion of this tooth overlaps buccally the heel of the anterior premolar and conforms closely to its shape, whereas its own heel is crudely overlapped by the anteriorly distended protoconid region of the posterior premolar.

The posterior premolar is a molariform tooth that is subequal in its mesiodistal length with the middle premolar and approximately two-thirds the width of M_1 . The basally swollen protoconid is broadly melded with the slightly smaller and rather posteriorly emplaced metaconid; a very compressed and bladelike paracristid courses down the face of the protoconid and extends quite far forward before kinking severely backward to proceed as a very thin structure that fades out at the base of the metaconid. Distally, the tall and melded protoconid and metaconid form a steep, flattened, obliquely oriented wall that faces upon the talonid. A stout, straight cristid obliqua courses from the large hypoconid to abut upon this wall inferiorly and just buccal to the midline of the trigonid cusps; the

metaconid thus broadly forms the apex of a quasi-triangular talonid basin and the protoconid borders anteriorly a moderately deep and wide hypoflexid notch. The relatively elongate talonid is about as broad as the trigonid but appears a bit narrower because the small and low entoconid is directed inward. The crest that emanates from this latter cusp to course around the lingual base of the metaconid thus truncates the talonid basin laterally; interestingly, this entoconid crest runs in parallel with the cristid obliqua.

The tall, pointed molar protoconids and metaconids are also broadly melded at their bases but their tips are widely separated (increasingly so from M_{1-3}) and the metaconid is only slightly displaced posteriorly. The paracristid is at best a faint structure coursing down the face of the protoconid but its base is distended slightly, and from it runs a moderately developed paraconid shelf that terminates at the base of the metaconid. The two trigonid cusps form a steep, flattened wall that faces the talonid, the basin of which is bounded anteriorly by the metaconid and almost the entire lingual half of the protoconid; the latter cusp is virtually bisected at its base by the terminus of the stout, rather straight cristid obliqua. By itself, this position of the cristid obliqua would not necessarily create a deep hypoflexid notch; but a fairly deep notch is present on M_{1-2} since the protoconid swells lingually. On M_{1-2} the entoconid is narrower, taller, and more pointed than the hypoconid and a sharp crest descends from it to the base of the metaconid, thus creating a deep lingual notch; in contrast, the interiorly flexed entoconid of M_3 is smaller and lower than the hypoconid so that the crest running from it to the base of the metaconid descends gently downward. When viewed from behind, the hypoconid and entoconid of M_{1-2} form the sides of a broadly U-shaped posterior edge that is slightly thickened and crenulated posterointernal to the entoconid; this minimal hypocristid subtends a thin, faint notch or pit at the base of the entoconid. The broad, well-excavated talonid basins of M_{1-2} therefore open posteriorly. In contrast, the elongate talonid of M_3 bears a well-developed heel that is rimmed by a very low crest that connects it to the hypoconid, but which terminates prior to reaching the entoconid. The

heel is emplaced quite lingually; there is thus a large, right-angled notch buccally to it behind the hypoconid. The three molars are subequal in mesiodistal length, but M_2 is broader than M_1 which in turn is markedly bulkier and broader than the posteriorly tapering M_3 .

GALAGO ALLENI

UPPER DENTITION (Figs. 28, 29, 30)

The central and lateral upper incisors are subequal in size and close together. They are very slender, very high-crowned teeth that are slightly angled palatally and gently curved medially; the crowns are slightly compressed buccolingually. The central incisors are set well apart.

The upper canine is very tall, standing at least twice the height of the molars; it is quite trenchant and gently curved backward. A small but distinct vertical heel receives an inferiorly distinct posterior crestlike edge; lingually both of these structures border a moderately excavated posterior depression. There is a much narrower and shorter lingual depression on the upper part of the anterior face of the tooth from which descends a faint cingulum that courses arcuately to the heel.

The anteriormost premolar is only slightly taller than the middle premolar, which is slightly taller than the posterior premolar, which in turn rises a little above M^1 . The anteriormost premolar is composed of a large, stout, somewhat lingually swollen paracone with a short, steep anterior edge and a long, sloping posterior edge. Both edges terminate in distinct styles; a lingual cingulum descends from the anterior style to thicken into an inferior swelling posterior to the vertical axis of the crown. This tooth is not closely approximated to either its anterior or posterior neighbor.

The middle upper premolar, which does abut its posterior neighbor, is longer and much broader than the anterior premolar; but in buccal outline the two are similar. A shelllike precingulum extends from the parastyle to incorporate a small, somewhat anteriorly displaced protocone (which is at the base of the broad paracone) and then continues steeply downward (as a protocone fold?) to incorporate a minuscule hypocone that lies at the

base of the protocone and at the anterior extremity of a large, distolingually distended heel. The low cingulum continues around this expanded talon and, as the postcingulum, meets the posterior style. Since it effectively opens posteriorly, being bounded buccally by a constriction below the posterior style, the talon is best seen as a lingual continuation of the paracone slope.

The molariform posterior premolar is almost as broad buccolingually as M^1 but is not as long. This tooth is similar to M^{1-2} in many features: the cusps are moderately bulbous; the paracone is much larger and more rounded than the metacone; the somewhat compressed metacone is obliquely angled, buccally distending the distobuccal corner of the tooth (this angle is accentuated by a short, but stout, postmetacrista); an equally stout centrocrista lies between the paracone and metacone; a distinct preprotocrista departs the somewhat anteriorly displaced and buccolingually compressed protocone to incorporate a small paraconule as it broadly bypasses the paracone as a shelllike structure that meets the small parastyle; the talon is markedly distended, especially distally, and bears a low but large and rounded hypocone; the distal edge of the talon is relatively straight-sided and is rather abruptly truncated near the base of the metacone; the shallow talon basin descends from the hypocone to open in a buccally oblique direction at this constriction; a weak postcingulum descends from the metastylar region to terminate at the constriction. The last premolar is more similar to M^1 in that the hypocone is connected to the side of the protocone by a thin but distinct prehypocone crista; this crest is even more extensive in the premolar. The trigon of the premolar is much narrower than it is in the molars; this is due, in large part, to the arcing of the postprotocrista to the anterior side of the metacone. The talon of this tooth is also not as lingually distended as it is on M^{1-2} .

M^1 is slightly longer than M^2 but is not as broad buccolingually. The postmetacrista is longer and more obliquely arcuate but does not terminate in as distinct a metastyle. The postprotocrista of M^1 bears a more distinct metaconule and the hypocone of this tooth is more distally and lingually distended than

it is on M^2 . The somewhat smaller and more marginally emplaced hypocone gives M^2 a larger talon basin. The smaller prehypocone crista of M^2 , located between the bases of the hypocone and protocone, may also be accompanied by a small, narrow pit. The prehypocone crista is more evident on M^3 , probably because this region is uncomplicated—the talon is only moderately expanded and bears a narrow ledge with a minuscule hypocone. Moreover, although the metacone-metastylar region is somewhat distended as it is on M^{1-2} , the protocone region is basally enlarged and bears a relatively large parastyle, thereby emphasizing the mesiobuccal aspect of the tooth. M^3 is almost as broad buccolingually as M^1 but is narrower than either.

LOWER DENTITION (Figs. 31, 32, 33)

The six anterior teeth are slender, moderately elongate, and bear strong, markedly raised, longitudinal central keels. These teeth are quite procumbent, but the extent of this horizontality is in part obscured by the degree to which the tips of the crown arc upward. The central four teeth are rather laterally compressed into a keel lingually and bear strong but thin and inferiorly emplaced lateral margocristids. The lateralmost teeth are more robust and deeper but are only slightly flared laterally and bear bladelike rather than crestlike lateral edges. The crowns of these teeth are oriented inward, so that the central keel comes to approximate a mesial edge.

The anteriormost lower premolar is a moderately robust tooth whose crown is tilted forward slightly and bears a strong but narrow lingual vertical protoconid pillar on either side of which are long, shallow, subequal depressions. These depressions are bounded externally by thin but distinct pre- and postcingulids that emanate from the tip of the crown and become confluent at the base of the protoconid pillar. The crown of this tooth curves gently inward toward the tip, creating a slightly convex buccal surface and a slightly concave lingual face that swells basally to form a moderately developed heel. In buccal outline, the somewhat outwardly arcuate ante-

rior edge descends rather steeply, whereas the longer distal edge curves gently to the heel. The horizontal axis of the tooth is at an oblique angle to the long axis of the mandible. This high-crowned tooth stands approximately twice the height of the molars but only one-third above the middle premolar.

The middle premolar is characterized by an extremely anteriorly displaced protoconid and an elongate, shallow, and basally expanded posterior face. There is a low, shelf-like expansion of cingulid posterobuccally that causes the talonid to open lingually. The middle premolar also bears a faint lingual cingulid that is most visible high anteriorly on the face of the protoconid; this cingulid borders a small, shallow, lingual depression.

The posterior premolar is only slightly taller than M_1 and is molariform. As in the molars, the cusps of this tooth are quite bulbous. The large protoconid and the smaller and posteriorly displaced metaconid are extensively melded, separated only at their tips; they form a rather tall wall that faces onto the talonid. A broad, low, and short paracristid descends the anterior face of the protoconid and then angles sharply inward to become a narrow shelf that terminates before circumscribing the base of the protoconid. The metaconid bears some cingulid at its base lingually. The talonid of the posterior premolar is characterized more by its breadth than by its length. This breadth is created by a large, somewhat buccally distended hypoconid and a small but posterolingually displaced entoconid. Although this axis is buccolingually oblique, the metaconid-entoconid crest is rather straight. The cristid obliqua is low and as broad as the hypoconid and terminates at the base of the protoconid. The width of the cristid obliqua effectively diminishes the expanse of the shallow talonid basin and causes this latter structure to appear to be shifted lingually. The posterior premolar is somewhat smaller than M_1 .

The molar trigonids are characterized by having a large protoconid and a smaller, slightly posteriorly displaced metaconid that form a relatively steep wall facing the talonid; although they are broadly melded at their bases, the tips of these cusps are quite sepa-

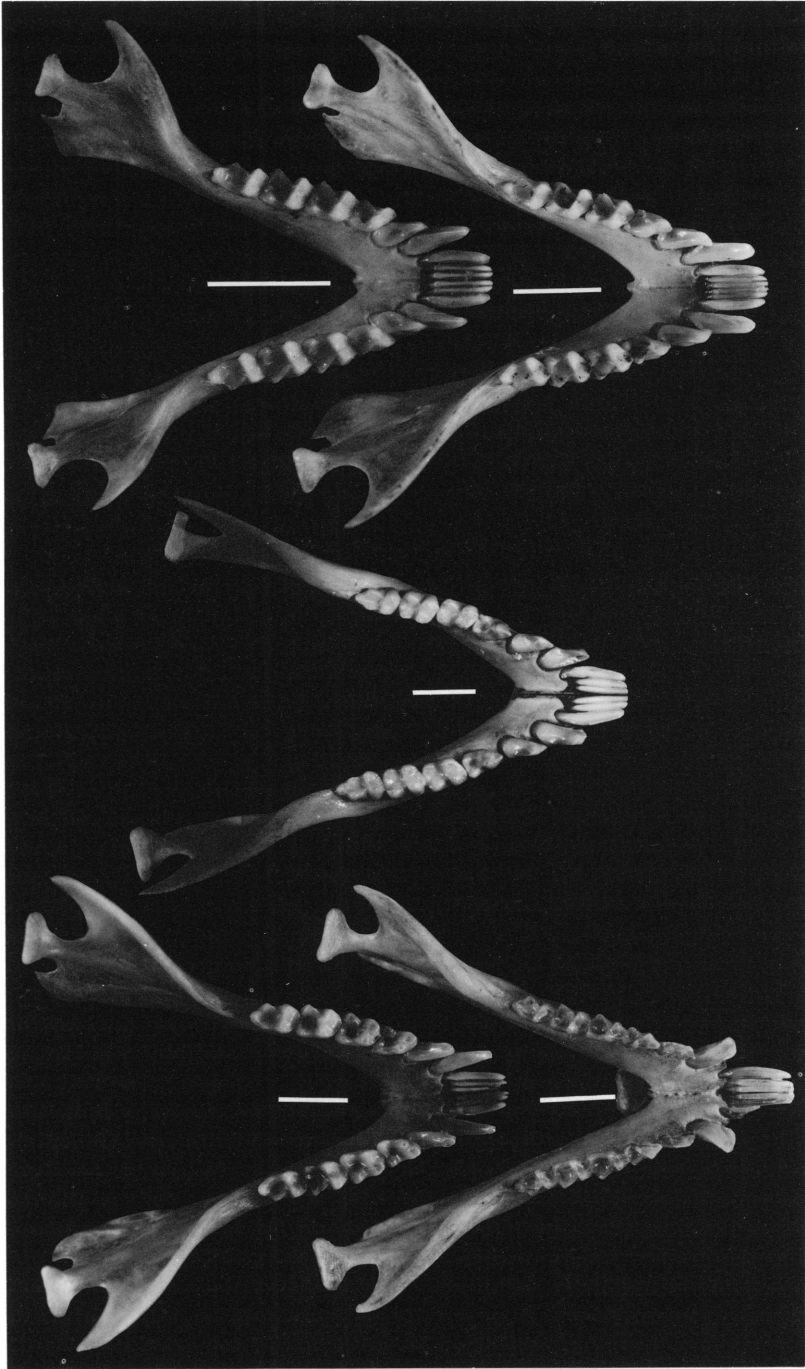


FIG. 32. Lower jaws of galagids in occlusal view. Top left: *Galago demidovii demidovii* (AMNH 241122); top right: *Galago senegalensis* (AMNH 180100); center: *Galago crassicaudatus monteiri* (AMNH 86405); bottom left: *Galago alleni* (AMNH 241119); bottom right: *Euoticus elegantulus* (AMNH 241126). All scales represent 5 mm.

rate. On all molars a broad but weak and anteriorly directed paracristid descends from the buccally displaced tip of the protoconid to angle sharply inward and proceed as a strong shelf to the base of the lingually oriented metaconid; this shelf broadens from M_{1-3} and thus borders a posteriorly increasing but nonetheless rather shallow and truncated trigonid basin. The protoconids and hypoconids of all three molars are swollen buccally such that M_{1-2} , especially, can be described as exodaenodont. Each molar also possesses a relatively straight and moderately broad cristid obliqua (of approximately the same width as the hypoconid) that terminates just medial to the long axis of the metaconid, just at the base of this cusp; on M_{1-2} this crest is part of a cresting system that incorporates the relatively low and marginally displaced hypoconid and entoconid and that circumscribes a relatively broad and moderately excavated talonid basin.

On M_{1-2} the talonid is broader than the trigonid; this is due, in large part, to the posterolingually displaced entoconid. The hypoconid-entoconid crest of M_{1-2} is only slightly arcuate (effectively "squaring-off" the talonid posteriorly), whereas the elongate talonid of M_3 , which is narrower than the trigonid, tapers to a distinct heel, somewhat lingually displaced. This relatively elongate hypoconulid is broadly separated from the hypoconid, but curiously there is a distinct if minuscule notch between the bases of these cusps.

GENUS *EUOTICUS*

EUOTICUS ELEGANTULUS

UPPER DENTITION (Figs. 28, 29, 30)

The central and lateral incisors are small, thin, and subequal in size; the crowns are moderately spatulate and lingually compressed. The central incisors are widely separated by the large anterior palatine fenestrae and the lateral of the set from the canines by small diastemata. The two incisors sit close together and side-by-side.

The upper canine is an extraordinarily large, trenchant, dagger-like tooth whose stout root impresses itself upon the maxilla externally; above the terminus of the root there is a deep

fossa. The tooth stands at least four times higher than the molars; its crown is markedly compressed laterally and the sharp tip curves gently outward. In buccal outline, the crown presents itself as a narrow triangle with slightly angular anterior and distal extensions at the base. The mesiodistal axis of the tooth is skewed somewhat outward, away from the long axis of the jaw. A fairly large fovea lingual to the root of the tooth accommodates the tip of the lower anterior premolar.

The anteriormost premolar is approximately two-thirds the height of the canine and is as markedly compressed and dagger-like. Its crown is more triangular: basally it is more acutely angular and inferiorly it is distended into styles. The tip of the tooth curves gently outward and the maxillary bone is molded around the robust root. This tooth is isolated from its anterior and posterior neighbors by small diastemata.

The middle premolar is a minute, laterally compressed, essentially bladelike tooth. If one did not know that it was a successional tooth (Schwartz, 1975), its size might cause one to identify it as a retained primary tooth. Nevertheless, the middle premolar of *Euoticus* is unique in size and morphology among strepsirrhines. The crown barely rises above the level of the posterior style of the anterior premolar but is surprisingly long mesiodistally, borne as it is by two relatively robust roots. The posterior edge of the tooth is longer than the anterior; the latter is further truncated by the presence of a large, compressed style from which extends lingually a cingulum that is only weakly expressed posteriorly. In its distal portion the tooth is skewed slightly inward, and is overlapped by the enlarged parastylar region of the last premolar.

Given the morphology of the molars, the posterior premolar of *Euoticus* can be described as molariform. In general occlusal outline the tooth is rather T-shaped, but is distended distolingually due to the presence of a moderately developed hypocone. Although the high, pointed, and partially compressed paracone and metacone are closely approximated and even melded extensively at their bases, the buccal side of the tooth is quite long mesiodistally. This is due to the development of a large, sharp, anteriorly oriented parastyle and its subtending cingulum,

as well as to the distal extension of the post-metacrista and hence the posterior edge of the metacone; these lateral extensions create the marked "waisting" of the tooth. The relatively low, pointed, somewhat compressed, centrally emplaced protocone subtends a moderately sized and excavated trigon basin. From this cusp diverge sharply stout, rugose protocristae that become confluent with the stylar regions; the postprotocrista is interrupted in such a manner as to suggest a separate metaconule. (It is interesting to note that the postprotocrista, and not a postcingulum, approaches the metastylar region; this feature also characterizes the molars.) The small but distinct hypocone is appressed distolingually to the base of the protocone; from this small cusp descends a relatively broad cingulum that fades out before the metastylar region and which enhances the "waisting" distally of the tooth. The tooth is subequal in height and mesiodistal length with the molars, but is only about two-thirds the width of M^{1-2} .

The molars also possess tall, pointed, somewhat compressed paracones and metacones, but these cusps are widely separated at their tips and are barely melded, if at all, at their bases. The lower protocone, which is nonetheless pointed and partially compressed, is quite far removed from the buccal cusps, creating a long, narrow trigon basin. From the protocone diverge well-developed protocristae which bear conules posteriorly and perhaps anteriorly, and which may be slightly crenulated in the portions that run to the stylar regions. Apart from a flexure in the slightly thickened paraconular region, the preprotocrista courses rather directly to the moderately enlarged parastyle; the postprotocrista runs initially toward the metacone, but "kinks" markedly outward at the metaconule to be diverted around the metacone, which it circles to meet the metastylar region. On M^{1-2} this region is greatly distended distally. On M^{1-2} , the posterior "waisting" to the side of the metaconule is extreme. This "waisting" to some extent isolates the metacone region of a basal cingulum that descends the distal face of the protocone as it proceeds lingually. On M^3 , this postcingulum terminates in a hypocone, which is quite small and appressed to the distolingual face of the pro-

tocone; on M^{1-2} , the hypocone is enlarged, pointed, and separated from the protocone by a narrow trough. The hypocone and protocone of M^{1-2} are, however, connected by a faint prehypocone crista that peaks as it crosses between the bases of the two cusps. We cannot detect a prehypocone crista on M^3 .

LOWER DENTITION (Figs. 31, 32, 33)

As a group, the lower six anterior teeth of *Euticus* are among the most laterally compressed, elongate and procumbent to be found in any strepsirhine toothcomb. Even the relatively large anterior premolar does not detract from their character. All teeth curve gently upward at their tips. The central four are the most markedly compressed; they bear strong longitudinal central keels that are bounded by distinct medial and lateral margocristids. The lateral teeth of these four are slightly wider than the central pair and bear somewhat thicker lateral margocristids. The most lateral anterior tooth is deeper and more robust and flares somewhat laterally; there are a distinct medial margocristid, somewhat inferiorly emplaced, and a thicker lateral margocristid, separated from the broad central keel by a narrow groove.

The anteriormost premolar, separated from the toothcomb by a diastema, is very tall, pointed, compressed, and dagger-like; its deep and robust root swells the mandibular bone externally. Even though it inclines forward slightly and its tip arcs gently backward, this tooth stands more than twice the height of the posterior cheek teeth. The crown bulges slightly anteriorly; the gently concave posterior edge of the tooth terminates in a minuscule, pointed heel at which terminates a weak but complete lingual cingulid.

The middle lower premolar is as unique as its upper counterpart; the crown of the lower tooth, however, is noticeably higher than the upper. This lower tooth is inclined a bit forward, emphasizing a very long and bladelike edge that, at its most distal extent, angles inward to form a heel. This heel directs lingually a long, shallow depression that parallels the posterior edge of the tooth. The very anteriorly emplaced apex of the tooth permits only a short anterior edge; a lingual proto-

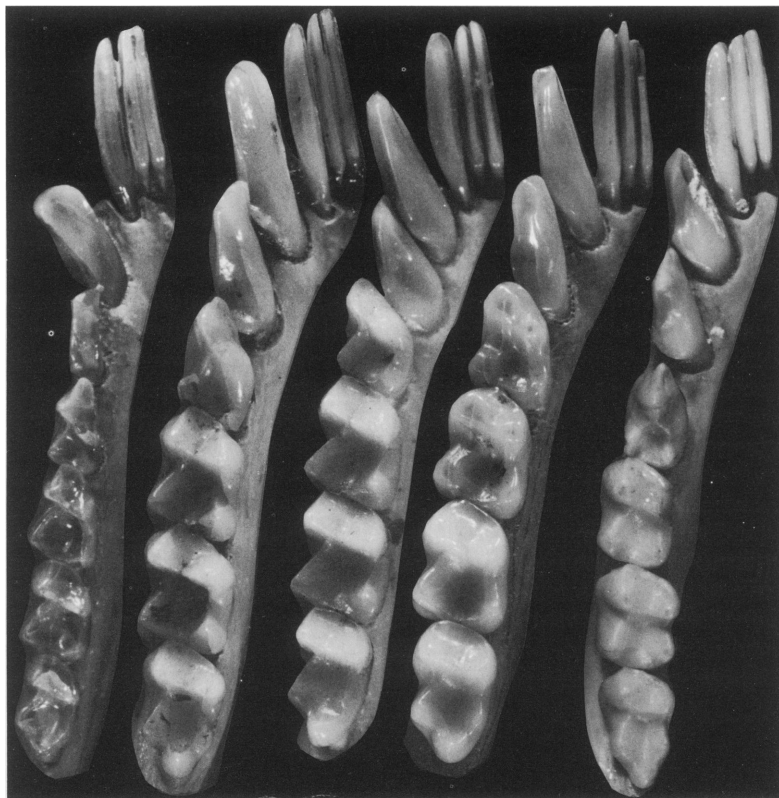


FIG. 33. Lower left dentitions of galagids in occlusal view. From left to right: *Euoticus elegantulus* (AMNH 241126); *Galago senegalensis* (AMNH 180100); *Galago demidovii demidovii* (AMNH 241122); *Galago alleni* (AMNH 241119); *Galago crassicaudatus monteiri* (AMNH 80801). Not to scale.

conid "pillar" delineates a very shallow depression. A weak lingual cingulid courses from the most anterior point of the crown to fade out reaching the posterior heel. Although the bladeliike crown is quite low, it is very long mesiodistally and sits on two relatively stout roots.

The posterior premolar may fairly be described as moderately molariform, although this tooth does differ in most features from the molars proper. Thus the small metaconid is not separated from, but is appressed distolingually to the quite tall and lingually flattened protoconid (hence looking more like a well-developed stylid than a cusp). The relatively long anterior edge of the protoconid lacks a paracristid and terminates in a broad but truncated lingual paraconid shelf that is not connected in any way to the metaconid; the trigonid as a whole is thus quite elongate

and compressed with a broad, very shallow basin that is almost entirely exposed lingually. No crest connects the entoconid with the metaconid, hence a deep and fairly broad notch is formed. This notch may show a small groove inferiorly between the cusps, opening the talonid basin lingually. The metaconid is extremely tall and appears as a pillar or appressed to the side of the protoconid. The hypoconid is displaced a bit buccally, but is not noticeably swollen; from this cusp emanates a stout, rather straight cristid obliqua that courses to the protoconid. A short, high, sharp and straight (but postero-obliquely oriented) hypocristid runs between the hypoconid and entoconid; internally, a groove of variable expression delineates the face of the hypoconid. Although the posterior premolar is narrower than M_{1-2} , especially, it is subequal to these teeth in mesiodistal length.

What the posterior premolar lacks in lingual swelling typical of the molars it replaces in its degree of exodaenodonty, especially over its anterior root.

All molars bear tall protoconids and metaconids that are separated and divergent at their tips but are broadly melded at their bases; they are also connected by a stout crest. The metaconid is emplaced slightly posterior to the protoconid and its tip angles increasingly lingually, away from M_{1-3} . The protoconid and metaconid form a broad, steep wall that faces upon the talonid. A prominent paracristid runs down the anterior face of the protoconid, to "kink" and proceed to the base of the metaconid as a broad shelf, weakly crenulated. The paracristid extends markedly outward on M_1 , less so on M_2 , and less again on M_3 , thereby reducing the expression of the trigonid on the posterior molars. The stout cristid obliqua terminates low on the protoconid-metaconid wall just to the inside of the former cusp; this creates a relatively deep hypoflexid notch that is further enhanced by

some buccal swelling of the protoconid, by the presence of a protostylid (which is more developed on M_{1-2} than M_3 , and which is a rare feature of primate teeth), and by some lingual swelling of the lower hypoconid.

M_{1-2} are subequal in talonid width, but M_1 appears narrower and more elongate as a result of its more closely approximated protoconid and metaconid, its more anteriorly extended paracristid, and its more posteriorly emplaced entoconid. Both anterior molars show a well-developed, slightly arcuate hypocristid that completes the enclosure of a broad and deep talonid basin. M_3 is subequal in mesiodistal length with M_{1-2} , but is a bit narrower because its hypoconid is not extended much farther buccally than its protoconid. The talonid of the last molar is distended by a low, narrow heel that is connected to the other talonid cusps by thin crests; the well-excavated talonid basin is thus also enclosed by continuous cresting, but the entoconid region is much lower and less distinct than in the other molars.

STREPSIRHINE RELATIONSHIPS

The foregoing dental descriptions make clear how great a diversity of dental morphology exists among the living "lower primates." In attempting to perceive the order underlying this diversity—an order reflecting the inclusive hierarchy of relationships produced by the evolutionary process—we have considered, and rejected, a large number of alternative hypotheses of relationship among these forms. The cladogram given in figure 34 represents our view of the optimum nesting of the primate genera involved, on the basis of the characters we have considered; necessarily, however, it embraces a considerable amount of parallelism. Thus, for example, the genera *Arctocebus* and *Loris* share with the galagids a large, submolariform last upper premolar; but we have been obliged to reject this as a synapomorphy of these two groups since *Arctocebus* and *Loris* are united with *Perodicticus* and *Nycticebus* by a substantial number of diversely derived cranial and postcranial features. Similarly, the phylogenetic scheme advanced here demands that

lower molar paraconid loss must have occurred independently on numerous occasions in the evolutionary history of the lemurs and lorises. For example, we unite *Hapalemur* with *Lemur* + *Varecia* on the basis of the uniquely shared possession of a large number of dental characters (see below), despite the possession by the former of a paraconid, which is absent in all other extant taxa considered here. Thus the loss of the paraconid must be regarded as independently synapomorphic in both the loridid-galagid-cheirogaleid clade, and that of the indriids + *Daubentonina* + *Lepilemur*.

We present below the synapomorphies which define the various clades and subclades recognized in the cladogram in figure 34. Within this assemblage, foresaking strictly cladistic principles of classification, we have chosen to recognize seven families. The synapomorphies uniting the taxa within each family are presented first, and relationships among the larger taxa are discussed subsequently.

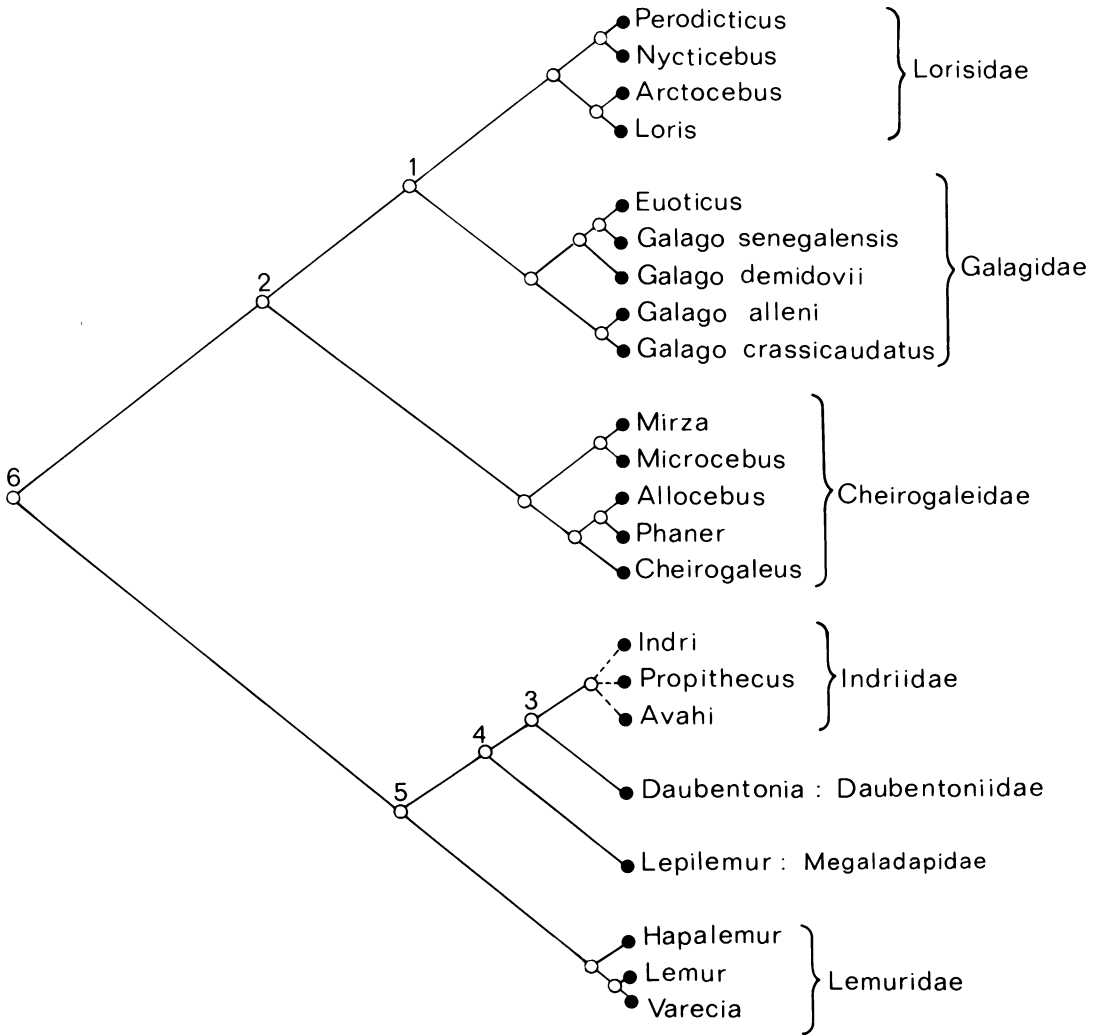


FIG. 34. Hypothesis of relationships among living strepsirhine primates.

FAMILY CHEIROGALEIDAE

This family consists of the five genera *Cheirogaleus*, *Microcebus*, *Mirza*, *Phaner*, and *Allocebus*, forms united as a whole by the possession of a complex of characters of the upper and lower molar teeth. These include: a buccal cingulid around the protoconid of M_{1-3} (smoothed out in the case of *Cheirogaleus* species); a buccally emplaced cristid obliqua on M_{1-3} ; very closely approximated and broadly melded protoconid and metaconid on M_{1-3} . Apart from *Phaner* and *Allocebus*, in which the talonid heel is lacking, the cheirogaleid genera are also linked

by the compression and lingual displacement of the talonid heel of M_3 . Cheirogaleids are united in the upper molars by possessing widely divergent protocristae, and thus relatively broad trigon basins, on M^{1-3} ; the molar stylar shelves are also well developed in all genera; and the upper molar protocones are bounded externally by a substantial cingulum. The upper incisors of all cheirogaleids are long, tusklike, and slightly procumbent.

Within the family, *Allocebus* and *Phaner* share dentitions that are extraordinarily similar except in point of absolute (but not relative) size. This similarity also extends to details of skull morphology such as the slen-

der, "unpinched" snout that is somewhat downturned on the cranial base, and indeed to certain postcranial characteristics such as keeled nails (R. D. Martin, personal communication). Dentally, the two genera are jointly distinguished most strikingly from other cheirogaleids by the marked reduction in size of the third molars, which lack any talonid heel, and by the enormous elongation and lateral compression of the upper and lower anterior premolars. In both genera the posterior dentition is reduced in size relative to the anterior teeth, and the toothcomb is remarkably elongate and procumbent, the lateral tooth being extremely slender.

The sister of the group formed by *Phaner* and *Allocebus* appears to be the lone genus *Cheirogaleus*. This genus is highly autapomorphic in lowering and rounding the relief of the cheek dentition, to the extent that cusps, crests, styles, and most cingula are only minimally distinct; this represents an exaggeration of the trend already evident in *Phaner* and *Allocebus*. *Cheirogaleus* also shares with these genera a condition whereby the lateral upper incisor is greatly reduced relative to the central, and the third lower molar is at least somewhat reduced relative to its anterior neighbors.

The group *Microcebus* + *Mirza* is clearly distinguished dentally from the other cheirogaleids by the complete buccal cingulids found on M_{1-3} ; the buccal excavation of the last lower premolar, which bears a thick basal cingulid; the buccal cingulum which bounds all the upper premolars of the two genera; the distinct protostyles in the anterolingual corner of M^{1-2} ; the thickening of the talon region of the relatively large M^3 ; and the posterior notching of the upper lateral incisors.

FAMILY LORISIDAE

Lorisidae, consisting of the four genera *Loris*, *Arctocebus*, *Perodicticus*, and *Nycticebus*, is united by a suite of synapomorphies most of which, however, do not reside in the dentition. The primary such dental character, and a very striking one, is the rather central emplacement of the cristid obliqua in M_{1-3} , such that the protoconid in its entirety subtends a deep hypoflexid notch, and the metaconid alone bounds the talonid basin anteriorly. Non-dental characters include expansion

of the gonial region of the mandible, convergent orbits, tubular lateral petrosal extension, and reduction of the second digit of the manus.

Within the family, *Arctocebus* is linked with *Loris* by the possession of an anteriorly prolonged premaxilla, and by dental characters that include: a large submolariform upper last premolar that bears a small hypocone; a paraconid shelf on the last lower premolar; buccal cingulids on M_{1-3} , which are complete on M_{1-2} ; and a large M^3 . In both genera the upper canine is anteriorly placed and transversely rotated. *Perodicticus* and *Nycticebus*, in contrast, are united by the "puffy" anterior maxillary region, distended by the very large roots of the upper canine, and by the robust zygoma. Dentally, the two share as synapomorphies somewhat lowered, broadened, and "puffy" upper and lower cheek tooth cusps; a pit lingual to the hypocone on M^2 ; robust and enlarged upper central incisor, upper canine and anterior premolar; and a more robust and less procumbent toothcomb than that of any other strepsirrhine.

FAMILY GALAGIDAE

The family Galagidae contains five species which pose nomenclatural problems that we are unable to pursue here. Our hypothesis of relationships is as shown in figure 34, and unites *Galago alleni* and *Galago crassicaudatus* as the sister of the other three species. The family is united by the following synapomorphic characters: pneumatization of the mastoid and bullar regions; elongation of the hindlimb; and development of molariform upper and lower last premolars, the upper of which bears a definite protocone fold, and the lower showing an anteriorly directed paracristid that terminates in a small swelling, creating an open and shallow trigonid basin. Within the family, the teeth of *Galago alleni* and *Galago crassicaudatus* are distinguished in sharing lower and more bulbous cusps; the upper posterior premolar of both is also quite distinct in that the preprotocrista arcs posteriorly and inward to terminate almost at the midline between the paraconid and the metaconid.

Euoticus elegantulus shares the following synapomorphies with *Galago senegalensis*: sharp, accentuated cheek tooth cusps, both

upper and lower; an elongate upper anterior premolar that lacks cingula; upper incisor crowns lowered; penultimate and last lower premolars compressed laterally and bearing sharp, bladelike edges; the last lower premolar with the talonid basin reduced in size and open lingually through a deep notch between the steep face of the metaconid and the entoconid. Both *Euoticus elegantulus* and *Galago senegalensis* share with *Galago demidovii* a compressed and bladelike anterior upper premolar and a posterior lower premolar in which the cristid obliqua terminates on the inside of the protoconid. On the upper last premolar through M^2 in all three species the preprotocrista runs posteriorly around the metacone.

FAMILY LEMURIDAE

In earlier contributions we have favored linking *Hapalemur* together with *Lepilemur* into a single taxon at the subfamily or family level. However, more detailed consideration of dental morphology has led us to another conclusion entirely. We now favor isolating *Lepilemur* in its own family, and we group *Hapalemur* with *Lemur* and *Varecia*, in the family Lemuridae. The synapomorphies which unite the *Lemur-Varecia-Hapalemur* clade are the following: greatly enlarged infraorbital foramen; upper incisors short, broad, and lingually excavated; buccolingual broadening and anteroposterior waisting of the posterior upper premolar; longitudinal orientation of the posterior lower premolar, which bears a distinct and peripherally emplaced cristid obliqua and a deep, centrally located talonid basin; cristid obliqua buccally positioned on M_{1-3} ; talonid crests of lower molars tall and incorporating peripheralized cusps, producing deep talonid basins; paracristid on M_{1-3} tall but straight and truncated anteroposteriorly; and upward deflection of the hypocristid, especially on M_3 . Within the group, *Lemur* and *Varecia* are united by a list of synapomorphies that include: lower anterior premolar triangular and compressed, separated from the middle premolar by a diastema; loss of paraconid on lower molars; well-developed trigonid basins in M_{1-3} that are defined by a smoothly rounded paracristid, especially on M_1 ; reduction of entoconid on M_1 ; upper canine elongate,

bladelike, and recurved; upper anterior premolar greatly reduced in size and separated from the canine by a diastema; protocone on M^{1-2} ringed by a lingual cingulum; anterolingual distension of M^2 ; reduction in size of M^3 .

FAMILY INDRIIDAE

The extant indriids form a close-knit group united by a variety of dental synapomorphies. Among these are: only two premolars present in each quadrant of the jaw; tooth-comb composed of only four teeth; upper premolars elongated, with compressed anterior and posterior edges; lower posterior premolar compressed and bladelike; cristid obliqua runs to the metaconid on M_1 ; M_2 quadricuspid and subrectangular; paracristid extremely broad on M_{2-3} . Within Indriidae, relationships are hard to interpret, to the extent that we represent the group on our cladogram (fig. 34) by an unresolved polychotomy. Intuitively, it seems reasonable to regard the dental condition represented by *Propithecus* as closest to that which is primitive for the group, largely since *Indri* and *Avahi* appear to diverge from it in separate directions. For example, in *Avahi* the crests in the molar teeth, both upper and lower, are more pronounced; in *Indri*, less. In *Avahi* the cusps are taller and more compressed; in *Indri* they are lower and more rounded. In *Avahi* the styles, especially the mesostyles in M^{1-3} and the metastyles in M^{1-2} , are enlarged and distinct, whereas in *Indri* the mesostyles are reduced and more rounded, and the metastyles are diminutive. In *Avahi* the postmetacristid of the upper molars is more pronounced, and bears a small but distinct metastylid; in *Indri* the posterior part of the metaconid is more compact. The enamel of the upper and lower cheek teeth of *Avahi* is highly crenulated; in *Indri* the molar enamel is smooth. In the absence of any clear pattern of synapomorphy linking either *Indri* or *Avahi* with *Propithecus*, we prefer to reflect uncertainty in our cladogram.

FAMILIES DAUBENTONIIDAE AND MEGALADAPIDAE

These two families are generically monotypic, at least as concerns their extant rep-

representatives; the autopomorphies of each genus will be evident from the descriptions already given.

RELATIONSHIPS AMONG THE STREPSIRHINE PRIMATE FAMILIES

Our cladogram (fig. 34) shows not only the relationships that we posit within the various strepsirhine families, but also the relationships among them. Characters synapomorphic for each family have already been given; in order to facilitate discussion we have numbered the nodes on the cladogram that represent the larger groupings, and will discuss below the characters defining and uniting each one.

Node 1, representing the common ancestor of Lorisidae + Galagidae, is defined by the following character states: tympanic ring completely fused to bullar edge; lower molars with tall protoconid and metaconid that are melded at their bases and connected by a stout crest, yet whose tips are widely divergent; sheer wall created by this cusp complex that faces on the talonid; M_{1-3} with deep hypoflexid notch accentuated by a buccally expanded protoconid; cristid obliqua terminates such that most of the protoconid fails to border the talonid basin.

Node 2 represents the common ancestor of the lorises, galagids, and cheirogaleids. Synapomorphies at this point include the presence of an "anterior carotid" (or ascending pharyngeal) artery; separation of the upper central incisors by the anterior palatine fenestrae; downward distension of the premaxillary alveolar margin; basally flexed paracristid that runs along the bases of the protoconid and metaconid; compressed trigonid basins, absence of paraconid on M_{1-3} ; hypocone present on M_{1-2} .

Node 3 represents the common ancestor of the Daubentoniidae plus the Indriidae. These families are united by: rounded, globular cranium; deepened splanchnocranium and mandible; expanded gonial angles; mandibular condyles that are rounded in the coronal plane; minuscule zygomatic foramina; M^{1-2} quadricuspid and subsquare, with broadened hypocone region; enlarged para- and metaconule regions on M^{1-2} ; anterior displacement of paraconule region on M^1 ; expansion of mesostylar region on M^{1-2} ; metacone of

M^3 reduced and shifted posteriorly; squaring-up of posterior face of M_{2-3} ; heel of M_3 reduced.

Node 4, which unites the group just discussed with the Megaladapidae, is characterized by the following: development of secondary articulation on posterior aspect of mandibular condyle; broad trigons with deemphasized postprotocristae on M^{1-3} ; distension of para- and metastylar regions on M^{1-2} ; posterior lower premolar deeply excavated distally; M_1 elongate, with metaconid more distended posteriorly than at Node 5.

Node 5 unites the group above with the family Lemuridae. Characters at this point include: downwardly sloping anterior nasal floor; compression of upper molar buccal cusps; distinct crests on buccal cusps of M^{1-3} ; broadening and lowering of protocone on M^{1-3} ; some distension posteriorly of metaconid on M_{1-3} ; anterior and middle lower premolars with anterior projection toward base.

The living strepsirhine ensemble, whose common ancestry is represented at Node 6, is effectively tied together by the possession of one character common to all: the toilet claw on the second pedal digit; it is also united by the toothcomb, which has been lost in *Daubentonia* (as in the subfossil *Hadropithecus*), but which was certainly present in the common ancestor of this genus and the indriids.

THE SUBFOSSIL MALAGASY LEMURS

Several strepsirhine genera are known from Madagascar that have become extinct within the last thousand years or so (see Tattersall, 1982, and references therein), almost certainly as a sequela of human arrival on the island. Although certain of these genera display specializations that are not characteristic of any of the surviving lemurs, all are closely related to taxa still extant in Madagascar. We summarize these relationships (not all of them certain in detail) in the cladogram given in figure 35.

The extinct indriids *Archaeoindris* and *Palaeopropithecus* (subfamily Palaeopropithecinae) are clearly demarcated from their extant relatives by their extremely large size and by certain cranial apomorphies (see Tattersall and Schwartz, 1974; Tattersall, 1982). However, their dentitions ally them unequivocally

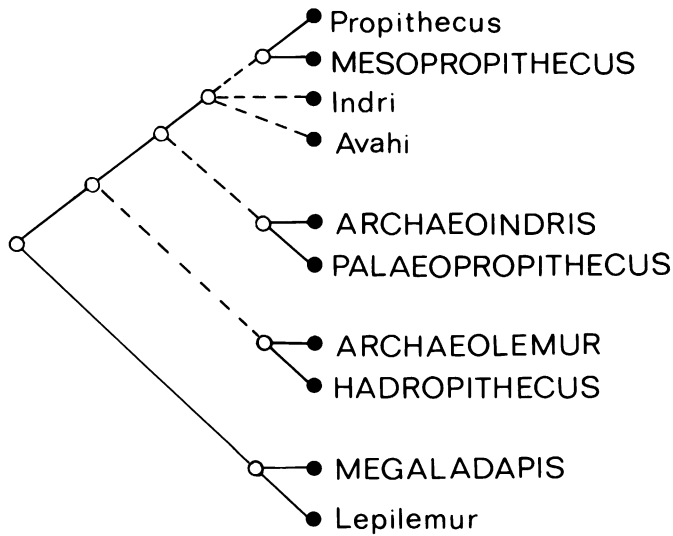


FIG. 35. Hypothesis of relationships among extinct Malagasy lemurs (upper case) and their closest living relatives.

cally with the living indriines, not only in detailed morphology, but also in the loss of a premolar in each quadrant of the upper and lower jaws. The two intermediate-sized genera *Archaeolemur* and *Hadropithecus* (subfamily Archaeolemurinae), in contrast, remain relatively primitive and indriine-like in cranial structure, but display notable specializations of the dentition (see summary in Tattersall, 1982). The arrangement of these taxa given in figure 35 is based on the sharing by living indriines and the palaeopropithecines of the apomorphic reduced molar number; the archaeolemurines retain the primitive premolar number of three per quadrant of the dentition. The remaining subfossil indriid genus *Mesopropithecus* is extremely close to *Propithecus* in virtually all cranial and dental characters apart from its greater robusticity.

The other notable member of the subfossil lemur fauna is *Megaladapis* (subfamily Megaladapidae), a very large and autapomorphic form which nonetheless betrays in its dentition and certain characters of the lower

jaw its close relationship to *Lepilemur*, hence the common membership of these two genera in the family Megaladapidae. Among the most striking of the characters that link the pair are the loss in both genera of upper permanent incisors; a short, anteriorly directed paracristid of M_{2-3} that opens the trigonid lingually; and the development of a large secondary articulation on the medial side of the neck of the mandibular condyle.

CLASSIFICATION

Since classification is not synonymous with phylogeny, which is the central concern of this paper, and since its ramifications extend beyond the taxa under review here, we have preferred simply to indicate the family-level groupings we recognize. The wider questions of primate classification, including the ordering of the lorises and the lemurs, are scrutinized elsewhere by one of us (Schwartz, in press b). Another review, based on an earlier and slightly different phylogeny, may be found in Tattersall (1982).

FOSSIL STREPSIRHINES

THE CONCEPT OF ADAPIDAE

The monolithic current notion of the family Adapidae descends directly from that ad-

umbrated by Gregory (1920) in his monograph on *Notharctus*. In contrast to Stehlin (1912, 1916), who had separated into differ-

ent families the large non-"tarsioid" North American Eocene primates and the larger European primates of that epoch, Gregory argued for a close relationship between the two groups, and lumped all the genera involved into a single family Adapidae. Despite a later attempt by Gazin (1958) to resurrect Stehlin's interpretation, Gregory's view continues to command virtually universal acceptance, and the generic content of Adapidae has continued to expand as newly discovered and/or named forms, both European and North American, have been classified within the family.

The end result of this ongoing process is that, while all recent authors would appear at least implicitly to regard Adapidae as a monophyletic assemblage, the family has in reality become a taxon of the "not-A" type: in other words, a wastebasket for all those Eocene primates that have not been categorized as "tarsioids." (It is interesting to note in this context that P. Schmid [personal commun.], who has been studying the European fossil "tarsioids," has reached the conclusion that this latter group is composed of forms that simply have in common not being "adapid"!)

In any attempt to understand the fossil "lemuroids," all of which have been classified as adapids, the first question to be approached must thus be whether the family Adapidae, as it is at present generally held to be constituted, is in fact a monophyletic grouping. We have for several years suspected that such is not the case (see, for example, Schwartz and Tattersall, 1979), and we have recently investigated the problem in a series of papers (Schwartz and Tattersall, 1982a, 1982b, 1983; Tattersall and Schwartz, 1983a, 1983b, 1984) dealing with various "adapids" of the European Eocene. We are now broadening these studies to embrace the North American forms. It is not our intention to recap all of this other work here; rather, we wish to approach a more specific problem that we have not broached elsewhere: namely, the question of the content and relationships of Adapidae in a strict monophyletic sense.

The type genus of the family Adapidae is of course *Adapis* Cuvier, 1821, the first fossil primate ever to be named. But *Adapis parisiensis*, from the late Eocene Quercy phos-

phorite deposits, was regarded by its describer as an ancient pachyderm, and it was not until the beginning of this century that Forsyth Major (1901) suggested that this species might be linked phylogenetically with the Malagasy lemurs. Four decades earlier, however, Rütimeyer (1862) had described *Caenopithecus lemuroides*, from the middle-to-late Eocene fissure fill deposits of Egerkingen, Switzerland, as a lemuriform primate. During the twentieth century the number of species assigned both to *Adapis* and to Adapidae has steadily grown; indeed, in 1977 Gingerich was able to list 28 adapid species from the Eocene of Europe alone, and to recognize eight species within the genus *Adapis*. Not all authorities are in agreement with the large number of species assigned by Gingerich to *Adapis* (indeed Szalay and Delson [1979] restricted the genus to the single species *Adapis parisiensis*); but there has been essentially no quarrel with the allocation of all these forms to the family Adapidae, although some authors have at least implicitly recognized that the family is not entirely homogeneous. Thus Szalay and Delson (1979) have divided their subfamily Adapinae (which excludes the North American forms) into five tribes (Protoadapini, Anchomomyini, Microadapini, Indralorisini, and Adapini, the last with two subtribes: Adapina and Caenopithecina), whereas Gingerich (1977) recognizes a "*Protoadapis* group" and an "*Adapis* group" within the European forms, the latter consisting purely of that author's many species of *Adapis*.

Since the content of the family Adapidae must ultimately depend on judgments of affinity deriving from comparisons with *Adapis parisiensis*, we briefly describe the dentition of this species below.

DENTAL MORPHOLOGY OF *ADAPIS PARISIENSIS*

The upper incisors of *A. parisiensis* are broad, spatulate, mesially distended, and concave lingually (fig. 36). The upper canines are broad and stout, and project only moderately beyond the occlusal level of the cheek teeth. The anterior upper premolars are small and only rudimentarily premolariform; the second and third upper premolars are larger but are not much more complex, being dom-

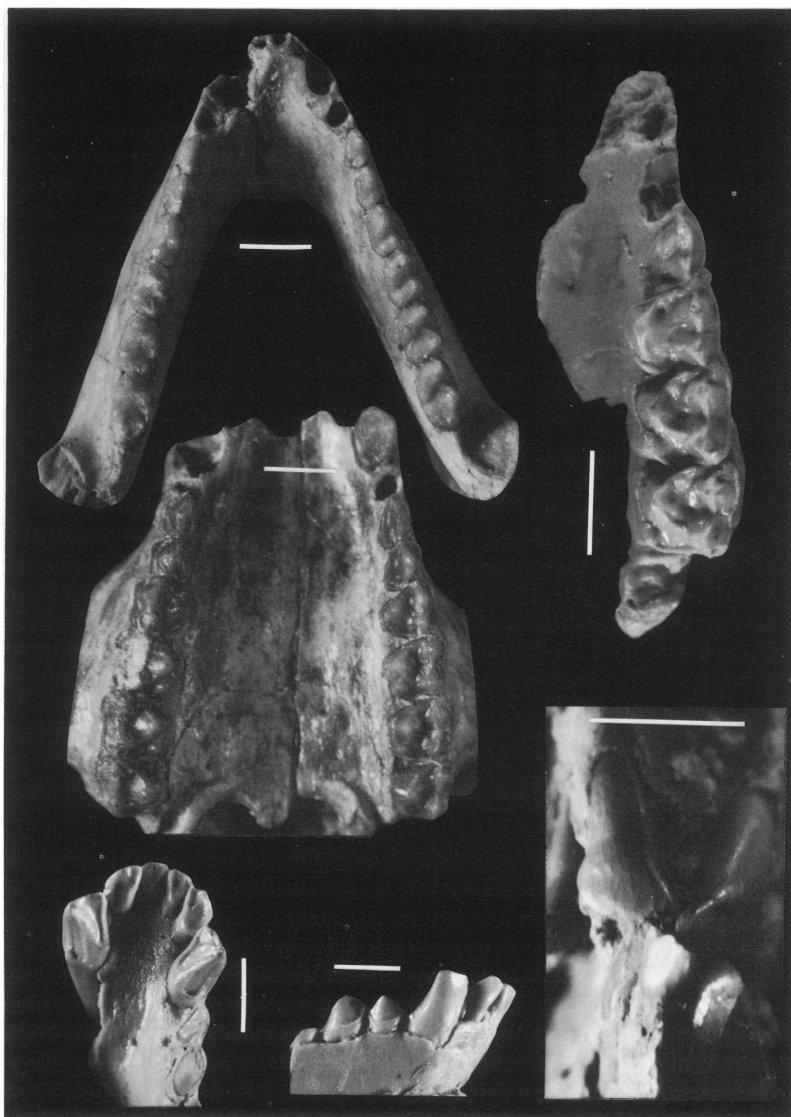


FIG. 36. Dentitions of *Adapis*. Clockwise from top left: *Adapis parisiensis*, lower jaw with cheek dentition (BMNH M 1634); *Adapis sudrei*, cast of type maxilla (Montpellier RBN-5120); *Adapis parisiensis*, anterior view of anterior dentition (MNHN QD 1); *Adapis parisiensis*, lateral view of anterior dentition (cast of MNHN 10957); *Adapis parisiensis*, occlusal view of anterior dentition (cast of MNHN 10957). All scales represent 5 mm.

inated by the paracone, from which emanate discernible pre- and postparacristae. These teeth also bear a small protocone. The last upper premolar is submolariform, bearing subequal paracone and metacone, closely approximated to each other and connected by a distinct centrocrista. The protocone is large, low, broad, and lingually distended; the tooth

is entirely ringed by cingulum. There is a sharp preprotocrista that runs anterior to the paracone to join a well-developed and anteriorly directed preparacrista; the postmetacrista is present but less prominent. The upper molars are similar in being quadrate and quadricuspid; the buccal cusps are somewhat compressed and bear stout cristae on all sides as

well as buccal pillars. A stout preprotocrista runs anteriorly around the paracone to the parastylar region; the small postprotocrista runs distally toward the hypocone, then fades out toward the metacone. All molars are almost entirely ringed by cingulum; M^{1-2} are subsquare and subequally sized, while M^3 is as broad buccolingually but is foreshortened mesiodistally.

The lower incisors are somewhat low-crowned and spatulate (see fig. 36), the lateral teeth of the pair being substantially larger and more noticeably flared laterally than the central. The lower canine is a broad and stout non-caniniform tooth that does not project beyond the plane of the incisors (fig. 36). The crown of the tooth appears to be flexed backward so that the apex of the protoconid lies on the same plane as the anteroinferior extent of the crown. There is a very prominent and vertically oriented posterior basin that is subtended inferiorly by a cingulid bearing a small heel. There is also a broad but shallow anterior depression lingually. The anterior lower premolar is a small, somewhat buccolingually compressed tooth, dominated by its protoconid. A complete lingual cingulid is present. The second and third lower premolars increase in size toward the rear, but both are simple and buccolingually compressed. The posterior lower premolar is quite molariform; the trigonid bears three distinct cusps, although the paraconid is diminutive and incorporated into the anteriorly directed paracristid. The metaconid lies just behind the protoconid, to which it is connected by a distinct crest. The shallow and lingually facing trigonid basin is bounded inferiorly by the inferiorly directed paracristid. The metaconid also bears a short postmetacristid that is somewhat thickened and reminiscent of a small metastylid. The well-developed talonid basin is bordered by a distinct hypoconid and entoconid, interconnected by a stout crest. An equally stout cristid obliqua runs to terminate just to the inside of the protoconid. The basin opens lingually, however, between the "metastylid" and the entoconid. There is a complete buccal cingulid. Overall, this tooth is almost as large as M_1 . The trigonids of M_{1-3} are quite similar to each other, and differ from that of the last lower premolar in that the paracristid does not extend as far anteriorly

before descending inferiorly, and that there is a better-developed metastylid. There is still a lingual opening of the talonid basin posterior to the metaconid-metastylid cresting complex. The cristids obliquae of M_{1-3} terminate more toward the metaconid, and the talonids are more expanded; indeed, M_3 bears a moderately developed heel. All three lower molars possess complete buccal cingulids.

WHAT CONSTITUTES ADAPIDAE?

Our studies noted above have demonstrated that the European species generally allocated to Adapidae form a highly diverse assemblage, and that relatively few of them show any of the constellation of dental characters that in general distinguish *Adapis* from the extant primate taxa already described. These distinctive characters of *Adapis* include the following:

1. Spatulate and mesially distended upper incisors.
2. Submolariform last upper and lower premolars.
3. Diminution of postprotocrista.
4. Accentuation of para- and metacristae.
5. Quadrateness of M^{1-2} .
6. Well-developed hypocone on M^{1-3} .
7. Buccal pillars on upper molars.
8. Emphasis of longitudinal shearing crests on buccal side of upper cheek teeth.
9. Ringing of cheek teeth with cingulum.
10. "Premolariform" and occlusally rotated lower canine.
11. Buccolingual compression of first three lower premolars, and emphasis of sharp trigonid and talonid crests on last lower premolar and M_{1-3} .
12. Distension of the metaconid into a metastylid on last lower premolar through M_3 .

If the possession of the characters enumerated above, or at least of a subset of them, is considered necessary to establish a phylogenetic position within the clade of *Adapis*, then the North American Eocene primates *Pelycodus*, *Notharctus*, *Smilodectes*, *Copelemur*, and *Mahgarita*, and also the Holarctic genus *Cantius*, are immediately eliminated

from that clade. So also are the following "adapid" genera from the Eocene of Europe: *Anchomomys*, *Periconodon*, *Microadapis*, *Huerzeleris*, *Agerinia*, *Protoadapis*, *Pronycticebus* (including *Europolemur*), and *Cercomanius*, together with some species often referred to *Adapis*, including *priscus*. The molar teeth of *Caenopithecus* do resemble those of *Adapis* in certain respects that have led to the association of the two genera; such features include size, the presence of metastylids on M_{1-3} , the complete cingulids around the lower molars, the subquadrate form of the upper molars, and the development of large para- and metacristae on the latter teeth. However, on other grounds it is preferable to associate *Caenopithecus* with the tarsiod group, as broadly defined (see Schwartz, in press a); among the most obvious reasons for such allocation is the presence in the front of the lower jaw of a pair of extremely large teeth, as indicated by well-preserved alveolae. As early as 1916 Stehlin noted this prominent feature and its incongruity with adapid affinities for its possessor, and this important observation was reiterated subsequently by Simpson (1940).

Thus among the primates of the Eocene there remain relatively few that can be considered to bear a reasonably close affinity with *Adapis parisiensis*. Of these, only Gingerich's (1977) *Adapis sudrei* (fig. 36) is sufficiently similar to *parisiensis* to be allocated to the same genus. Most remaining species in this category are allocable to the genera *Leptadapis* and *Paradapis*, the latter containing only the species *Paradapis ruetimeyeri* (Stehlin, 1916) (see Tattersall and Schwartz, 1984). *Paradapis* differs from *Adapis* and *Leptadapis* in having "puffier" cusps, upper molars that are less square, more filled-in basins on the upper and lower molars, a hypocone on the upper posterior premolar, the metastylid apparently restricted to M_1 , and the paracristid (and the trigonid generally) more truncated.

Leptadapis, in the form of the type species *L. magnus*, is almost as well known in terms of quantity of specimens as is *Adapis parisiensis* itself. In addition to its much larger size, *L. magnus* differs from species of *Adapis* in having less distinct hypocones, especially on M^{2-3} , upper M^3 relatively smaller, upper

and lower canines more trenchant, the lower non-molariform premolars less compressed buccolingually, penultimate premolar with a distinct metaconid and hypoconid, and the metastylid on the last lower premolar and M_{1-3} markedly more pronounced (fig. 37). A poorly known second species of *Leptadapis*, *L. stintoni* (originally named as a species of *Adapis*), is distinguished from *magnus* by its slightly smaller size, more mesiodistally compressed trigonids, much more pronounced metastylids emplaced in stouter metacristids, more buccolingually compressed, non-molariform lower premolars, and broader and more rounded heel of M_3 .

Two other genera from the Eocene of Europe, both poorly known, also seem to belong in this clade. The first of these is the recently named *Alsatia*, known certainly only from isolated upper molars but most closely resembling *Paradapis ruetimeyeri* (Tattersall and Schwartz, 1984). This form shows complete cingular banding, compressed buccal cusps with buccal pillars, strong para-, meta-, and postprotocristae, and a large, swollen hypocone; but it differs from *Paradapis* in the development of the protostylar region. The second such genus allocable to this group is *Simonsia*, known only from lower jaws with M_{2-3} , and which also most closely resembles *Paradapis* (Schwartz and Tattersall, 1982b). It shows a stout, short paracristid and a very truncated trigonid; a stout, tall crest connecting the protoconid and metaconid; somewhat filled-in talonid basins; and buccal cingulids. *Simonsia* is, however, substantially smaller than any other taxon in this clade, and M_2 bears a fat, flat, truncated hypocristid.

Adapis, *Leptadapis*, *Paradapis*, *Alsatia*, and *Simonsia* thus form a relatively cohesive clade that is quite distinct from any other group of Eocene primates. It is only meaningful to regard this restricted assemblage as constituting the family Adapidae. Many of the distinctive characteristics of this family as a whole when contrasted with other Eocene primate taxa must of course be derived from its better-known members alone. Such characters include spatulate and mesially distended upper incisors, molariform upper and lower last premolars, non-caniniform lower canines, stout, anteriorly directed paracristids on M_{1-3} , buccal cingulids on M_{1-3} , presence of high

crests connecting protoconid and metaconid, metastylid at least on M_1 , and expansion of the hypocone region, at least on M_{1-2} . If all of these characters prove with further knowledge to unite all the genera listed above as a clade and to separate them from all other Eocene primates, then we may consider the following as additional apomorphies of the group: upper molars bounded at least in part by cingulae; upper molar buccal cusps somewhat compressed and bearing distinct cristae on all sides, with pillars buccally; and symphyseal fusion.

AFFINITIES OF ADAPIDAE WITH EXTANT PRIMATES

Adapidae has in a broad sense long been considered to be "close to" the ancestry of the living "lower primates." Gregory (1920) specifically pointed to similarities between *Adapis* and *Lepilemur*, and concluded that the former was the ancestor of the lemurs as a whole, among which he regarded *Lepilemur* as the most primitive. Gingerich (1975) found a closer comparison between *Adapis* and *Hapalemur*, and argued similarly for an adapid derivation of the modern lemurs. Schwartz and Tattersall (1979) argued that the morphologies of *Lepilemur* and *Hapalemur* are in fact derived, and that similarities with *Adapis* and other Eocene taxa indicate a nesting of the fossil forms within Strepsirhini, rather than their placement at the origin of the clade. In this section, we re-examine the potential relationships between the adapids (as restricted here) and the modern lemurs. Necessarily, our comparisons are largely between the extant forms and the best-known adapids, *Adapis parisiensis* and *Leptadapis magnus*.

Whereas previous comparisons between adapids and modern lemurs have invariably involved members of the families Lemuridae and Lepilemuridae, the detailed scrutiny to which we have subjected all living strepsirhines in the earlier part of this contribution has led us to a radically different comparison, but one that we find much more satisfactory. In previous studies we experienced difficulty in determining the phylogenetic position of the indriids—so different in gestalt from the

"exemplar" lemur taxa—among the lower primates. As a clade, this family is highly autapomorphic among the living lemurs; but a broader base of comparison, extended to embrace the primates of the Eocene, reveals that a significant number of these apparent autapomorphies is in fact shared with another taxon: namely, Adapidae *sensu stricto*.

Such shared characters include deep faces and deep mandibles with expanded gonial regions and digastric attachment areas (fig. 38); low-crowned, spatulate and mesially distended upper incisors; quadrangular M^{1-2} , with expanded hypocone regions and compressed buccal cusps that bear distinct cristae and buccal pillars; and stout paracristids, somewhat truncated trigonids, and compressed and posteriorly distended metacoenids. Further, we might at this point add one particularly significant observation: if the affinities of *Adapis* and *Leptadapis* do indeed lie with the indriids, the peculiar conformation of the "lower canine" of these forms is quite easily explained. The morphology of this tooth, especially when corrected for the rotation of its anterior surface, compares far better with that of the anterior lower premolar of the smaller indriids than it does with the classic "caniniform" pattern. Like the premolariform tooth posterior to it, the adapid "lower canine" is notably characterized by an excavated talonid basin bounded by distinct crests buccally and lingually. This is especially true of the two lower premolars of the extant indriids also. Similarly, the upper middle premolars of *Adapis* and *Leptadapis* have very distinct crests delineating a talon basin in a way that recalls the two upper premolars of extant indriids. We might also note that, if the "lower canine" of the adapids is indeed homologous with the "caniniform" lower premolar of the indriids, then there are four teeth, rather than six, anterior to the front premolars in both adapids and indriids, which would furnish yet another synapomorphy binding the two families. As an aside, we might suggest that recognition of this homology, if substantiated, might lead to a rather entertaining argument that runs as follows: if all lateral teeth of the strepsirhine toothcomb are homologous, if the lateral teeth of the indriid toothcomb are homologous with the lateral anterior teeth of the adapids, and

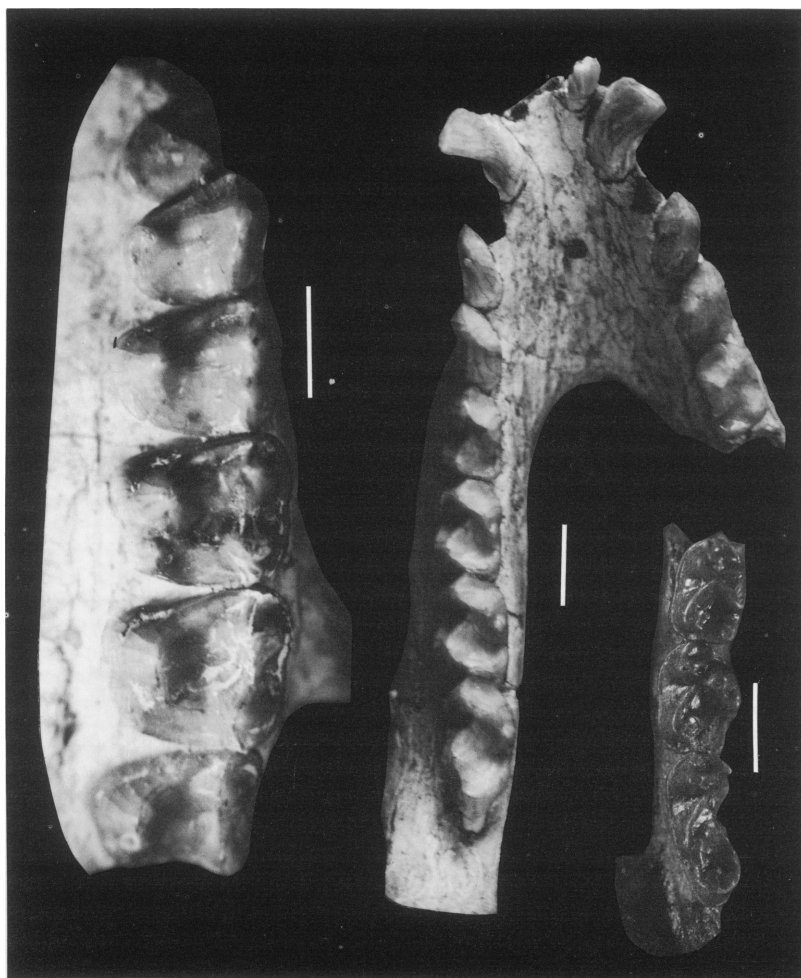


FIG. 37. Upper (left, MNHN QU 10893) and lower (center, NMB QD 13) dentitions of *Leptadapis magnus*; lower molars of *Leptadapis stintoni* (BMNH 3215 a). All scales represent 5 mm.

if those lateral teeth are incisors, then the lateral teeth of all strepsirhine toothcombs must be incisors—even where the toothcomb consists of three teeth bilaterally (as suggested by E. Geoffroy as long ago as 1812!). Should this argument perchance prove to be correct, the entire major clade represented at the basal Node 6 in figure 34 would be united by an apomorphic loss of the lower canine tooth.

If the first molariform tooth of the extant indriids is compared to the last deciduous premolar of both *Leptadapis* and *Adapis* (fig. 39), it is possible to find even finer points of similarity than those elaborated above between the dentitions of adapids and indriids.

In the upper jaw each of these teeth shows a protocone fold that becomes confluent with a postcingulum enclosing an expanded talon basin. There is also in both a similar emphasis of the precingulum which sweeps widely around the paracone and forms a distinct parastylar shelf. These features are seen to a less pronounced degree in M^1 of the fossil forms, from which it may be concluded that the M^1 of indriids is homologous with the last deciduous upper premolar of *Adapis* and *Leptadapis*.

A similar comparison is also evident in the lower dentition (fig. 39). In extant indriids M_1 is characterized by the expansiveness of

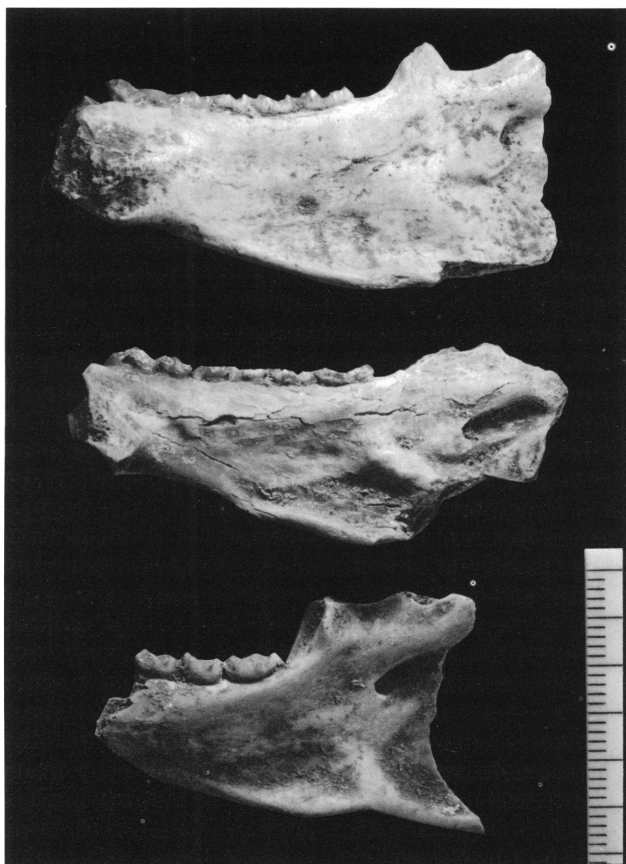


FIG. 38. Internal views of three dentaries of *Adapis parisiensis*. Descending from top: Leuven PLV 48, PLV 51, PLV 38. Scale graduated in mm.

the trigonid, whereas the posterior molars both have greatly reduced trigonids. In *Adapis*, e.g., BNM QD 54 and QW 1601, the last deciduous lower premolar resembles M_1 of indriids. M_{1-2} of *Adapis* and *Leptadapis*, on the other hand, are more comparable, especially in trigonid configuration, to M_{2-3} of the extant indriids. Indriids are distinctive in their lower molars in emphasizing the metaconid on M_{2-3} , but this feature is seen to a lesser extent in the molars of *Adapis* and *Leptadapis*. The two groups are further similar in having a tiny and medially positioned paraconid and in the strong posterior crest of the metaconid. This is most marked in the last deciduous lower premolar of the fossil forms and in M_1 of the extant taxa, which displays a cristid obliqua terminating at the base of the metaconid. Other similarities between the

last deciduous lower premolar of *Adapis* and *Leptadapis* and the lower molars of the extant taxa lie in the common possession of a distinct and deep lingual notch between the metaconid and entoconid. The extant forms are more derived than the fossils in their de-emphasis of the protoconids, especially M_{2-3} , and in the reduction of the premolar complements of both jaws.

Lepilemur bears strong resemblances to the indriids and *Adapis* and *Leptadapis* in the posterior excavation of its premolars, especially the lowers; in the de-emphasis of molar transverseness and the emphasis of length; in the lateral compression of the molar cusps and the accentuation of shearing crests; and in the medial orientation of the strong paracristid of the lower molars. In this last feature *Lepilemur* appears to be more derived than

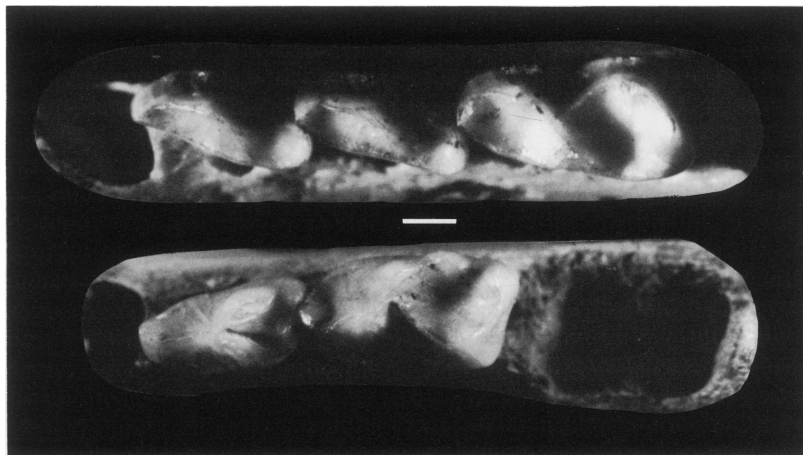


FIG. 39. Partial deciduous lower dentitions of *Adapis parisiensis*, BNM QE 1601 (above) and BNM QD 54. Scale is 1 mm.

the other taxa to the extent that the open and expansive trigonid seen in the last deciduous lower molar of *Adapis* and *Leptadapis* and in M_1 of the indriids is expressed in this form throughout the lower molar series. In the upper molars *Lepilemur* lacks any talon expansion but instead shows continuous thickened lingual cingulae. The cusp that appears in the lower molars to be the entoconid may in fact be no more than a metastylid placed on a posterior extension of the metaconid. The posterolingual opening on M_{1-2} of *Lepilemur* is located between this stylid and the strong hypocristid, and the entoconid has probably been lost.

OTHER RELATIONSHIPS

If, then, Adapidae (in our restricted sense) seems to bear some specific relationship to the indriids among the extant lemurs, can any similar relationships be discerned between other living strepsirhines and those fossil forms that we have excluded from Adapidae? We believe so. Some of the synapomorphies which bind together the lorisid + galagid + cheirogaleid clade are also to be found in certain of the Eocene primates of Europe. Notable among such characters are the lack of a paraconid on the lower molars, the possession of a paracristid that runs down the face of the protoconid to kink sharply toward the metaconid, compressed talonid basins, and the hypocone most distinct on M^1 . These

characters are found in all taxa subsumed by Node 2 in our cladogram, and are also possessed by certain European Eocene forms, including *Anchomomys gaillardi* and *Periconodon helveticus* (uppers and referred lower teeth, contra Tattersall and Schwartz, 1983a: see below).

At an early stage of our analysis of the extant strepsirhines it became apparent that the lorisid + galagid + cheirogaleid clade was also united by the possession of a prehycocone crista on M^{1-2} . Among putative fossil relatives this character is also present in the "adapids" *Anchomomys gaillardi*, *Periconodon helveticus*, *Huerzeleris quercyi*, and "*Adapis*" *minimus* from the Geiseltal. However, it is also present in *Tarsius* and in certain fossil "tarsioids" (see Schwartz, in press a), among them *Omomys* and *Hemiacodon*. In addition to the prehycocone crista, this larger assemblage is also united dentally by the steep wall facing the talonid basin formed by the lower molar protoconids and metaconids, and by an angular, buccally projecting hypoconid. In a recent contribution (Tattersall and Schwartz, 1983a) we have suggested that *Periconodon helveticus* bears omomyid affinities rather than the "adapid" ones that have been generally assumed in recent years. This conclusion was based largely on the configuration of the upper molar trigon, notably the disposition of the pre- and postproto-cristae and on the long lingual slope of the protocone; and the upper molars of this form



FIG. 40. Comparison of upper dentitions of *Huerzeleris quercyi* (type, BNM QH 470) and *Phaner furcifer* (AMNH 100829). Each scale represents 1 mm.

also bear prehypocone cristae. It now seems, however, that this constellation of characters of the upper molar teeth may not help to resolve the affinities of *P. helveticus* beyond its membership in a more inclusive clade that embraces the “tarsioids” as well as the lorioids. But whereas we were formerly reluctant to accept as *Periconodon* the referred lower teeth from the middle Eocene Alsatian site of Buxwiller because they lack the paraconid typical of omomyid lower molars (especially M_1), we may conclude from this new perspective that the lack of the paraconid in these teeth, the course of the paracristid down the protoconid and sharply across to the metaconid, and the compression of the trigonid, are all characters that indicate affinity with the lorisoid clade.

Elsewhere (Schwartz and Tattersall, 1983) we have detailed the more specific similarities of *Anchomomys gaillardi* to *Microcebus* and *Mirza*, and of *Huerzeleris* to *Phaner* (fig. 40). We might add here the possibility that “*Adapis*” *minimus* shows potential galagid affinities. The type and only specimen of this species consists of a left maxillary fragment with one complete molar and the lingual moiety of the tooth anterior to it that appears to have been molariform but not identical to the molar. The hypocone of this broken tooth is distinct and distolingually projecting, and

the protocone is somewhat buccally and anteriorly displaced. The “molariform” upper last premolar of the galagids is similarly conformed and distinct from the first molar. Also as in galagids, the putative molariform upper premolar of the fossil bears a long prehypocone crista. On the basis of these premolar characters it is at least possible to suggest an affinity between “*Adapis*” *minimus* and the extant galagids.

STREPSIRHINI OR PROSIMII?

We have chosen not to treat the fossil forms we discuss here in precisely the same manner as the living ones simply because we do not have comparable amounts of information on the two groups: the fossil genera are in most cases known from less than complete dentitions, and cranial and postcranial data are almost invariably lacking. For example, the only two apomorphies that unite the entire clade at Node 6 in figure 34 are the possession of the “toilet claw” on the second pedal digit, and the presence of the toothcomb in the lower dentition. Only one known Eocene fossil specimen convincingly possesses the former character: the rear half of an “adapid” specimen described by von Koenigswald (1979) from the Messel. Unfortunately, this specimen lacks any other diagnostic charac-

ters that might indicate its affinities within Strepsirhini. Further, in the fossil record strepsirhine toothcombs are known only in Miocene lorisoids that bear close relationships to existing genera. But although it is in this case necessary to assume that the anterior lower teeth of *Adapis* must have been foreshortened considerably from the primitive condition (see Schwartz and Tattersall, 1979), it seems reasonable to conclude that the various apomorphies shared between the fossil and living forms we have discussed do warrant at least the consideration of certain broad relationships. Because of the dearth of information currently available, however, we have not attempted to incorporate fossil forms into our cladogram.

We should note at this point that the suggestion we have made that *Tarsius* and the fossil "tarsioids" might conceivably nest *within* the clade we have been referring to as Strepsirhini does not violate the characters used to define Node 6 on the cladogram. *Tarsius* does indeed possess a toilet claw on the second pedal digit (as also on the third, but this would seem to be an additionally derived character); and although *Tarsius* fails to display a toothcomb, it also apparently lacks the entire set of teeth that would comprise it (Schwartz, 1983). We do not know whether or not any fossil "tarsioid" possessed a grooming claw; but recent interpretations of the anterior lower dentition in some of these forms (Schmid, 1983; Schwartz, in press a), both in terms of their morphology and of their wear patterns, have led to the conclusion that they did indeed possess toothcombs, albeit comprising only two teeth. In the light of this it certainly seems reasonable at least to enquire whether the dental apo-

morphies of *Tarsius* and the fossil "tarsioids," namely the possession of a prehypocone crista, the buccally distended hypoconid, and the protoconid-metaconid wall, might indicate the nesting of these taxa within the clade characterized in figure 34. It has lately been fashionable to emphasize the differences from the taxa represented in figure 34 of the highly autapomorphic *Tarsius* (a form sometimes referred to, albeit less frequently than *Daubentonia*, as "aberrant"); but it remains true that for many years it was standard practice to associate *Tarsius* with these forms in the suborder Prosimii in contradistinction to the catarrhine and platyrrhine "higher primates," as, in some quarters, it still is.

Perhaps, then, it may after all be Prosimii, rather than Strepsirhini, that has reality as a monophyletic grouping. And if it is, Prosimii now has ancestral characters to define it that were not available before: the toilet claw and the toothcomb. However, a Prosimii thus constituted would still exclude many of the fossil primates that it was formerly thought to contain, for example, *Pelycodus*, *Notharcus*, *Smilodectes*, *Copelemur*, *Cercamonius*, and of course the plesiadapiforms. Our study of the North American "adapid" forms of the Eocene is still incomplete, but they may well prove to be the sister of the clade represented by figure 34, the whole assemblage perhaps defined basally by the possession of a *Lemur*-type auditory bulla (apomorphically lost in some forms). And while on the basis of the rather slender evidence available at present we hesitate to suggest a wholesale revision of the systematics of the fossil and living lower primates, it does seem that this may ultimately be found to be necessary.

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