

CRANIAL ANATOMY OF THE
ARCHAEOLEMURINAE
(LEMUROIDEA, PRIMATES)

IAN TATTERSALL

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ABSTRACT

UNTIL RELATIVELY RECENTLY about 16 lemuroid genera existed on Madagascar; due to the intervention of man, only 10 of these survive today. Sites of recovery of subfossil lemuroids are widely distributed over the island; available C¹⁴ dates range from 2850 to 980 years B.P.

The extinct indriid subfamily Archaeolemurinae contains three species: *Archaeolemur majori*, *A. edwardsi*, and *Hadropithecus stenognathus*. This group of prosimians was studied with three objectives in view: to determine to what extent they were, as has been claimed, "advanced" relative to other prosimians; to elucidate their dietary preferences and adaptations; and to explain, as far as possible, their cranial architecture in functional terms.

The present study indicates that the archaeolemurines were not advanced over the general indriid condition in their neural or peripheral sensory organization; a typical prosimian pattern is retained in the brain and in the visual, olfactory, and auditory systems. For instance, it is virtually certain that the archaeolemurines possessed all the external attributes of the prosimian olfactory apparatus, including labial vibrissae, a naked, tethered rhinarium, and a naked philtrum. It is also likely that their eyes retained afoveate retinas. These animals most closely approached the Old World higher primates in their masticatory apparatus, but analysis shows this resem-

blance to have been entirely superficial, albeit probably related to the action of similar selective pressures.

Cranial structure in the archaeolemurines was largely governed by the masticatory system, which was very strongly developed, particularly in *A. edwardsi* and *Hadropithecus*, but which was at the same time designed to eliminate the occurrence of stresses at the temporomandibular joint during mastication. In elevation of the jaw this was accomplished essentially through the action of the posterior temporalis and the masseter-internal pterygoid muscles as a couple acting around the mandibular insertion of the sphenomandibular ligament, while during lateral movement a similar result was achieved by the geometry of a system relying chiefly on the action of the contralateral posterior temporalis. The resultant occlusal forces at the dentition were absorbed through a pyramidal facial structure ideally designed to perform such a function.

The adaptations of the crania, and especially the dentitions, of the archaeolemurines indicate that these animals represent a radiation closely paralleling that of the large terrestrial African monkeys. *Archaeolemur* appears to have been a browser similar to the common baboon *Papio*, whereas *Hadropithecus* represents a highly specialized grazer reminiscent of the gelada baboon, *Theropithecus*.

INTRODUCTION

ISOLATED ON THE ISLAND OF MADAGASCAR for upward of 40 million years, the lemuroid primates have undergone a wide adaptive radiation. The modern Malagasy prosimian fauna gives a distorted picture of the extent of this adaptive radiation since, during the last thousand years or so, many genera have become extinct. Of these extinct forms the Archaeolemurinae, in particular, has been regarded as greatly advanced relative to the extant groups. The present study was undertaken primarily to determine to what extent the archaeolemurine lemuroids *Archaeolemur* and *Hadropithecus* may, in fact, be regarded as "advanced," to elucidate their ecological relationships, and to explain their cranial architecture, as far as possible, in functional terms.

It is, however, quite evident that any attempt at a comprehensive functional analysis of an

extinct mammal is, given the present paucity of relevant knowledge of living forms, impossible. Only the most preliminary approach to the functional cranial anatomy of the archaeolemurines is therefore presented here; more thorough treatments must await the requisite experimental evidence that studies of living primates will, hopefully, provide in the future.

METHODS

The only method employed herein that may require separate explanation is that of Trend Surface Analysis (p. 100). The basic concept involved in the production of deformation grids by trend surface analysis is the comparison of changes in shape between two or more specimens. A number of homologous points on the specimens are identified. When a rectangular

cartesian coordinate system is superimposed on a two-dimensional image of the specimens, coordinates on the X and Y axes can be given each of the points. If X_{ha} is the X coordinate of point h on specimen a, and X_{hb} is the coordinate of the same point on specimen b, then $Z_{Xh} = X_{ha} - X_{hb}$ is the displacement of point h on the X axis when a is compared with b. If Z_{Xh} is calculated for all homologous points a polynomial can be derived which will express Z_{Xh} in terms of X_{ha} and Y_{ha} . The result is a polynomial which expresses the amount of displacement on the X axis of the homologous points of specimen a required to position the points as they occur on the X axis of specimen b. If the same process is performed calculating $Z_{Yh} = Y_{ha} - Y_{hb}$, a second polynomial is calculated expressing the displacement on the Y axis of the points on specimen a.

The ability of the polynomial to express the displacement of any given homologous point is a function of the power of the polynomial and the number of homologous points used. The concepts involved can best be understood if the system is viewed as a topographical model with the horizontal position of a point being determined by its values X_{ha} and Y_{ha} , and its vertical position by the value Z_{Xh} . If the number of points is three, a polynomial of power one ($Z_{Xh} = a_1 + a_2 X_{ha} + a_3 Y_{ha}$, where a_1 — a_3 are the calculated coefficients) can fit a flat plane to the three points exactly. If the number of points is increased to four, an additional complexity may be introduced in the topographical contour of the model. If the power of the polynomial is not increased, the polynomial must fit the four points as well as it can. If the power of the polynomial is increased, however, it is possible to describe the additional complexity exactly. The number of points that can be fitted exactly by a polynomial is equal to the number of calculated polynomial coefficients.

The formation of transformation grids is accomplished by superimposing a cartesian coordinate system on the image of the specimen which was used in calculating the polynomials in X and Y. This figure now becomes the model on which the deformations are based. The intersection of the X and Y coordinate points of the grid lines are fed into the polynomial that describes the trend in X to determine the position on the X axis of the point if it were on figure b. The process is repeated using the poly-

nomial for the trend in Y to determine the new Y coordinate. When these new intersection positions are plotted and joined by lines, the deformed grid represents the deformation (displacement of points) which figure b has undergone when compared with figure a.

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ABBREVIATIONS

The following abbreviations are used in the text for names of institutions:

AM, Académie Malgache, Tananarive

AMNH, the American Museum of Natural History,

New York, Department of Vertebrate Paleontology

BM, British Museum (Natural History), London

VNHM, Naturhistorisches Museum, Vienna

ORIGIN, ISOLATION, AND EXTINCTION OF THE SUBFOSSIL MALAGASY LEMUROIDS

IT IS GENERALLY RECOGNIZED that the Malagasy lemuroids are descended from a group, or groups, of early Tertiary African prosimians, possibly related to the Holarctic family Adapidae. If, as is beginning to seem likely, Lemuriformes as at present constituted is not a monophyletic grouping, a fundamental division exists between the Cheirogaleinae and the other lemurs; the cheirogaleines possess a number of characteristics not shared with the other Malagasy forms, for instance orbital exposure of the os planum of the ethmoid (Clark, 1959), and penetration of the basicranium by the internal carotid artery anterointernal to the bulla (e.g. Gregory, 1915), although their aural structure is otherwise of the lemuriform type. Moreover, Charles-Dominique and Martin (1970) have demonstrated the close similarity in social behavior between *Microcebus murinus* E. Geoffroy and *Galago demidovii* Fischer. Cartmill (1972) has suggested that the cheirogaleines represent a very early type in the adaptive history of the primates; the existence by the early Eocene of adapids which relatively closely resemble the lemurines, particularly *Lepilemur* I. Geoffroy, suggests that, if this is indeed the case, the cheirogaleines and lemurines could not be descended from a common ancestor peculiar to Madagascar. It also appears possible that the lemurine and indriid prosimians may be descended from stocks which split before the arrival of the ancestral indriids and lemurines on Madagascar.

Unfortunately, primates are unknown in Africa prior to the Oligocene of the Egyptian Fayum. The Fayum primate fauna, however, includes no prosimians, the earliest African members of this suborder having been found in East African deposits of Miocene age. These latter show close affinities to the modern African lorises (MacInnes, 1943; Simpson, 1967). In the absence of direct paleontological evidence it is necessary to rely on comparative osteological evidence in deciding between a monophyletic, diphyletic, or polyphyletic origin of the Malagasy primates, and this evidence, although suggestive, is not conclusive. It is intended to undertake a detailed examination of this problem elsewhere; provisionally, therefore,

the conventional taxonomy of the Malagasy prosimians is retained in the lists on pp. 98–100, with the realization that the scheme may soon require drastic modification.

Few authorities would now disagree that the island of Madagascar was derived from continental Africa through the process of continental drift; the structural integrity of the two land masses leaves no doubt of this. Opinions differ, however, as to precisely where the two were adjoined. Thus Du Toit (1957) believed that Madagascar broke away from the mainland in the area now occupied by the Miocene islands of Zanzibar and Pemba, whereas Walker (ms) preferred an alternative location off the coast of Mozambique. Numerous lines of evidence suggest that the former location is the correct one, the island having drifted south and east relative to the mainland, rather than almost due east. Active drifting appears to have been in progress from the Late Cretaceous, i.e. from about the time of origin of the primate order, until the end of the Eocene. A southeasterly direction of drift would have involved the close proximity of the two land masses for a much greater length of time, assuming a constant rate of drift, than would movement toward the east, although any colonization of the island from the mainland by primates which would have made plausible ancestors of the modern Malagasy prosimian fauna would necessarily have been via a "sweepstakes" route, probably rafting. Multiple invasion of the island at different times during the early Tertiary is therefore not more improbable than a single invasion by primates during that time, although post-Eocene colonization seems unlikely.

In isolation, the Malagasy lemuroids underwent a wide adaptive radiation, involving until recently about 16 genera, of which only 10 presently survive. Much has been written in attempts to explain this large-scale extinction, and most contributions espouse one or the other of two major theories of lemuroid extinction: climatic change, and the agency of man. The former theory has generally emerged from studies of the subfossil faunas from the dry south and southwest of the island (e.g. Lamberton,

1934; Mahé and Sourdat, In press); these authors, noting that most of the deposits represent the remains of ancient, now-dry lakes, believed that the lemurs died out as a result of the gradual aridification of these areas of Madagascar. However, these lakes are now dry because of changes in local drainage patterns since the time of deposition of their fossiliferous sediments. As there is no evidence of any dramatic change in the rainfall regime of Madagascar in the recent past, it seems most plausible to attribute the recutting of water-courses and other modifications of the drainage patterns largely to the increased runoff of ground-water from the interior of the island resultant upon its deforestation, which was (and is), plainly effected by human intervention.

The argument of climatic change therefore indirectly implicates man in the lemuroid extinctions. There is, however, much more direct evidence that man was the agent responsible for such extinctions. This evidence has most recently been reviewed by Battistini and Vérin (1967) and Walker (1967). Battistini and Vérin have noted reports of pottery and other evidences of human presence contemporaneous with subfossil lemurs at Ampasambazimba and other sites, and that native folklore includes tales of animals that cannot be identified with any extant Malagasy mammals.

Walker (1967) has more thoroughly investigated the agency of man in the destruction of the Malagasy fauna. He noted archeological evidence of the contemporaneity of man and the subfossils at the sites of Taolambiby and Andrahomana, and reported that the latter locality has yielded subfossil bones bearing traces of cutting and burning; one *Archaeolemur*

majori cranium (BM M7374), in particular, shows a depressed fracture of the frontal bone which could only have been caused by a blow from an axe or a similar implement. Further, Walker has noted that all the subfossil forms are relatively to extremely large compared with extant lemurs, and has suggested that they were all diurnal (except, presumably, *Daubentonia robusta* Lambertson, whose cranium is not known) on the basis of the size of their orbits. In addition, whereas all extant lemurs are more or less arboreal, the archaeolemurines were terrestrially adapted. Thus we find that large, diurnal forms, those presumably most vulnerable to human predation, are extinct, whereas the smaller, more agile forms have survived. The only extant lemuroid which rivals the smallest subfossil species in size is *Indri*, now relatively rare, and protected from man in its remaining areas of occurrence by native *fady*, or taboos.

The intervention of man, then, both as a deforester and as a predator, provides the only plausible mechanism for selective extinction of the type seen among the Malagasy fauna. The time of arrival of man in Madagascar is not known, but is unlikely to have been earlier than 1000 or 1500 B.P. at most. The most recent absolute date on a subfossil-bearing deposit is 1000 years, for Itampolo. Presumably some or all of the subfossil lemuroid genera survived until much more recently than this, just possibly beyond the time of first European contact with Madagascar. Tragically, this extinction appears to be an ongoing process, and continued deforestation of the island threatens the disappearance in the near future of a unique and remarkable fauna.

SUBFOSSIL SITES OF MADAGASCAR

DESPITE THE relatively large numbers of subfossil lemurs which have been recovered during the past three-quarters of a century, the sites from which they have come are all small, isolated deposits of recent date that cannot be stratigraphically correlated, and which lie within modern, active, drainage systems (Walker, ms). Mahé (1965) has classified these sites into three categories: (1) Marshes in volcanic areas (e.g. Morarano and Ampasambazimba). (2) Coastal marshes (on the southwest coast, e.g. Bevoha, Itampolo). (3) Caves (in the cliffs near Fort-Dauphin: Andrahomana).

Unfortunately collectors, in particular the early ones, were far more interested in the fossils than in the sites from which they came, and in most cases little information as to the nature of the latter can be gleaned from the literature. Recent surveys have been made of some sites (Walker, ms; Raison and Vérin, 1968; Mahé and Sourdat, In press), and it is hoped that further work will enlarge this new knowledge.

The following section provides descriptions, where information is available, of the sites which have yielded remains of subfossil lemurs.

AMPARIHINGIDRO: Near Majunga; C¹⁴ dated at 2850 ± 200 years B.P. (Mahé, 1965).

Amparihingidro is the most recently discovered of the subfossil sites, having come to light in 1961 when a farmer accidentally uncovered the first subfossil. Mahé assigned this site to his second category; apparently the bones and sediments accumulated in a closed depression in an Eocene cliff formation (Mahé and Sourdat, In press). In the past the excavation of such sites proved very difficult, as Grandidier (1905) recorded, in the case of Lamboharana: "On est obligé de tâter les ossements immergés soit avec une bêche, soit avec le main ou le pied, selon la profondeur à laquelle ils sont situés sous l'eau et de les retirer un par un, en un mot d'opérer à l'aveuglette" (p. 37). Mahé, however, employed pumps to keep the excavations at Amparihingidro dry, and was able in consequence to collect sedimentary samples suitable for palynological analysis. The results of this analysis are not yet available. The C¹⁴ date quoted above was made on a piece of wood

obtained from the base of the fossiliferous layer, at a depth of 2.2 m.

No complete list is yet available of the fauna recovered at Amparihingidro, but *Archaeolemur* Filhol, *Palaeopropithecus* G. Grandidier, *Lemur* (*Pachylemur*) Lamberton, and *Lemur sensu stricto* Linnaeus are represented.

AMPASAMBAZIMBA: In the province of Miarin-arivo, 1.5 km. southwest of the village of Tsarazaza; longitude 49°25'E, latitude 21°05'S; 1010 m. in altitude (Walker, ms). Ampasambazimba is the only site on which there is any extensive literature (Raybaud, 1902; Jully and Standing, 1904; Grandidier, 1905; Standing, 1907; Fontoynont, "1908" [1909]; Perrier de la Bathie, 1927; Lenoble, 1940; Walker, ms). Both Raybaud and Standing published stratigraphic sections of the site.

Ampasambazimba forms part of the Lake Itasy area, a region abounding in dormant volcanic cones from which radiate extensive lava streams. As Standing described the site:

The fossiliferous marsh [now under cultivation as a rice paddy] itself is roughly circular in form. It is bounded on its semicircular [southern] contour by the River Mazy, the bed of which now lies some five metres below the surface of the marsh. On its other sides it is limited by a stream of lava, the surface of which shows it to be of much more recent date than that traversed by the river in its higher reaches.

A calcareous deposit several metres thick and of great hardness separates the marsh from the river, and it is no doubt to the presence of this broad bank of limestone that the preservation of the fossiliferous deposits is due.

The marsh when trenched presents considerable variety in the sections exposed. Over large areas there are deposits of travertin in varying thickness. This in many parts forms an unbroken sheet which greatly impedes the work of exploration; here and there this sheet is replaced by detached nodules, and over considerable areas the lime-deposits are absent. Mineral springs are abundant, but all are now cold. They are of varying mineral constituents, some being strongly impregnated with iron and many highly charged with carbonic acid. From these springs the deposit of lime is still forming (1908a, p. 63).

Standing also described a section through the deposit [this section agrees closely with that of Raybaud (1902)] thus:

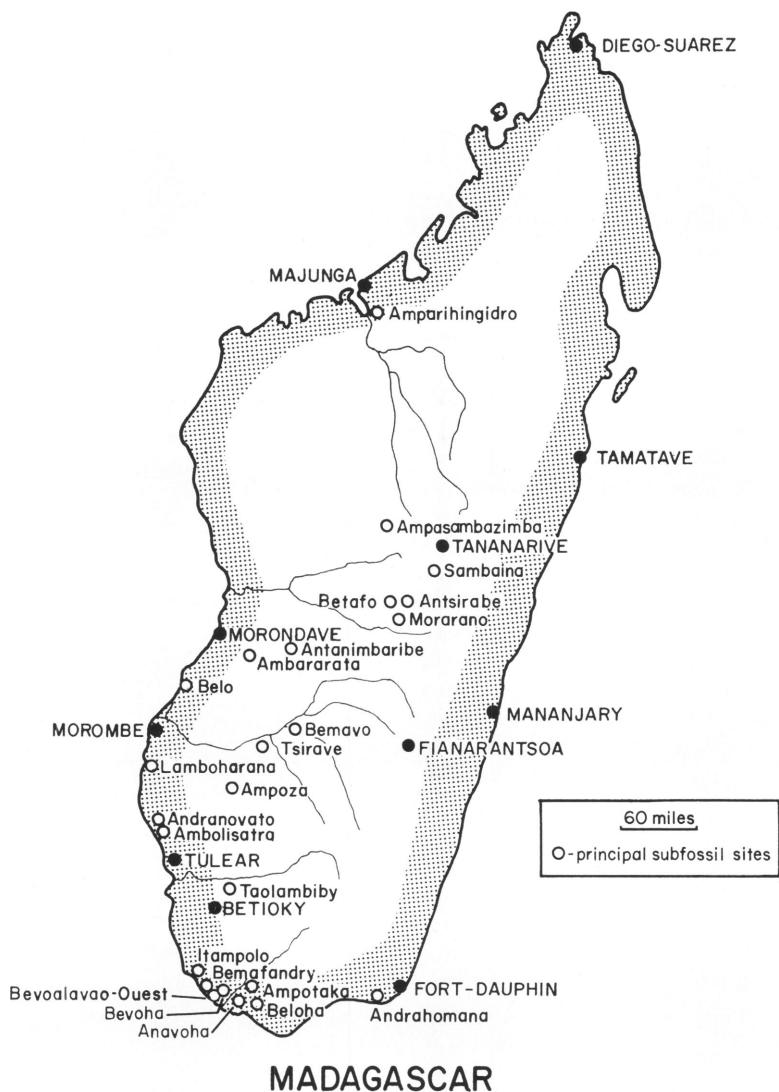


FIG. 1. Subfossil-bearing sites of Madagascar.

To a depth of about 1 metre below the present surface the deposits consist of recent vegetable remains succeeded by a fine black humus which rapidly turns to mud on admixture with water. This is superposed on a stratum of forest debris, consisting of leaves, twigs, seeds, and fruits of numerous species. Below this again a layer of larger branches and tree-trunks is frequently encountered . . . The bones begin to appear in general with this layer of wood, though they are occasionally met with nearer the surface.

In several places the bed of the marsh has been uncovered. It is found to consist of a compact layer of pebbles cemented together by mineral deposits and frequently presenting a metallic sheen. These pebbles

apparently form a nearly horizontal floor about three metres below the present surface.

Primate remains are found at all depths (pp. 63, 65).

Walker (ms) has summarized the lengthy discussion in the literature as to the origin of the deposit as follows:

We can say that the deposit formed in a large lake, probably originally formed by the damming of the Mazy river by lava streams (although the drainage patterns may have altered completely during the period of vulcanicity) and that the pebble bed, the

forest and bone bed and the travertines are successive deposits representing the gradual infilling and drying up of the lake. During this period occasional lava flows, restricted in distribution, may have poured into the area. The final drainage of the marsh was probably due to the breaching of the western lava dam by the Mazy (pp. 433–434).

For a number of reasons, Standing regarded the deposit as of recent origin, suggesting a maximum age for the fossils of 500 years. He concluded that "One may, at any rate from a biological point of view, regard all these sub-fossil Malagasy lemuroids as the contemporaries of extant species in other parts of the island" (p. 71). Walker noted that samples from Ampasambazimba have been submitted for radiocarbon dating, but results are not yet available.

Perrier de la Bathie (1927) analyzed a collection of fruits and seeds made by Lambertson from the peat surrounding the major fossiliferous area at Ampasambazimba. This study led him to the conclusion that "Toutes ces plantes sont des espèces des bois des pentes occidentales, formation qui devait couvrir, avant son déboisement, le massif d'Itasy tout entier et dont on retrouve encore les vestiges aux alentours du lac" (p. 25). It is probable that the word "occidentales" represents a misprint for "orientales"; the fauna from Ampasambazimba, containing *Indri* and *Avahi*, is of eastern aspect, while the Itasy area falls within the eastern floral region as delimited by Battistini and Vérin (1967). None of the plants represented at Ampasambazimba suggested to Perrier de la Bathie that any notable climatic change had taken place "depuis le temps des Aepyornis et des Megaladapis"; the modern flora of the area is entirely a product of deforestation by man.

A list of mammal species from Ampasambazimba follows:

PRIMATES

Archaeoindris fontoynonti Lambertson
Palaeopropithecus ingens G. Grandidier¹
Archaeolemur edwardsi Standing
Hadropithecus stenognathus Lorenz
Megaladapis grandidieri Standing
Mesopropithecus pithecoides Standing
*Lemur (Pachylemur) insignis*² (Standing)

¹*Palaeopropithecus maximus* of other authors; *P. maximus* and *P. ingens* are here regarded as conspecific.

²*Lemur (Pachylemur) jullyi* of other authors; the two "species" are regarded here as conspecific.

Avahi laniger Gmelin
Indri indri Gmelin
Cheirogaleus E. Geoffroy sp.
Propithecus Bennett sp.
Lemur sensu stricto Linnaeus sp.
Hapalemur griseus I. Geoffroy
Lepilemur mustelinus I. Geoffroy

OTHER MAMMALS

Cryptoprocta ferox Bennett
Cryptoprocta spelea G. Grandidier
Galdictis Geoffroy sp.
Pseudailurus edwardsi Filhol
Plesiorycteropus madagascariensis Filhol
Hippopotamus lemerlei A. Grandidier
Centetes Illiger sp.

AMBOLISATRA: Situated on the west coast of Madagascar between Manombo and Tuléar, about 25 km. north of the latter.

Although Ambolisatra has been known since 1865, when Alfred Grandidier found the first remains of extinct Malagasy mammals there, very little is known of this site. Walker, who visited there in 1965, reported (ms) that all that can now be seen of this lagoonal swamp deposit, protected by modern dunes, is a coconut plantation with its drainage ditches. Nevertheless, bone fragments are still to be found in these ditches.

Mammalian remains from Ambolisatra include the following:

PRIMATES

Megaladapis madagascariensis Major
Megaladapis edwardsi G. Grandidier
Palaeopropithecus ingens G. Grandidier
*Lemur (Pachylemur) insignis*³ (Filhol)
Archaeolemur Filhol sp.

OTHER MAMMALS

Hippopotamus lemerlei A. Grandidier
Potamochoerus Gray sp.
Sus Linnaeus sp.

AMPOZA: Approximately longitude 44°35'E, latitude 22°20'S, according to 1:500,000 map (Institut Géographique National, Tananarive, 1963); 620 m. above sea level. Ampoza lies 3 km. north of the village of Ampoza, some 22 km. east of Ankazoabo, on a river variously named the Ampoza or Sakavanaka. Radiocarbon dated at 1910 ± 120 years B.P. (Mahé and Sourdats, In press).

³*Lemur (Pachylemur) jullyi* of other authors.

Ampoza has been worked by Lamberton (1924, 1925), and White (1930) who collected large quantities of subfossil vertebrate material there. It was also visited by Walker (ms), who has provided the most comprehensive existing account of the site, although he noted that detailed geological mapping is still required.

The river flows in a westerly direction, toward its confluence with the Ampanihy River, across a series of sandstone strata that dip gently toward the east, cutting a steplike series of shallow basins across which the river flows in a series of small waterfalls. According to Walker:

The basins seem to represent the bottom of what was once a much larger series of basins for the river itself has been recut through a series of soft sediments up to 2 feet in thickness (but in places considerably thinner). The sediments are rather haphazardly arranged—which may indicate resorting but equally well may represent recutting through several basins. The fossils are found scattered throughout the beds but are to be found in profusion in the thinner, dark humic beds (p. 452).

Walker noted that the large collections of lemuroid remains made there by White give a false impression of the composition of the fauna represented at Ampoza; although several hundredweight of bones of *Crocodilus* Linnaeus, *Hippopotamus* Linnaeus, and *Testudo* Linnaeus were recovered in a single afternoon, no lemuroid remains were found.

The radiocarbon date quoted above was taken on bones found at a depth of 2 m. at the bottom of the fossiliferous beds.

The fauna from Ampoza includes:

PRIMATES

Archaeolemur edwardsi
Megaladapis edwardsi
Megaladapis madagascariensis
Palaeopropithecus ingens
Lemur (Pachylemur) insignis
Propithecus verreauxi

OTHERS

Hippopotamus lemerlei
Aepyornis I. Geoffroy sp.
Mullerornis A. Grandidier and Milne-Edwards sp.
Crocodilus niloticus Laurenti
Testudo grandidieri Vaillant

ANAVOHA: One of the sites in the Lower Menarandra Valley, south of Ampanihy on the boundary between the Préfectures of Tuléar and

Fort-Dauphin; Radiocarbon dated at 1954 ± 110 years B.P. (Mahé and Sourdat, In press).

The sites in the Lower Menarandra Valley have been discussed by Lamberton ("1932" [1933], 1934, 1936a, 1936b), Walker (ms), and Mahé and Sourdat (In press). These sites, presently surrounded by sand dunes, represent the remains of former marshes or lakes which once existed as part of the drainage pattern of the Menarandra River. The fossiliferous beds, which lie, according to Lamberton ("1932" [1933]) on an impermeable sand [stone?], are commonly under 60 cm. in thickness, and consist primarily of a dark brown, sandy marl; they are overlain by beds of marly clay of similar thickness, frequently heavily calcified, which support the modern soil surface. The total sequence is usually about 1.5 m. thick.

Lamberton was mystified by the heavy concentrations of bones of an enormous variety of animals in these deposits; to account for these he suggested that a drying trend had forced the animals of the region to collect around the diminishing water holes now represented by the fossiliferous sites, until finally, with complete aridification, they died out. This is a theme which has recently again been taken up by Mahé and Sourdat. However, as Walker has pointed out, Lamberton's difficulty lay in that he did not recognize a death assemblage, but assumed that the animals in the deposit constituted a representative sample of a living fauna. The bones found by Lamberton were doubtless initially swept together from widely distant parts of the Menarandra drainage pattern.

The radiocarbon date for Anavoha recorded above was determined from a piece of wood recovered at a depth of 77 cm.

The subfossil fauna of the Lower Menarandra Valley includes:

PRIMATES

Megaladapis madagascariensis
Megaladapis edwardsi
Palaeopropithecus ingens
Archaeolemur majori
Hadropithecus stenognathus
Propithecus verreauxi
Lemur (Pachylemur) insignis

OTHER MAMMALS

Hippopotamus sp.
Hypogeomys A. Grandidier sp.
Centetes sp.

ANDRAHOMANA: Cave site situated about 35 km. west-southwest of Fort-Dauphin, on the southern coast of the island. Collections have been made at this spot by Sikora, Allaud, Gaubert, and Guillaume Grandidier; the site was most recently visited by Walker. The only records of the cave site itself have been made by Grandidier (1905) and Walker (ms); the two accounts are very similar.

According to Walker:

The cave is formed by the gouging of a series of sink holes in calcareous Pleistocene sands. These sands are massive and overlie the gneissic basement rocks in a great unconformable sheet.

The cave has two or three small and one large outlet on the seaward side.

The collapse of blocks between adjacent sinkholes has resulted in the roof being open over great areas and the floor beneath littered with enormous blocks weighing many tons. Only in a few places can the original floor be reached (p. 457).

Grandidier estimated the average height of the cave, which at the turn of the century, when collecting was in progress, apparently had but a single large entrance, as about 20 m. In Grandidier's time, as now, the sandy cave floor between the fallen blocks supported a luxurious vegetation.

Human occupation of the cave is indicated by the presence of ashes, and by the fact that many of the subfossil bones bear indications of cutting or burning (Walker, 1967).

Andrahomana has yielded remains of the following:

PRIMATES

Archaeolemur majori
Hadropithecus stenognathus
Megaladapis madagascariensis
Megaladapis edwardsi
Lemur (Pachylemur) insignis
Cheirogaleus sp.

OTHERS

Aepyornis sp.
Centetes sp.
Cryptoprocta ferox
Cryptoprocta spelea
Crocodylus niloticus
Testudo grandidieri

ANDRANOVAO: Site on west coast somewhat north of Ambolisatra; bears same relation to coast as does Ambolisatra (Walker, ms).

ANJEDAVA: Lower Menarandra site; see entry for Anavoha.

ANTANIMBARIBÉ: Site approximately 30 km. west of Tsiroanomandidy, Prefecture of Miarinarivo, on a tributary of the River Manambolo.

ANTASATRY: Lower Menarandra site; see entry for Anavoha.

ANTSIRABÉ: Made famous by the collections of Major, but the site itself is described only by Jullé (1899). Marsh site probably of similar origin to Ampasambazimba, close to the town of Antsirabé about 170 km. south of Tananarive on Route National 7.

BELO-SUR-MER: On the west coast, approximately 70 km. south of Morondava. Described by Grandidier (1905) as a coastal marsh site, similar to Ambolisatra, "comprise entre la bande de sable littoral et des dunes cotières" (p. 36).

BELOHA: Situated slightly to the east of the Lower Menarandra Valley, Beloha is the administrative center of the district. Fossils described as coming from here are probably in fact derived from one or another of the Lower Menarandra sites, most likely Anavoha.

BEMAFANDRY: Lower Menarandra site near the village of Bemafandry to the west of Bevoha; Radiocarbon dated at 1980 ± 90 and 2060 ± 150 years B.P. (Mahé and Sourdats, In press).

Situated in the middle of the vast Sadaona series of sand dunes, close to the coast. The site apparently formed much as did those at Itampolo described by Mahé and Sourdats (In press). The radiocarbon dates given above were made, respectively, on wood found at a depth of 98 cm. (the bottom of the fossiliferous layer) and on a fragment of turtle carapace found "in association" with the wood.

BEMAVO: Approximately 30 km. northeast of Beroroha, at the confluence of the Manamaty and Mangoky rivers. No other information.

BETAFO: Approximately 20 km. west of Antsirabé on Route National 34. Central plateau marsh site.

BEVOALAVAO-OUEST: Dune site slightly to the north and west of the town of Bevoalavao-Ouest, on the Baie de Bevoalavao about 10 km. west of the Menarandra estuary. According to Mahé and Sourdats (In press), Bevoalavao-Ouest consists of two fossiliferous deposits similarly formed, evidently in a manner analogous to Itampolo.

BEVOHA: Lower Menarandra site to west of the river; Radiocarbon dated at 2160 ± 110 years

B.P. (Mahé and Sourdat, In press). The date was obtained on a fragment of turtle carapace recovered at a depth of 148 cm. (the bottom of the fossiliferous layer). Numerous remains of *Megaladapis edwardsi* have been recovered from Bevoha; for faunal list and other information see entry on Anavoha.

ITAMPOLO: Two to 3 km. north of Itampolo village on the southwest coast, a short distance inland from the Baie de Sapaly; Radiocarbon dated at 2290 ± 90 years B.P.; also at 980 ± 200 years B.P. (Mahé and Sourdat, In press).

Itampolo is discussed briefly by Walker (ms) and at greater length by Mahé and Sourdat (In press). According to Walker, the site is a small lake, lined with calcareous sand and apparently permanent, separated from the sea only by a series of sand dunes; fossils are to be found both above and below the present water level.

Mahé and Sourdat described two fossiliferous sites which form part of a series of small, saline, hydromorphic depressions in the dune formations. They provide the following section:

0–60 cm.: a sandy clayey horizon, watery gray in color.

60–90 cm.: a clay-sandy layer quite distinct from that above, brownish in color, with a high organic content. Contains bones.

90–115 cm.: a layer of partly consolidated sand, fragmented into blunt blocks. Cementation is calcareous.

115–125 cm.: a further horizon of organic, fossiliferous sediment.

125 cm. plus: coarse coralligenous sand, white in color.

The radiocarbon dates quoted above were taken respectively from a piece of wood recovered at a depth of 120 cm. (almost the bottom of the lower fossiliferous horizon), and from a hippopotamus bone found at a depth of 15 cm. (well above the top of the upper fossiliferous horizon).

The dominant faunal element of Itampolo is *Hippopotamus*.

LAMBOHARANA: On the west coast about 45 km. south of Morombe, on the Baie des Assassins, near Itampolo; Radiocarbon dated at 1220 ± 80 and 2350 ± 120 years B.P. (Mahé and Sourdat, In press).

Excavated by Grandidier, Lamberton, and White; in origin Lamboharana appears to be similar to Ambolisatra and many other sites, i.e. patches of alluvial deposits behind sand dunes (Walker, ms). Grandidier recorded that bones are discovered at depths of less than 200 cm.,

and complained of the difficulties of working a site where the excavations are immediately invaded by water, and the compact humus surrounding the bones is rapidly turned to mud (see p. 10).

The fauna from Lamboharana includes *Megaladapis edwardsi*, *Archaeolemur*, and *Mesopropithecus*.

The radiocarbon dates quoted above were made respectively on bones recovered at depths of 40 cm. and 60 cm.

MANOMBO: Identified only as "les gisements de la région de Manombo" (Lamberton, "1933" [1934], p. xxiii). Manombo is an administrative center about 50 mi. north of Tuléar on the estuary of the Manombo River. According to Lamberton, the sites consist of dried-up marshes.

Since Lamberton described these sites in common with Taolambiby, it is difficult to tell which of the genera in his faunal list come from which site, or whether the entire fauna is common to both. The list includes:

Megaladapis madagascariensis

Megaladapis edwardsi

Palaeopropithecus ingens

Archaeolemur majori

"Petits lémurien," carnivores and insectivores are rare, as are remains of *Aepyornis* and *Mullerornis*.

MORARANO: Situated near the village of Morarano, about 20 km. due east of Betafo. Central plateau site; marsh deposit in volcanic region, cf. Ampasambazimba. Excavations by Lamberton in 1919 produced remains of *Archaeolemur*, *Megaladapis*, and *Palaeopropithecus* (Lamberton, "1919" [1921]).

SAMBAINA: Central plateau site, about 34 km. north of Antsirabé on Route National 7. Worked by Lamberton from mid-October to mid-November, 1927. According to Lamberton ("1927" [1928]) Sambaina lies on a broad plain in the neighborhood of a mineralized spring. The surface at this point is covered with a layer of travertine. Beneath this lies a sandy clay containing some peat, and lower still, at a depth of 4 m., a sandy layer with no organic content. Bones occur in the peaty sand.

The fossil yield of this site has been disappointing. Hippopotamus bones predominate to the extent that only two other mammals are represented: *Archaeolemur* by two femoral heads, and the large rodent *Hypogeomys* by a humerus.

TAOLAMBIBY: Approximately longitude 44° 30' E, latitude 23° 40' S, 1:500,000 map (Institut de Géographie, Tananarive, 1963); 200 m. above sea level; Radiocarbon dated at 2290 ± 90 years B. P. (Mahé and Sourdat, In press); 20 km. east of Betioky.

Taolambiby has been surveyed by Walker (MS) and by Raison and Vérin (1968), with similar results. According to Walker this site

is a river bank section in part of the Sakamena drainage system, although the Sakamena and most of its tributaries are dry for the greater part of the year.

The fossiliferous beds are a series of travertines and sands, the travertines forming a basin below a periodic waterfall. The surrounding basement rock forming the waterfall is hard Mesozoic sandstone overlying blue clays with thin red marly bands.

The travertines at the base of the fossiliferous section are an indication of a former shallow basin of quiet, lime-rich water below a waterfall (pp. 438, 444).

Walker provided the following section of an area lacking travertine: a variable thickness of modern soil overlies 60 cm. of white and brown sands with alternating leached and humic layers. Below this is 50 cm. of black humic sand overlying 85 cm. of fawn-colored sands. Between this layer and 100 cm. of blue clays which extend to the bottom of the measured section (present water level) is a layer, varying in thickness, of hippopotamus and crocodile bones.

Within the section, the 85 cm. of fawn sands yield bones of *Hippopotamus lemerlei*, *Crocodilus* sp., and *Testudo grandidieri*, but the most highly fossiliferous layer is that which overlies it, the 50 cm. of black humic sands (which in fact forms part of the same sand unit), which has yielded the remains of seven lemuroid genera, fossil and living.

Walker interpreted the sequence as having been laid down in a lake which almost dried up:

The original basin was shallow and became lined with travertine before becoming filled with sediments. The concentration of humic material in the higher beds indicates a change to swampy conditions before increased river action overspilled and downcut the present course through the travertine rim (p. 445).

Fragments of coarse pottery were found in the layer which yielded the lemuroid remains; this

is one of the few definite associations of man with the subfossil forms. Since the arrival of man in Madagascar was comparatively recent, a late date for the site is suggested. The radiocarbon date quoted above, however, is far older than would therefore be expected. Mahé and Sourdat said that the date was obtained from turtle bones recovered at a depth of 190 cm., which is apparently equivalent to somewhere in the fawn sands of Walker's section (where *Testudo* does indeed occur). It seems likely that the dated material antedates the lemuroid remains, then, although by how much remains debatable, as Mahé and Sourdat did not state the exact provenance of their sample, and the rate of deposition is unknown. Walker stated that a sample from the black sands has been submitted for radiocarbon dating; the result of this test should resolve the problem.

The primate fauna of Taolambiby includes:

Archaeolemur majori
Palaeopropithecus ingens
Lemur (Pachylemur) sp.
Lemur (sensu stricto) sp.
Propithecus verreauxi
Lepilemur mustelinus
Cheirogaleus sp.

TSIRAVÉ: Site approximately 20 km. south of Beroroha on a normally dry portion of the Isahena River, shortly before its confluence with the Malio River, a tributary of the Mangoky. Lamberton learned of this important site in 1930, and described it only once, in a verbal presentation to the Académie Malgache in the following year (Lamberton, "1931" [1932]). Unfortunately, although the Comptes Rendus of the Académie Malgache normally contain a full account of such reports, in this case the only mention of this part of Lamberton's presentation is: "Après avoir fait une brève description du gisement, M. Lamberton . . ." ("1931" [1932], p. xxiii).

Crocodile, turtle, and hippopotamus dominate the Tsiravé fauna; the lemurs are represented by *Hadropithecus stenognathus*, *Archaeolemur majori*, *Lemur (Pachylemur) insignis*, *Daubentonia robusta*, and "quelques os des grands lémuriens."

TSIHOMBÉ: Lower Menarandra site. See entry for Anavoha.

HISTORY OF STUDY

GENUS *ARCHAEOLEMUR*

ALTHOUGH THE FIRST SUBFOSSIL LEMUR to be brought to scientific attention was the type specimen of *Megaladapis madagascariensis* (Major, verbal communication to the Royal Society, June 15, 1893, published 1894), the first such specimen to be described in print (Major, 1893) was an incomplete calvaria (BM M4874) of a subadult *Archaeolemur majori* which had been discovered by the collector Last "in a marsh on the southwest coast of Madagascar" (Major, 1893, p. 532). However, although at that time Major clearly recognized its lemuroid affinities, basing his comparison on a skull of *Hapalemur*, he refrained from naming the specimen as "there is some probability that more complete and more adult specimens may before long come to hand" (p. 535). It was therefore left to Filhol (1895) to name the species *A. majori* which he based on the humerus and the proximal portions of a radius and ulna discovered by Grevé at Belo. The name *Archaeolemur majori* bears positional priority in Filhol's paper over *Lophiolemur edwardsi*, a genus and species erected to accommodate "two mandibles and several postcranial bones" (p. 13) collected at the same site as the *Archaeolemur majori* material, and clearly conspecific with it, despite the fact that in this case Filhol noted "only remote resemblances to *Hapalemur*."

In the following year Major (1896) reported on material recovered during his excavations at Antsirabé, consisting of the facial portion of a skull (BM M7075) and a left dentary (BM M7072). On these he based the genus and species *Nesopithecus roberti*, which, largely on the basis of its dental characters and on the (erroneous) supposition that the orbital and temporal fossae had been separated by a bony wall, he interpreted as representing a previously unknown monkey, although naturally enough he felt it necessary to assign the form to a new family of Anthropoidea, Nesopithecidae, "intermediate in some respects between the South American Cebidae and the Old World Cercopithecidae, besides presenting characters of its own" (p. 436).

During a discussion of the endocast of the juvenile calvaria BM M4874, which he had left unnamed four years earlier, Major (1897) ap-

plied the name *Globilemur flacourti* to this specimen. However, in 1899 (Major, 1899a), while describing a new species of *Nesopithecus*, *N. australis*, founded on a virtually complete skull and associated right mandibular ramus (both BM M7374), he remarked that this specimen demonstrated the specific identity of *Globilemur* with *N. roberti*, besides possessing features, such as the form of the auditory bulla, in common with the extant lemurs. At that time Major posed, but left unresolved, the question of whether "*Nesopithecus* is the most highly evolved of Lemuroidea or the lowest of Anthropoidea."

The next contribution followed shortly, when Grandidier (1899b) reported on the results of further investigations at Belo, and described a mandible and fragmentary maxilla as belonging to a new genus, closely related to *Lophiolemur* and *Nesopithecus*, which he named *Bradylemur* because of its robust appearance, and of which he suggested that *Lophiolemur* and *Nesopithecus* might represent ancestral types. The new species, *Bradylemur robustus*, was shortly joined by *Bradylemur bastardi*, based on a partial left maxilla from Ambolisatra (Grandidier, 1900a).

Also in 1900, Lorenz von Liburnau described and figured a new genus and species, *Protoindris globiceps*, based on a photograph of a skull sent him from Andrahomana by the collector Sikora, while Grandidier (1900b) listed seven species of *Archaeolemur*-like primates from Madagascar. Little wonder, then, that in the same year Major (1900) thought it necessary to review current knowledge of subfossil Malagasy primates. Although he did not formally propose synonymies, Major grouped together *Archaeolemur*, *Lophiolemur*, *Nesopithecus*, *Globilemur*, *Bradylemur*, and *Protoindris*, remarking that the last of these had been founded by Lorenz on a photograph of the skull, BM M7374, which Major had already described as the type of *Nesopithecus australis*. At the same time Major also took the opportunity to discuss the broader relationships of this group of fossils, which he identified with his own genus *Nesopithecus*, although he did state that, should they all prove to be congeneric, "the name *Lophiolemur* . . . or rather probably *Archaeolemur*" would have priority (p. 495). *Nesopithecus*, in Major's view, appeared

"to form a side-branch of the evolving line from lemurs to monkeys, branching off close below the Cercopithecidae" (p. 499). It was left to Grandidier (1902) formally to synonymize *Lophiolemur*, *Dinolemur*, *Nesopithecus*, *Globilemur*, and *Protoindris* with *Archaeolemur*, although he retained his *Bradylemur* as a separate genus. Grandidier also reduced the number of species of *Archaeolemur* to two, retaining *N. australis*, *P. globiceps*, and *B. bastardi* in *A. majori*, while, "Quant à la deuxième espèce, qui a été décrite par Filhol sous le nom de *Lophiolemur edwardsi*, elle doit, en réalité, prendre celui d'*Archaeolemur edwardsi* et admettre comme synonyme *Nesopithecus roberti*" (p. 501).

In 1905 the first large-scale monograph on the Malagasy lemurs appeared (Grandidier, 1905). Although at the beginning of this work Grandidier formally synonymized his genus *Bradylemur* with *Archaeolemur*, later in the study it becomes clear that Grandidier intended this synonymy to apply only to the material he had assigned to his species *B. bastardi*, while he retained his belief in the generic distinctness of *B. robustus*. The taxonomic views expressed by Grandidier in 1905, then, remained identical with those he had held three years earlier. As far as the broader systematic position of the Malagasy subfossils was concerned, Grandidier took the opposite stance to Major's: "Il est d'abord hors de doute qu'il faut les ranger parmi les Lémuriens" (pp. 135-136). The features which had led Major to the opinion that *Archaeolemur* might most properly be classified as a monkey were, to Grandidier, "les caractères acquis par une similitude de vie" (p. 136). *Archaeolemur*, *Bradylemur*, and *Hadropithecus* were classified together in the subfamily Archaeolemurinae, distinct only at this taxonomic level from the Indriinae and Lemurinae.

In the same work Grandidier put forward a new zoogeographic scheme to explain both the recent uniqueness of the Malagasy fauna and the similarities borne by it to the Holarctic fauna of the Eocene: "Cet ensemble de caractères communs à des animaux d'âges si différents serait inexplicable si . . . il n'y avait eu des communications entre l'Europe et Madagascar . . . qui seront peut-être établies par l'Afrique" (p. 138). Grandidier replaced the prevailing concept of Madagascar as the remnant of a vast continent stretching to the east almost as far as Australia with the notion that for a short time

during the Tertiary the northwest coast of Madagascar was joined to Africa via an isthmus, of which a remnant is represented by the Cormoro Islands. Grandidier was therefore the first scientist to recognize that the Malagasy prosimian fauna represents an isolated radiation derived from an early Tertiary African primate stock or stocks.

Between 1903 and 1909 Standing (1903, 1904, 1905, 1908a, 1908b, 1909; Jully and Standing, 1904) published several notes on the geology and fauna of the subfossil site of Ampasambazimba, which had been discovered by Raybaud in 1902. Standing's major contribution was that of 1908 (1908a), in which he described all subfossils then known from Ampasambazimba in a comprehensive monograph that contained for the first time a diagnosis of the subfamily Archaeolemurinae, and in which was emphasized the individual variation present in the series of 10 skulls of *Archaeolemur edwardsi* known at that time from Ampasambazimba. Most importantly, this variation revealed that the triangular form of the third molar, which had been considered by Grandidier the chief diagnostic characteristic of the genus *Bradylemur*, in fact fell well within the range of variation shown by this series of *Archaeolemur* skulls. At the same time, however, Standing was sufficiently impressed by the distinctness of one skull (AM 311024) in the collection to base on it the new species *Archaeolemur platyrrhinus*.

In his discussion of the phyletic position of *Archaeolemur*, Standing referred to Grandidier's views on the specialized (i.e. parallel) nature of the "simian" characteristics of *Archaeolemur*, but chose himself an alternative hypothesis, in accord with the interpretations of Major. Standing believed that "there is much more reason for regarding these simian features as general ancestral characters and the condition of the recent genera of Malagasy lemurs as specialized" (1908a, p. 103).

In the conclusion to his memoir, Standing expanded on his reasons for adopting this position. Rejecting, as had Grandidier, the notion of an eastward-extending supercontinent, he adduced faunal and floral evidence to support the hypothesis of a land connection between South America, Africa, and Madagascar, lasting at least to the end of the Mesozoic and probably well into the Tertiary. Although the connection between South America and Africa disappeared

much earlier, Madagascar and Africa were joined possibly as late as the Miocene. On this southern land mass "there is strong presumptive evidence that . . . there was during the Eocene period a race, or races, of Primates which had already acquired most of the distinctive Simian characters" (*op. cit.*, p. 159). The inference was therefore strong that "the race or races of Primates isolated in Madagascar at the time of its severance from the Mainland would already have acquired most of the characteristic features of the 'Anthropoidea'" (*op. cit.*, p. 159). In his descriptions and comparisons Standing discovered that the "affinities" of the subfossil fauna lay primarily with the South American monkeys, but he also noted some characters which accorded most closely with those of catarrhine primates. All these he ascribed to the primitive "Indrisine" condition from which all higher primates sprang.

Continuing this line of argument, Standing compiled a list of "diagnostic" prosimian and higher primate features, and demonstrated the intermediacy shown by *Archaeolemur* (which he classified within the Indriidae) and other subfossil Malagasy primates, making considerable use of the evidence gathered by Major (1901) in a study of the cranial characteristics of a wide variety of prosimians and higher primates, in which *Nesopithecus*, and particularly *N. roberti*, were shown to possess higher primate characteristics in the lacrimal region. On the basis of this, Standing argued, "it seems no longer necessary, or indeed possible, to separate the Primates into the two sub-orders of Lemuroidea and Anthropoidea" (*op. cit.*, p. 162).

Although Standing's misconceptions and the weaknesses inherent in his arguments (to which scant justice has been done here) are readily apparent to the modern reader, Standing's work represented a considerable tour de force for the period, and was highly influential. Gregory, however, was not impressed, and in 1915 wrote of *Archaeolemur* and *Hadropithecus* that "these forms, by reason of their large braincase, forwardly-directed orbits, and macaque-like molar teeth, have given rise to the preposterous hypothesis that they indicate a special affinity between the Indridae and the Anthropoidea" (pp. 440-441). He accepted, however, the affinities of *Archaeolemur* with the Indriinae, and incorporated Standing's classification of *Archaeolemur* within the Indriidae in his own scheme.

Despite the fact that Lamberton, the foremost student of the extinct Malagasy fauna, had been writing on the primates of the island since 1910, study of *Archaeolemur* languished until 1936, when Carleton published the first full-scale study of the postcranial skeletons of the extinct lemurs. Although Carleton's work was primarily descriptive, she did venture an opinion on the locomotor habits of *Archaeolemur*, thus: "every bone of *Archaeolemur* gives evidence of its increased mobility [as compared to *Lemur* (*Pachylemur*)]. One may well suppose that it had begun to experiment with brachiation, but failed to reach the level attained in higher primates" (p. 284). She failed, however, to produce any substantial evidence for this point of view. Carleton assigned some postcranial specimens of *Archaeolemur* in the collections of the British Museum (Natural History) to *Bradylemur* on the grounds that their measurements were closely similar to those reported for *Bradylemur* by Grandidier, although at the same time she remarked that "On the evidence of the limb-bones only, one would be inclined to question the propriety of separating this genus from *Archaeolemur*." She retained the genus *Bradylemur*, however, because "Grandidier's distinction . . . is based on differences in the skulls" (p. 284). This in spite of the fact that Standing, whose work she quoted elsewhere, had long before demonstrated the invalidity of the distinction, and had been followed by such authorities as Gregory (1915) and Abel (1931) in assigning *B. robustus* to *A. edwardsi*.

Despite his voluminous contributions to the study of the extinct Malagasy lemurs, Lamberton never devoted a monographic study to *Archaeolemur* specifically. However, in 1937 ("1937" [1938]) Lamberton figured, without describing, a complete restoration of the skeleton of *A. majori*, and in the same year (1937), in his study of *Hadropithecus*, comprehensively described the skeleton of *Archaeolemur* for comparative purposes. In this latter work, Lamberton suggested that *Archaeolemur* was an arboreal form which had perhaps begun the attempt to brachiate, but had not yet perfected this mode of locomotion. Later Lamberton (1939a), in the course of a discussion of the possible evolutionary relationships of the lemurs, wrote: "Pour les Archaeolemuridae, ils ont dû se détacher du stock ancestral [of quadritubercular dental types] bien avant les *Archaeoindris*" (p. 49), and placed

the time of separation at a point early in the Quaternary. This was the first indication that Lamberton regarded *Archaeolemur* and *Hadropithecus* as together deserving separate familial status. Shortly thereafter (1939b) Lamberton more fully described the osteology of the foot of *Archaeolemur* as then known. He also (1939c) described two crania and a mandible of *Archaeolemur edwardsi* which possessed four molars bilaterally instead of the normal three, and reviewed the literature on supernumerary teeth among primates. Having discovered that while extant prosimians possessing extra teeth normally have them in the form of pre-molars, higher primates are prone to possess supernumerary molars, Lamberton asked: "Faut-il rappeler que, par leurs molaires quadrituberculées, les *Archaeolemurs* se rapprochent des Simiens?" (1939c, p. 154). He also remarked that: "il ne semble pas déraisonnable de penser que l'origine [of fossil lemurs] doit être recherchée très loin dans le passé et il est possible que les ancêtres aient eu 4 molaires" (*op. cit.*, p. 154).

The milk dentition of *Archaeolemur* was described for the first time in 1938, in the course of Lamberton's survey of the milk dentition of the subfossil forms. Besides recording his morphological observations, he presented several conclusions, among which the most interesting is that "la dentition temporaire prend un développement beaucoup plus grand et persiste jusqu'à une taille, et probablement un âge, beaucoup plus considérables que dans les espèces actuelles" (p. 79-80).

In the same year Sera (1938) published his enormous work on the subfossil lemurs, in which he claimed an almost exclusively arboreal habitat for *Archaeolemur edwardsi* and a primarily arboreal, but partly also terrestrial, mode of existence for *A. majori*, despite the fact that he believed the calcaneum and tibia of *Archaeolemur* to demonstrate the impossibility of opposition of the hallux. *Archaeolemur platyrrhinus*, on the other hand, known only from a single cranium, had, although arboreal, only very recently abandoned an aquatic existence. Sera also reinvestigated the problem of the relationships of the subfossil lemurs to higher primates and concluded that the "advanced" features of the subfossils represented characteristics of the beginning of the higher primate radiation. In Sera's view, it was possible to speak of a lemurian phase, followed

by platyrrhine and catarrhine phases, the entire sequence ultimately derivative from an aquatic condition. Later, in an equally enormous contribution, Sera (1950) was to extend his theory of aquatic derivation to almost every known fossil primate, *Archaeolemur* becoming completely aquatic in the process.

In 1941 Lamberton published a study of the ear region among the subfossil lemurs and added a wealth of detail to the knowledge of the structure of this region in *Archaeolemur*, although it had long been known that the bony ear of this genus very closely resembles that of the living Indriinae. Lamberton's conclusions were confirmed by the later studies of Saban (1956, 1963).

Although Major had in 1897 briefly described an endocast of his *Globilemur calvaria*, and Burckhardt (1901) and Smith (1903, 1908) had reviewed currently available knowledge of the brains of the subfossil lemurs, the first full-scale studies of the endocranial cavity of *Archaeolemur* were those of Piveteau (1948, 1950). Piveteau noted the relatively high degree of "cerebralisation" shown by *Archaeolemur*, but ultimately concluded that "les lémuriformes, même les plus évolués comme *Archaeolemur* . . . ne conduisent pas vers les groupes de Primates supérieurs. Ni les Simiens, ni les Anthropomorphes, ni l'homme n'ont traversé, au cours de leur histoire paléontologique, une phase lémurienne" (1948, p. 170). Nevertheless, Clark (1959) was led to conclude that "the brain of *Archaeolemur* has a remarkably pithecoïd appearance, though the resemblances to the brain of a monkey are offset by the poor development of the frontal lobes" (pp. 249-250).

Following Edinger's studies of 1942, Lamberton ("1949" [1952]) published some observations on the relationships between hypophyseal development and body size in a variety of subfossil lemurs. He found that, in the case of *Archaeolemur*, "la fosse pituitaire est nettement creusée . . . mais elle n'est pas aussi grande qu'on aurait pu supposer *a priori*, étant donnée la taille de l'espèce" ("1949" [1952], p. 34), a situation unique among the fossil lemurs. Lamberton's final contribution appeared in 1956 ("1956" [1957]) not long before his death, and consisted of a long, thoroughly documented refutation of Sera's theories. Most of the paper concerns genera other than *Archaeolemur*, particularly *Palaeopropithecus*, which had borne the brunt of Sera's theory building, but, *inter alia*, Lamberton

disposed of Sera's views on the aquatic derivation of *Archaeolemur* and the lack of prehensility in its foot.

The two most recent studies of *Archaeolemur* have both concerned the postcranial anatomy of the genus. The earlier, that of Jouffroy (1963), is primarily directed toward interpretation of the relationships of the animal. Carleton to the contrary, Jouffroy showed that *Archaeolemur* clearly differs from *Lemur* (*Pachylemur*), although "l'Archéolemur porte dans son squelette appendiculaire les caractères essentiels du groupe des Prosimiens" (p. 153).

The other contribution, that of Walker (ms), is, on the other hand, functionally oriented, the section on *Archaeolemur* forming part of a comprehensive survey of locomotion among the subfossil lemurs. Walker clearly established that *Archaeolemur* bears throughout its postcranial skeleton an array of terrestrial characters, and that its nearest locomotor analogues lie among the ground-living cercopithecoid monkeys.

HADROPITHECUS

The initial remains of *Hadropithecus stenognathus* were discovered by the collector Sikora in the cave of Andrahomana. Sikora sent his finds to Lorenz von Liburnau of the Naturhistorisches Museum in Vienna, who in 1899 described a right dentary as the type specimen of the new genus and species. This specimen was neither figured nor identified, but from its description it is evidently VNHM 1934 XV 1/1. Hill (1953) erred in stating that the type specimen is immature. Lorenz was impressed by the resemblance of the (heavily worn) teeth and of the jaw to those of man and apes, concluding provisionally that the material might represent a hitherto unknown Malagasy ape. He also considered that his specimen was female, for the rather obscure reason that "Der Eckzahn ist klein, mit der Spitze wenig über die Backenzähne hervorragend, was, dafür spricht, das der Unterkiefer einem weiblichen Thiere angehört" (1899, p. 256).

Shortly thereafter, Lorenz (1900a) figured and further described this mandible, together with a photograph of the first of only two crania of the genus known (VNHM 1934 IV 1), which, however, he described as the type of a new genus and species, *Pithecodon sikorae*. It was in this publication that Lorenz expressed for the first time his view that *Hadropithecus* was closely

related to *Archaeolemur*. Lorenz's most substantial study of *Hadropithecus* appeared in the next year (Lorenz von Liburnau, 1902), when he reviewed all known material of the genus (for many years to be known only from Andrahomana), synonymized *Pithecodon sikorae* with *Hadropithecus stenognathus*, and described and figured the contents of a further consignment of fossils from Sikora, which included a variety of maxillary and mandibular fragments with both permanent and deciduous dentitions represented. Lorenz also reaffirmed his belief in the proximity of *Hadropithecus* and *Archaeolemur*, and quoted Major's (1900) view that the two genera represented a side branch in the evolutionary progression from lemurs to higher primates, with the comment that present knowledge held nothing to dispute this view. In his paper of 1900 Major had expressed agreement with Lorenz's 1901 opinion as to the close relationship of *Hadropithecus* and *Archaeolemur*, and their dental similarities and differences, although in the latter he was misled in places because, working from illustrations, he was unaware of the heavy wear on the teeth of the *Hadropithecus* specimen under discussion.

Major's conclusion was echoed in 1902 by Grandidier (1902), who stated that "il n'y aucun doute qu'on doit ranger dans le même groupe ces deux genres" (p. 591). In his monograph of 1905 Grandidier exhaustively described the *Hadropithecus* material known at the time, all of it from Andrahomana, and supported his earlier statement with a wealth of detail, but refrained from stating at which taxonomic level the "groupe des *Archaeolemur*" deserved distinction. It was left to Standing (1908a) and later to Gregory (1915) to diagnose the Archaeolemurinae, containing *Archaeolemur* and *Hadropithecus*, as a subfamily of the Indriidae. Gregory was also the first scholar to suggest that *Hadropithecus* was in some way more "advanced" than *Archaeolemur*. Gregory's taxonomic views have received general acceptance, but Abel (1931) disagreed to the extent that he proposed the Hadropithecinae as a separate subfamily within the Indriidae.

The major monograph on *Hadropithecus* is that of Lamberton ("1937" [1938]), in which he reported the discovery of, and described, an almost perfect cranium and a left mandibular corpus, with symphysis, which he had recovered from the site at Tsiravé in 1931, together with a

series of postcranial bones which he assigned likewise to *Hadropithecus stenognathus*. In 1932 Lamberton had discovered, in the Lower Menarandra Valley, a humerus, tibia, and various small mandibular fragments; these he also dealt with in 1937. Lamberton described a variety of differences between the Tsiravé and Andrahomana crania (the latter of which he had never seen except in illustration), not least that of size. He wrote: "On voit que le spécimen de Vienne est notablement plus petit que le notre, mais, peut-être qu'avec l'âge, il aurait pu atteindre à la même taille" (p. 2).

In view of the numerous detailed differences he found between the two skulls, Lamberton considered whether in total they justified specific distinction, but decided that they should be regarded as age changes, or as individual variations, "plutôt que de compliquer la nomenclature avec un nouveau nom spécifique" (p. 4).

Lamberton demonstrated that resemblances to *Archaeolemur* are not confined to the skull of *Hadropithecus*, but are abundant throughout the skeleton. He therefore explicitly rejected Abel's taxonomic recommendations, suggesting that the cranial differences between the two were largely related to diet, and that the genera were about as close as *Palaeopropithecus* to *Archaeoindris*. *Hadropithecus* and *Archaeolemur* were, in Lamberton's opinion, "des rameaux issus d'un tronc commun encore hypothétique et dont le développement s'est longtemps poursuivi côte à côte" (p. 44).

The fresh condition of the bones of *Hadropithecus* from the southern sites suggested to Lamberton that the extinction of this animal was of recent date, and led him to repeat his

earlier speculation ("1931" [1932]) that *Hadropithecus* might have been the subject of the legend of the "Kalanoro," a myth still current among the Bara people of the Ankazoabo region. According to Lamberton: "Aux dires des Bara, les *Kalanoro* sont de petits hommes à longue chevelure qui habiteraient encore les forêts de la région et qui en sorteraient la nuit pour venir dans les villages rôder en quête de nourriture. Ils courent et grimpent avec beaucoup d'agilité" ("1937" [1938], p. 44).

In 1950 Sera posited an aquatic habitat for *Hadropithecus*; six years later Lamberton ("1956" [1957]) disposed of this theory.

Piveteau (1956) was the first scholar to consider the brain of *Hadropithecus*, however briefly. He found the genus to resemble *Archaeolemur* and the *Archaeolemurinae* to differ from all other lemuriformes, in general brain morphology. Saban (1956, 1963) studied in detail the temporal region of *Hadropithecus* and agreed with the findings of Lamberton (1941) on the structure of the ear region, which is of the general lemuriform type and closely similar to that of *Archaeolemur*.

In the course of his survey of locomotion among the subfossil lemurs, Walker (ms) studied the postcranial skeleton of *Hadropithecus* and concluded:

What elements we have of *Hadropithecus* show the same features as *Archaeolemur*, but on the whole the bones are more gracile and elongated. Probably *Hadropithecus* was to *Archaeolemur* as *Erythrocebus* is to *Papio* today; *Hadropithecus* and the patas monkey being more slender, longer-limbed creatures, more terrestrially committed than the coarser, more adaptable *Archaeolemur* and baboon" (p. 317).

SYSTEMATICS

ORDER PRIMATES LINNAEUS, 1758

INFRAORDER LEMURIFORMES GREGORY,
1915

FAMILY INDRIIDAE BURNETT, 1828

SUBFAMILY ARCHAEOLEMURINAE
G. GRANDIDIER, 1905

INCLUDED GENERA: *Archaeolemur* Filhol, 1895;
Hadropithecus Lorenz von Liburnau, 1899.

DISTRIBUTION: Madagascar, Recent.

AMENDED DIAGNOSIS: Extinct indriids of moderate size, distinguished from both the Indriinae and Palaeopropithecinae by the possession of an additional premolar in each jaw, upper and lower. Dental formula thus probably $\begin{smallmatrix} 2.1.3.3. \\ 2.0.3.3. \end{smallmatrix}$. Lower incisors not procumbent. Mandibular symphysis fused and relatively vertical; inferior transverse torus present.

GENUS *ARCHAEOLEMUR* FILHOL, 1895

TYPE SPECIES: *Archaeolemur majori* Filhol, 1895.

AMENDED DIAGNOSIS: Substantially larger than the extant indriines, but close in cranial morphology to *Propithecus*. Premolars laterally compressed, blade-like; molars bilophodont, lacking mesostyle. Upper incisors large, spatulate. Quadrupedal adaptations in postcranial skeleton.

Archaeolemur majori Filhol, 1895

HOLOTYPE: Humerus from Belo, presently unlocated.

AMENDED DIAGNOSIS: Small archaeolemurine, more gracile than *A. edwardsi*; invariably lacks sagittal and nuchal crests. Facial angle somewhat less steep than in *A. edwardsi*. Dentition

morphologically identical to that of *A. edwardsi*, but some 15 percent smaller in mean measurements.

Archaeolemur edwardsi (Filhol, 1895)

HOLOTYPE: "Two lower jaws and several postcranial bones" (Filhol, 1895); no provenance given; presently unlocated.

AMENDED DIAGNOSIS: Some 15 percent larger than *A. majori* in linear dimensions and more robustly built. Sagittal and nuchal cresting invariably present, but to varying degrees. Dentition morphologically indistinguishable from that of *A. majori*, but larger in proportion to overall dimensions. Facial profile relatively steep.

GENUS *HADROPITHECUS*
LORENZ VON LIBURNAU, 1899

TYPE SPECIES: *Hadropithecus stenognathus* Lorenz von Liburnau, 1899.

AMENDED DIAGNOSIS: Monotypic genus; diagnosis as for species *H. stenognathus*.

Hadropithecus stenognathus Lorenz von Liburnau,
1899

HOLOTYPE: VNHM 1934 IV 1/1, right dentary from Andrahomana.

AMENDED DIAGNOSIS: Broadly similar in size to *Archaeolemur edwardsi*, but face much shorter anteroposteriorly, and deeper; neurocranium somewhat more highly situated relative to facial skeleton. Incisors, upper canine, and lower caniniform premolar (P_2) greatly reduced; molars and P_4 greatly expanded, with complex cresting on crowns. Some degree of sagittal and nuchal cresting invariably present, in some cases pronounced.

DISTRIBUTION AND TAXONOMY OF THE ARCHAEOLEMURINAE

IT IS UNFORTUNATE that a lack of records prevents a precise account of the geographical distribution of known archaeolemurine material. The only means of obtaining information on the distributions of *Archaeolemur* and *Hadropithecus* is by consultation of published faunal lists and of the records accompanying the fossils themselves. Both sources are imperfect. Because the vast majority of specimens of *Archaeolemur* consists of fragmentary mandibles and maxillae, which rarely permit accurate specific recognition, many specimens whose provenance is recorded are of no utility in distributional reconstruction. The map in figure 2 is doubtless incomplete even as far as known material is concerned, and not all areas of the island have been sampled.

A fairly clear picture of the distribution of species of *Archaeolemur* emerges from the figure, however, especially if the reported *A. edwardsi* from Ambolisatra has been misidentified and is, in fact, *A. majori*. This is quite possible, as to this writer's knowledge there are no complete

Archaeolemur crania or calvariae known from this site. The single cranium of *Archaeolemur* from Amparihingidro is identified in the Museum of the Académie Malgache as an individual of *A. majori*, but is probably better viewed as *A. edwardsi*. If this identification is correct, Amparihingidro is the only coastal site to have yielded *A. edwardsi*, the species being otherwise confined to the central plateau. *Archaeolemur majori* is found widely in the south and southwest of the island.

Since the advent of man, Madagascar has become largely deforested in consequence of land clearance by burning. At the present time only about 7 percent of the land surface of the island remains covered by aboriginal vegetation. Reconstruction of the prehuman vegetational pattern has hardly been begun, but since the basic climatic pattern appears to persist (Battistini and Vérin, 1967), some broad inferences may be made.

The central plateau sites yielding *Archaeolemur edwardsi* appear to represent humid, densely forested conditions, particularly in light of the observations of Perrier de la Bathie (1927), already cited, on samples of fruits and seeds from Ampasambazimba. Such forests now persist on the western side of the island, but over a drastically reduced area.

The collection areas, or sites of deposition, of the death assemblages of the southwest coast were probably originally covered by deciduous forests which flourished in a drier, more seasonal climate than that of the center, whereas the most southerly sites, such as those of the lower Menarandra, represent even drier conditions, although gallery forests may well have existed along the banks of the Menarandra and other rivers, as they do along parts of the Mandrany today. The belief that aridification in the south caused local extinction of lemurs through the drying-up of lakes and watercourses is probably, as we have seen, without substance.

Thus, if Ambolisatra *Archaeolemur* is indeed *A. majori*, there would appear to be a clear ecological distinction between the two species of *Archaeolemur*, apart from the probable appearance of *A. edwardsi* at Amparihingidro. This



FIG. 2. Distribution of the archaeolemurines.

latter site, however, is far removed geographically, and possibly ecologically, from the other coastal sites.

Hadropithecus stenognathus, on the other hand, apparently occupied almost the full range of ecological settings available to it on the island. If more than one species of this genus actually existed, present material is insufficient to show it, although it should be borne in mind that, given only the evidence of the dentition and of the jaws, it would be difficult to justify the retention of two species of *Archaeolemur*. However, since *Hadropithecus stenognathus* was evidently much more stenotypic than either species of *Archaeolemur*, unrecognized speciation seems less likely.

Because some recent authors continue to recognize Standing's *Archaeolemur* "*platyrrhinus*," it is as well to state here that this specimen is incontrovertibly an individual of *A. edwardsi*; both multivariate statistical and morphological analyses demonstrate unequivocally that this is so.

Sites which have yielded archaeolemurine material include the following:

Hadropithecus stenognathus

Ampasambazimba
Ampoza
Andrahomana
Belo-sur-Mer
lower Menarandra
Tsiravé

Archaeolemur edwardsi

Ampasambazimba
Antsirabé
Morarano
Sambaina

Archaeolemur majori

Ampoza
Andrahomana
Belo-sur-Mer
Bemafanary
Itampolo
Lamboharana
lower Menarandra
Manombo
Taolambiby
Tsiravé

Archaeolemur ?sp.

Ambolisatra
Amparihingidro

MORPHOLOGICAL DESCRIPTION¹

Archaeolemur majori

GENERAL DESCRIPTION OF CRANIUM

COMPARED WITH that of its congener, *A. edwardsi*, the skull of *A. majori* gives above all the impression of lightness and gracility; it resembles most closely, among the crania of extant forms, that of *Propithecus*. In dorsal view the most striking features are the round, almost globular, braincase and the widely bowed zygomatic arches (maximum bizygomatic width [10 specimens] 96.4 mm. against maximum length of 130.6 mm. [mean of 17 individuals]). Postorbital constriction is pronounced (mean width across frontals at postorbital constriction 32.2 mm. [16 individuals]). The orbits are laterally directed by about 20 degrees, and in relation to the plane of the palate are dorsally directed by about the same amount. The frontal and malar bones participate about equally in their formation; there is no postorbital closure. The frontal bone, apart from its orbital processes, is approximately lozenge-shaped, meeting the sagittal suture at about the longitudinal midpoint of the neurocranium; the metopic suture tends to remain clearly distinct until a relatively advanced age. Robust lateral development of the zygomatic process of the temporal plays a major role in the bowing of the zygomatic arcade.

In lateral view, the dorsal profile of the skull is almost perfectly semicircular from the tip of the nasal bones to the occipital angle, the continuous curvature of this outline being interrupted only by a slight depression in the nasals at the level of the lacrimal foramen, which is situated in the orbital margin and which is bounded by the lacrimal posteriorly and by the maxilla anteriorly. In profile the snout beneath the nasals is composed almost entirely of the maxilla, the premaxilla occupying, in this view, only the lateral borders and the anterior tip of the floor of the nasal aperture. Ventrally, however, the suture uniting the premaxilla and maxilla runs posteriorly along the medial border of the canine tooth before progressing to the

midline at the level of the posterior extremity of the large anterior palatine fenestra; this aperture therefore lies virtually entirely within the premaxillary bone, only its most posterior tip being bounded by the maxilla.

Posterior to the premaxilla, the palate is primarily of maxillary formation, the maxillary-palatine suture originating posterior to the last molar and traveling anteriorly parallel to the tooth row as far as the level of the first molar, where it turns medially in a curve paralleling that of the posterior border of the palate. This last is deeply incurved, the palate being fully roofed by bone only anterior to the middle of the first molar. The postpalatine torus is only feebly developed; posterior palatine foramina, which may be single or multiple, are confined to the palatine portion of the palate, and communicate with the orbit, emerging on the internal aspect of the maxilla, close to the inferior margin of the sphenopalatine foramen.

The palatine bone also functions in the formation of the strong hamulus at the head of the deep pterygoid fossa; the medial and lateral pterygoid plates are both of sphenoid origin.

The lateral marginal bar of the orbit is strongly built; although the orbits are well rounded, there is a slight angulation at the frontomalar suture. The malar flares considerably, in consequence of which the angle of the long maxillomalar suture is oriented from its superior extremity inferiorly and posteriorly at about 45 degrees. Infraorbital foramina penetrating from the orbital aspect of the malar to the maxilla are invariably multiple; those entirely malar in formation may be either single or multiple. The posteromedial wall of the orbit is formed dorsally by the parietal and ventrally by the alisphenoid. Medially the orbit is bounded by the frontal, with a small contribution from the orbitosphenoid; anterior to these lies the small lacrimal bone, variable in shape from triangular to rectangular, and bounding the posterior border of the relatively large lacrimal foramen. The floor of the orbital fossa, which occupies a roughly conical area, is provided for its full length by the maxilla, which extends further posteriorly beneath the cranium than in almost any other primate. This aspect of the

¹As in the case of the other lemurs, the species of the Archaeolemurinae lack any sexual dimorphism in the osteological characteristics of the skull; accordingly, a single description suffices for both sexes.

TABLE 1
CRANIAL DIMENSIONS (IN MILLIMETERS) OF *Archaeolemur majori*

	Mean	Standard Deviation	Sample Size	Overall Range
Maximum length	130.6	5.7	17	122.3–135.0
Facial length (nasion to alveolare)	48.2	3.4	16	43.0–50.6
Maximum bizygomatic width	96.4	5.1	12	88.8–98.0
Minimum frontal breadth at the postorbital constriction	32.2	2.5	16	25.8–34.2
Maximum height of zygomatic arch	13.6	1.6	14	11.5–16.3
Palate length	48.3	2.1	15	45.4–49.5
Palate width at M ¹	23.5	1.4	17	21.0–25.0
Maximum width of occiput	60.6	3.0	17	55.0–63.9
Maximum length of foramen magnum	15.6	1.0	16	13.6–17.3
Maximum width of foramen magnum	17.4	1.7	16	16.3–19.0
Maximum nasal height	18.9	1.3	7	17.9–19.2
Maximum nasal width	18.1	1.3	16	15.0–19.4
Maximum orbital height	28.6	1.7	16	26.5–31.8
Maximum orbital width	24.6	1.2	16	23.3–25.0
Greatest vertical dimension of postglenoid process	11.1	1.1	9	9.2–11.8
Basion to alveolare	109.7	6.5	16	100.4–116.7
Basion to nasion	88.1	4.7	15	82.7–93.0
Perpendicular distance from nasion to alveolar margin	43.7	2.4	16	39.8–45.9

maxilla takes the form of a broad, very gently convex shelf of bone which extends sufficiently superiorly at its medial margin to enclose the large sphenopalatine foramen.

At the apex of the orbital cone lie three foramina: most medially, the optic foramen, a relatively small orifice whose endocranial counterpart is tiny; lateral, and generally somewhat inferior to this, the large foramen rotundum, which in this animal fulfilled also the function of the superior and inferior orbital fissures of human anatomy; and medial and superior to both, a small venous foramen representing the orifice of a canal conducting an emissary vein to the large temporal dural sinus.

The zygomatic arch is in most individuals robustly built, and averages 13.6 mm. in maximum height (14 individuals). At its anterior inferior extremity there is a pronounced downward-pointing process formed jointly by the maxilla and malar. The suture uniting the zygomatic processes of the malar and temporal bones runs obliquely anteriorly and superiorly at a low angle; in consequence the greater part of the superior border of the arch is temporal in formation, while most of its inferior margin is malar in composition.

The superior temporal lines are rarely strongly marked, and almost never closely

approach the sagittal midline of the cranium. The parietal bones are gently rounded, but in a small area at their posterolateral angles are sharply concave. A small oval interparietal bone is sometimes present in the midline, just posterior to the coronal suture; in one specimen in Paris (Institut de Paléontologie, Muséum National d'Histoire Naturelle 1931–1936) a narrow strip of parietal intrudes anteriorly into the frontal bone, to the level of the supraorbital lines, bilaterally. The squamous suture runs horizontally almost in a straight line. The glenoid fossa is elevated considerably above the plane of the tooth row, and is almost totally plane; behind it is a pronounced postglenoid process (mean maximum height 11.1 mm. in nine individuals), anteroposteriorly relatively slender, but broad transversely and confluent with the bulla medially. This process is generally pierced medially by a small foramen which opens into the glenoid fossa.

In posterior view, the cranium of *Archaeolemur majori* is smoothly rounded, the parietal contour being steep but slightly less so than in *Propithecus*. As among prosimians in general, the lambdoid suture coincides with only a very small section of the nuchal ridge; an almost equilaterally triangular segment of occipital bone runs superiorly and anteriorly from the center one-

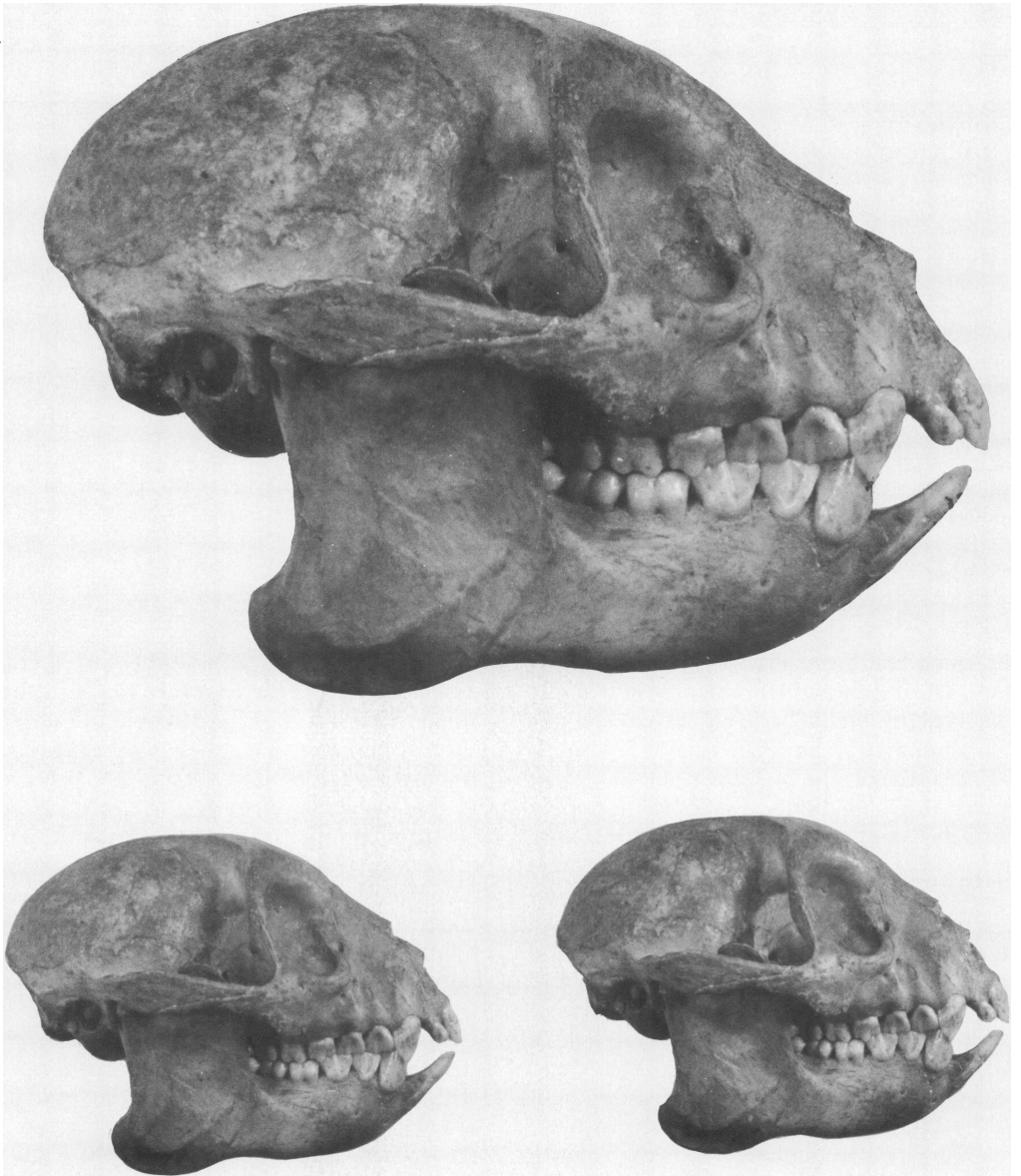


FIG. 3. *Archaeolemur majori*, BM M7374, Andrahomana. Natural size. Stereophotograph of same below.

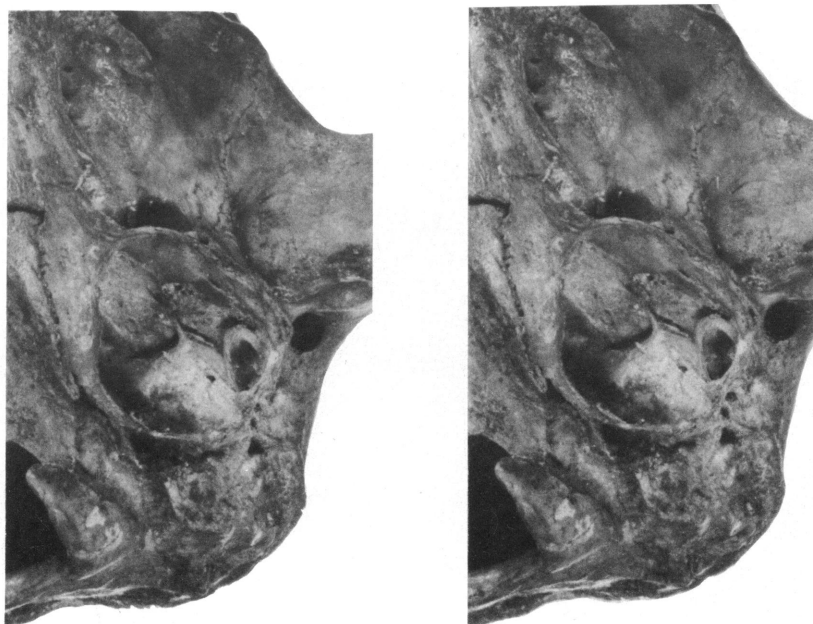


FIG. 4. *Above:* *Hadropithecus*, AM uncatalogued, Tsiravé, stereophotograph of auditory region. *Below:* *Archaeolemur majori*, AMNH 30007, stereophotograph of ventral view of auditory region. Most of bulla has been broken away. Not to scale.

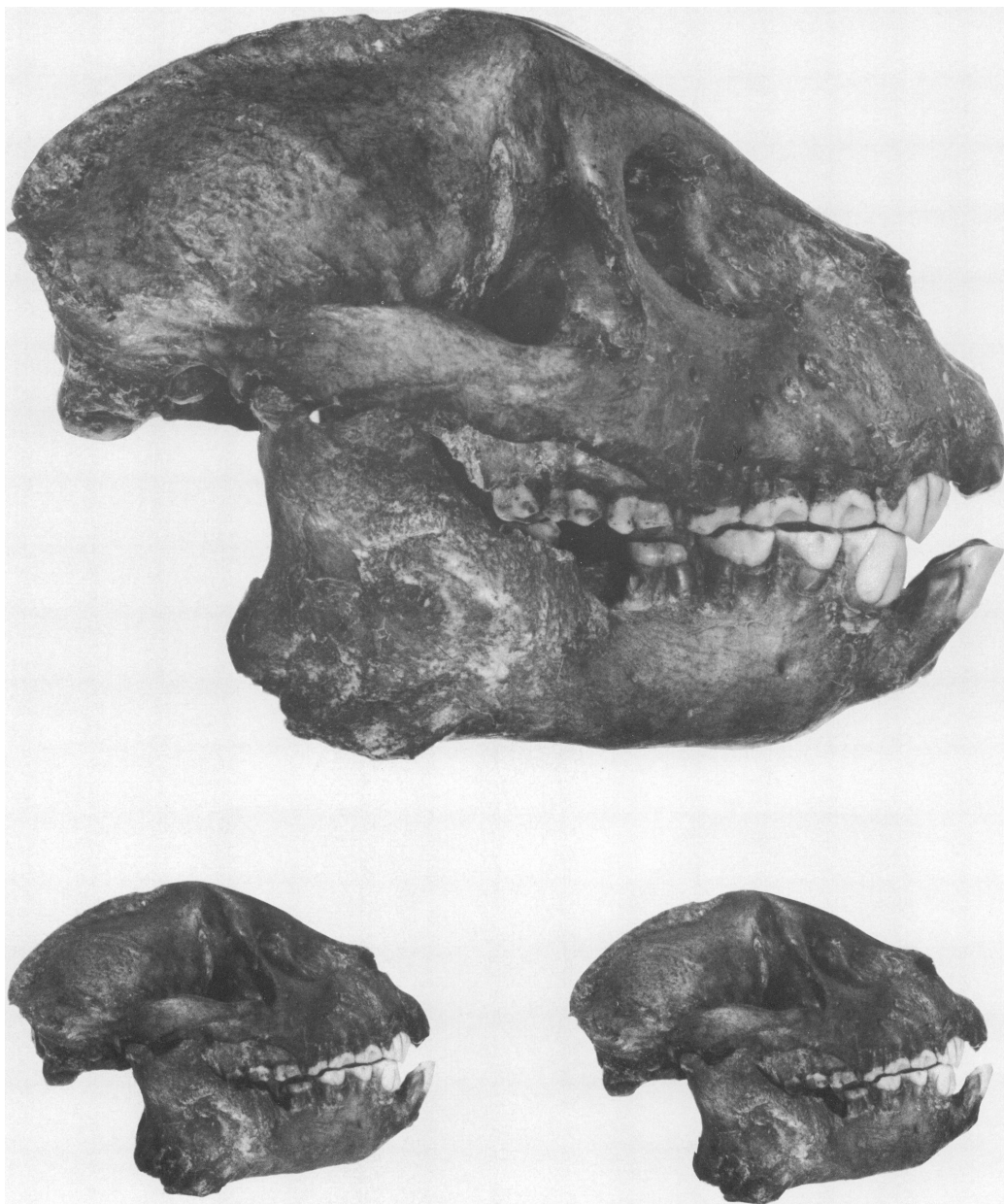


FIG. 5. *Archaeolemur edwardsi*, BM M9909 and M9910, Ampasambazimba, lateral view of articulated cranium and mandible. Stereophotograph of same below.



FIG. 6. *Hadropithecus stenognathus*, AM uncatalogued, Tsiravé, lateral view of cranium and mandible. Stereophotograph of same below.

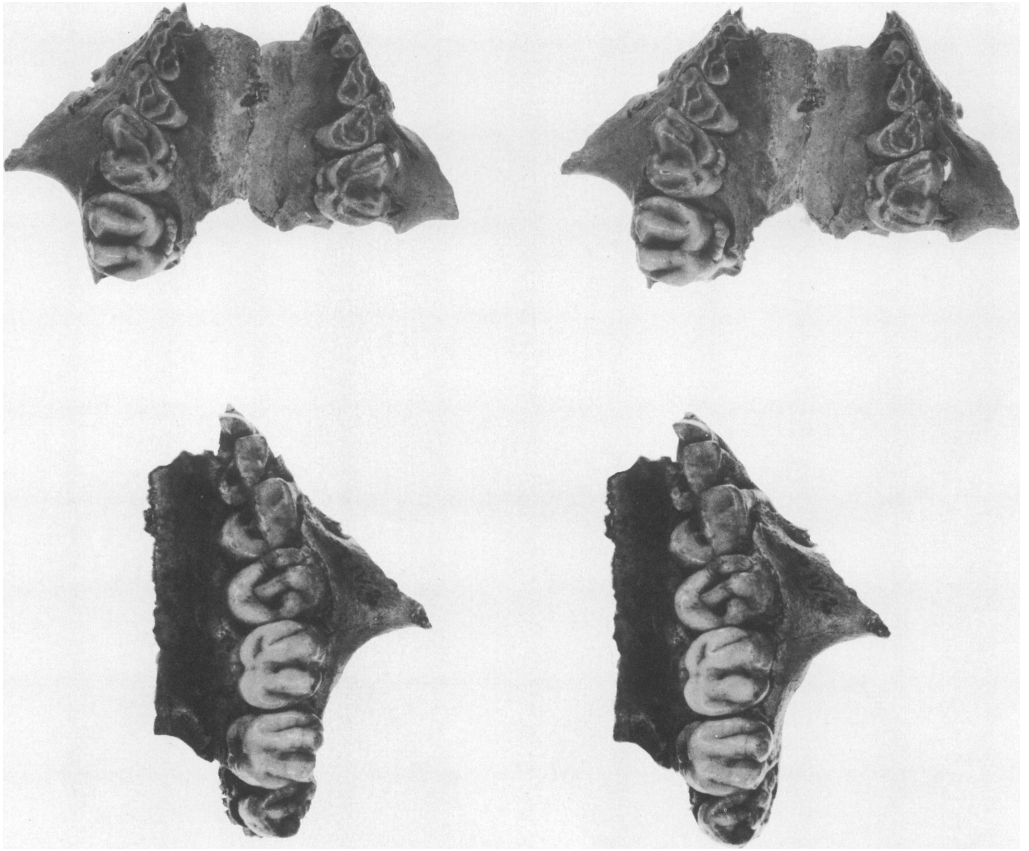


FIG. 7. *Hadropithecus stenognathus*, Andrahomana, stereophotographs of maxillary specimens. *Above*: VNHM 1934 IV 4a and 4b. *Below*: VNHM 1934 IV 2. Both natural size.

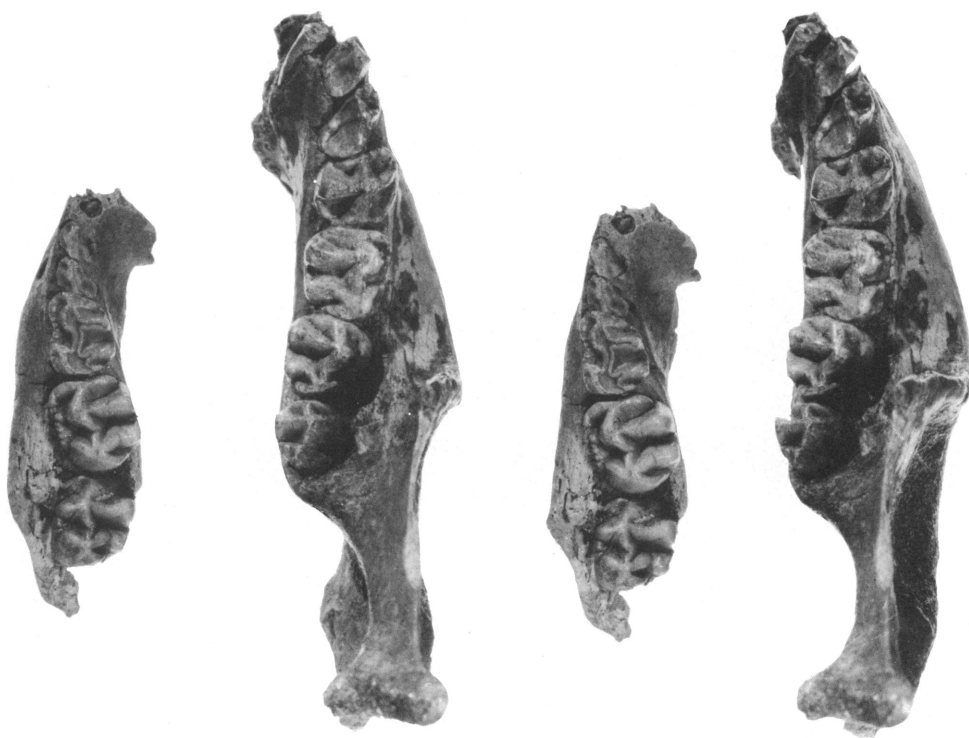


FIG. 8. *Hadropithecus stenognathus*, stereophotographs of mandibular specimens. *Left pair*: from Andrahomana (VNHM 1934 IV 3). *Right pair*: VNHM 1934 IV 2/1a. Both natural size.



FIG. 9. *Above: Archaeolemur majori*, AM 311027, Tsiravé, cranium, lateral view. *Below: Archaeolemur edwardsi*, BM M9965, Ampasambazimba, cranium, lateral view. Both natural size.

third of the moderately developed nuchal ridge to meet the sagittal suture, whereas the lateral margins of the occiput are formed by the temporals. The nuchal segment of the occipital is rugose, and divided into lateral moieties by a low central ridge extending from inion to opisthion. Laterally, in the temporal portion of this area, are double postmastoid foramina.

The foramen magnum is subcircular and bounded laterally and anterolaterally by articular condyles resembling those of genus *Lemur*. Lateral to these lie the paroccipital processes, moderately developed in an obliquely oriented, semiflattened peg shape. Mastoid processes as such are absent, a rugose area lateral to the paroccipital process having provided for the insertion of the lateral flexors of the head.

Internally, the skull is characterized by the strong development of frontal and maxillary sinuses. The former occupies a cavity invading much of the length of the frontal bone and extending into the orbital processes; it connects with the nasal cavity through bilaterally paired oval frontonasal foramina. The maxillary sinus is small, and lies just anterior to the sphenopalatine foramen, invading the root of the zygomatic arch. All specimens examined having been damaged in this area, the exact nature of the communication between the nasal cavity and the maxillary sinus cannot be determined.

THE EAR REGION

The auditory bulla of *Archaeolemur majori* is formed entirely by the petrosal, apart from a small portion of its wall, lying in contact with the postglenoid process, which is of temporal derivation. It is a large globular structure, slightly oval in plan, with its long axis situated at an angle of about 45 degrees to the sagittal plane; its maximal and minimal dimensions in the plane of the cranial base are about 25.0 and 20.0 mm. respectively. Parallel to the long axis, but anterior to it, the bulla is traversed by a small but sharp crest.

The external auditory meatus is large and almost perfectly circular, with a radius of about 10 mm.; its superior, anterosuperior, and posterosuperior borders are formed in the temporal bone, whereas the remainder of its margin is formed by the petrosal, as part of the lateral bulla wall. Within the meatus, the large tympanic annulus lies free on the anteroinferior half of its circumference, as in living indriines

and lemurines, and is markedly inclined ventrally and medially. The free edge of the ring is therefore separated by a considerable space from the inferior margin of the external auditory meatus. In life this space must have been enclosed by the annular membrane which in living forms connects the tympanum with the exterior.

It is of interest here, in regard to the origin of the tympanic ring in *Archaeolemur*, to record the little-known but unique observations of Major (1899a) on the ontogenetic development of the bulla among lemuroids:

In the youngest stage available to me for examination, the foetus of a *Chiromys*, there is no trace of an osseous bulla; the completely ossified annulus lies almost horizontally underneath the periotic. In a second stage (*Lepidolemur*) ossification begins to be developed from the lower sharp margin of the periotic, which adjoins the annulus. In the third stage (*Lepidolemur*) this outgrowth appears increased, and has a shell-like shape, with the concavity turned outward; the annulus is gradually being uplifted by it. In a fourth stage (*Lemur rubriventer*) the shell-like ossification is still more increased, and begins to cover the median part of the annulus; and this state of things is still more increased in the fifth (*Lepidolemur*) and sixth stage (*Avahis laniger*), with the result that first the median part, and eventually the remainder of the annulus becomes invisible when viewed from below, being shut by the periotic. In the adult . . . the annulus is represented by a bony ring . . . which hangs in the tympanic cavity, being coalesced with the *squamosum* only in one part, viz. anteriorly to the stylomastoid foramen. Ontogeny therefore teaches us that the annulus of the adult is not a secondarily detached part of the bulla (pp. 987-988).

The postglenoid foramen opens into the posterointernal aspect of the postglenoid process, and abuts onto the anterosuperior border of the external auditory meatus. It is large in size, relatively more so than in extant lemurs, and communicates internally with the temporal dural sinus.

The petrous process of the bulla is not very strongly developed, as it is, for instance, in *Megaladapis*, although it is distinct, and is joined inferiorly to the medial pterygoid plate by a thin lamina, a large pterygoid foramen thereby being formed superiorly. This junction is rarely preserved in the fossils. The process is expressed as a rugose crest on the anterior surface of the bulla which in basal view partly obscures the depression, lying immediately superior to it, which accommodates both the oval foramen and

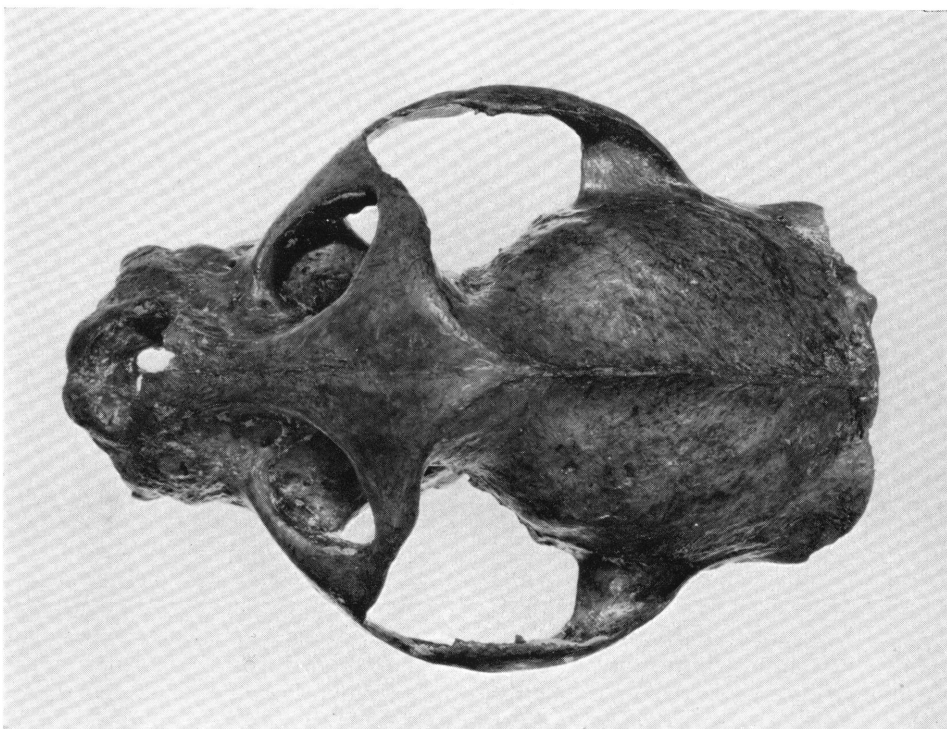
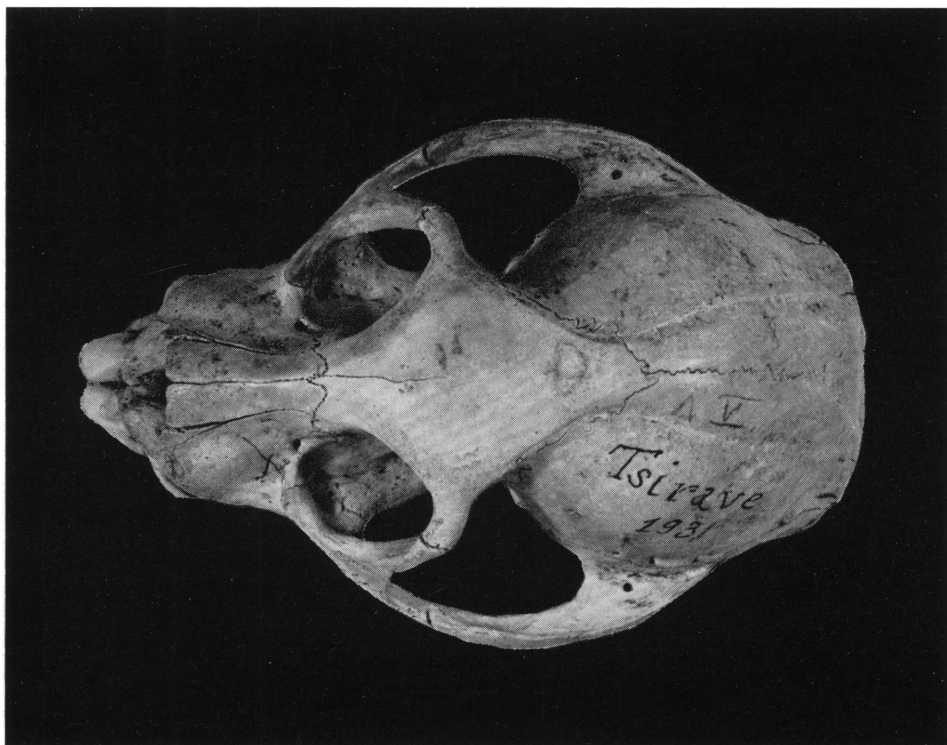


FIG. 10. Above: *Archaeolemur majori*, AM 311027, Tsiravé, cranium, dorsal view. Below: *Archaeolemur edwardsi*, BM M9909, Ampasambazimba, cranium, dorsal view. Both $\times 5/6$.

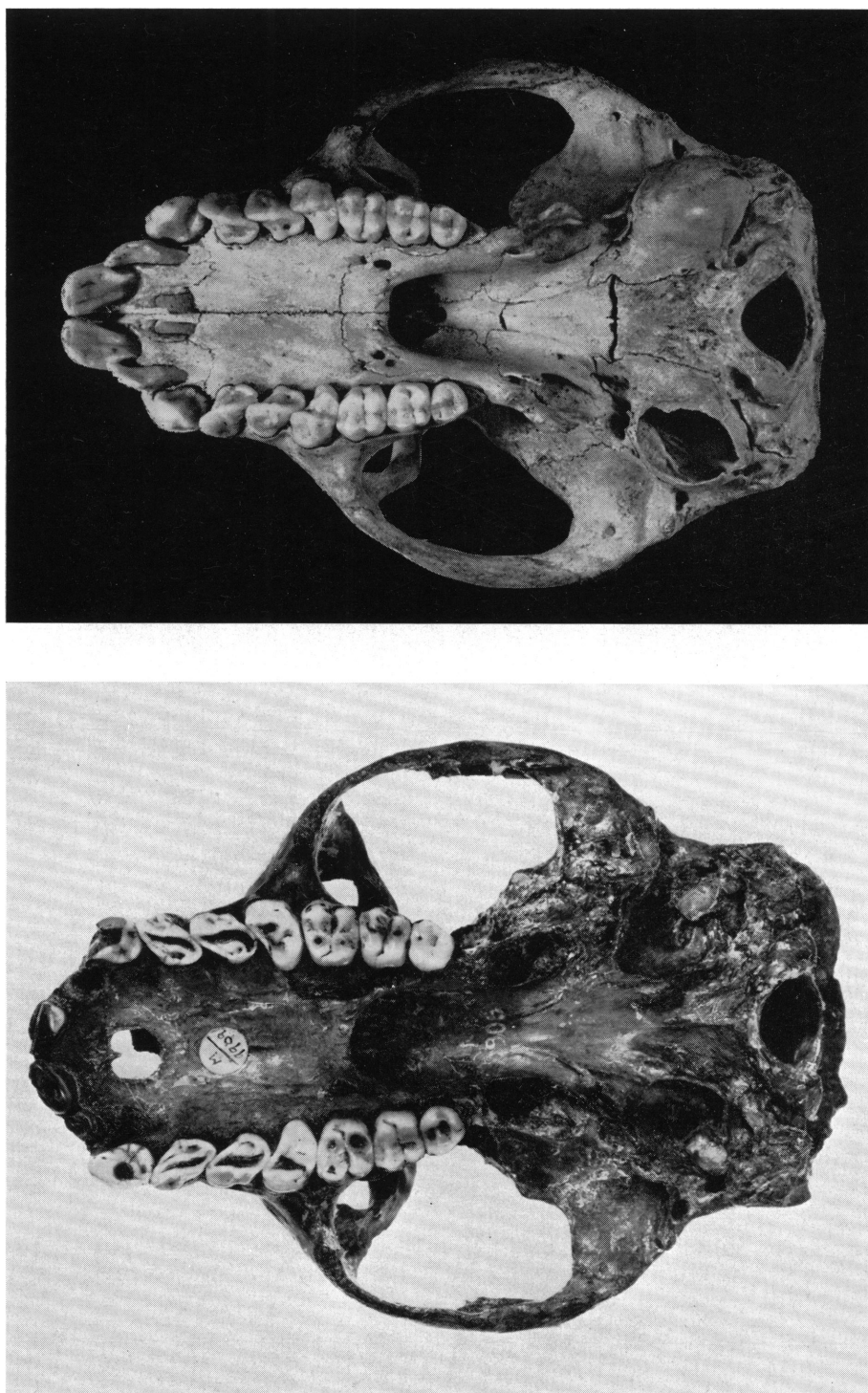


FIG. 11. Above: *Archaeolemur majori*, AM 311027, Tsiravé, cranium, ventral view. Below: *Archaeolemur edwardsi*, BM M9909, Ampasambazimba, cranium, ventral view. Both $\times 5/6$.

the opening of the auditory (Eustachian) tube. The first of these is large and elongated; it is separated from the small orifice of the auditory tube, lying posterior and ventral to its posterior border, by a thin bony lamina.

Lamberton (1941), Piveteau (1948), and Saban (1963) have discussed the foramina of the cranial base in *Archaeolemur* in relation to temporal circulation. The orifice of the internal carotid canal is a tiny foramen situated on the posterolateral angle of the bulla, in the same vertical plane as the cochlea, which lies close medially to the tympanic ring. The internal carotid artery entered the bulla by way of this foramen, and then coursed superiorly, through a partly free bony canal attached to the posterior bulla wall only by a thin lamina of bone, to the cochlea, where it divided into two. One branch, the stapedia artery, ran superiorly through a bony canal on the posterointernal aspect of the cochlea, at right angles to the parent vessel, to cross the stapes, and the other, the entocarotid proper, traversed the cochlea anteroinferiorly in a shallow groove, and rejoined the bulla wall anteriorly, to enter the neurocranium. Evidently the vertebral (foramen magnum) and middle meningeal (foramen ovale) arteries predominated in cerebral irrigation.

The complex of the posterior lacerate foramen, lying along the posteromedial wall of the bulla, houses two principal foramina, both associated with venous drainage from the posterior portion of the transverse sinus, as well as with the transmission of cranial nerves IX, X, and XI. Two small foramina strung out anterior to the posterior lacerate foramen along the medial face of the bulla also communicated with the transverse dural sinus, doubtless conducting emissaries to the internal jugular. The principal pathway of dural venous drainage was via the postglenoid foramen, associated with a more anterior portion of the transverse sinus.

Further details of the archaeolemurine temporal circulation may be found in the discussion of *Hadropithecus*.

Slightly anterior and internal to the mastoid rugosity, and directly posterior to the external auditory meatus, lies the small stylomastoid foramen which, besides transmitting the stylomastoid artery and the auricular branch of the vagus nerve, also provides the external orifice of the facial (Fallopian) canal, which conducted the facial nerve from the internal auditory

meatus around the lateral base of the cochlea, and through the floor of the epitympanic recess to this foramen.

The hypoglossal canal, of moderate diameter, runs from an orifice just posterior and inferior to the jugular spine internally, to the base of the anterolateral aspect of the condyle. Occasionally there is a second perforation slightly anterior to this canal.

THE MANDIBLE

The lower jaw of *Archaeolemur majori* is robustly built, with a high ascending ramus and a deep, broad (compared with extant indriines) corpus. (It is not possible to quote mean measurements of many of these dimensions since almost all specimens are damaged.) The anterior border of the ascending ramus begins to rise in most individuals at about the level of the front of M_3 , i.e. considerably more anteriorly than among the Indriinae, and arches backward in a continuous, very gentle, curve toward the broad, rounded coronoid process, which exceeds the condyle somewhat in elevation. The condyle itself is exceedingly reminiscent of the condyle in *Homo*. The mandibular notch nevertheless gives the impression of shallowness, because the profile of the condyle is virtually continuous with its posterior margin. The posterior border of the ascending ramus is vertical above the level of the tooth row, but inferior to this is sharply convex posteriorly, due to the large posteroinferior expansion of the gonial angle.

The angle of the long axis of the fused symphysis is variable, but normally stands at about 45 degrees to the plane of the tooth row. Commonly the long planum alveolare slopes only very gently posteriorly toward the superior transverse torus; in profile, the genial fossa appears as a step, rather than as an excavation in the bone. Thus in this case the superior transverse torus does not take the classic form of a torus, but merely forms the posterior border of the planum alveolare. The posterior limit of the symphysis is marked by a strong, rounded inferior transverse torus, the posterior edge of which lies at about the level of the center of P_3 . The anterior profile of the symphysis is smoothly rounded except in individuals with very large incisors, where, to accommodate the roots of these teeth, the superior portion of the profile bulges anteriorly to varying extents. The mylohyoid line is well marked in many specimens,



FIG. 12. *Archaeolemur majori*, BM M7374. Andrahomana, mandible, lateral (above) and medial views. Natural size.

and runs obliquely superiorly and posteriorly from the region of the genial fossa to terminate just superior to the mandibular foramen.

A single mental foramen is invariably present at mid-depth of the mandible below P₃; multiple mental foramina commonly occur inferior to the caniniform. The mandibular foramen lies in the plane of the tooth row, in line with the tip of the coronoid process; the lingula protecting it takes the form of a smooth ridge of bone. The mylohyoid groove is deep, but short.

The mandible is strongly marked internally and externally by muscle scars, the degree of development of which appears largely to be a function of age. Further discussion of these may be found in the section dealing with myology.

PERMANENT DENTITION

The dental formula of *Archaeolemur*, ^{2.1.3.3}/_{2.0.3.3} differs from that of living indriines, which possess eight teeth bilaterally in the upper jaw and seven in the lower. The interpretation of the dental formula in the Indriinae hinges on the identification of the lateral procumbent tooth of the lower jaw; if this is an incisor, as the embryological work of Spreng (quoted by Hill [1953]) would seem to suggest, the dental formula is ^{2.1.2.3}/_{2.0.2.3}. In any event, *Archaeolemur* has retained one tooth above and below which are absent in the modern indriine condition. Small diastemata are sometimes present between I₂ and P₂, and between I² and C in *A. majori*. One of the most striking features of the *Archaeolemur* dentition is the extreme mesiodistal packing of the cheek teeth, particularly the molars; this is not purely a mechanical phenomenon, as it is in the case of some other primates, but is also a genetic one, related to the occlusal function of the basin thus formed by the combination of the posterior and anterior foveae of adjacent teeth. Another such feature is the extreme thickness of the enamel coating of the teeth (apart from the lingual aspect of the incisors); the enamel commonly measures up to 1.75 mm. in thickness (measured directly with needlepoint calipers on heavily worn specimens).

For dental measurements see tables 2 and 3.

UPPER DENTITION: I¹⁻²: In impressive contrast to the small upper incisors of indriines and lemurines, those of *Archaeolemur majori* are strongly developed, particularly the central incisor, a large and orthally implanted tooth with its long axis oriented at about 45 degrees to

the cutting edge. Gingivally and distally the buccal aspect of the tooth is buttressed by a distinct pillar so that at its cervical border its crown is broader labiolingually than mesiodistally; in profile the labial border of the tooth is smoothly rounded. Labially the enamel layer of the tooth is relatively thick, although not so thick as that of the molars; lingually, however, the enamel coating is very thin.

The lateral upper incisor is much reduced compared with I¹; small and slightly spatulate, it bears much the same relationship to the central incisor as does its homologue in *Pongo*, i.e. it lies against the lateral border of that tooth, the tip of its crown falling several millimeters short of that of the central incisor. Thus I¹ is invariably heavily worn before the lateral incisor begins to become incorporated into the biting edge.

C: This is a short but stout tooth which rarely projects significantly beyond the occlusal plane of the tooth row. Roughly oval in cross section at its gingival margin, it is almost conical in buccal profile apart from a posterior extension which is represented on the lingual surface by a gutter running down the posterior margin of the tooth. At the base of the crown

TABLE 2
MEASUREMENTS OF UPPER DENTITION
(IN MILLIMETERS) OF *Archaeolemur majori*

	Mean	Standard Deviation	Sample Size	Overall Range
I ¹ width	5.3	0.9	10	4.0-7.8
I ¹ length	8.1	0.8	10	7.3-9.5
I ² width	3.6	0.8	14	2.0-4.4
I ² length	5.4	0.7	14	4.1-7.0
C width	7.2	0.8	17	5.9-8.4
C length	9.2	0.9	17	8.2-10.6
P ² width	8.2	0.8	21	6.4-9.3
P ² length	9.7	0.8	21	9.1-10.7
P ³ width	8.0	0.7	23	6.2-9.1
P ³ length	9.7	0.7	23	9.2-10.5
P ⁴ width	10.0	1.2	23	8.5-11.8
P ⁴ length	8.3	0.8	23	7.1-10.1
M ¹ width	9.2	0.7	23	7.4-11.1
M ¹ length	8.1	0.6	23	7.3-10.0
M ² width	8.5	0.6	22	7.3-9.6
M ² length	7.2	0.4	22	6.5-8.0
M ³ width	8.0	0.5	20	6.1-7.8
M ³ length	6.3	0.8	20	5.7-7.1



FIG. 13. *Archaeolemur* and *Hadropithecus*; comparison in dorsal view of mandibles. *Bottom*: *Archaeolemur* sp., probably *A. majori*, AM uncatalogued, no provenance. *Top*: *Hadropithecus stenognathus*, VNHM 1934 IV 1/1 and 1/2, Andrahomana. $\times 7/8$.

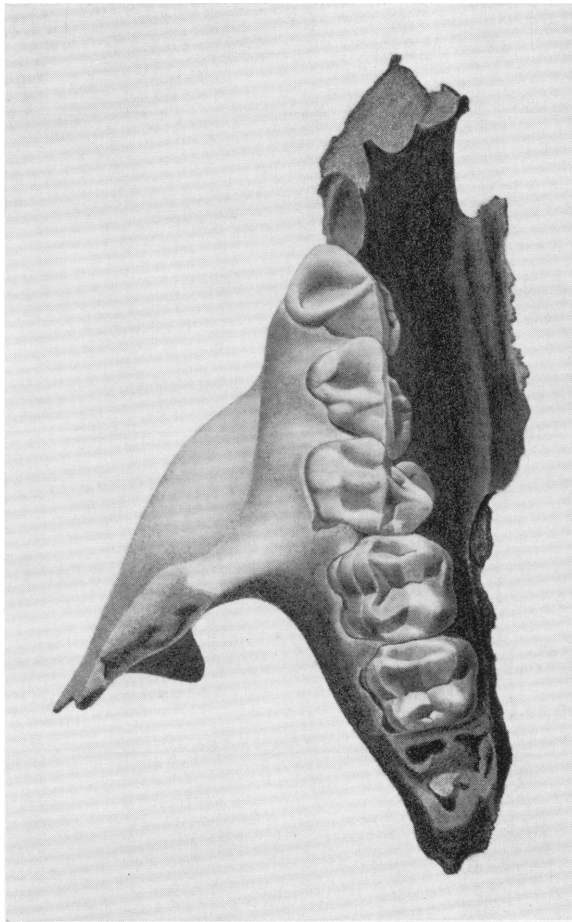


FIG. 14. *Archaeolemur* sp., AMNH 15865, upper cheek dentition. $\times 1.5$. Drawn by Carl R. Wester.

this groove turns anteriorly to form a postero-internal basal cingulum which occasionally bears a small posterior cusp. The tooth bears a very robust root, approximately twice the length of the crown, which curves gently posteriorly.

P²⁻⁴: The premolars embody the most specialized and characteristic adaptation of the *Archaeolemur* dentition, having evolved into elongated shearing blades. The second and third upper premolars are built on much the same plan, bearing a high longitudinal shearing surface, convex in profile. These teeth are given a somewhat skewed appearance by the presence of a basal anterointernal swelling at the confluence of two buttresses which run superiorly from the front and midpoint of the cutting

surface respectively, and by the existence internally, on the central and posterior aspects of this side, of a similar but larger protuberance likewise formed by the confluence of anterior and posterior buttresses, but sometimes also by a central buttress. Dishing tends to occur in the spaces between the buttresses. The roots of the anterior two premolars are set obliquely to the long axis of the tooth row, and are longer and stouter than those of the other cheek teeth. The premolar shearing surfaces are aligned with respect to each other in such a way that they form a continuous, unbroken edge.

The posterior premolar, although of unique construction, is easier to describe in terms of conventional terminology than its predecessors;

this is primarily because it represents a functional intermediate between, or rather, fulfills the functions of both, premolars and molars. P⁴ is almost L-shaped, the dominant cusp being the paracone, which stands in the angle of the L. Anterior and posterior to the paracone lie, respectively, a parastyle and a mesostyle, each slightly lower than the principal cusp and confluent with it. Buccal to this longitudinal structure the crown slopes very gently toward its gingival border; all along the buccal base of the crown there is a swelling, possibly representing an incipient cingulum. Lingual and fractionally posterior to the paracone, and at a much lower level, lies a distinct protocone, from which low crests radiate to meet the parastyle, paracone, and mesostyle. Between these crests lie a small anterior fovea, and, posterior to it, a slightly larger central fovea. Lingual to the protocone the crown of the tooth slopes more steeply than on its buccal aspect toward the gingival border; however, the basal swelling is more pronounced on this side, giving the impression of decreased slope.

The posteroexternal extremity of P³ fits into the angle of the L in such a way that the parastyle-paracone-mesostyle crest of P⁴ is confluent with the longitudinal shearing surface of P³. Microscopic examination of the shear surfaces of the premolars, both upper and lower, of certain specimens of both species of *Archaeolemur* reveals the presence of series of perikymata (enamel growth-rings) on these surfaces, indicating the former presence of small cusps, rapidly removed by wear. Such cusps were not directly observed on any of the numerous *Archaeolemur* specimens examined.

M¹⁻³: The upper molars of *Archaeolemur majori* are roughly square, somewhat bilophodont, and moderately high crowned. The four cusps of M¹ are arranged almost in a square, although the paracone and metacone lie fractionally anterior to, respectively, the protocone and hypocone. The outer cusps are slightly higher than the internal pair; the paracone is more salient than the metacone. Each transverse pair of cusps is joined by a shallow V-shaped, centrally pointing crest; so is each longitudinal pair, giving the tooth a slightly waisted look. Occasionally, the posterior transverse pair of cusps is more widely spaced than the anterior pair. At the base of the lingual constriction there frequently forms a small, anterosuperiorly sloping cingulum. Buc-

cally, the base of the crown also swells slightly above a well-defined line, hinting at incipient cingular development. There is a moderately deep central fovea; anterior and posterior foveae are, respectively, developed between small crests running anterointernally from the paracone and protocone, and posterointernally from the metacone and hypocone.

M² is essentially similar to M¹, but the internal cusps are more salient than the external pair, reflecting the torsion of the occlusal surface along the tooth row (from internally facing anteriorly to externally facing posteriorly). The tooth is also compressed buccolingually compared with M¹, and the lingual cingulum tends to be less strongly developed.

M³ is smaller and more circular (occasionally triangular) in outline compared with the preceding teeth, and is dominated by the protocone; the hypocone and metacone are reduced. The tooth lacks cingula and a posterior fovea; the anterior fovea is tiny. The occlusal surface is oriented still further toward the lingual side than is that of M².

The molars are very closely packed and in consequence bear well-marked interproximal attrition facets; direct measurement of enamel thickness indicates the possibility of losses of enamel in excess of 0.5 mm. of enamel at each end of a tooth only 9 or 10 mm. long.

Within *A. majori* there is considerable variation in dental morphology, but this is generally limited to differences in the degree of expression of the features described above rather than to the absence of any of the characteristics listed or to the presence of traits not described.

LOWER DENTITION: I₁₋₂: These teeth are very clearly derived from those of a form possessing a dental comb, although they vary a little in the degree of their procumbency. Commonly they form an angle of about 45 to 50 degrees to the plane of the tooth row. Essentially cylindrical in form, the incisors taper gently in profile but not in section. As in forms possessing a dental comb, the lateral lower incisor is larger than the central, and is usually somewhat convex laterally. The distribution of enamel is as on the upper incisors: thick enamel labially and laterally; very thin enamel lingually and medially.

\overline{C} : Not present if the lateral procumbent tooth is interpreted as an incisor.

P₂₋₄: The anterior lower premolar is a stout,

TABLE 3
MEASUREMENTS OF LOWER DENTITION
(IN MILLIMETERS) OF *Archaeolemur majori*

	Mean	Standard Deviation	Sample Size	Overall Range
P ₂ width	9.2	0.9	16	8.0–10.8
P ₂ length	9.7	0.8	16	8.3–11.8
P ₃ width	7.8	0.9	18	6.7–9.0
P ₃ length	9.4	0.6	18	8.3–11.5
P ₄ width	8.5	0.8	19	7.4–9.6
P ₄ length	8.9	0.6	19	8.1–9.6
M ₁ width	8.3	0.7	21	7.4–10.4
M ₁ length	8.2	0.5	21	7.2–10.1
M ₂ width	8.1	0.6	21	7.1–9.4
M ₂ length	7.7	0.5	21	6.9–9.3
M ₃ width	7.3	0.6	20	6.7–8.7
M ₃ length	7.1	0.6	20	6.6–9.0

approximately conical tooth relatively much shorter anteroposteriorly than its counterpart in modern indriines, although it does possess a posterior heel which serves to initiate the premolar shearing surface. The tooth tends to project slightly above the general occlusal level of the lower tooth row, with the consequent rapid obliteration of the heel by wear against the rear of the anterior upper premolar. P₂ has a robust and extremely long root which extends almost the full depth of the jaw.

P₃ is closely reminiscent of its upper counterpart, although mirror-imaged. Its lateral root is situated anterior to its medial root, and this determines the orientation of the long axis of the tooth; but the elevated longitudinal shearing blade lies along the axis of the tooth row. A skewed appearance is therefore given the tooth by an anterolateral boss lying above the anterior root and a posteromedial boss in similar relation to the posterior root. At the base of the latter tuberosity there frequently lies a small, rounded cingulum.

P₄ is the most complex of the lower premolars. From a high central protoconid cusp radiate a series of ridges: posteromedially a metaconid crest; anteriorly a paraconid crest; and posteriorly a small protostylid crest. Laterally the protoconid is buttressed by a vertical pillar; along the anterior and posterior margins of this run deep grooves. At the base of the crown, internal to the metaconid crest, lies a slight swelling which may be interpreted as a lingual

cingulum. The anterior extremity of the paraconid crest is longitudinally aligned with the rear of the shearing surface of P₃, and is continuous with it.

M₁₋₃: M₁ and M₂ are in most cases almost identical. Roughly square in outline, they possess open occlusal surfaces with the four cusps arranged at the corners of a square. The protoconid and metaconid anteriorly, and the hypoconid and entoconid posteriorly, are connected by low, transverse lophs. The anterior and posterior cusp pairs are separated by internal and external vertical grooves at midlength of the crown. A paraconid crest anteriorly encloses an anterior fovea, while the loph pairs delineate a distinct central fovea. The posterior fovea is

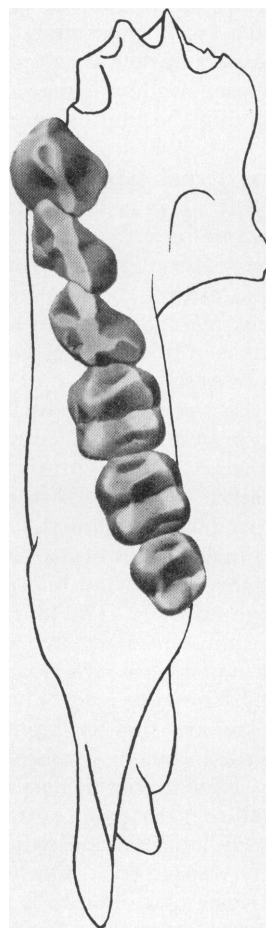


Fig. 15. *Archaeolemur majori*, AMNH 30008, lower dentition. $\times 1.5$. Drawn by Carl R. Wester.

small, little better than a shallow wrinkle. In both teeth the metaconid is the highest cusp, the lateral pair being more salient than the medial pair of cusps; in M_2 , however, the latter feature is less marked than in M_1 .

M_3 is slightly smaller and more rounded than M_1 and M_2 ; in this tooth the external cusps tend to be slightly higher than the internal ones, with a consequent lingual tilt to the occlusal surface. There is no trace of a hypoconulid such as is found on the M_3 of the bilophodont cercopithecoid monkeys.

As in the case of the upper teeth, individual variation in lower dental morphology among *A. majori* is largely confined to differences in the degree of expression of a constant set of features. Enamel thickness is likewise equal to that of the upper teeth.

DECIDUOUS DENTITION

The milk dentition of *Archaeolemur*, in so far as it is known, has been comprehensively described by Lamberton (1938); it seems unnecessary to repeat those descriptions here.

Archaeolemur edwardsi

GENERAL DESCRIPTION OF CRANIUM

Somewhat larger in linear dimensions (6–7 percent in skull length) and considerably more robust than *Archaeolemur majori*, *A. edwardsi* is distinguished from its congener primarily by differences consequent upon a greatly expanded cranial musculature. Its facial profile is generally described as being more orthal than that of *A. majori*, and its muzzle, in consequence, as being shorter. These differences are in fact largely illusory; the more swollen frontal region in this genus conveys a more pronounced impression of flatness, whereas the proportion of the dental arcade lying anterior to the inferior root of the zygomatic process of the malar is generally very slightly greater in *A. edwardsi* than in *A. majori*. Differences in orbital orientation between the species have also been overemphasized. Hill (1953) is in error in stating that the lacrimal foramen lies within the orbital margin; rather, it is marginal to the orbit, as in *A. majori*, the anterior and posterior lacrimal crests marking the respective limits of the orbital margin.

TABLE 4
CRANIAL DIMENSIONS (IN MILLIMETERS) OF *Archaeolemur edwardsi*

	Mean	Standard Deviation	Sample Size	Overall Range
Maximum length	147.0	4.0	17	139.6–153.5
Facial length (nasion to alveolare)	55.0	2.2	16	52.2–58.4
Maximum bizygomatic width	108.4	3.3	7	104.6–111.5
Minimum frontal breadth at the postorbital constriction	35.2	5.6	16	26.0–38.8
Maximum height of zygomatic arch	15.2	1.1	17	13.2–17.3
Palate length	53.9	2.0	15	49.2–56.5
Palate width at M^1	26.5	1.5	17	24.7–29.8
Maximum width of occiput	66.6	2.0	16	62.7–69.8
Maximum length of foramen magnum	17.1	1.5	15	16.1–19.8
Maximum width of foramen magnum	18.6	1.6	16	17.6–21.9
Maximum nasal height	20.9	3.1	10	17.7–21.9
Maximum nasal width	21.5	1.7	14	19.0–25.6
Maximum orbital height	31.1	1.9	16	28.4–35.0
Maximum orbital width	25.8	1.4	16	23.9–27.1
Greatest vertical dimension of postglenoid process	10.7	1.4	5	10.0–12.5
Basion to alveolare	121.3	3.7	16	115.4–126.6
Basion to nasion	97.7	4.1	15	91.2–105.0
Perpendicular distance from nasion to alveolar margin	50.2	2.8	16	46.1–53.3

The frontal bone in *A. edwardsi* is inflated by the enormous development of the frontal sinus, which extends the entire length of the bone, and penetrates the orbital processes to the level of the frontomalar suture. Anteroinferiorly the sinus communicates with the nasal cavity through large, oval, bilaterally-paired frontonasal foramina. The maxillary sinus is also considerable, divided into anterior and posterior moieties by the intrusion of dental roots, and penetrating the orbital floor to the maxillomalar suture. Again, the exact extent of this sinus and the nature of its communication with the nasal fossa cannot be established for want of undamaged specimens.

The coronal suture is more posteriorly placed and runs more vertically than in *A. majori*, with the result that the parietal is excluded from the formation of the posterior wall of the orbit. Orbital formation is otherwise as in *A. majori*.

The supraorbital lines are strongly marked and continuous with the sharp lateral edge of the postorbital bar. They curve posteromedially to meet the midline somewhat anterior to the cornal suture, where they become confluent with the strong sagittal crest. This crest is invariably present, even in those cases (such as *A. "platyrrhinus,"* AM 311024) in which it is not

strongly developed. Posteriorly the sagittal crest joins with the transverse nuchal crest, which reaches its strongest development laterally. The paroccipital process is relatively much larger than its homologue in *A. majori*; lateral to it lies a distinct mastoid rugosity.

The zygomatic arches are higher and more robust than are those of *A. majori*, and the tuberosities on their anteroinferior roots are more pronounced than in that species. The pterygoid plates are stronger and more rugose, and define a depression deeper than that in *A. majori*.

The foramen magnum in *A. edwardsi* is slightly more posteriorly placed than in *A. majori*, reflecting a marginally less steep occipital profile. The ear region is virtually identical in the two species except for some deepening of the bulla in *A. edwardsi*. Apart from the foregoing differences, the crania of the two species of *Archaeolemur* are closely similar.

For cranial measurements of *A. edwardsi*, see table 4.

THE MANDIBLE

The lower jaws of *A. majori* and *A. edwardsi* are extremely similar in morphology, and can overlap in size; they also share the age changes mentioned earlier. It is impossible, therefore, to list diagnostic characters which infallibly discriminate between the species, but mandibles of *A. edwardsi* may generally be recognized on grounds of greater size and robusticity.

DENTITION

The dentitions of the two species of *Archaeolemur* are so similar as to be indistinguishable, apart from the mean size difference, which is of little assistance in discriminating between individuals as the ranges of dental size in the two species overlap. In *A. edwardsi* the diastemata between I^2 and \bar{C} and between I_2 and P_2 tend to be larger and more frequently present, but are far from constituting diagnostic characters.

For measurements, see tables 5 and 6.

Hadropithecus stenognathus

GENERAL DESCRIPTION OF CRANIUM

The following description is based on the almost complete cranium found by Lamberton at Tsiravé in 1931, which is now in the collections of the Académie Malgache. This individual

TABLE 5
MEASUREMENTS OF UPPER DENTITION
(IN MILLIMETERS) OF *Archaeolemur edwardsi*

	Mean	Standard Deviation	Sample Size	Overall Range
I^1 width	8.3	—	1	—
I^1 length	8.4	—	1	—
I^2 width	5.5	—	2	4.4–6.7
I^2 length	5.8	—	2	5.3–6.3
\bar{C} width	7.9	0.5	5	7.1–8.6
\bar{C} length	10.7	1.1	5	8.8–11.7
P^2 width	9.4	1.0	8	8.2–11.2
P^2 length	11.1	0.6	8	10.3–11.7
P^3 width	8.7	0.8	9	8.2–9.9
P^3 length	10.9	0.6	9	9.9–11.7
P^4 width	11.8	0.9	9	10.1–12.7
P^4 length	9.1	0.6	9	8.1–9.8
M^1 width	10.7	0.5	9	10.3–11.3
M^1 length	9.2	0.5	9	7.9–9.8
M^2 width	10.0	0.5	9	9.2–10.8
M^2 length	7.9	0.5	9	7.0–8.7
M^3 width	8.3	0.5	7	7.5–8.8
M^3 length	7.1	0.4	7	6.8–7.6

TABLE 6
MEASUREMENTS OF LOWER DENTITION
(IN MILLIMETERS) OF *Archaeolemur edwardsi*

	Mean	Standard Deviation	Sample Size	Overall Range
P ₂ width	9.7	0.6	17	8.6–10.8
P ₂ length	10.7	0.7	17	9.4–11.8
P ₃ width	8.2	0.7	18	6.9–9.6
P ₃ length	9.9	0.8	18	9.3–11.5
P ₄ width	9.0	0.7	18	7.5–9.6
P ₄ length	9.7	0.6	18	8.7–10.7
M ₁ width	9.2	0.7	18	8.4–10.6
M ₁ length	9.3	0.5	18	8.3–10.3
M ₂ width	8.8	0.6	17	8.2–9.5
M ₂ length	8.8	0.5	17	7.7–9.7
M ₃ width	8.2	0.5	17	8.0–9.0
M ₃ length	8.0	0.6	17	7.4–9.0

differs in some ways from the Andrahomana cranium, VNHM 1934 IV I; these differences will be discussed following the formal description.

The general foreshortening and broadening of the skull of *Hadropithecus* as compared with that of *Archaeolemur* is at once evident in the comparison of major dimensions. Whereas the maximum cranial length of Tsiravé *Hadropithecus* is 141.8 mm., somewhat less than the mean of 17 individuals of *A. edwardsi* (147.0 mm.), its maximum bizygomatic width can be reliably estimated at 114.5 mm., which exceeds the mean of seven *A. edwardsi* (108.4 mm.). In lateral view the most striking manifestation of this is the relatively orthognathous facial region, and in dorsal view the wide flaring of the zygomata.

In some respects the orthognathy of *Hadropithecus* relative to *Archaeolemur* is deceptive, since in large part it is due to the anterior inflation of the frontal sinus, which has shifted the highest point on the frontal bone forward, to lie immediately above the orbital process of the bone. The profiles of the face and cranial roof are therefore sharply angled relative to one another, rather than being more gradually confluent. This represents a continuation of the trend toward an increased facial angle seen in the series *A. majori*–*A. edwardsi*. The frontal sinus, as the foregoing suggests, is yet more capacious than that of *A. edwardsi*, penetrating the entire length of the frontal bone and invading the orbital processes, as in that species, but

attaining a somewhat greater vertical dimension. The disposition of the coronal suture recalls the condition seen in *A. edwardsi*, in descending almost vertically from bregma, but the suture is placed further anteriorly, bregma lying only slightly posterior to the narrowest point on the postorbital constriction. The supraorbital lines are less marked than in *A. edwardsi*, in consequence of the more swollen frontal region; however, the most anterior part of the sagittal crest nevertheless lies on the frontal.

The orbits of *Hadropithecus* are still more frontally directed than those of *Archaeolemur*; the malar bones are therefore more widely flared laterally, and less retreating, than in the latter. They are, in addition, deeper dorsoventrally, and the anteroventral tubercle is yet more strongly marked. The orbital processes of the malars are broad and robust, as are the descending orbital processes of the frontal. The long

TABLE 7
CRANIAL DIMENSIONS (IN MILLIMETERS) OF
Hadropithecus stenognathus

	Tsiravé	Andrahomana
Maximum length	141.8	128.2 ^a
Facial length (nasion to alveolare)	51.2	45.0 ^a
Maximum bizygomatic width	114.5 ^a	108.0 ^a
Minimum frontal breadth at the postorbital constriction	21.8	24.4 ^a
Maximum height of zygomatic arch	18.7	15.1
Palate length	54.3	—
Palate width at M ¹	26.9	23.8
Maximum width of occiput	66.9	63.8
Maximum length of foramen magnum	16.8	18.4
Maximum width of foramen magnum	17.8	18.4
Maximum nasal height	19.1	—
Maximum nasal width	20.0	15.8 ^a
Maximum orbital height	29.0	—
Maximum orbital width	27.0	26.4
Greatest vertical dimension of postglenoid process	12.0	13.0
Basion to alveolare	110.2	100.0
Basion to nasion	94.8	88.0
Perpendicular distance from nasion to alveolar margin	53.6	50.3

^a A reliably estimated dimension.

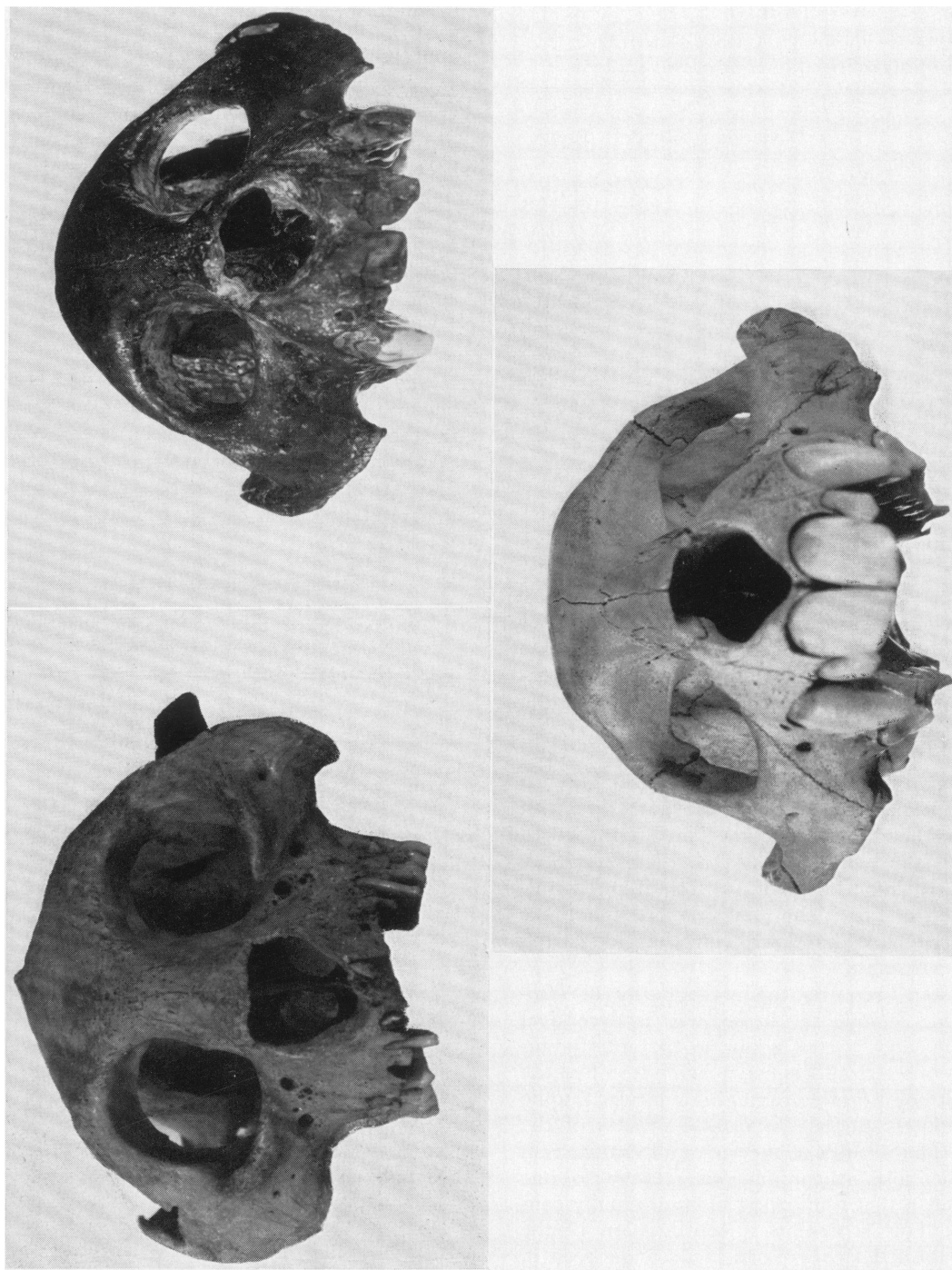


FIG. 16. Facial view of the three archaolemurine species. *Above left*: *Hadropithecus stenognathus*, AM uncatalogued, Tsiravé. *Above right*: *Archaolemur edwardsi*, BM M9909, Ampasambazimba. *Below*: *Archaolemur majori*, AM 311027, Tsiravé. Not to scale.

maxillomalar suture is oriented much as it is in *Archaeolemur*. The orbits are almost circular, the vertical dimension barely exceeding the lateral one. The interorbital distance (15.8 mm.) is slightly less than is usual in *A. edwardsi*. Lamber-ton ("1937" [1938]) has suggested that an oblique crest, beginning on the lower part of the parietal and running on to the alisphenoid, represents incipient orbital closure, but this feature is, in fact, functionally related to the temporalis muscle. The orbital margins are sharply defined; the ventral orbital border is produced anteriorly into a low, rounded ridge. Construction of the medial and posterior orbital walls is as in *A. edwardsi*, i.e. the parietal, due to the perpendicular descent of the coronal suture, takes no part in the formation of the latter. Foramina at the apex of the orbital cone are likewise disposed similarly to those of *Archaeolemur*, with an additional small venous foramen ventral to the optic foramen. For its entire length the orbital fossa is floored by the dorsal surface of the massive maxilla, which is far more strongly developed in *Hadropithecus* than in *Archaeolemur*.

The nasal bones are short, but relatively broad in their anterior portions. Obliteration of the maxillopremaxillary sutures in the Tsiravé individual, and damage to this region in VNHM 1934 IV 1, renders impossible determination of the extent of the premaxillae in *Hadropithecus*; presumably, as in *Archaeolemur*, these bones were reduced, forming only the most anterior limits of the nasal aperture, and the palate anterior to the rear of the anterior palatine fenestrae.

The form of the palate itself is rather less quadrangular than in *Archaeolemur*, largely due to its anterior narrowing, a reflection of the reduced anterior dentition. The posterior border of the palate is deeply incurving, although not to the extent seen in *Archaeolemur*; its most posterior point in the midline is level with the midpoint of M^2 . There is no trace of a postpalatine torus. Single, small posterior palatine foramina lie bilaterally in the palatine, level with the midpoint of M^1 ; two larger, paired, foramina lie posteriorly, within the sphenoid portion of the palate. The alveolar processes project ventrally to a slightly greater extent than they do in the case of most *Archaeolemur*, although the projection is nevertheless not substantial; it is most marked posteriorly, in correlation with the curve of Spee.

The zygomatic arches are extremely robust and widely projecting. The anterior part of the malar orbital process projects perpendicularly to the sagittal plane before turning sharply posteriorly; this has the effect of broadening considerably the anterior parts of the temporal and infratemporal fossae, particularly since the flexion occurs at the level of the narrowest part of the postorbital constriction. The maxilla takes part in the formation of the strong, ventrally directed tubercle adjacent to the inferior root of the zygomatic process of the malar. The zygomatic process of the temporal bone likewise projects strongly laterally, while its root is also broad in its anteroposterior dimension. The dorsal border of the zygomatic arch is strongly inclined medially.

Viewed from the side, the zygomatic arch is high, its maximum vertical dimension reaching 18.7 mm., as compared with the mean of 15.2 mm. for 17 *A. edwardsi*. The arch is oriented more obliquely than in *Archaeolemur* because its posterior root is raised relative to the anterior one. The temporomalar suture is for most of its length oriented horizontally, as in *A. edwardsi*, but turns sharply in a dorsal direction just posterior to the orbital process of the frontal.

As in *Archaeolemur*, the entire maxillary molar row lies posterior to the ventral root of the zygomatic process of the maxilla, although, because of the relatively reduced anterior dentition in *Hadropithecus*, the proportion of the dentition lying beneath the calvaria is considerably greater.

One of the most striking suites of differences between *Hadropithecus* and *Archaeolemur* is due to the elevation of the neurocranium relative to the splanchnocranium in the former. It is this elevation which has led to the forward displacement of the frontal sinus and the raising of the temporal zygomatic process already mentioned. In concert with this have occurred the deepening of both the face and the subglenoid portion of the temporal bone and corresponding portions of the bones anterior to it. Facial deepening is almost entirely due to a downward extension of the maxilla. The malar has deepened only slightly, with the result that the anteroinferior root of the zygomatic arch, lying almost at the level of the tooth row in *A. majori*, and only slightly above it in *A. edwardsi*, is in *Hadropithecus* raised considerably above this level. The perpendicular distance between the most ventral



FIG. 17. *Hadropithecus stenognathus*, lateral view of two crania. *Above*: from Tsiravé (AM uncatalogued). *Below*: from Andrahomana (VNHM 1934 IV 1). Both $\times 7/8$.

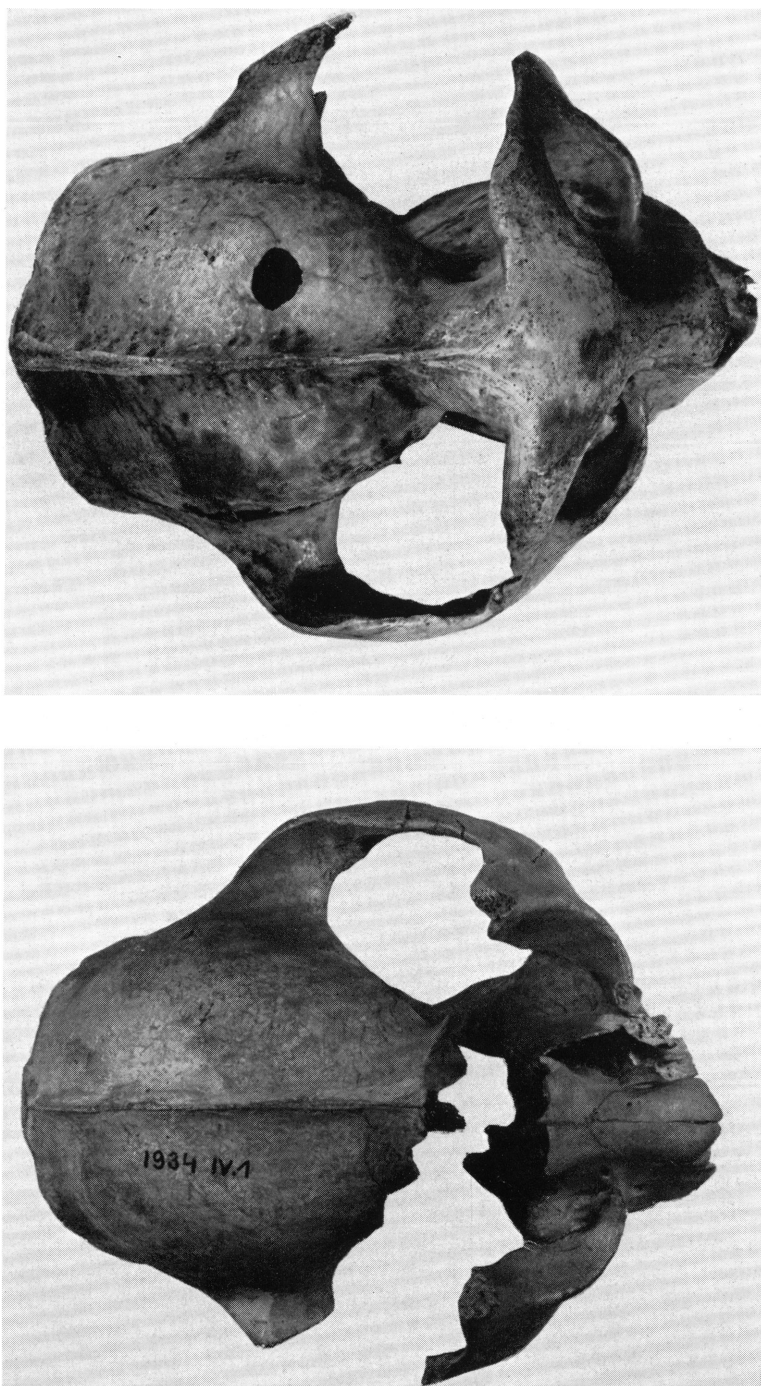


FIG. 18. *Hadropithecus stenognathus*, dorsal view of two crania. *Above*: from Tsiravé (AM uncatalogued). *Below*: from Andrahomana (VNHM 1934 IV 1). Both $\times 3/4$.

point on the malar and the alveolar border is in the Tsiravé specimen about 13.0 mm. as compared with 3.0–4.0 mm. in *A. edwardsi*; and in this specimen there is considerable alveolar resorption.

In the temporal bone an even more dramatic deepening has occurred, restricted to that part of the bone lying ventral to the inferior face of the zygomatic process. The squamous suture maintains the same broad relations as that of *Archaeolemur*, although its course is a little more convex dorsally than in that genus. The palatine bone, which is concerned in the formation of the pterygoid hamulus, is deepened in this portion, as are the sphenoids, which form the pterygoid plates. These (particularly the medial plates), are damaged in both crania of *Hadropithecus* but were evidently strongly built; they are more widely flaring, and subtend a wider and deeper area than do their homologues in *Archaeolemur*. The lateral pterygoid plates evidently did not make bony contact with the anterior faces of the deep bullae, although a cartilaginous connection may have existed. This is quite contrary to the condition seen in *Archaeolemur* and the indriines.

The remaining dominant feature of the cranium of *Hadropithecus* in side view is the sagittal crest, whose anterior extremity, as noted earlier, intrudes on to the frontal bone. In vertical dimensions this crest is not larger than that seen in the most robust specimens of *Archaeolemur edwardsi*, except in its posterior portion, which is most pronounced. Especially in this latter part, the crest is T-shaped in transverse section, showing pronounced lipping at its dorsal margin.

The nuchal crest is more pronounced in occipital than in dorsal view, but is nonetheless prominent and rugose. As in *Archaeolemur* and other indriids, the nuchal area is not entirely composed of the occipital bone, its lateral moieties being of temporal derivation. Multiple postmastoid foramina lie in these latter portions. A pronounced median vermis separates the halves of the occiput dorsally and is confluent with the nuchal crest. The paroccipital processes are only slightly more pronounced than in *A. edwardsi*, and are in somewhat closer relation to the posterior aspect of the bulla; their muscle-attachment surfaces are comparable in extent to those of *A. edwardsi*. Lateral to these processes lie distinct mastoid rugosities. Foramen magnum is almost circular, and is intermediate in its dimensions between the means of those of *A.*

majori and *A. edwardsi* (tables 1, 4, 7), while the occipital condyles are likewise similar in morphology and position to those of *Archaeolemur*. The extent of the supraoccipital portion of the occipital bone is obscured in the Tsiravé individual because of sutural obliteration; in the Andrahomana specimen it is comparable with that in *Archaeolemur*, although posteriorly it is slightly more flared, as the transverse portion of the lambdoid suture does not coincide with the nuchal crest but runs slightly dorsal to it.

The form of the glenoid fossae in the Tsiravé *Hadropithecus* is somewhat different from that in *Archaeolemur*; the posterior portion is more excavated; in the Andrahomana cranium this difference is yet more apparent. In both individuals the postglenoid processes are somewhat more robust, and are posteriorly more concave, than in *Archaeolemur*, although they are nonetheless anteroposteriorly compressed and pierced laterally by a small foramen. The postglenoid processes are broadly confluent medially with the lateral bulla walls; postglenoid foramina are present and similar in size to those of the robust species of *Archaeolemur*.

THE EAR REGION

The auditory bulla in *Hadropithecus* is larger than that of *Archaeolemur edwardsi*, primarily because of its considerable downward extension, although because of the general shortening of the cranial base in this animal the bullae are distinctly compressed anteroposteriorly, so that their long axes in basal view run perpendicular to the sagittal midline. As in *Archaeolemur*, the bulla is petrosal in formation, although sutural obliteration in both crania prevents the precise determination of the contribution of other elements. The anterior bullar face is flattened, and, as noted above, separated from the external pterygoid plate. However, it does show medially, as Saban (1956) has pointed out, rugose markings which indicate attachment of the medial pterygoid muscle, and a contact with a posterior prolongation of the medial pterygoid plate, dorsal to which a pterygoid foramen is formed. A low medial extension of this prolongation travels posterolaterally to the postglenoid process. The petrotympanic fissure is shallow, and interrupts the course of this ridge. The lateral part of the posterior aspect of the bulla in the Tsiravé individual shows two vertical furrows, the medial one shallower than the lateral. The

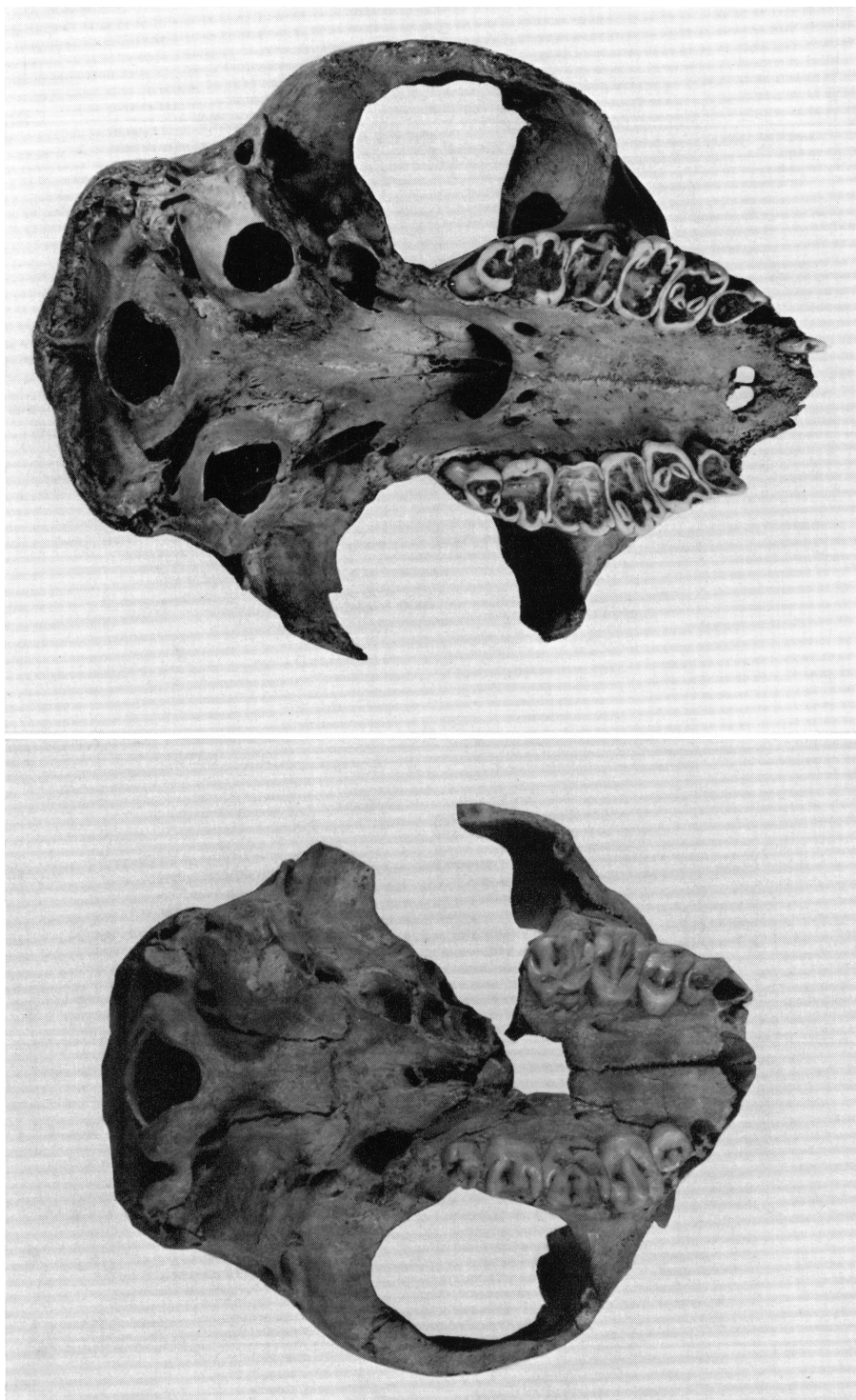


FIG. 19. *Hadropithecus stenognathus*, ventral view of two crania. *Above*: from Tsiravé (AM uncatalogued). *Below*: from Andrahomana (VNHM 1934 IV 1). Both $\times 3/4$.

Andrahomana specimen only shows one such furrow, which apparently corresponds to the medial groove in the Tsiravé subfossil. The medial groove originates in the deep, if small, tympanohyal fossa, and was thus presumably associated with the stylopharyngeal and stylohyoid muscles. A dissection of *Propithecus* by Saban (1956) showed such an association to exist in that animal. The lateral groove in the Tsiravé specimen appears to have been associated with the digastric muscle, the greater muscularity of the Tsiravé individual probably accounting for its appearance in this specimen.

The external auditory meatus is almost circular in both individuals of *Hadropithecus*, but in each case, and particularly in the Tsiravé specimen, its ventral border bears a small tuberosity lacking in *Archaeolemur*. The tympanic ring, as in other lemurs, is free anteroventrally, and its free margin is inclined medially. Just posterior to the external auditory meatus, in both crania of *Hadropithecus*, lie double stylomastoid foramina. The small, circular superior stylomastoid foramen, situated at the base of the mastoid rugosity, is interpreted by Saban (1956) as having been a nervous orifice (auricular branch of the facial nerve). Within this orifice also lies the opening of the canal of the chorda tympani, which ran along the petrotympanic suture to open into the tympanic cavity. There is also a communication between the superior stylomastoid foramen and its inferior counterpart. The inferior stylomastoid foramen lies in a depression immediately ventral to the former in the Andrahomana specimen, and somewhat ventrally and posterior to it in the Tsiravé skull. The inferior orifice was vascular in function, having transmitted both the stylomastoid artery and the corresponding vein. A branch of this opening, too, communicates with the tympanic cavity. Both foramina are associated with the facial canal. The depression accommodating the inferior stylomastoid foramen also holds the opening of a small canal which communicates with an opening at the base of the groove which contained the occipital artery.

The large postglenoid foramen, anterior and lateral to the dorsal border of the external auditory meatus, is comparable in size with that in *A. edwardsi*, and presumably, as in the latter, communicated endocranially with the temporal sinus. In the Tsiravé individual, a number of tiny canals communicate between an area just

anterior to the anterior root of the postglenoid process, and the interior of the postglenoid foramen; Lamberton (1941) has termed their anterior orifices "perforations ectoglenoïdienne."

The oval foramen in *Hadropithecus* lies in a round depression tightly approximated to the anterior bullar wall. The roundness of this depression is a reflection of the extreme shortening of the cranial base. The opening of the auditory tube lies, as in *Archaeolemur*, in this same fossa.

Along the base of the oblique, medially facing posterior wall of the bulla lies the complex posterior lacerate foramen, which extends sufficiently far medially to enclose the exocranial orifice of the condylar canal. The area of the posterior lacerate foramen is much deeper than that of *Archaeolemur* or of the indriids. Anterior to the condylar foramen lies a foramen communicating with the endocranial transverse petrosal sinus; lateral to this lies, beneath a bony projection, the external orifice of the lateral petrosal sinus. Yet more lateral lies the opening of the lateral petrosal sinus, and more lateral still the opening of the cochlear canal. The lateral part of the posterior lacerate foramen accommodates the foramen conducting the tympanic branch of the glossopharyngeal nerve, and, external to this, double foramina presumably related to the occipital vein. Anterior to these, in the posterior bullar wall, lies the internal carotid foramen. Strung out lateral to the posterior lacerate foramen along the petro-occipital suture, as in *Archaeolemur*, lie a pair of small foramina communicating with the inferior petrous sinus.

Because the bullae of the Andrahomana individual are undamaged, and those of the Tsiravé specimen are broken only at their ventral extremities, it is difficult to describe the interior of the tympanic cavity, which appears, as far as can be told, to resemble that of *Archaeolemur*. The reader is referred to Saban's (1956) remarkable study for further information.

TEMPORAL CIRCULATION

Saban (1956) has reconstructed the temporal circulation of *Hadropithecus* on the basis of an extremely detailed study of temporal morphology. The following is based on his discussion, and it is evident that there are few substantial differences between *Hadropithecus* and *Archaeolemur* in this respect. Three arterial systems are

involved in the temporal circulation of *Hadropithecus*: the internal carotid, the stylomastoid, and the tympanic, of which the last two are primarily concerned with the tympanic region.

The tiny internal carotid entered the bulla via the carotid foramen; on the surface of the cochlea, it separated into two branches; a stapedia artery, which passed between the legs of the stapes above the oval fenestra and penetrated the endocranium after passing across the epitympanic recess; and an entocarotid, which traveled to the front of the cochlea, ran along the longitudinal septum of the tympanic cavity, and entered the neurocranium behind the oval foramen to pass anteriorly to join the cerebral arterial circle (of Willis). The tiny internal carotid evidently played a minor part in cerebral irrigation, the brunt of this task having been borne by the vertebral arteries.

The stylomastoid artery branched off from the occipital artery in the region of the posterior lacerate foramen. Almost immediately an inferior branch was given off; this entered the tympanic cavity after passing through the tympanohyal fossa. The main trunk passed through the secondary orifice of the stylomastoid fossa, turned back again through the inferior stylomastoid foramen, and shared the facial canal with the facial nerve before giving off a superior branch to the annular region, and passing between the two stylomastoid foramina. A median branch entered the tympanic cavity by way of the canal of the chorda tympani to serve the tympanic membrane, then rejoined the facial canal.

The tympanic artery traveled with the chorda tympani after branching off from the internal maxillary artery, and once in the tympanic cavity anastomosed with the branches of the stylomastoid artery.

Venous drainage of the neurocranium was primarily by way of a system linked to the lateral and inferior petrous sinuses. The lateral sinus connected with the internal jugular vein via the jugular foramen of the posterior lacerate complex. The associated temporal (petrosquamous) sinus was drained via the postglenoid foramen by the external jugular vein. The mastoid vein, likewise associated with the lateral sinus, followed the mastoid canal after passing through a foramen in the petrosquamous suture, medial and anterior to the posterior lacerate foramen.

The inferior petrous sinus, associated with the cavernous dural sinus, connected with the internal jugular at the posterior lacerate foramen. The stylomastoid vein, whose path closely followed that of the corresponding artery, received middle and superior branches before passing through the foramen of the tympanohyal fossa, and an inferior branch subsequently, then joined the occipital vein in the region of the posterior lacerate foramen.

GROSS DIFFERENCES BETWEEN THE TWO CRANIAL SPECIMENS OF *Hadropithecus*

As Lamberton ("1937" [1938]) pointed out, considerable differences do exist between the two known crania of *Hadropithecus*. The Andrahomana specimen is rather smaller in overall skull length (128.2 mm. as compared with 141.8 mm.) than is that from Tsiravé, but the difference is easily matched within either species of *Archaeolemur*. The specimen VNHM 1934 IV 1 has suffered considerable damage: virtually the entire frontal bone is missing, the posterior part of the palate is lacking (particularly on the right side, where M²⁻³ are lost), the pterygoid areas are heavily damaged, and most of the right zygomatic arch is missing; but it is clear that the facial profile of this specimen differs from that of the Tsiravé individual in being slightly less steep, although this difference has probably been exaggerated by Lamberton ("1937" [1938]) and subsequent authors. The nasal bones are, however, rather more salient in VNHM 1934 IV 1, although, of course, this is itself a reflection of facial shortness.

The Vienna specimen is rather more brachycephalic than that from Tsiravé, since its bizygomatic width is not reduced proportionally to its length (respectively, the cephalic indices are 85.6 [VNHM 1934 IV 1] and 81.0), but such a difference can hardly be regarded as particularly significant. The maxillary tooth rows of the Académie Malgache specimen and those of VNHM 1934 IV 1 show similar curves of Spec.

The primary difference between the two specimens lies in the stronger development in the Tsiravé cranium of muscle-related crests and ridges. In the Andrahomana individual the sagittal and nuchal crests are far less pronounced than in the Tsiravé specimen, although they are nevertheless distinct. However, to judge from the degree of sutural obliteration and dental

wear in the two specimens, the Tsiravé individual was of much greater age than the apparently newly adult Andrahomana individual. Seth (1964) has noted that in *Nycticebus coucang* both sagittal and nuchal crests become much more pronounced with age, apparently to the extent that in most cases it is possible to estimate relative age solely on the grounds of crest development. On the basis of this work alone, it is possible to agree with Lamberton ("1937" [1938]) that "les différences . . . auraient pu s'atténuer, et peut-être même s'effacer, avec l'âge" (p. 3).

Cranial measurements of the two specimens are shown in table 7.

THE MANDIBLE

Age differences in the mandibles of *Hadropithecus* are even more striking than those existing in the cranium. The following description is based on younger material, particularly VNHM 1934 IV 2/1a and b, because it is generally better preserved; differences apparent in older specimens are discussed subsequently.

Whether in young individuals or in old, the mandible of *Hadropithecus* is massively constructed. The ascending ramus is higher than in *Archaeolemur*, and the corpus is broader, although no shallower. The mandible is particularly broad in the region of M_2 - $_3$, although its ventral border is excavated medially, in the area of origin of the anterior belly of the digastric muscle. The ascending ramus is extremely long anteroposteriorly (44.0 mm. in VNHM 1934 IV 2/1a), and both its anterior and posterior borders rise vertically relative to the long axis of the corpus (in fact, they slope slightly anteriorly relative to the plane of the tooth row, corresponding to the curve of Spee). The ascending ramus is more anteriorly placed than is that of *Archaeolemur*, its anterior border beginning its rise at about the midpoint of M_2 . In all extant indriines the entire tooth row lies in front of the anterior border of the ascending ramus, a reflection of the relatively longer faces of the group.

The entire gonial angle is not preserved in any specimen, but it is almost certain that there is very little material missing from the angle in

VNHM 1934 IV 2/1a, which is smoothly rounded and which projects both posteriorly and ventrally. It is also somewhat incurved. The masseteric fossa is well marked and deep. The corresponding medial surface of the mandible is strongly excavated, due to both the incurving noted above, and the breadth of the bony buttress accommodating the tooth row, which lies immediately anterior to it. This alveolar bone is displaced medially by the breadth of the shelf between the alveolar bone and the anterior border of the ascending ramus. The mandibular foramen, unprotected by a lingula, is large, and lies at the level of the tooth row.

The coronoid process, whose dorsal extremity is rugose, exceeds the condyle in height by as much as 7.0–8.0 mm. The mandibular notch is nonetheless relatively shallow; the condyle is anteroposteriorly more restricted than in *Archaeolemur*, and is divided into lateral moieties by an anteroposterior waisting.

The corpus is, as remarked earlier, massive, and composed almost entirely of hard compact bone, with cancellous tissue immediately around and between the dental roots. It is widest posteriorly, narrowing anteriorly as the long axis of the tooth row comes into line with that of the corpus. Mental foramina are variable in number; for instance, VNHM 1934 IV 1 probably had only a single large foramen at mid-depth of the corpus, below the rear of the caniniform, while in VNHM 1934 IV 2/1a three small foramina are strung in line high up on the corpus from the level of the rear of P_3 to that of the rear of the caniniform.

The angle of the fused symphysis is somewhat more vertical than that of *Archaeolemur*; the symphyseal cross section is generally similar in both genera. The anterior surface of the symphysis recedes in a gentle curve, the diminution of the incisors obviating the dorsal bulge often seen in *Archaeolemur*. The planum alveolare slopes very steeply ventrally and posteriorly, so that the genial fossa appears as a pit inset into a highly oblique surface. There is in consequence no recognizable superior transverse torus, while the inferior transverse torus is smoothly rounded and not very high.

FIG. 20. *Hadropithecus stenognathus*, lateral views of the three most complete mandibular specimens. Above: from Tsiravé (AM uncatalogued). Center: Andrahomana (VNHM 1934 IV 1/1). Below: Andrahomana (VNHM 1934 IV 2/1a). All $\times 5/6$.



Age changes in the mandibular morphology of *Hadropithecus* are most pronounced in the angular region. Given the very small sample sizes it is dangerous to generalize, but a clear picture does emerge from available evidence. The two relatively complete mandibular specimens belonging to individuals of advanced age are the holotype of the genus, VNHM 1934 IV 1/1, with its left-side counterpart VNHM 1934 IV 1/2, and the partial mandible associated with the Tsiravé cranium, now also in the collections of the Académie Malgache. Both individuals show an extremely sharp medial inclination of the gonial angles. The angle is more projecting than it is in the younger specimens, and both medial and lateral surfaces are a great deal more rugose, particularly in showing rugged crests running roughly in the orientation of the attached muscles. The absence of the coronoid process in both these individuals unfortunately precludes any observation of age changes in this feature. It is noteworthy that the Académie Malgache specimen shows the characteristics described above more strongly than does VNHM 1934 IV 1/1-2, as the dental wear on this individual is more advanced than in any other specimen.

PERMANENT DENTITION

The same problems exist in the interpretation of the dental formula of *Hadropithecus* as do in that of *Archaeolemur*, and the same formula is preferred, namely: $\frac{2.1.3.3}{2.0.3.3}$. No known specimen of *Hadropithecus* possesses the diastemata between I₂ and P₂ and I₂ and C which occur in many individuals of *Archaeolemur*, but the two genera do share the extremely thick dental enamel coating and the close mesiodistal packing of the cheek teeth.

The description of the teeth of *Hadropithecus* given here is based on a variety of specimens. That of the upper dentition apart from the incisors and M¹ (the latter is described from the isolated BM M7869) is based on a beautifully preserved subadult maxilla, VNHM 1934 IV 2, whereas the sole upper incisor (I²) is known from the Tsiravé cranium. The lower premolars and molars are described from VNHM 1934 IV

TABLE 8
MEASUREMENTS OF UPPER DENTITION (IN MILLIMETERS) OF *Hadropithecus stenognathus*

	Mean	Standard Deviation	Sample Size
I ¹ width	3.7	—	1
I ¹ length	—	—	—
I ² width	2.1	—	1
I ² length	6.3	—	1
C width	—	—	—
C length	—	—	—
P ² width	7.8	1.5	3
P ² length	9.4	1.0	3
P ³ width	7.2	0.5	4
P ³ length	9.7	1.1	4
P ⁴ width	14.2	1.0	4
P ⁴ length	9.3	1.0	4
M ¹ width	12.8	0.4	5
M ¹ length	10.9	1.1	5
M ² width	12.3	0.3	4
M ² length	10.0	0.8	4
M ³ width	8.6	1.0	4
M ³ length	7.8	1.7	4

2/1a, the lower incisors from the Tsiravé mandible, VNHM 1934 IV 1/1 and IV 3.

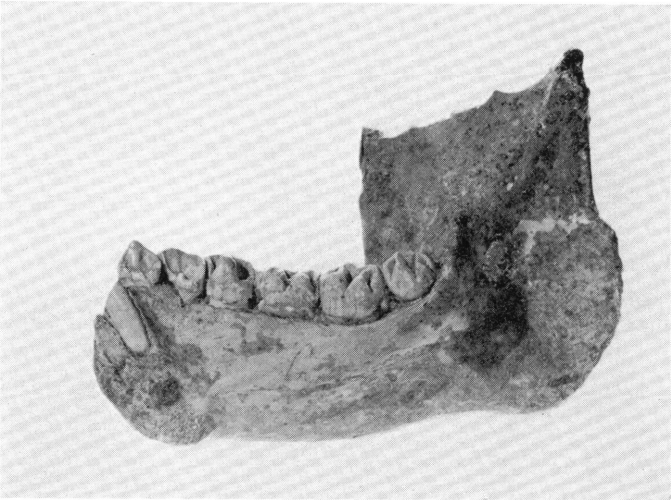
Dental dimensions are in tables 8 and 9.

UPPER DENTITION: I¹⁻²: As noted above, only a single upper incisor of *Hadropithecus* is known, I² in the Tsiravé cranium. The same specimen, however, contains the root of I¹, the crown of which was evidently similar in size to that of its neighbor. I² is a small, simple tooth, of mesiodistally compressed peg shape. It is orthally implanted, small-rooted, and possesses a horizontal wear surface.

C: This tooth is greatly reduced compared with the already relatively diminutive condition of its homologue in *Archaeolemur*, and is also morphologically much changed. It is a mesiodistally short, laterally compressed tooth with a crown no higher than those of adjacent teeth, and is triangular in profile. Its labial face is gently convex, its lingual face yet more gently concave, with a faint lip posteromedially.

P²⁻⁴: The upper premolars form a series of increasing complexity posteriorly. P² is some-

FIG. 21. *Hadropithecus stenognathus*, medial views of the three most complete mandibular specimens. Above: from Tsiravé (AM uncatalogued). Center: from Andrahomana (VNHM 1934 IV 1/1). Below: Andrahomana (VNHM 1934 IV 2/1a). All $\times 5/6$.



what bladelike, as in *Archaeolemur*, with a high shearing edge, somewhat V-shaped in outline, running anteroposteriorly along the lateral side of the tooth, and a much lower crest running posteromedially to its anteromedial border to meet a similar crest running medially from the posterior extremity of the lateral crest. The three crests together border a small, triangular depression.

In P³ the posterior crest has disappeared, but a large, selenodont protocone has formed lingually, to form the entire medial border of the tooth. The lingual border of the protocone slopes steeply toward the alveolar margin of the tooth. Buccally, there is a relatively distinct paracone, with a bladelike parastyle and mesostyle traveling anteriorly and posteriorly from it, respectively. Buccally, the parastyle is deeply indented in its posterior portion, forming a cleft between its anterior part and the paracone; this cleft terminates dorsally in a small cingulum. There is a deep, V-shaped central fovea between the protocone and the buccal blade.

The broad P⁴ is still more complex, and is almost rectangular, apart from its lingual margin; it is more high crowned than its predecessors. The paracone is still the highest cusp, and its parastyle and mesostyle are distinct cusps closely approximated, but slightly lingual, to it. The protocone is morphologically similar to, but much larger than, that of P³, and likewise forms the entire lingual margin of the tooth. A large transverse crest, which nevertheless fails to make complete contact with the protocone, runs lingually from the paracone, dividing the central basin of the tooth into anteroposteriorly constricted, but deep, anterior and posterior foveae.

M¹⁻³: The upper molars are remarkably broad and high crowned, and decrease in size from front to back. The only completely unworn M¹ known to the writer is BM M7869, an isolated molar from Andrahomana. This tooth is steep-sided, and roughly square. The large, lobular paracone and metacone lie, anteriorly and posteriorly respectively, on the central portion of the buccal side of the tooth; in most individuals a small cingulum lies externally at the base of the cleft between them. The protocone and hypocone are not distinct cusps; rather, they are in the form of high, rounded, medially convex crests. High, rounded transverse crests cross the tooth between the paracone and proto-

cone, and the hypocone and metacone, forming deep, distinct, anterior, central, and posterior foveae. The anterior fovea is bounded mesially by a buccally curving extension of the protocone crest; the posterior fovea is bounded distally by a similar extension of the hypocone crest. Lingually, at the base of the protocone, and in the cleft between the protocone and hypocone, lies a large, beaded cingulum raised some way beyond the alveolar margin of the tooth.

M² is built on the same plan as M¹, but is somewhat shorter mesiodistally; its internal cingulum is generally slightly reduced compared with that of M¹.

M³ is greatly reduced, and approximately triangular in shape. There is no recognizable metacone or hypocone, although the relatively small paracone and protocone are linked by a transverse crest, as in the other molars. A parastyle runs mesiobuccally from the paracone, while a crest runs from the paracone to meet it; another crest runs distobuccally to terminate in what might be regarded as a small metacone. Anterior and central foveae are therefore present, but there is no cingular development.

LOWER DENTITION: I₁₋₂: The only unworn incisor of *Hadropithecus* known is the erupting I² in VNHM 1934 IV 3. This is a very small tooth, laterally compressed at its root, but with a labiolingually compressed upper part of the crown, which terminates superiorly in a knife-edge. In frontal view it is narrowly rectangular; in lateral profile the anterior border of the tooth is gently convex, while the posterior border is steeply sloping. The central incisor, present in VNHM 1934 IV 1/1 and in the Tsiravé mandible, is essentially similar but is narrower mesiodistally. These teeth resemble their homologues in *Archaeolemur* far more than do their upper counterparts.

P₂₋₄: The lower premolars, like their upper counterparts, form a series of increasing complexity posteriorly. P₂ is a simple tooth, larger than, but reminiscent of, the upper canine. Inverted V-shaped in lateral profile and laterally compressed, the tooth consists of a central pillar coinciding with the apical axis of the V; anteriorly and posteriorly the pillar is bounded by sharp, steeply sloping crests. P₃ is an elaboration of the same basic pattern, but the anterior and posterior crests are less steeply sloping, forming a blade reminiscent of that of the homologous tooth in *Archaeolemur*. The anterior



FIG. 22. *Hadropithecus stenognathus*, mandibular specimens. *Left*: from Tsiravé (AM uncatalogued). *Right*: Andrahomana (VNHM 1934 IV 1/1). Both natural size.

crest turns buccally at its anterior extremity, and the posterior crest turns lingually at its posterior extremity; posteromedially there lies a small cingulum. P_2 and P_3 are closely approximated, and their blades are longitudinally aligned.

P_4 is basically cruciate in form, and square in outline. The protoconid is situated at the center of the tooth, with crests radiating laterally, anteriorly, and posteriorly from it. The largest of these is the medially projecting metaconid lobe, which broadens medially to form the anterior lingual border of the tooth. Anteriorly from the protoconid runs a paraconid crest, which terminates in alignment with the blade of P_3 , to which it is closely approximated. A transverse crest, into which the paraconid crest

runs, marks the anterior border of the tooth. Crests similar to that of the paraconid run laterally and posteriorly from the protoconid; a fovea is thereby formed at each corner of the tooth.

M_{1-3} : The lower molars approximate to mirror images of the upper ones, and decrease in size posteriorly. In M_1 the metaconid and entoconid are lobular, as are the paracone and metacone of M^1 , and are linked to the protoconid and hypoconid, respectively, by rounded transverse crests. These latter cusps are linked by a bulbous crest which runs anteriorly into a large, transverse paraconid crest which forms the anterior border of the crown. A small crest also runs medially, and somewhat posteriorly,

TABLE 9
MEASUREMENTS OF LOWER DENTITION (IN
MILLIMETERS) OF *Hadropithecus stenognathus*

	Mean	Standard Deviation	Sample Size
P ₂ width	5.9	0.6	4
P ₂ length	8.2	1.3	4
P ₃ width	7.7	1.4	5
P ₃ length	10.2	1.4	5
P ₄ width	11.0	0.6	8
P ₄ length	11.7	2.7	8
M ₁ width	10.9	1.2	12
M ₁ length	12.2	0.7	13
M ₂ width	11.7	0.8	14
M ₂ length	11.9	0.8	15
M ₃ width	10.0	1.0	10
M ₃ length	10.6	0.2	10

from the hypoconid along the posterior border of the tooth. A pronounced, beaded external cingulum is situated at the base of the protoconid, and in some cases also runs some distance along the base of the hypoconid. The cingulum is raised well above the alveolar margin of the

tooth. Anterior, central, and posterior foveae are present, but are less marked than in the upper molars.

M₂, although smaller, is similar in form to M₁, but the anterior crest and the entoconid are somewhat reduced; in addition, the hypoconid is usually shifted slightly posteriorly, into contact with the posterior transverse crest. The external cingulum is generally reduced or lacking. M₃ is round in outline, and generally reduced relative to the other molars. The protoconid and metaconid remain, linked by a high transverse crest, but the hypoconid is reduced, and buccally shifted; the entoconid has become a tiny cuspule closely approximated to the lingual aspect of the hypoconid. A crest links the hypoconid with the protoconid, and the small transverse paraconid crest is likewise linked with this cusp. The anterior and central foveae are open lingually.

DECIDUOUS DENTITION

The milk teeth of *Hadropithecus* have been well described by Lamberton (1938); it is unnecessary to repeat those descriptions here.

MASTICATORY MUSCULATURE

ARCHAEOLEMUR

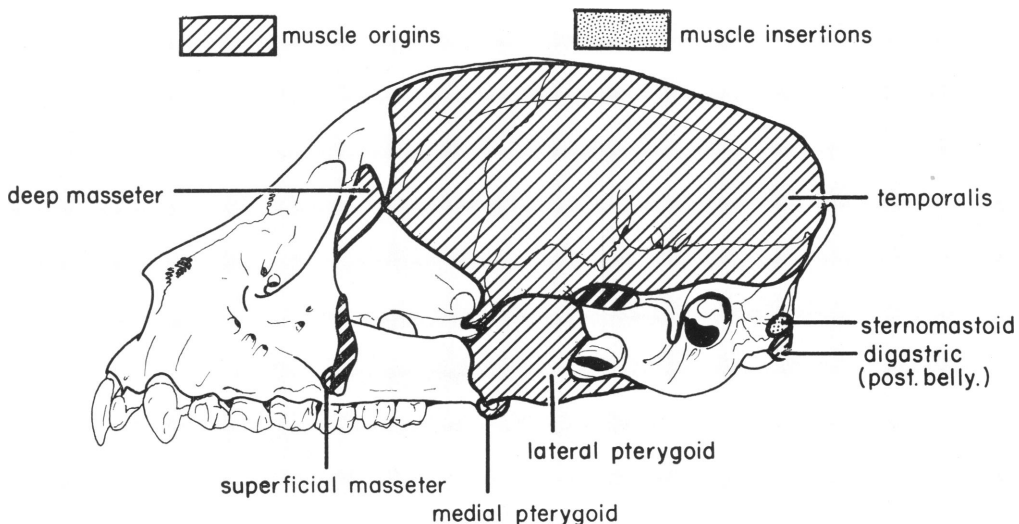
It is now becoming increasingly clear that the form of bone is not in itself a primary seat of genetic activity. Rather, the morphology of a given bone is largely, if not entirely, the result of its ontogenetic interaction with the surrounding soft tissues, whose form is much more closely determined genetically (cf. Grüneberg, 1963). Thus a great deal of information regarding the influence of the cranial musculature on skull form can be derived by considering the problem under three related headings: the local, external effects upon the skull of the demands of muscle attachment; the more general effects of these demands; and, less directly, the results of evolutionary forces acting to produce the optimum muscular disposition. In this section the first category of effects is considered as part of (indeed, makes possible) the reconstruction of the masticatory myology of *Archaeolemur*; the others are discussed later.

M. TEMPORALIS

The degree of development of M. temporalis represents one of the most striking distinctions between *Archaeolemur majori* and *A. edwardsi*, the

most prominent result of the relative hypertrophy of this muscle in *A. edwardsi* being the almost invariable presence of a sagittal crest.

Temporalis in *A. edwardsi* took origin over the entire postorbital area of the lateral and dorsal aspects of the cranial vault. The temporal lines, which are confluent with the lateral posterior margin of the postorbital bar, and mark the posterior border of the swollen frontal convexity, indicate that temporalis extended well forward, its most anterior portion originating from the posteromedial aspect of the postorbital bar. In most cases this area of origin extends almost as far along the postorbital bar as the frontomalar suture. Inferior and slightly posterior to this, the area of temporalis insertion is demarcated from the orbital fossa by a small, variably developed ridge of bone which generally corresponds to the superior limit of the orbital cone. Inferiorly, this ridge generally terminates in an anteriorly directed process lateral to foramen rotundum. From this process, a similar ridge runs almost horizontally toward the anterior origin of the zygomatic process of the temporal, demarcating the inferior limit of the area of origin of temporalis. Variably present is a long, low bony



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FIG. 23. *Archaeolemur edwardsi*, muscle attachment areas on the cranium, lateral view.

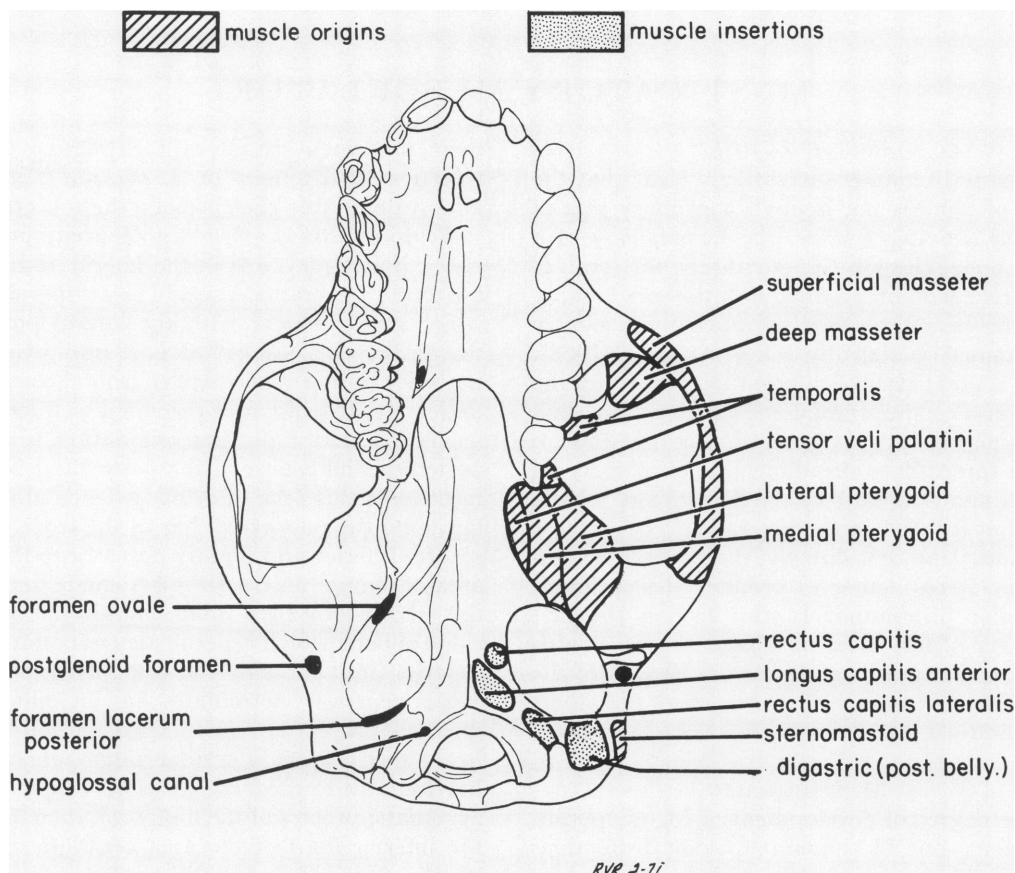


FIG. 24. *Archaeolemur edwardsi*, muscle attachment areas on the cranium, ventral view.

ridge which runs posterodorsally up the parietal from around the point of intersection of the frontoparietal suture with the squamous suture. If projected anteroinferiorly, the line of this ridge coincides with the tip of the coronoid process in the temporal fossa when the teeth are in full occlusion. This feature is presumably due to a broad fascial attachment of the muscle, and may well indicate a functional division of the separately innervated anterior and posterior moieties of the temporalis.

It is not completely clear to what extent the internal surface of the zygomatic arch was utilized in temporal attachment. It seems likely, however, that the part of the arch constituted by the zygomatic process of the temporal bone, i.e. its posterior and dorsal portion, gave rise to short fibers of the temporalis.

Temporalis inserted down the anterior border of the ascending ramus of the mandible almost

to the occlusal level of the lower tooth row, the attachment along this border apparently having been fascial. On the medial surface of the coronoid process insertion was wide, although difficult to delineate precisely because of the paucity of relevant subfossil material. The studies of Washburn (1947), who showed that total resorption of the coronoid process takes place when temporalis is removed completely, and of Avis (1959), who found that coronoid shape changes markedly subsequent to removal of part of the muscle, indicate the profound effect of temporalis development on coronoid form. The robustness of this process in *A. edwardsi* suggests a temporalis of great bulk. The height of the sagittal and nuchal crests, both of which frequently exceed 10.0 mm. at their maximum, similarly suggests that temporalis was a very substantial muscle, as does the breadth of the area of origin on the posterior aspect of the

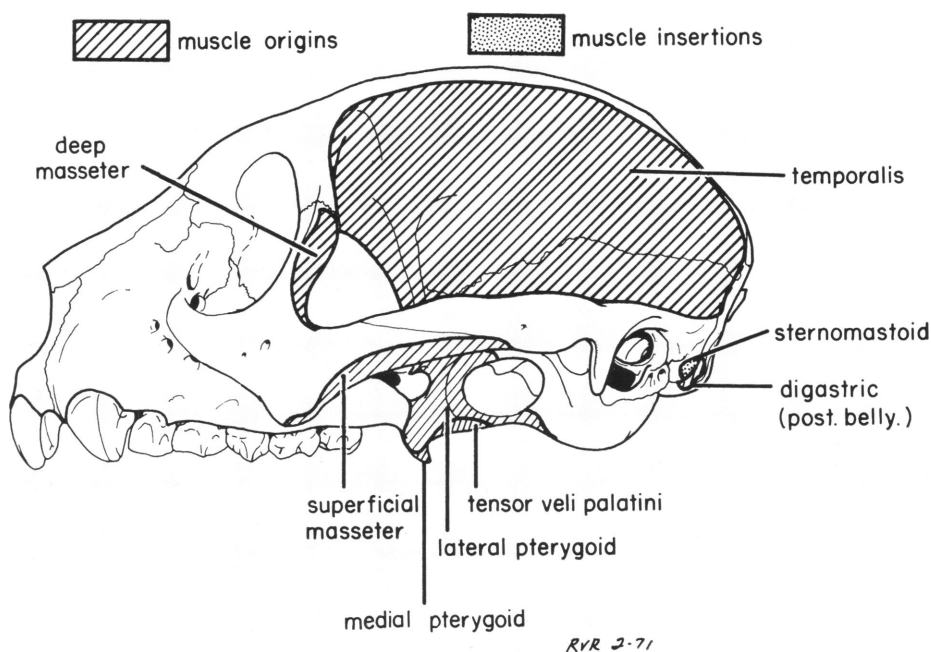


FIG. 25. *Archaeolemur majori*, muscle attachment areas on the cranium, lateral view.

orbital process of the frontal. Minimum thickness appears to have been attained for a short distance along the nuchal ridge, adjacent to its junction with the sagittal crest. Very strong development of the pars horizontalis of this muscle is suggested by the great width of the horizontal surface of the zygomatic process of the temporal bone, and the expansion of the nuchal crest posterior and slightly dorsal to this. Great temporalis bulk is also indicated by the great breadth of the temporal fossa, a characteristic achieved by the narrowness of the post-orbital constriction as well as by the lateral bowing of the zygomata.

Archaeolemur majori, although considerably more gracile than its congener, likewise possessed a large temporalis relative to the remainder of its masticatory musculature. The elevation of the superior temporal lines is variable (the distance between the most dorsal points on the left and right lines ranging from approximately 4.0 mm. to about 24.0 mm.), and sagittal cresting never occurs, but the boundaries of temporalis origin are nonetheless invariably well marked. Expansion anteriorly of temporalis is limited by the relative smallness of the frontal convexity, which displaces the anterior area of temporalis origin ventrally and somewhat

laterally on to the posterointernal aspect of the frontal orbital process. The importance in this animal of the posterior fibers, and particularly of the pars horizontalis of temporalis, is emphasized by the depression of the parietal adjacent to the lateral part of the nuchal ridge.

M. MASSETER

The division of this muscle in *A. edwardsi* into deep and superficial portions is clearly evident in its areas both of origin and of insertion. The superficial masseter took origin from almost the entire length of the ventral face of the zygomatic arch, from a point posterior to the ventral portion of the temporomalar suture and just anterior to the most forward boundary of the capsule of the temporomandibular joint, to the tip of the process marking the anteroventral margin of the zygomatic arch. This tubercle presumably marked, as it does in extant lemurs, the position of a concentrated tendinous attachment of the superficial masseter. The surface of attachment of this portion of the muscle is rugose, and is inclined laterally for most of its length, presumably to maximize its area. In its posterior half, the dorsal boundary of this laterally inclined surface is generally coincident with the temporomalar suture.

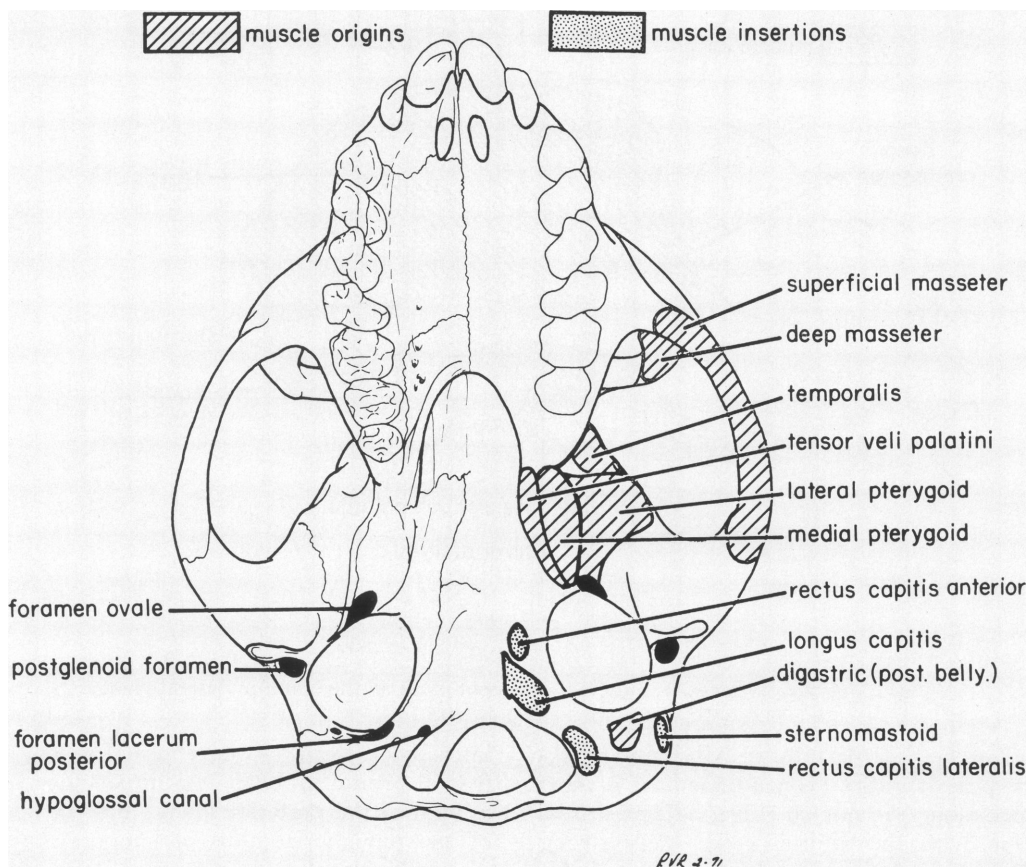


FIG. 26. *Archaeolemur majori*, muscle attachment areas on the cranium, ventral view.

The superficial masseter inserted broadly over the lateral surface of the rounded mandibular angle, posterior and ventral to the masseteric fossa. This area is variably rugose, most commonly showing low crests which run obliquely across its surface and were presumably related to tendinous or fascial muscle attachment. The posterior and ventral borders of the gonial area show a rugose cresting and become increasingly medially deflected with age; this cresting marks the confluence of the tendons of insertion of the superficial masseter and internal pterygoid muscles.

The masseteric fossa of the mandible, in which the deep masseter inserts, is strongly excavated and only slightly variable in extent, occupying the area inferior to the coronoid process and anterior to the rear of the mandibular notch, but not intruding upon the angular process. The surface area of insertion of this

part of the masseter was therefore approximately the same or slightly greater than that available to the superficial part of the muscle. The deep masseter originated tendinously along a sharp, inwardly turned ridge running along the superior edge of the zygomatic arch and up the posterior edge of the lateral margin of the post-orbital bar, to the level of the frontomalar suture. A deep impression occupying the entire posterior surface of the orbital process of the malar testifies to wide origin of the deep masseter in this area, as on the medial aspect of the zygomatic arch. The superior tendon of origin was presumably confluent with the temporal fascia, which must likewise have attached along the superior aspect of the zygomatic arch and on the lateral border of the malar orbital process. That this was a very substantial connective tissue sheet is suggested not only by the presence of the ridge already

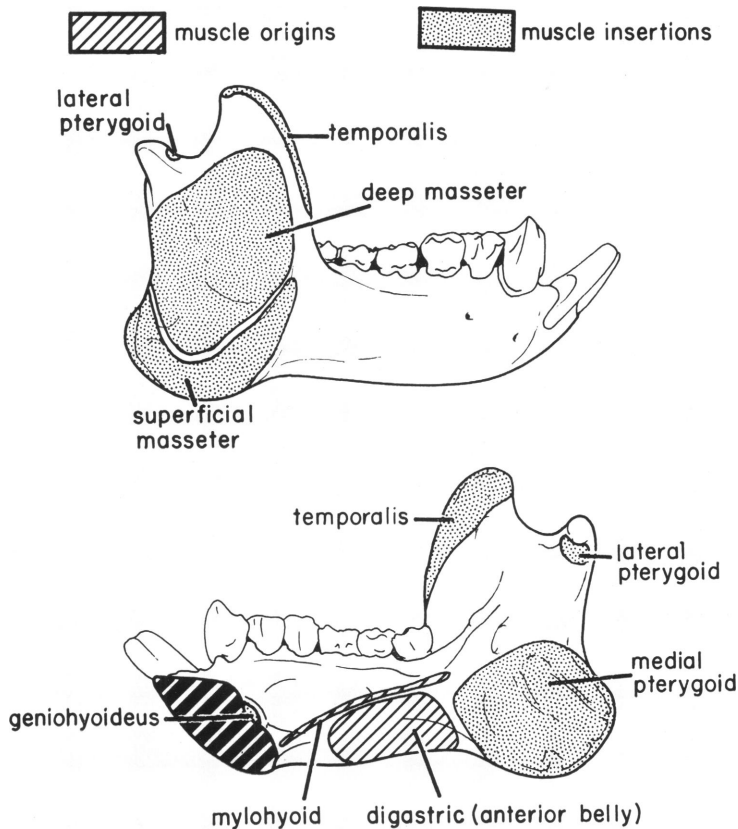


FIG. 27. *Archaeolemur*, medial and lateral views of muscle attachment areas on the mandible. Based on *A. majori* (BM M7374). There is no significant difference between the species.

referred to, but also by the slightly thickened superior edge of the sagittal crest in some individuals.

Archaeolemur majori apparently did not differ materially from the larger species in masseteric arrangement, although the area of origin of the deep masseter is generally less well marked.

M. PTERYGOIDEUS MEDIUS

The pterygoid fossa of *A. edwardsi* is deep and relatively wide, although somewhat circumscribed medially by strong development of the medial pterygoid plate (which is, nonetheless, dwarfed by the robust lateral plate). A small, variably present crest running along the roof and anterior wall of the pterygoid fossa, and slightly displaced medially, probably indicates the medial boundary of origin of the internal pterygoid. The fossa itself is deeply excavated,

and oriented slightly medially, providing a maximal area for attachment of the medial pterygoid. The origin of this muscle continues strongly on to the posterior aspect of the robust hamulus of the palatine.

Insertion of the medial pterygoid was broad over the medial surface of the mandibular angle, inferior to the level of the lingula of the mandibular foramen. The insertion extends almost to the level of the rear of the third molar at its most anterior point. This area of insertion is deeply excavated; its concavity is emphasized by the general inversion of the angle and by the sharp inward turning of its border, the site of attachment of the medial pterygoid tendon. All this seems to indicate that the medial pterygoid was a more powerful muscle than the superficial masseter. The internal surface of the gonial area is strongly rugose, the primary features of this

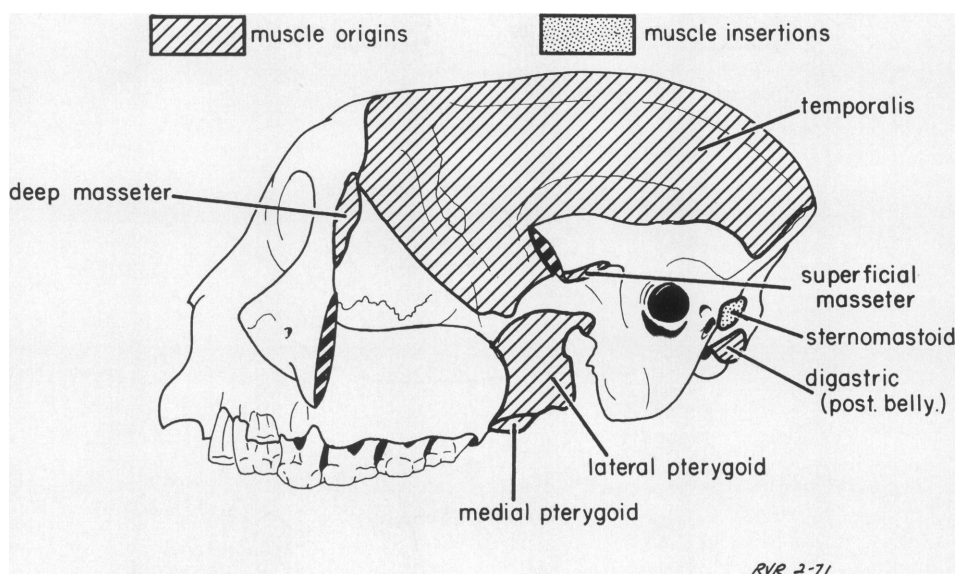


FIG. 28. *Hadropithecus stenognathus*, Tsiravé, lateral view of muscle attachment areas on the cranium.

rugosity consisting of ridges running from the angular border roughly in the line of action of the muscle.

M. PTERYGOIDEUS LATERALIS

The lateral pterygoid muscle took origin widely over the lateral surface of the lateral pterygoid plate, and also over the broad infra-temporal portion of the alisphenoid, where it was bounded anterolaterally by the crest marking the ventral boundary of temporalis. Posteriorly, the attachment extends for a short distance on to the ventral surface of the temporal bone. As the insertion of the lateral pterygoid was presumably largely related to the meniscus and capsule of the temporomandibular joint, it is impossible to say much regarding it, but as the anterior and medial surfaces of the condyle dorsal to the articular surface, and of the neck of the condyle, are heavily rugose, the insertion was probably strong.

Apart from the factor of size, there does not appear to have been any substantial difference in the pterygoid musculature between the two species of *Archaeolemur*.

M. DIGASTRICUS

The surface of origin in *Archaeolemur* of the anterior belly of the digastric shows this muscle

to have been relatively enormous. Small in *Lemur*, hardly larger in other lemurids, and only moderately developed in indriines, the digastrics reached the zenith of their development in the extinct lemurs. In *Archaeolemur* the rugose area of origin of the anterior belly occupies the entire depth of the mandible below the mylohyoid line from the level of the rear of P₃ to the anterior limit of the anterior process, slightly posterior to M₃. A tuberosity at midlength of the inferior border of this area suggests strong tendinous attachment at this point.

The posterior belly of the digastric attached to the paroccipital process, lateral to the occipital condyle and just posterior to the posterior bullar wall. Whereas the surfaces of origin of the anterior belly of the muscle are relatively of about the same size in both species of *Archaeolemur*, there is a considerable difference in the size of the paroccipital process; the area of origin of the posterior belly of the digastric in *A. majori* is commonly in the region of 30.0 mm.², while the figure in *A. edwardsi* is generally around 65.0–70.0 mm.², although there is some intra-species variation.

HADROPITHECUS

M. TEMPORALIS

Temporalis in *Hadropithecus* is still more

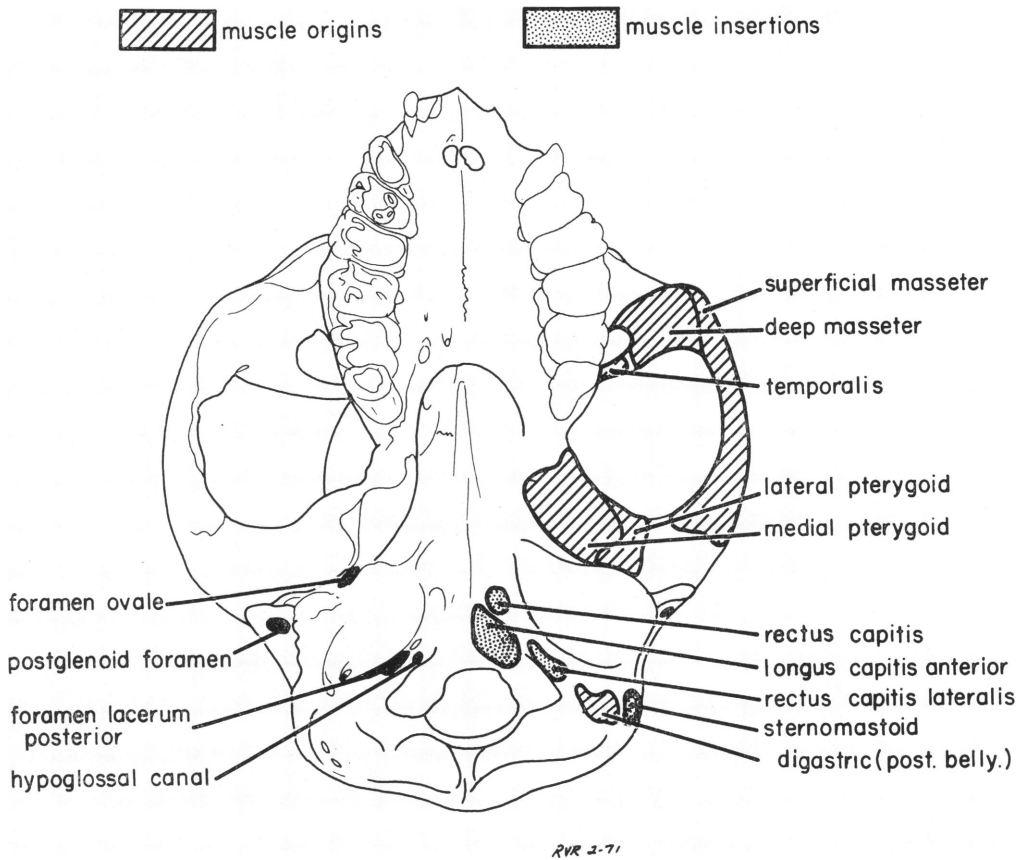


FIG. 29. *Hadropithecus stenognathus*, Tsiravé, ventral view of muscle attachment areas on the cranium.

strongly developed than in *Archaeolemur edwardsi*. The sagittal crest in the fully mature Tsiravé individual is well developed, particularly posteriorly; the muscle was evidently most bulky in its posterior portion. This is not to imply, however, that the anterior part of temporalis was at all weakly developed; the inflated frontal area and general elevation of the brain provided ample attachment area anteriorly for temporalis, whose area of origin spread on to the posterior aspect of the orbital process of the frontal. Ventral to this, an oblique crest denoting the dorsal boundary of the orbital fossa delimits also the margin of temporalis origin in this area. From the base of this crest, somewhat ventral to the inferior root of the zygomatic process of the temporal bone, the horizontal fibers of temporalis took origin along a line passing just dorsal to the zygomatic process and then slightly ventrally to meet the lateral extremity of the nuchal crest.

The dorsal border of the sagittal crest, notably on its posterior part, shows a considerable lateral lipping. This is interpreted to imply the attachment of a particularly well-developed temporalis fascia. Development of such a fascia appears to be associated not so much with the development of temporalis as with that of the masseteric muscles; Eisenberg and Brodie (1965) have demonstrated experimentally that the temporal fascia plays a major role in resisting the downward forces on the zygomatic arch caused by masseteric contraction. A strong temporalis fascia is also suggested by the inward turning and ridging of the dorsal border of the zygomatic arch, on which it attached.

Only a single specimen of *Hadropithecus*, VNHM 1934 IV 2/1b, the left dentary fragment associated with the Vienna cranium, preserves the coronoid process of the mandible. The tip of the coronoid and its anterior border, down to the occlusal level of the teeth, show

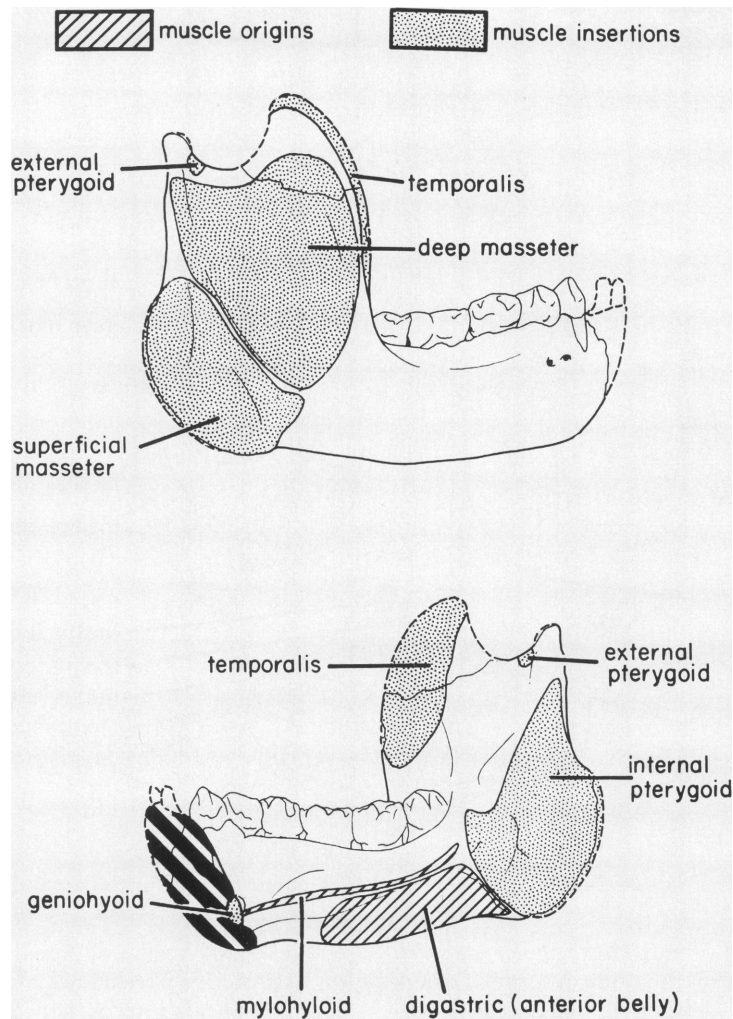


FIG. 30. *Hadropithecus stenognathus*, medial and lateral views of muscle attachment areas on the mandible.

considerable rugosity, which in this relatively gracile individual implies a strong and extensive temporalis insertion.

M. MASSETER

The existence of superficial and deep portions of this muscle is as clearly shown in *Hadropithecus* as it is in *Archaeolemur*. The superficial masseter took origin all the way along the ventral border of the zygomatic arch, from a point just anterior to the glenoid fossa to the anterior tubercle, level with the back of P⁴. This tubercle marks the point of attachment of a very strong anterior masseteric tendon. The ventral border of the

arch presents a relatively broad, rugose horizontal surface of muscle attachment. As no complete mandibular gonial angles of *Hadropithecus* are known, it is impossible to chart the precise extent of the insertion of the superficial masseter, but it is clear that it was considerable, the muscle having attached over the entire angular surface posterior and ventral to the anterior two-thirds of the masseteric fossa.

The deep masseter took origin along the tall medial aspect of the zygomatic arch and over the posterior aspect of the orbital process of the malar bone. This latter area of attachment extends even farther dorsally than in *Archaeo-*

lemur edwardsi. The area of insertion of the deep masseter is likewise greater and more strongly marked than in *Archaeolemur*; the masseteric fossa is extremely deeply excavated. The posterior margin of this area slopes ventrally and anteriorly from just below the neck of the condyle to a point somewhat below mid-depth of the mandibular corpus and posterior to the anterior border of the ascending ramus, then curves dorsally and closely parallels the anterior border. The deep portion of the masseter thus probably exceeded the superficial part of the muscle in bulk.

M. PTERYGOIDEUS MEDIUS

Unfortunately, the pterygoid plates have been damaged in both crania of *Hadropithecus*, and in the case of the Vienna specimen, almost totally destroyed. However, in the Tsiravé individual enough remains to permit a relatively accurate reconstruction of the areas of origin of the pterygoids.

In concert with the general deepening of the ventral part of the cranium in *Hadropithecus*, the pterygoid plates are considerably enlarged dorso-ventrally compared with those of *Archaeolemur*. The medial pterygoid plate, most of which is unknown, evidently curved laterally more strongly than do those of *Archaeolemur*, as do the lateral plates. The medial plate appears to have contacted the anterior bullar wall dorsally, just medial to the oval foramen, but it is uncertain whether any more ventral contact was made, although there are strong markings on the anterior face of the bulla, ventral to this, which imply attachment of the medial pterygoid. The pterygoid fossa is deep, and the lateral face of

the medial pterygoid plate, and the hamulus, afforded a large surface area for medial pterygoid attachment.

The medial surface of the large gonial angle provided an ample area for medial pterygoid attachment. The muscle inserted widely over the angle posterior to the back of M_3 , but avoided the area of the mandibular foramen.

M. PTERYGOIDEUS LATERALIS

The deepening of the lateral pterygoid plate provided an extensive area of origin for the lateral pterygoid, which also spread laterally on to the infratemporal portion of the alisphenoid where, as in *Archaeolemur*, its anterior margin is marked by the crest indicating the most ventral extent of temporalis. Rugose markings on the anterior face of the condylar neck suggest a strong insertion.

M. DIGASTRICUS

The anterior belly of this muscle in *Hadropithecus*, as in *Archaeolemur*, was huge. Its surface of origin occupies the full depth of the mandible, ventral to the mylohyoid line, between the mid-point of M_1 and the rear of M_3 . The area of origin of the posterior belly of the digastric was also large, although not proportionally so, the paroccipital process being developed similarly to that of *A. edwardsi*.

Briefly, then, the primary differences between the masticatory musculature of *Hadropithecus* and that of *Archaeolemur* were as follows: the musculature of *Hadropithecus* was generally more expanded; in the case of temporalis and the deep masseter, greatly so. Temporalis was shifted forward, as, to some extent, were the masseters.

MANDIBULAR MOVEMENTS AND DENTAL FUNCTION

ARCHAEOLEMUR

THE FACETS FORMED BY WEAR on the occlusal surfaces of the teeth of mammals have been used by several authors to reconstruct both the function of individual teeth (e. g. Butler, 1952; Mills, 1955, 1963, 1964, 1966; Butler and Mills, 1959; Welsch, 1967a, 1967b; Jenkins, 1969; Crompton and Hiiemäe, 1969a; Crompton and Situlumsden, 1970) and mandibular movements (Mills, 1966, 1967; Crompton and Hiiemäe, 1969a, 1969b, 1970), and have provided indexes of age in individual animals (Welsch, 1967a, 1967b). Although, as Crompton and Hiiemäe (1969a, 1969b, 1970) have pointed out, mandibular movements cannot be elucidated from wear facets alone where the dentaries are joined in a mobile syndesmosis, in animals where the halves of the jaw are united in an immovable synostosis the procedure is admissible.

A number of studies of mastication in extant mammals have been carried out using the technique of cineradiography. Experimental animals have included the rabbit (Ardran, Kemp, and Ride, 1958), the wallaby (Ride, 1959), the rat (Hiiemäe and Ardran, 1968), and the American opossum (Crompton and Hiiemäe, 1969b, 1970). Numerous authors have studied masticatory movements and forces in man, using a variety of ingenious techniques; recent examples are the studies of Adams and Zander (1964) and of Atkinson and Shepard (1967).

Crompton and Hiiemäe (1970) have recently combined both analysis of dental wear and cineradiography in the interpretation of molar occlusion and mandibular movements in the opossum, *Didelphis* Linnaeus. They distinguish in this animal a three-phase chewing cycle consisting of a preparatory stroke, a power stroke, and a recovery stroke. These three phases are, however, arbitrarily delimited, as the whole cycle forms a single smooth movement. Mastication in *Didelphis*, as in most mammals, is anisognathic, i.e. takes place on only one side of the mouth at a time; the cycle may be repeated 20 or 30 times on one side of the mouth before the food is shifted to the other side.

The preparatory masticatory stroke in *Didelphis* begins at the point of maximum gape of the lower jaw, and ends with the first contact of

opposing teeth, or of the upper teeth with the food. This stroke therefore involves both elevation and a slight lateral movement to line up the opposing teeth. The power stroke begins with the tooth rows in the final position of the preparatory stroke, i.e. with the mandibular dentition of the active side directly below the maxillary tooth row of the same side, and the lower dentition of the balancing side internal to its maxillary counterpart. At this stage the symphysis lies on the active side of the palatal midline. The exact form the power stroke takes depends on the nature of the food material being processed and the extent to which it has already been chewed. In the case of tough, bulky material the power stroke assumes a "crushing-puncturing" function, involving only tooth-food-tooth contact. When the food has been sufficiently triturated in this manner a shearing element dominates the power stroke, with tooth-tooth contact predominating. In both cases the mandibular movement is similar, the corpus on the active side moving upward and medially. The stroke terminates with the protocones of the upper molars locked firmly into the talonid basins of the lower molars. The recovery stroke consists of a simple vertical depression of the jaw, during which the condyle moves anteriorly over its articular surface.

Despite the fact that the dentition of *Didelphis* approaches very closely the primitive tribosphenic mammalian type, that it possesses a mobile symphysis, and that its masticatory musculature is not highly differentiated (Hiiemäe and Jenkins, 1969), Crompton and Hiiemäe believe (personal commun.) that the basic masticatory pattern of this animal is similar to that of man and other primates, particularly in showing an anterior slide following the power stroke of a three-stroke masticatory cycle.

The types of dental wear to be observed on molar teeth correspond to the two types of power stroke. Wear produced by the crushing-puncturing action is expressed in a gradual rounding and lowering of the cusps, whereas shearing wear results in the appearance on the shearing surfaces of the tooth of distinct contact facets. Microscopic examination of such facets frequently reveals the presence of tiny striations

running in the plane of the movement which produced the facet. In practice, these two types of wear often interact to maintain the capacity of the teeth for efficient functioning; as the removal of dental material by crushing wear reduces the height of the cusps, their sharpness is renewed by shearing wear.

In *Archaeolemur*, between the two species of which there appears to have been no difference in masticatory pattern, there were three discrete dental functions: incisal (nipping); premolar (shearing); and molar (crushing/grinding). The evidence for each of these three functions is discussed below. The incisors of *Archaeolemur*, both upper and lower, rapidly become heavily worn, to broad, flat surfaces. The acquisition and maintenance of such surfaces on the lower incisors, whose occlusal area is much greater than that of their upper counterparts, was assured by the thinness of the enamel coating on the posterior aspects of these teeth; this coating, and subsequently the unresistant dentine, was quickly abraded to produce a flat surface, "horizontally sharp" in the sense of Every (1970). Both incisal morphology and incisal wear strongly recall the condition seen in *Papio*. It seems probable that the incisal biting cycle in *Archaeolemur* was reminiscent, in essentials, of the molar cycle described by Crompton and Hiimäe for *Didelphis*, the critical phase again being the power stroke, which striations on the incisal surfaces suggest was produced by elevation together with strong bilateral retraction of the condyles.

The sequence of mandibular movements involved in incisal biting was thus probably as follows: the mandible dropped at the end of the previous cycle, and the condyles slid forward bilaterally; the mandible then swung upward until tooth-tooth or tooth-food-tooth approximation was achieved, the symphysis remaining in the midline. After the achievement of contact, the elevation of the mandible was continued, but the dominant movement was produced by strong bilateral retraction of the condyles, constantly symmetrical in position, into the glenoid fossae.

The premolar complex of *Archaeolemur* is unique, and without doubt represents the most specialized condition of this dental region to have arisen among the primates since the Paleocene. As we have seen, P², P³, and the anterior portion of P⁴ are laterally compressed

and aligned to produce a single shearing blade which works against a similar blade formed from P₂, P₃, and the anterior part of P₄. In a young adult *Archaeolemur* each tooth in the premolar series forms in profile a shallow V-shape, the apex of the V coinciding with the vertical buccal buttress of the tooth. During shearing these apexes move against the troughs formed at the contacts of successive teeth in the opposing row. The posterior shearing surface of P₂ moves against the anterior surface of P², the anterior surface of P₃ against the posterior surface of P², and so forth. This pattern of shear is slightly modified in the case of P⁴ and P₄ because of the molarization of the posterior moieties of these teeth. The development in P⁴ of a protocone and of ridges linking this cusp with the paracone and mesostyle provides additional shearing surfaces, which are opposed in the lower posterior premolar by the slight buccal extension of the protoconid and by the protostylid crest, in conjunction with the medial rotation of the metaconid crest. Although even in the freshest *Archaeolemur* posterior premolars the primary cutting edges have developed distinct shearing facets, it appears that the accessory edges come into use somewhat later in ontogeny.

The shearing facets on the premolar series in *Archaeolemur*, buccal in the lower jaw, lingual in the upper, are clearly marked, and are continuous along the entire series. They are set at about 45 degrees to the sagittal plane in young adults, and bear striations which run directly transversely; these are without doubt the products of tooth-tooth shearing wear. The mandibular movements involved in premolar shearing appear to have been as follows: the ipsilateral condyle moved posteriorly on its articular surface as the mandible was elevated to the point of dental approximation. A transverse movement then occurred, guided by the interlocking of the teeth, during which the ipsilateral condyle rotated medially, while locked in the back of the glenoid fossa against the postglenoid process; the contralateral condyle simultaneously translated backward into the articular fossa, total movement being in the order of 7.0 to 8.0 mm. The locking of the ipsilateral condyle assured the stability of movement necessary for strong, constant tooth-tooth approximation during single-surface vertical shear.

Compared with the amount of wear generally

to be observed on the incisors and premolars, wear on the molar teeth of *Archaeolemur* appears at first sight to be limited. Only very rarely does an individual show exposure of the dentine along the entire molar row, whereas an equivalent condition on all teeth anterior to the molars is relatively common. To some extent, however, this comparison is unfair, since the molar cusps of *Archaeolemur* appear to be entirely composed of enamel. For instance, the protocone and hypocone may be reduced almost to the level of the central fovea which they border before enamel perforation occurs. The enamel of the shearing premolars, on the other hand, while uncontestedly thick, covers an uncomplicated surface in a layer of uniform depth, and never reaches a thickness comparable with that obtained on cusps of the molar teeth.

Although there is a good deal of individual variation, enamel attrition appears, at least in the anterior portion of the molar row, to be shared about equally between the two types of attrition. Wear facets are never so sharply defined as in the case of the premolars, but can be detected in many individuals; distinct striations are less frequently present. However, it is possible to build up a composite picture by utilizing information gathered from a number of individuals, a process which reveals that mandibular movement during the power stroke was upward and transverse. The most striking gross effect of molar wear is the reduction or removal altogether of the lower buccal and upper lingual cusps, particularly of the anterior molars, a phenomenon readily explained by examination of occlusal relations in *Archaeolemur*.

Essentially, the molar rows of *Archaeolemur* consist of series of transverse ridges and valleys, the upper series complementary to the lower. These shear transversely across each other. Thus, during the power stroke, the M_1 protoconid passes through the basin formed by the combined anterior and posterior foveae of P_4 and M^1 respectively. Similarly, the combined anterior and posterior foveae of P_4 and M_1 move across the protocone of P_4 . The profiles of both basins and cusps are perfectly complementary. In the same manner, the central fovea of M_1 passes across the protocone of M^1 , the hypoconid of M_1 across the central fovea of M^1 , the posterior-anterior foveae of M_{1-2} across the hypocone of M_1 , the protoconid of M_2 across the posterior-anterior foveae of M^{1-2} , the central fovea of M_2

across the protocone of M^2 , the hypoconid of M_2 across the central fovea of M^2 , the posterior-anterior foveae of M_{2-3} across the hypocone of M^2 , the protoconid of M_3 across the posterior-anterior foveae of M^{2-3} , the central fovea of M_3 across the protocone of M^3 , and the hypoconid of M_3 across the central fovea of M^3 . At the end of this stroke, the entoconids of the lower molars are locked into the lingual spaces between the protocones and hypocones of the upper molars, with their tips fitting against the internal cingula of the latter, while the internal aspects of the buccal cusps of the lower molars are approximated against the internal aspects of the low ridges which connect the lingual cusps along the upper molar row.

For initial descriptive purposes the model of molar occlusion in *Archaeolemur* has been somewhat simplified. In practice it is slightly complicated by the decrease in absolute lateral movement toward the rear which occurs during ipsilateral rotation, and by the torsion, already described, of the occlusal surface along the molar rows. In the upper molar rows, the buccal cusps of M^1 are higher than the lingual ones; in M^2 they are slightly, and in M^3 considerably, lower. The reverse applies to the opposing molar rows. Thus while, in the case of the first molars, a pure transverse and upward action of the sort described above takes place, in the case of the second molar a crushing function is evident, and, in the case of the third molar, is dominant. It is therefore evident that the exaggerated wear of the buccal cusps of M_1 and the lingual cusps of M^1 compared with the other molars is due as much to a slight difference in function as to the delay (relative to *Indri*) in eruption of M_{2-3} referred to by Lamberton (1938), or to the nature of the animal's diet.

Most of the foregoing remarks are based on observations made on young adult individuals; age, with its attendant dental wear, brings about a small change in the masticatory pattern. In many young adult *Archaeolemur*, premolar shear and molar occlusion required two discrete movements; if an animal was using its premolars, then wished to shift function to the molars, it had to disengage the upper and lower dentitions by lowering the jaw and rotating the mandible slightly ipsilaterally about the ipsilateral condyle. In older animals, however, it was possible to incorporate the two functions as successive phases of a single smooth movement. This was

achieved through the wearing down of the premolars, which eventually became almost flat as the transverse component of movement during shearing increased at the expense of the vertical one. At the same time, molar relief was also decreased, although not to a comparable extent. In older individuals of *Archaeolemur* the posterior face of the upper canine has become worn by the tip and superior part of the anterior face of P₂, and thus has become functionally incorporated, to a limited extent, in the premolar row. The occasional presence of a few longitudinal striations on this wear surface in addition to the common transverse scratches, suggests that the preparatory mandibular stroke had a propalinal component.

The mandibular movement associated with the power stroke was very similar to that producing premolar shear. The stroke began with the condyle of the ipsilateral side at the back of the articular surface, but with the symphysis standing well to the ipsilateral side of the palatal midline. Lateral movement was produced by contralateral rotation of the ipsilateral condyle about itself, and the translation backward of the contralateral condyle to a locked position against the postglenoid process, at which time the mandible was symmetrical about the midline and centric relationship of the molars was achieved.

THE TEMPOROMANDIBULAR JOINT

The temporomandibular joint shares with those of wrist and knee the possession of an intra-articular meniscus. Parsons (1900) demonstrated that the absence of a meniscus in the knee-joint of the bat is associated with the animal's inability to rotate the lower leg; conversely, many marsupials possess an astragalo-fibular meniscus that permits a rotation of the ankle of a type impossible for placentals. Mills (1967) has therefore suggested that the function of the temporomandibular meniscus is to divide this joint into two components, one concerned with rotation, the other with a gliding, translatory motion. He concluded that

Generally . . . the presence of a meniscus within a joint would seem to be associated with the need for two types of movement combined with a rotation. In the mandibular joints of . . . [many] . . . mammals there are three movements: translation combined with rotation about a vertical axis, during lateral jaw movement, and also a hinge-like opening movement . . . It would seem extremely probable that translation

takes place in the upper joint and rotation in the lower. This is confirmed by the morphology of the joints; the upper surface of the disc is closely applied to the under surface of the squamosal with a lax capsule to this joint, to allow movement, while the lower surface of the disc is usually deeply concave, as one would expect in a ball-and-socket joint, with a more closely applied capsule (Mills, 1967, pp. 658-659).

MacConnaill and Basmajian (1969) have recently figured the movement of the human mandibular condyle in the glenoid fossa during depression of the lower jaw. From this figure it is clear that there is considerable translatory movement of the condyle of the mandible during this action in man, and the same was evidently true for *Archaeolemur*. Rotation of the ipsilateral condyle in *Archaeolemur* during the power stroke naturally demanded, given the fused symphysis, a motion of the contralateral condyle posteriorly along an arc of the circle whose diameter was the intercondylar space. This arc is so small relative to the diameter of the circle that it may be regarded as a simple fore-and-aft translatory motion. Examination of the bony morphology of the temporomandibular joint of both species of *Archaeolemur* indicates that the condyle had abundant anteroposterior freedom; the temporal articular area is extensive and very little concave, whereas the condyle was anteroposteriorly narrow. A strong sphenomandibular ligament is suggested by well-marked attachment areas. A specimen of *Lemur fulvus rufus* dissected by the writer possessed, despite strong ligamentous attachment, a condylar freedom similar to that posited for *Archaeolemur*; the condyle was allowed by the joint capsule and ligaments to move anteroposteriorly through a distance approximately equal to the length of the talonid basin of the first molar.

HADROPITHECUS

For a variety of reasons related to preservation and individual age as well as to dental usage, there are few facets of occlusal wear on known dental specimens of *Hadropithecus*, and almost none of those that do exist is striated. Virtually all such evidence of mandibular movement, which may be gained from material available to the writer for microscopic examination, comes from M¹ of VNHM 1934 IV 2. Unfortunately, this evidence is not entirely unequivocal. The tooth is worn lingually to the extent that the

enamel has been breached in the area of the protocone, and leveled on the hypocone. In the area of the longitudinal lingual crest there are relatively strong transverse striae, particularly on the hypocone; on other areas of the tooth, which are much more lightly striated, the pattern is less consistent. On the buccal tip of the paracone lobe are a few light scratches running anterolaterally; internal to these further faint striae run almost anteroposteriorly. A similar situation is found in the case of the metacone lobe, with the exception that the buccal striae fan out, being oriented transversely to anteroposteriorly. Thus the area of heaviest wear shows transverse striae, whereas the scratches on other areas of the tooth show no consistent orientation. This latter feature is not an artefact of cusp morphology. The fact that no sharp, plane facets are formed by wear at this stage is significant in terms of the type of matter processed.

Such evidence as the analysis of wear facets produces can be combined with manual occlusion of associated upper and lower jaws (i.e. the aged Tsiravé mandible and cranium, and the young adult VNHM 1934 IV with VNHM 1934 IV 2/1a and 1934 IV 2/1b) to suggest the masticatory pattern described later.

Ironically, the only upper and lower incisal association known (Tsiravé: all mandibular incisors known, but only L1² of the upper jaw) represents an example of malocclusion. Plane facets of wear exist on all lower incisors, but in all except L1₂, these facets are tilted anteriorly by about 45 degrees. That of L1₂ is approximately horizontal, as is that of its opponent in the upper jaw. As the incisors in the type mandible VNHM 1934 IV 1/1 conform to the latter type of wear, L1₁₋₂, RI₁ in the Tsiravé mandible represent an occlusal anomaly. Unlike the case in *Archaeolemur*, there are no striae on the facets to indicate the direction of movement. The degree to which the incisors are worn, however, indicates that, compared with the posterior teeth, they were little used. In the Tsiravé cranium, for instance, M¹ is almost totally worn out, and the other cheek teeth show very considerable wear, but the relatively less hypsodont incisors are comparatively little worn. In an *Archaeolemur* of equivalent dental age they would have been worn almost to their alveolar borders. Similarly, in the rather younger, but nonetheless dentally relatively old VNHM 1934 IV 1/1, the incisors show very little wear indeed, i.e. no more

than the amount required to produce the initial breach of the relatively thin enamel. This is not necessarily a phenomenon related to the dental eruption sequence; in the subadult VNHM 1934 IV 3, the permanent lateral incisor is almost as advanced in its eruption as is M₂ (see radiograph in fig. 31).

In young adult *Hadropithecus* the postincisor anterior dentitions formed morphological units similar to those of their homologues in *Archaeolemur*; the canine and anterior premolar above, and P₂₋₃ below, form in profile a saw-toothed slicing edge morphologically suited for a scissoring action, the posterior border of the upper canine forming the most anterior component of this sequence. The buccal longitudinal crest of P³ and the paraconid crest of P₄ also form part of this shearing series, but the medial portion (protocone crest) of P³, and the remainder of P₄, are clearly united functionally with the molar series.

Manual occlusion of the opposing dentitions suggests that the basic occlusal pattern of *Hadropithecus* is not as dissimilar to that in *Archaeolemur* as a superficial assessment of the complication of the molar crowns might imply. The basic differences in *Hadropithecus* appear to be directed toward hypsodonty and the maximization of the available grinding surface. Occlusion during the power stroke appears to have been as follows: the metaconid lobe, and then the protoconid, of P₄ passed across the closely approximated posterior and anterior transverse crests of P³ and P⁴ respectively, while the posterior longitudinal crest of P₄ passed across the median transverse crest of P₄. The paraconid crest and protoconid: metaconid crest of M₁ passed across the mesostyle and posterior transverse crest of P₄, and the anterior transverse crest of M¹, respectively. The entoconid-hypoconid crest of M₁ passed through the laterally open central fovea of M¹, and the hypoconulid (posterior transverse) crest of the same tooth and the paraconid crest of M₂ passed over the rear of the hypocone-metacone and posterior transverse crests of M¹. And so on, posteriorly.

Thus, as in the case of *Archaeolemur*, there is in *Hadropithecus* morphological evidence for three types of dental function: incisal nipping, premolar shearing, and molar grinding. However, the progression of wear in *Hadropithecus* suggests that functionally the picture is simpler. Unfortunately there is a dearth of fossils of this

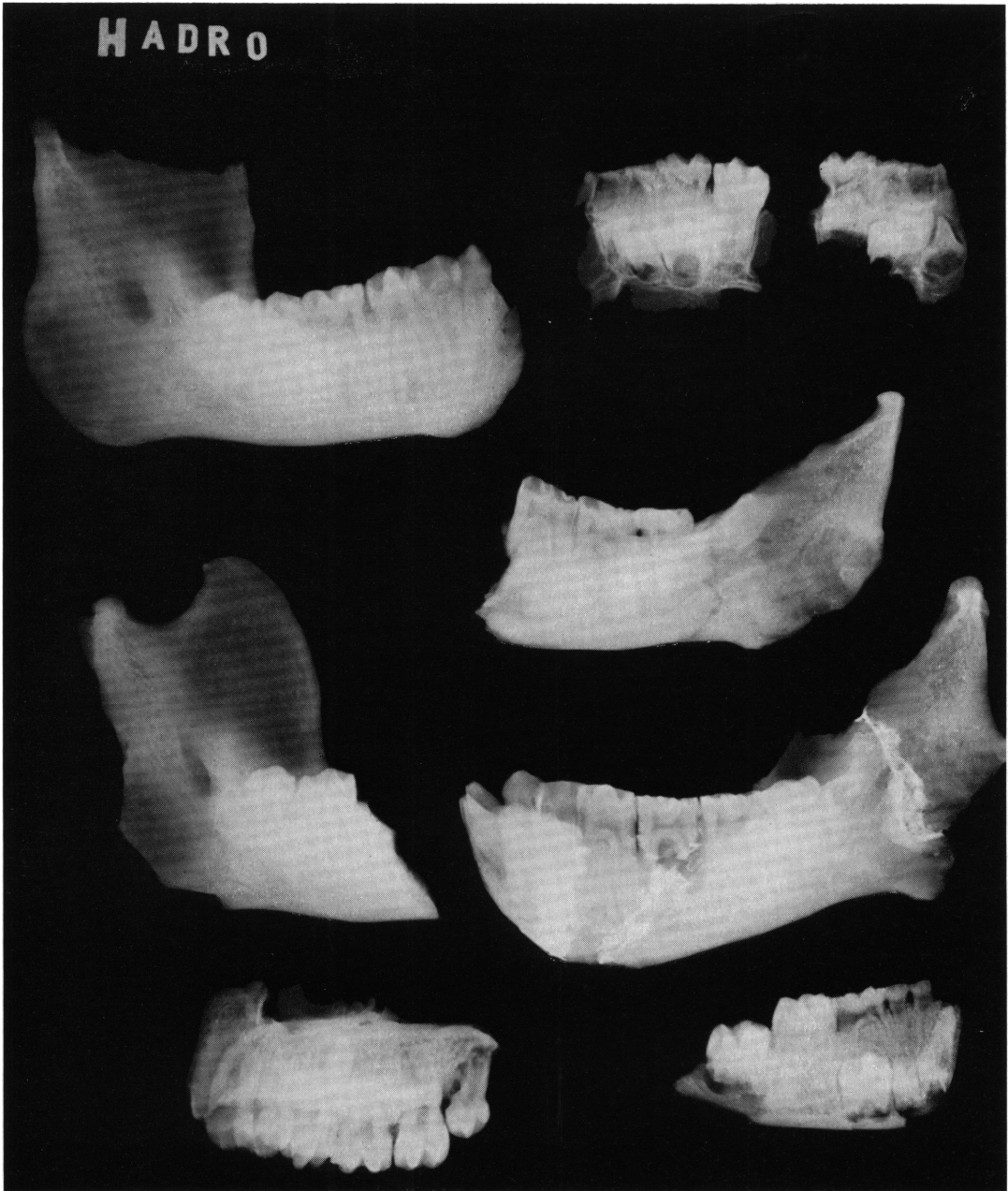


FIG. 31. *Hadropithecus stenognathus*. Radiographs of maxillary and mandibular specimens in the collections of the Naturhistorisches Museum, Vienna. *Top row (left to right)*: VNHM 1934 IV 2/1a; 1934 IV 4a; 1934 IV 4b. *Second row*: 1934 IV 1/2. *Third row*: 1934 IV 2/1b; 1934 IV 1/1. *Bottom row*: 1934 IV 2; 1934 IV 3. All $\times 4/5$.

genus showing intermediate stages of wear, but the type specimen VNHM 1934 IV 1/1, in which wear is advanced, although by no means so far as in the Tsiravé specimen, shows some

very interesting developments. The anterior lower premolar, morphologically part of a shearing complex, does not show a great deal of wear; such as there is, is almost completely

horizontal, only the tip of the tooth having been abraded away. The "shearing" premolar immediately posterior to this tooth shows rather more wear, but is likewise horizontally worn; P_4 also shows a flat surface, and is not strikingly worn.

The molars, on the other hand, although flat, are fairly heavily worn, showing a great deal of dentinal exposure. In part, this wear differential is due to the eruption sequence of the teeth; VNHM 1934 IV 3 and 1934 IV 4a show (see radiographs in fig. 31) that when M_2 is erupting the premolars are still deep in their crypts, and have not yet begun to displace their predecessors. Molar eruption appears to have been in quick sequence; M_1 in VNHM 1934 IV 3 is almost completely unworn when M_2 has already broken the alveolar surface. This explains the lack of a very distinct wear gradient posteriorly along the molar row.

What is of primary importance here, however, is not the quantity of wear in various parts of the tooth row, but its quality. All wear on the cheek teeth is horizontal. By the time the advanced stage of wear seen in the Tsiravé cranium and mandible is achieved, molars and premolars alike are reduced virtually to their alveolar outlines, with the effect that, for instance, P^2 appears molarized.

One interesting observation is that the torsion of the occlusal surfaces along the tooth row, already noted in the case of *Archaeolemur*, and equally pronounced in young adult *Hadropithecus*, remains in the aged Tsiravé specimen. The significance of this phenomenon, if not to produce a crushing component, is obscure; it is presumably related to the total mandibular geometry, but is apparently not necessarily associated with the curve of Spee, since the latter is lacking in *Archaeolemur*.

In no specimen of *Hadropithecus* is it possible to ascertain the position of the condyles with the teeth in centric occlusion with perfect precision, as in the Andrahomana skull the neurocranial and facial portions have become detached in such a way that it is not possible to restore their relative positions with total accuracy. It seems almost certain, however, that the masticatory movements of the mandible took the same basic form as did those of *Archaeolemur*, i.e. symmetrical bilateral retraction of the condyles during incisal biting, and contralateral rotation around the ipsilateral condyle in addition to elevation during the power stroke of molar occlusion. The posterior movement of the contralateral condyle would have introduced a small component of anteroposterior movement to the lateral chewing motion.

CRANIAL BIOMECHANICS

WE HAVE ALREADY DISCUSSED the repertoire of individual actions possible for the muscles of mastication, and we have demonstrated by analysis of the occlusal patterns the movements made by the mandible during chewing. How, then, did the masticatory musculature act to produce these chewing motions?

Anyone with experience in dissecting the heads of mammals will be well aware that the muscular contents of the temporal and infra-temporal fossae do not present a simple picture. These muscles frequently exchange fibers, are divided by numerous fascial planes, and are in some cases composed of fibers with widely differing orientations. This in itself suggests that any analysis dependent on average lines of pull of discrete units is bound to represent an oversimplification, especially where, as is inevitably the case in paleontology, the power and sequence of contraction of different muscles (and in many cases, of different muscle parts) are unknown. An average vector of pull may approximate to reality where a muscle is a prime mover, but in cases where it is acting as a stabilizer or as an antagonist or synergist of other muscles, this is clearly not necessarily the case.

The simple analysis presented below is, therefore, tentative, and does not pretend to "explain" muscular disposition in any but the broadest sense.

As we have seen, premolar and molar occlusion in the archaeolemurines was achieved by contralateral rotation of the ipsilateral condyle, combined with elevation. The gross effects of dental wear through life suggest that inward rotation was the dominant component of this action. Because the ipsilateral condyle was effectively fixed, rotating around a point within itself, it is tempting to regard the system, as many authors have done in other mammal groups (e.g. Crompton and Hiiemäe, 1969b) as a simple bent lever arrangement, the ipsilateral condyle providing the fulcrum. But this would be a mistake. The prime mover in contralateral rotation was the contralateral posterior temporalis, which exerted what was effectively a direct posterior pull on the backward sliding contralateral condyle. This movement was presumably stabilized by the contralateral external pterygoid.

The geometry of the system, however, is such that the force exerted by the posterior temporalis would have tended to make the food the fulcrum of the system, and to rotate the ipsilateral condyle in an anterolateral direction. This tendency must have been resisted by the ipsilateral posterior temporalis, which was ideally situated to perform this function. The net effect would have been to eliminate any reaction force at the ipsilateral jaw joint. Reduction to zero of the force at the point of rotation obviates the possibility that the system acted as a lever, and would greatly have enhanced its efficiency. The contralateral medial pterygoid and the ipsilateral superficial masseter may have acted synergistically with the contralateral posterior temporalis during lateral excursion of the jaw, but this is unlikely.

Again, it would at first sight seem reasonable to suppose that the jaw in elevation worked as a third-class lever. However, if the mandible is viewed as a lever rotating around the temporomandibular joint, it follows that the anterior adductor muscles (the masseters and the medial pterygoid; as fig. 32 shows, their lines of action in lateral view are virtually identical) in all archaeolemurine species would have had a moment arm during premolar shearing of about 40 percent of the length of the resistance arm of the system, if the resultant force were tangent to the arc of adduction. During molar occlusion this figure would have been raised to 50 percent. Were this the case, the resultant force at the jaw joint during masticatory activity would have been half as large again as the force exerted at the premolars and equal to the occlusal force during molar grinding.

Apart from the inherent improbability of so inefficient a system, such an arrangement is ruled out by the morphology of both elements of the jaw joint. The condylar neck is sufficiently weak for it to be said categorically that it could not have withstood the forces that would have been imposed upon it in a lever system. A similar observation may be made both of the postglenoid process, a gracile structure which acted as no more than a locating device, and of the bony buttressing of the temporal articular surface. In addition, it should be pointed out

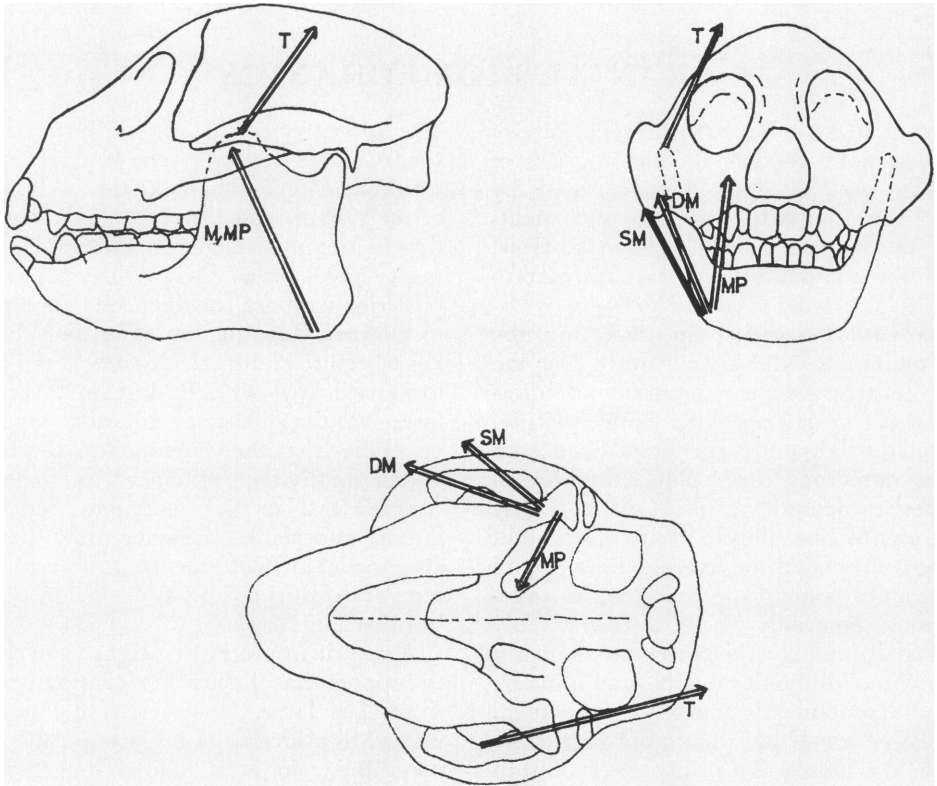


FIG. 32. *Archaeolemur edwardsi*, orientations of the masticatory muscles.

Abbreviations: DM, deep masseters; M,MP, masseters and medial pterygoid; MP, medial pterygoid; SM, superficial masseter; T, temporalis.

that the temporomandibular joint of mammals is lined with fibrocartilage rather than hyaline cartilage. Whereas hyaline cartilage is relatively well adapted to withstand compression, fibrocartilage is not, and is, in fact, best suited to provide a sliding surface.

Similarly, the structure of the archaeolemurine facial skeleton argues against the mandible acting as a lever, and also provides the key to the operation of the masticatory system in *Archaeolemur* and *Hadropithecus*. Basically, this region is designed as a bilateral tripod, its base formed on each side by the massive maxillae. The apex of the tripod is formed by the most elevated point on the frontal bone (whose position is determined by the size and shape of the frontal sinus), which in each case is aligned with the approximate center of origin of the anterior temporalis muscle. The legs of the tripod are formed by the frontal facial profile, by the anterior root of the zygomatic arch and postorbital bar, and by a

strong trabecular structure, clearly visible in radiographs of BM M9965 (fig. 35), which runs from the region of the pterygoid hamulus to meet the two anterior struts at the apex of the structure. This bilateral facial structure is further strengthened by the medial septa of the nasal cavity and the frontal sinus.

The operation of the archaeolemurine lower jaw as a lever around the temporomandibular joint would have produced a resultant force at the dentition oriented perpendicular to a line connecting the fulcrum and the bite point, i.e. tangential to the arc of adduction. Such a resultant would have made nonsense of the pyramidal stress structure formed by the facial skeleton. Had such a force been generated, only one component of it would have been contained within the structure; the other, anteriorly oriented, would have been directed out of the structure, and would have placed the posterior portion of the palate and the maxillae in tension.

Bone, although strong in compression, is weak in tension, and it is well known that musculo-skeletal structures are designed to reduce or eliminate tensile forces.

If, on the other hand, the resultant force at the bite point was directed toward the apex of the pyramidal stress structure there is no need to postulate component forces. Further, the vectors representing the temporalis and masseter-medial pterygoid muscle complexes would be readily reduced into a simple parallelogram of forces, the resultant of which would coincide in magnitude and direction with the postulated force at the bite point.

The face of *Hadropithecus* represents a modification of the scheme described above on the basis of *Archaeolemur*, related to the diminution in function as well as in size of the incisors and the anterior premolars. Dental activity in *Hadropithecus* was concentrated on the last premolar and first molar, which lie directly beneath the anterior root of the zygomatic arch. The orthognathism of *Hadropithecus* therefore correlates with the more vertical orientation of the resultant force of occlusion, as does the slight anterior migration of the origin of the temporalis. Facial depth, one of the most striking differences between this genus and *Archaeolemur*, is related to a more powerful masticatory mode; Davis (1964) has pointed out that deepening of the facial skeleton permits the resolution of more powerful forces. The great depth of the maxilla in *Hadropithecus* is, however, also due to the necessity of accommodating extremely long-rooted teeth (fig. 31); the roots of the teeth of *Archaeolemur* are puny compared with those of *Hadropithecus*, which penetrate almost the entire depth of the maxilla.

The greater masticatory power of *Hadropithecus* relative to either species of *Archaeolemur* is likewise reflected in the internal structure of the mandible and maxillae. Pneumatization of the maxilla in *Archaeolemur* is not extensive, but in *Hadropithecus*, in contrast to all other primates (Cave and Haines, 1940), radiographic evidence indicates a complete absence of pneumatization (fig. 31). Radiographs also show that the maxillae and dentaries (particularly the latter) in *Hadropithecus* are composed primarily, if not entirely, of compact or trabecular bone; these structures in *Archaeolemur* are less dense, although they are nonetheless robust.

On the assumptions that a) no force was

exerted at the jaw joint during mastication, and b) the resultant force at the bite point was constantly directed toward the apex of the facial structure, a simple model was constructed to permit investigation of the roles played by the various muscles of mastication during mandibular elevation. The model demonstrates unequivocally that, given the arrangement of the masticatory musculature present in the archaeolemurines, it is quite possible to produce a resultant force at the teeth possessing the optimal orientation, without exerting any reaction force at the jaw joint. The mandibular mechanics change slightly at different points along the jaw, but the mandible is held in equilibrium during occlusion essentially by a couple action between the posterior temporalis and the anterior adductors, combined with the upward pull of the anterior temporalis. The posterior temporalis-anterior adductor couple produces an anticlockwise torque around a point intermediate between the insertions of these two muscle groups. As the condyle lies posterior to this point, the effect of the couple is to rotate the condyle ventrally. Such rotation is resisted by the antagonistic pull of the anterior temporalis.

Under this model (based on *A. edwardsi*) different combinations of muscular efforts are employed to produce the requisite resultant at different bite points along the tooth row, and at different degrees of gape. At an anterior bite point, with a small food object, the anterior temporalis contributes only a small, constant force to the system, whatever the resultant force. Occlusal force is produced virtually entirely by the posterior temporalis-anterior adductor couple, with the posterior temporalis producing the bulk of the effort. Since the masseter is producing essentially a balancing force at this bite point, the effort of the posterior temporalis increases far faster than that of the masseter-internal pterygoid as bite force is increased. At a wider gape, which effectively moves the bite point back, the masseter plays a greater role, although the posterior temporalis still predominates. Thus at this anterior bite point the posterior temporalis has to produce a disproportionate amount of force, as it both balances the jaw and provides almost all the bite force, while not in a particularly mechanically advantageous position to do the latter. This presumably explains the presence of an alternative system for the production of incisal biting.

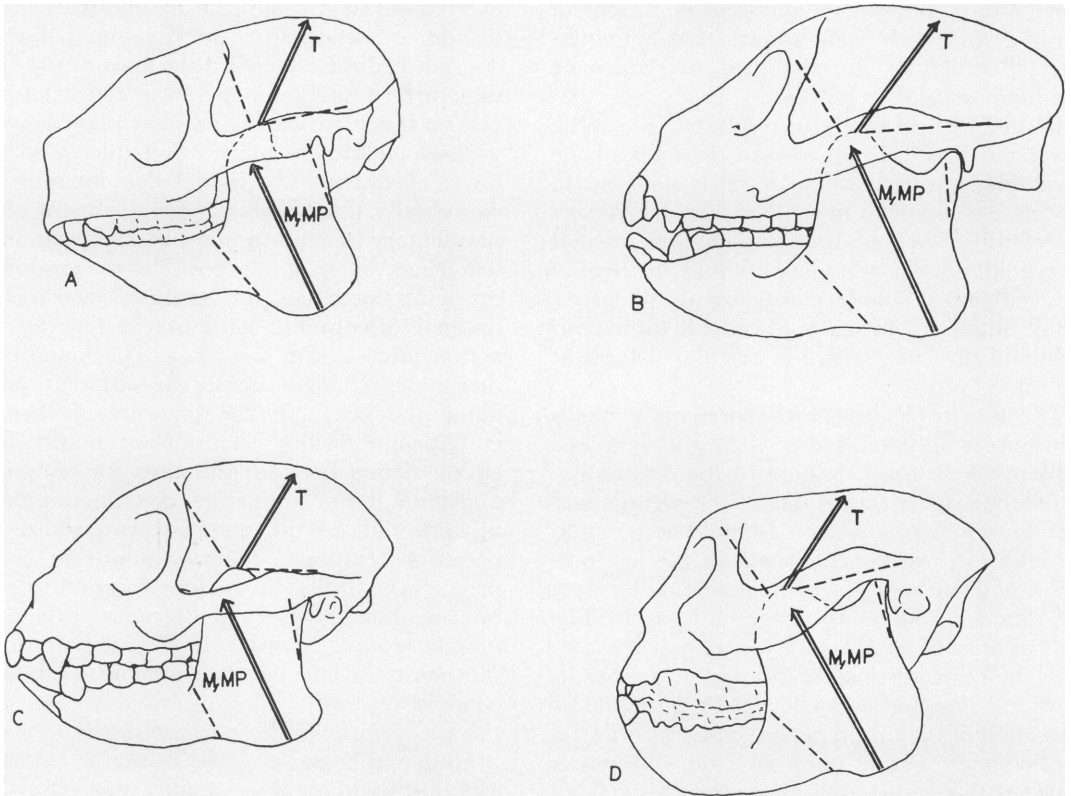


FIG. 33. Orientations of the mandibular adductor muscles. A. *Propithecus verreauxi*. B. *Archaeolemur edwardsi*. C. *Archaeolemur majori*. D. *Hadropithecus stenognathus*.

Abbreviations: M,MP, masseters and medial pterygoid; T, temporalis.

If the bite point is moved farther back to the region of P^4 and M^1 , where masticatory activity was clearly concentrated, the anterior temporalis assumes a more dominant role, while the masseters and internal pterygoid are entirely relegated to a balancing function, i.e. their contribution increases hardly at all as bite force becomes greater. At a wider gape, which, as we have noted, brings the bite point back, in this case almost directly beneath the line of action of the anterior temporalis, the couple balances the jaw at a relatively constant effort, while the anterior temporalis produces most of the occlusal force. The power exerted by this muscle thus increases almost proportionally with the resultant force.

A similar set of activities is apparent if the bite point is located at M^3 , with the couple muscles balancing each other while the bulk of the bite force is again provided by the anterior

temporalis. Despite the mechanical advantage-ousness of elevation at this position, the size of M^3 indicates that relatively little dental activity was concentrated at this point. This is presumably to be explained by the fact that very little lateral movement is possible at M^3 .

During the muscular activities described above, the resultant force at the dentition remains constantly directed toward the apex of the facial structure. There can be no tangential component of the resultant force since, although the jaw hinges up and down during free elevation and depression, there is no rotary movement around the condyle during power occlusion, and no force is exerted at the jaw joint. This is not to say, of course, that because the forces exerted at the teeth sum to zero during equilibrium, the resultant force at the dentition equals all those muscular forces acting to produce it. This is because some muscular effort is

expended in balancing the jaw through the couple, although the couple contributes in most positions a substantial proportion of the total bite force, and equilibration requires a relatively low level of muscular activity. It is also because subsidiary forces are raised at muscular origins and insertions and in the mandible.

Under this system almost all the major forces are compressive. The only large tensile force is that imposed on the zygomatic arch by the masseters, and this is resisted not by any bony structure but by the temporalis fascia. The predominant force, that at the dentition, is resolved by a structure ideally designed for that function. It is clear, in any case, that mechanically this system is far more efficient than a lever arrangement.

The system suggested also explains two features of the temporalis muscle: its division into separately innervated anterior and posterior components, and the fact that it is pinnate, as opposed to the parallel-fibered anterior adductor muscles. The temporalis, in both its portions, clearly plays a more important role in the production of occlusal force than do these latter muscles; pinnation permits the exertion of greater force for a given physiological cross section than does a parallel-fibered arrangement.

It is well known (e.g. Becht, 1953; Smith and Savage, 1955) that among the ungulates, the mammals that are most strongly specialized for lateral grinding during mastication, the medial pterygoid muscle is vastly enlarged, and appears to be responsible in large part for lateral mandibular motions. In the archaeolemurines the medial pterygoid was voluminous, although, unlike that of the ungulates, it was dwarfed by the temporalis; and as figure 28 shows, its lateral leverage was not great. It seems most plausible in the case of the archaeolemurines, then, to regard the large medial pterygoid merely as the product of a general hypertrophy of the masticatory musculature. Lateral motion was predominantly, if not entirely, a function of the contralateral temporalis.

When the archaeolemurine masticatory system is compared with that of a living indriine, for instance *Propithecus*, numerous similarities are at once apparent. In this animal, too, jaw movement takes the form of elevation plus internal rotation around the ipsilateral condyle, although the vertical component of this movement appears to predominate in this case.

Comparison of muscular orientations between archaeolemurines and indriines also reveals extreme similarities in the mechanics of jaw closure, at least as far as elevation is concerned (figure 33). There is one extremely important difference, however. Living indriines possess an unfused mandibular symphysis. The work of Crompton and Hiimäe (1969a, 1970; Hiimäe, personal commun.) has shown that a mobile symphysis indicates a totally different pattern of mastication from that obtaining in mammals possessing synostosed dentaries: one in which the two dentaries may move independently of one another.

The most striking differences, aside from tooth morphology, between the archaeolemurine and indriine masticatory apparatuses, lie in the form of the symphyseal region of the mandible, in the robustness of the mandibular corpus, and in the manner in which the dentaries are joined. The symphyses of *Archaeolemur* and *Hadropithecus* are extremely reminiscent of those of hominoid higher primates; in figure 34 symphyseal cross sections of *Hadropithecus* and

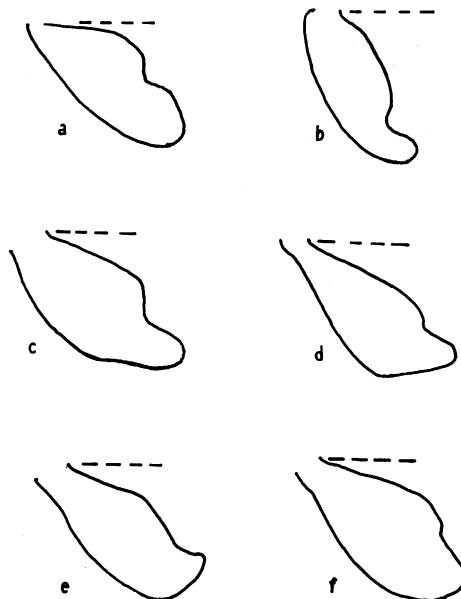


FIG. 34. Symphyseal cross sections of (a) *Archaeolemur* (*A. majori*, BM M7374), and (b) *Hadropithecus* (reconstruction, based on VNHM 1934 IV 1/1) compared with (c-f) similar sections of the mandibles of four adult individuals of *Gorilla gorilla*; c-f from Goodman (MS).

Archaeolemur are compared with those of a number of gorillas.

In the sifaka, given a mobile symphyseal syndesmosis, it is clear that the contralateral temporalis cannot function to provide internal movement of the ipsilateral dentary. Other muscular combinations, irrelevant here and requiring cineradiographic and electromyographic studies to elucidate, must be operative to produce a similar result. As Smith and Savage (1955) have pointed out in connection with the diminution of the temporalis in ungulates, internal movement of the mandible by contraction of the posterior temporalis of the contralateral side would require extreme stressing of the lower jaw; these stresses would have to be transmitted anteriorly, around the symphysis, and back again along the ipsilateral corpus. Despite this disadvantage, such a situation is precisely what we find among the archaeolemurines, together with massive jaws and an extremely strongly buttressed symphysis, characterized in particular by the possession of a strong inferior transverse torus.

Goodman (ms) has recently discussed the relation between form and function in the pongid symphysis. By stressing both a photoelastic model and pongid mandibles coated with a strain-sensitive lacquer, Goodman established that the inferior transverse torus of the pongid symphysis represents an adaptation for withstanding laterally directed forces, i.e. those which would tend to spread the dentaries apart. This torus is well developed in the mandibles of

all three archaeolemurine species (figure 34), while the forces developed in this area of the mandible during contralateral temporalis contraction would have been very much of the sort Goodman described.

It is thus clear that the archaeolemurine masticatory system could have been very simply derived from one similar to that of the extant indriines. It is suggested, therefore, that this system was derived from a primitive indriid masticatory system, largely retained by *Indri*, *Propithecus*, and *Avahi*, by fusion of the mandibular symphysis. Other modifications, such as the dominance of the contralateral temporalis in lateral movements, change in symphyseal form, and increased robustness of the mandible, are all correlates of this fundamental shift, and presumably reflect a change toward a more powerful masticatory pattern. The genetics of symphyseal fusion are, to this writer's knowledge, unknown, but it is unlikely that they are complex, and it seems probable that only a very minor genotypic modification would have been required to produce this change. Presumably the shift toward such a masticatory mode took the shape it did, with minimal modification of the pre-existing apparatus, because the skull of the common ancestor of the Indriinae and Archaeolemurinae was already relatively highly specialized toward the modern indriine condition. If this were indeed the case, subsequent evolution of a line adapting as the archaeolemurines did would have been strictly channeled.

THE BRAIN AND CRANIAL SENSORY ORGANS

ARCHAEOLEMUR

IN EARLY STUDIES of the subfossil Malagasy lemurs (e.g. Major, 1894) the assumption was frequently made that brain development was restricted, or at least strongly channeled, by osteological structures related to other skull functions. Now, however, it is known that the development of the brain and that of the immediately surrounding neural capsule are intimately related, and that it is the neural capsule which responds to the expansion of the brain. A series of developmental studies, summarized by Moss and Young (1960), have elucidated the relationship between the developing brain and neurocranium in some detail. At the foetal stage, the neural capsule comprises the entire mass of soft tissues surrounding the brain; this mass reacts with extreme sensitivity not only to the requirements of the expanding neural mass, but to anything within the skull which is expanding. Even if the cerebrum is reduced or absent, the cranial vault will develop normally if the capsule encloses a compensatory amount of fluid; this is seen in the case of hydranencephaly (Minckler, McCurdy, and Iwerson, 1941; Johnson, Warner and Simonds, 1951). As the foetus develops, the tissues of the cerebral capsule become differentiated into meninges, bone, and scalp. Ossification begins in the tissues of the capsule immediately overlying the dural layer, and proceeds radially outward from each of a number of ossification centers, while the capsule enlarges at an overall rate determined by the rate of expansion of the neural mass. Moss and Young offer the parietal bone as an example:

This bone is *passively* carried outwards by capsular expansion while it is growing. The growth of the parietal itself has nothing to do with its relocation in space during this period of development. Through this early enlargement, the parietal is merely ossifying a portion of the cerebral capsule (1960, p. 282).

As these authors pointed out, the outer layer of the cranial dura and the inner periosteal layer of the calvarial bones are identical, with the result that both the size and shape of the inner surface of the bony neurocranium are determined by the form of the dura, which in its turn is determined by the form of the brain. Experiments in in-

duced hydrocephaly and microcephaly in rats reported by Moss and Young demonstrate that the final form of the cerebral capsule constitutes a direct response to the mechanical demands upon it made by its contents during development. Clinical evidence corroborates this observation; it is known, for instance, that the cerebral shrinkage which occurs in old age is accompanied by a corresponding alteration of the inner table of cranial bone, while no apparent change takes place in the external table. Likewise, pathological loss of parts of the neural mass is compensated for by proliferation of the inner table of the cranial vault.

Weidenreich (1924, 1941) has termed the neural capsule, interpreted here as consisting of the meninges, and, more importantly to the present analysis, the inner table of the bones of the cranial vault, the *Grundform* of the skull. For the purposes of the present discussion, the *Grundform* may be regarded as functionally unrelated to the outer table of bone, or at least as being able to vary independently of it. Weidenreich used the term *Aussenform* to describe the outer aspect of the skull, that aspect whose shape is determined not by the cerebral capsule but by the demands of muscle attachment, stress resolution and so forth. In those cases where the functional demands upon the *Aussenform* are discordant with those on the *Grundform*, pneumatization of the calvarial bone invariably occurs, leading to the development of what Weidenreich called "dead" or "functionless" spaces. Hofer (1969) has objected that since these spaces do indeed serve a function, this terminology is somewhat misleading, but the description is, in fact, accurate in the sense that no stresses are transmitted through these spaces. Weidenreich's original intent, as Hofer recognizes, was to emphasize that, for instance, paranasal and paratympanal sinuses have no necessary functional relationship to the sense organs with which they are topographically associated.

A comparative survey very quickly shows that the thickness of unpneumatized vertebrate cranial bone rarely exceeds more than a few millimeters, even in the largest animals. The only exception to this known to the writer occurs in the case of the "dome-headed" pachycephalo-

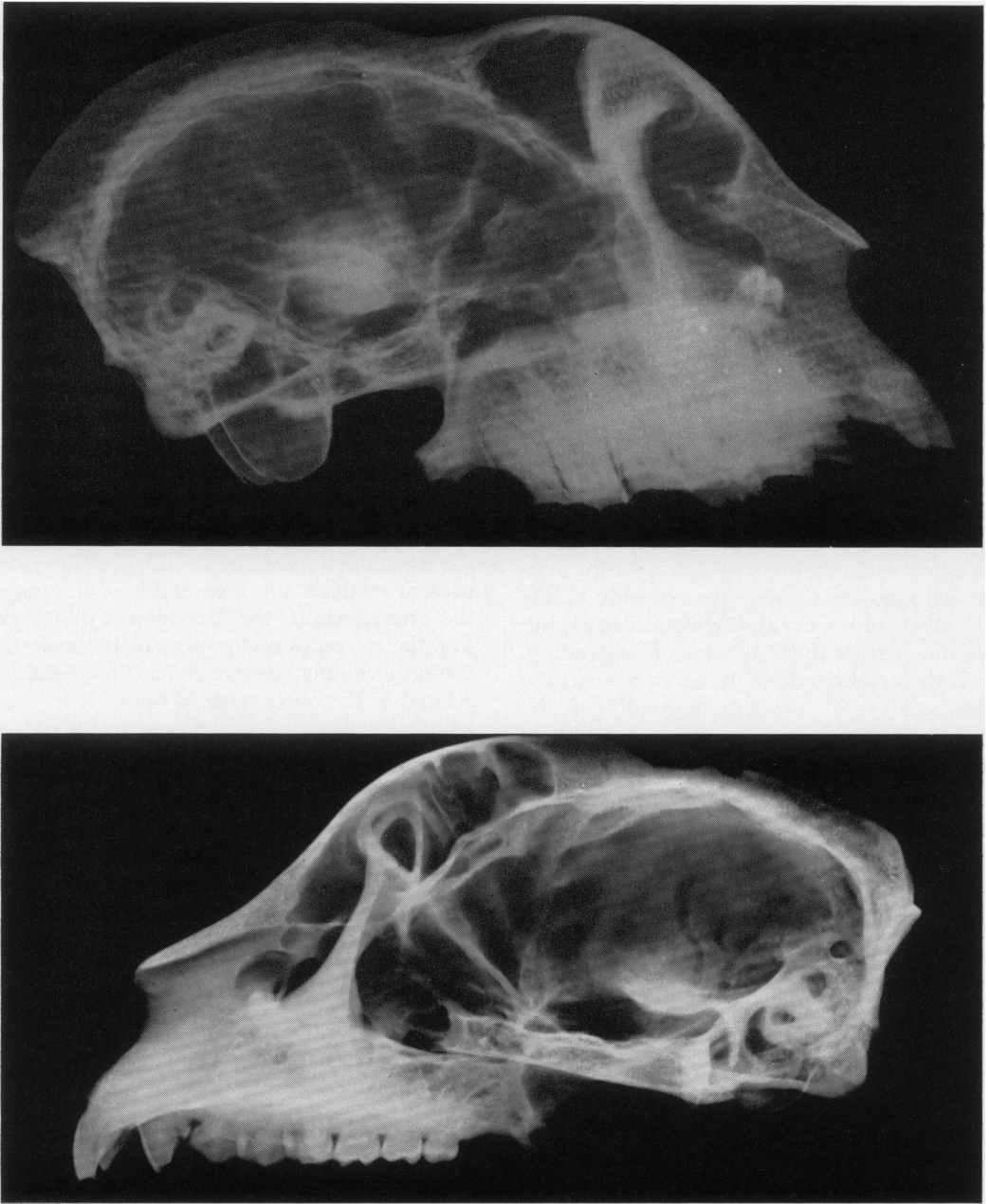


FIG. 35. Radiographs in lateral view. Above: *Hadropithecus*, Tsiravé. Below: *Archaeolemur edwardsi*, BM M9965. *Hadropithecus*, courtesy of Dr. Roger Saban.

saurid dinosaurs, among males of which the thickness of compact bone above the cranial cavity reached as much as 9 inches in a 2-foot-long skull. This remarkable condition, has, however, been convincingly shown by Galton (1970,

1971) to have had a special adaptive purpose, related to intraspecific competition between males.

There is a great deal of evidence, then, that whenever there is more than a very slight dis-

cordance between the Grundform and Aussenform of a skull, or, indeed, between any two separate functional components, a space is formed, which may or may not be filled with cancellous tissue. Where a cancellous diplöe is present, this tissue may be more or less dense, according to its functional purpose. The significance of diplöe has been relatively little studied, but it is clear from the work of Endo (1966) and of McElhaney et al. (1970), that the distribution of diplöe in cranial bones is of considerable mechanical importance.

Both species of *Archaeolemur*, as indeed the subfossil lemurs in general, are remarkable among primates in the development of extremely large frontal sinuses. In *Archaeolemur edwardsi* the frontal sinus invades almost the entire frontal bone, anteroposteriorly almost from the coronal suture to the junction of the frontal with the nasals, a length frequently in excess of 55.0 mm.; and laterally from the frontomalar suture of one side to that of the other, a width in many cases greater than 75.0 mm. The sinus may attain a maximum depth in this species of more than 20.0 mm. In *Archaeolemur majori* the sinus is smaller, both relatively and absolutely, although it remains substantial. The development of the frontal sinus in both species is primarily related to the demands made by temporalis on the Aussenform. As discussed, temporalis in *Archaeolemur*, and particularly in *A. edwardsi*, extends far forward, taking origin anteriorly over the expanded posterior aspect of the orbital process of the frontal, and over that part of the frontal posterior to the supraorbital line. In the absence of the frontal sinus, the superior part of the postorbital bar would be greatly reduced, and the posterior part of the frontal would shrink to a negligible proportion of its actual area. The area available for attachment of temporalis would therefore be totally inadequate to meet the functional demands of the muscle. In addition, the anterior portion of the external face of the braincase would recede to well below and behind the superior margin of the orbits; this would grossly interfere with both the orbital contents and with the transmission of stresses from the facial to the neurocranial skeleton.

The two species of *Archaeolemur* in fact provide a test case for this interpretation of the significance of the frontal sinus. The large-muscled *A. edwardsi*, whose brain is some 20 percent larger on average than that of the more gracile *A.*

majori (the mean neurocranial volume of nine *A. edwardsi* crania is 121.5 cm.³; that of six *A. majori* is 98.6 cm.³),¹ but which is only some 6–7 percent larger in mean cranial length, possesses frontal sinuses whose volume may surpass the volume of those of *A. majori* by as much as 250 percent. This huge discrepancy is apparently due to the disproportionately larger musculature of *A. edwardsi*. As Klatt pointed out as long ago as 1913, the power of a muscle is roughly proportional to its cross-sectional area, and not to its volume. The cross section of a muscle, as a plane surface, increases only as the square of its dimensions, while its volume increases as the cube. Thus a species which in linear dimensions is only slightly larger than another, closely related, species, may be expected to require a disproportionately larger musculature. This is precisely what we find in the case of *A. edwardsi* and *A. majori*. In the latter the temporalis is much smaller than in *A. edwardsi*, and its requirements in terms of attachment area are greatly reduced. Concomitantly, the frontal sinus is relatively much diminished. Of course, it is clear that the Aussenform is composed of not one but several functional components, and no attempt is made to claim that the form of the frontal sinus, situated at the junction of several of these (braincase, orbital and nasal capsules), is solely due to the demands of muscle attachment. However, it is clear that the musculature played a preponderant role in determining the degree of sinusal development, and that this condition is a correlate of the possession of a small brain and large, forward shifted masticatory muscles. The maxillary sinus may have played a similar role in relation to the attachment of the deep masseter.

Of the many functions postulated for the paranasal sinuses in man, the most ancient and most frequently quoted is that of reducing cranial weight to facilitate proper balance of the head. Biggs and Blanton (1970) have recently re-investigated this problem, and have concluded that weight reduction is not, in man at least, the explanation of the presence of sinuses rather than of solid bone. The approach adopted by these authors was to employ electromyography to measure the response of the postural neck

¹The author is grateful to M. Joël Mahé for providing the data on which these means are based.

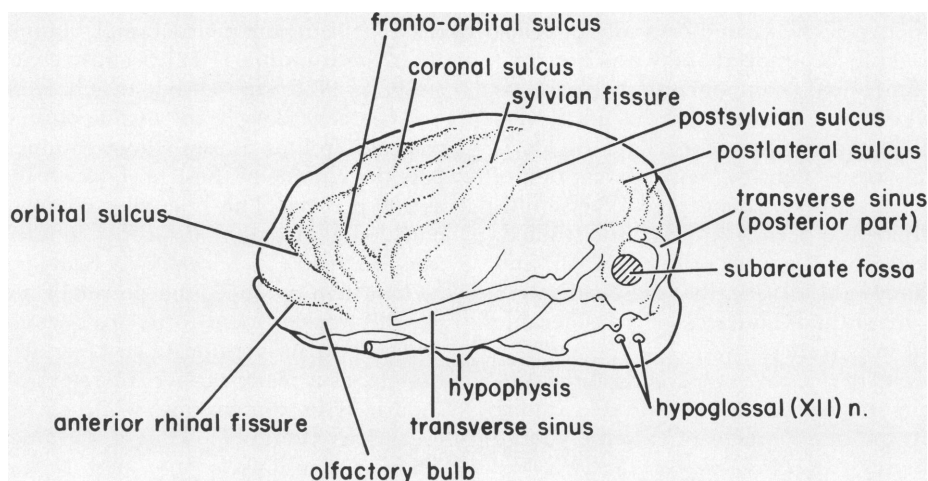


FIG. 36. *Archaeolemur edwardsi*, BM M9965, lateral view of endocranial cast, showing tentative identification of cerebral sulci.

muscles to loading of the head anterior to the point of balance. No significant muscular activity was observed until the added weight far surpassed that of the amount of compact bone required to fill the sinuses. Maintenance of the minimum weight, then, does not appear to be related to the mechanism causing sinusal development, rather than bone thickening, to occur when discordances arise between different functional units, although lightening is obviously a large secondary benefit in the case of the many animals, including the lemurs, whose crania possess sinuses far larger than those present in man. More likely physiological economy or a related phenomenon is involved.

It appears, then, that the brain in *Archaeolemur* played only a negative role in the determination of external skull form anteriorly, although posteriorly, apart from the formation of sagittal and nuchal crests, the external morphology of the braincase closely follows its internal, cerebral, contour.

In this study, the external morphology of the brain of *Archaeolemur edwardsi* was observed by means of a latex endocast prepared from the left side of a sagittally hemisected cranium, BM M9965 (figs. 36, 37). Most of the information derived is shown in the figures. The endocranial volume of this individual is estimated to be approximately 136 cm³. Since the internal aspect of the neurocranium develops during ontogeny in a very close relationship with the brain and

meninges, an endocast might be expected to reveal most of the details of external brain anatomy, although in accord with Radinsky's (1968) observation that sulci tend to show up less clearly on endocasts of larger species, the sulcal detail on the present endocast appears to be less pronounced than on that illustrated by Radinsky (1970) of an individual of *A. majori* (AMNH 30007).

Studies of the brain of *Archaeolemur* by Clark (1945, 1959) and Piveteau (1950) led these authors to the belief that in this organ *Archaeolemur* was reminiscent of catarrhine primates. However, as was pointed out as early as 1908 by Elliot Smith, and has been restated by Radinsky (1970), the brain of *Archaeolemur* is close in its external morphology to those of living indriines. Radinsky (1970) plausibly attributed differences in the lower portion of the frontal lobes between his endocast of *A. majori* and living indriines to the larger size and smaller orbital impressions of *Archaeolemur*; in BM M9965, however, the orbital impressions are more pronounced than is apparently the case in Radinsky's specimen. This appears to be due to the generally narrower interorbital space of *A. edwardsi*. Indriids in general tend to have more forward-directed orbits than do other prosimians; as this trend is not seen among other vertical clinging and leaping prosimians, while it is shared with the closely related but quadrupedal archaeolemurines, it is probably not a necessary correlate of truncal

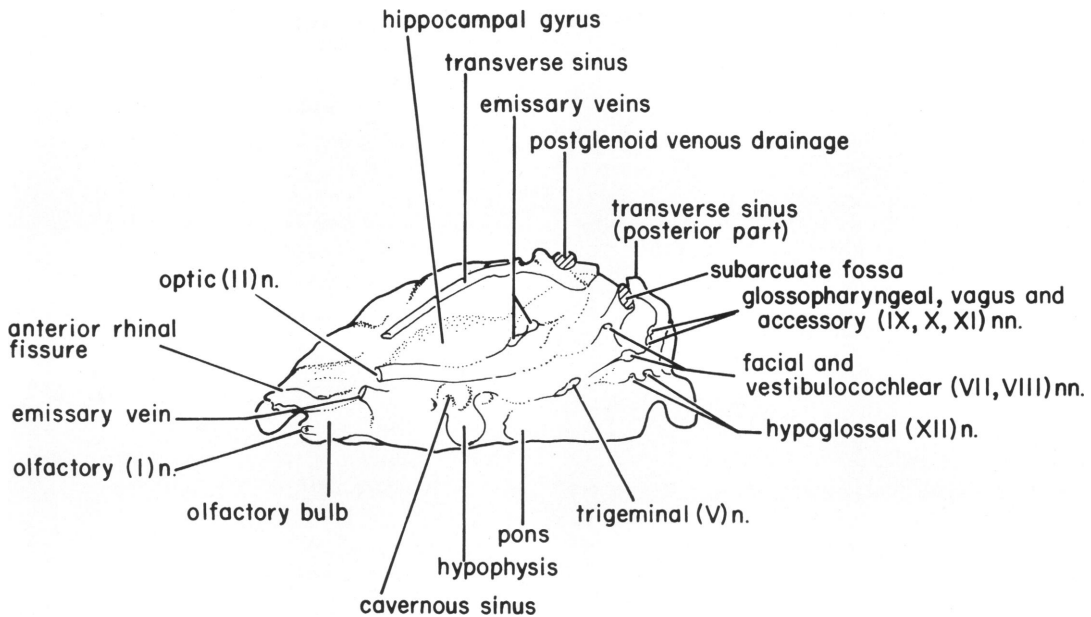


FIG. 37. *Archaeolemur edwardsi*, BM M9965, ventral view of endocranial cast, showing cranial nerves.

erectness during rest and locomotion. Possibly it is correlated with feeding or some other non-locomotory activity.

Radinsky (1968) has suggested that among the indriines the proportions of the frontal lobes, which in this group are consistently broader than among the lemurines, may be due to the expansion of this area of the brain into the additional neurocranial area made available by forward rotation of the orbits. It should be noted, however, that the relatively large interorbital width among the indriines does not necessarily appear to be correlated with the orientation of the orbits; in *Indri* and *Propithecus* the forward orientation of the orbital margins is produced by the forward projection, as a thin bony sheet, of the dorsal and dorsolateral orbital margins. *Avahi*, on the other hand, shares this feature only to a limited extent, although this is probably because, as a smaller animal and a nocturnal one, *Avahi* requires relatively larger eyes than its fellow indriines. To maintain an orbital orientation similar to that seen in *Indri* and *Propithecus*, *Avahi* would have either to expand the orbit medially, while retracting its medial margin, which would grossly interfere with its olfactory apparatus, or to expand the zygoma laterally, while maintaining the rela-

tive position of the orbital process of the malar, which would disorganize the musculature of the temporal and infratemporal fossae. Whether or not the condition represented by *Avahi* is primitive (probably not) the orbital orientation of this animal relative to the diurnal indriines can be explained by regarding the posterior displacement of the orbital process along the malar as the route of least resistance in orbital expansion.

In *Archaeolemur* a degree of orbital frontality equivalent to that of the diurnal indriines is maintained, not by anterior projection as a bony shelf of the postorbital bar (indeed, the bar in *Archaeolemur* is at its midpoint broader laterally than it is anteroposteriorly), but by the anterior expansion of the frontal sinus and its invasion of the superior and dorsolateral margins of the orbit. The orbits of *Archaeolemur* are, however, rather more closely approximated than are those of *Propithecus* and *Indri* (more so compared with the former than to the latter, whose interorbital distance is deceptively large), while the interorbital distance in *A. majori* exceeds that in *A. edwardsi*. The breadth of the frontal lobes appears in each of the above-mentioned animals to be positively correlated with interorbital breadth. *Propithecus*, with relatively the least approximated orbits, has in dorsal view the

most rounded anterior contour of the brain (Hill, 1953, fig. 157). *Archaeolemur edwardsi*, whose brain is more sharply angled around the frontal pole than is that of its congener, has the most closely approximated orbits. This correlation appears to apply, however, only within the Indriidae. *Lemur*, for instance, has narrow frontal lobes coupled with a broad interorbital space. Nevertheless, within the Indriidae, the broadening of the anterior part of the brain observed by Radinsky appears to be more closely linked to orbital approximation than to orbital frontality.

VISION

Unfortunately, the area of the visual cortex, whose superficial exposure would have been limited anyway, is obscured on the endocast of BM M9965 by the impression of a complex of sinuses; however, there is nothing about the brain to suggest any substantial difference in visual acuity between the diurnal indriines and *Archaeolemur*.

A perennial problem confronting primatologists has been the question of the significance of postorbital closure. Standing (1908a) who, as we have seen, believed in a close relationship between the lemurs and higher primates, attempted to explain the absence of postorbital closure in *Archaeolemur* and other subfossil lemurs as follows:¹

In the various families of Monkeys the frontal post-orbital region is generally so broad that the space to be filled in by the septum between the brain-case and the orbital bar is only a small fraction of the circumference of the eyeball—that is to say, a quite short outgrowth of the malar and frontal bones is sufficient to bridge across the vacant space between the orbital bar and the braincase . . .

In the case of the Malagasy Lemuroids which we are considering the narrowing of the skull has carried the frontal, orbito-sphenoid and alisphenoid far away from the post-orbital bar, so that supposing a septum did exist in a position analogous to that which it occupies in the Apes, it would have to wall in a space . . . equivalent to from 70 to 90 per cent of the transverse diameter of the orbit (p. 147).

The inadequacy of this explanation for the absence of postorbital closure is at once apparent

¹In actual fact, Standing was arguing here for the loss of the postorbital septum, which he believed had been present in the ancestral indriids, as a result of narrowing of the postorbital frontal region; however, the argument would apply both ways.

when *Tarsius* Storr is considered. Certainly the septum in *Tarsius* is not complete, but this is to permit the attachment of pterygoid musculature to the medial orbital wall (Hill, 1955); the presence of a septum in a form with a pronounced postorbital constriction demonstrates that the mere presence of a wide gap to be filled does not of itself prevent the formation of a septum. Quite simply, it would appear that in *Tarsius* a bony septum is required to support the enormous eye, whereas among the lemurs, even those nocturnal ones with relatively large eyes, such a requirement does not exist.

Given that *Tarsius* represents a special case, what is the purpose of postorbital closure? Simons (1962) has suggested a protective function. However, since the optic axes among primates appear to be generally more convergent than the axes of the bony orbits, leaving the orbital contents vulnerable from the side even in man, this would appear unlikely; further, the musculature of the temporal fossa presumably acts as an excellent insulator from shock.

A more plausible explanation is that closure serves to insulate the eye from the movements of the musculature in the temporal and infra-temporal fossae, and also provides a more stable support for the orbital contents. Collins (1921) may have had both of these factors in mind when he wrote that “the closing of the outer wall of the orbit in Primates ensures steadiness of the movements of the eye in the interests of binocular vision” (p. 15). Such an interpretation accords well with the fact that the retina in prosimians is considerably less advanced than is that of higher primates (Wolin and Massopust, 1970); for instance, no prosimian (except possibly *Tarsius*; contrast Castenholz [1965] with Rohen [1966]) possesses a retinal fovea. The visual significance of the fovea has long been debated, but recent evidence presented by Weale (1966) and Wolin and Massopust (1970) has demonstrated unequivocally that the fovea performs an important function, and is an intimate correlate of advanced retinal organization.

Possibly the relationship of stability of the eye to visual acuity is not so critical at the prosimian level of visual organization as it is at the more advanced level of the higher primates. If this is indeed so, it is not difficult to understand why selective pressures should have existed among the early Anthropoidea or their immediate ancestors to isolate the eye from the heaving

mass in the temporal fossa, whereas the necessity never arose among prosimians. The precise nature of the selective pressures leading to increased sophistication of the visual system of higher primates remains obscure, as higher primates are not notably more acrobatic or swift in locomotion than are many groups of prosimians.

OLFACTION

The olfactory bulbs of the living indriids, particularly *Indri*, are relatively considerably smaller than those of other extant prosimians (Stephan and Andy, 1969), and are even relatively reduced compared with those of some platyrrhine primates, for instance *Aotus*. The relative size and external morphology of the olfactory bulbs and tracts of *Archaeolemur edwardsi* (insofar as can be told from the specimen at hand) do not appear to differ materially from the condition seen in *Indri*; they are relatively small, and apparently did not project markedly beyond the frontal pole of the brain.

Very little of the internal nasal structure is preserved in BM M9965; much of the following description is based on Piveteau's (1948) account of *A. edwardsi*.

In general, the internal architecture of the indriid nasal capsule is closely reminiscent of that of lemurids (Kollmann and Papin, 1925), and *Archaeolemur* provides no exception. As among the diurnal indriines, the anterior transverse lamina of the sphenoid is situated rather high, providing a capacious choanal passage, but at the same time limiting the vertical extent of the olfactory fossa. The cribriform plate is oval in outline, and is somewhat more vertically oriented than is usual among lemurs. The thin nasal septum is formed dorsal to the transverse lamina by the perpendicular lamina of the ethmoid, and ventral to it by the vomer, which is deeply incurved both anteriorly and posteriorly. The frontal sinus was evidently similarly sagittally divided, communicating with the olfactory fossae bilaterally via the large nasofrontal fenestrae. In Piveteau's specimen there appears to be a very small sphenoid sinus, but there is no evidence of such a feature in BM M9965.

According to Piveteau (1948), the maxilloturbinal in *A. edwardsi* is of approximately the same relative extent as that in *Lemur*; it is not described by Piveteau, but Kollmann and Papin

(1925) stated that the maxilloturbinal is doubly rolled in *Lemur*, whereas in other prosimians the element consists merely of a single scroll. It seems unlikely, then, that the maxilloturbinal of *Archaeolemur* was doubly rolled. The functional significance of the maxilloturbinal is at present hypothetical; Scott (1954, 1958) has suggested a thermoregulatory function of the inferior turbinate processes, particularly the maxilloturbinal, and has related reduction of this element, and of the nasal cavity in general, through the primates, to increasing efficiency of the cutaneous thermoregulatory mechanism. The fact that the skin of *Tarsius* bears a greater density of sweat glands than does that of marmosets (Perkins, 1968, 1969; Arao and Perkins, 1969) does not vitiate this hypothesis (in fact, it lends credence to it), since in *Tarsius* the turbinal system is closely similar to that of higher primates, possessing, for example, "a small and attenuated maxilloturbinal" (Clark, 1959, p. 272).

Piveteau interprets the nasoturbinal in *Archaeolemur*, represented in his specimen only by its impression, as having been slender; the other ethmoturbinals were short, although the posterior extremity of the fourth came into contact with the sphenoid sinus. The internal architecture of the nasal fossa in *Archaeolemur* was thus of the general lemuriform type, and close in morphology to that of the modern indriids.

As the mechanisms of olfaction are obscure, it is difficult to assess the adaptive significance of a nasal cavity of this type, except by reference to broad levels of turbinal complexity. If, for instance, the absolute surface area of the olfactory mucosa determines the sensitivity of the olfactory apparatus, then *Archaeolemur*, purely by virtue of its greater size, had greater olfactory acuity than, say, *Propithecus*. However, it is far from clear that this is the case; certainly there is no consistent pattern, as might be expected on the basis of this hypothesis, of relative reduction in size of the nasal fossa and its contained elements in larger forms. Moreover, although Moulton (1967) stated that "The structure of the olfactory epithelium is remarkably uniform throughout the vertebrates, and there is little to distinguish the epithelium of one mammalian species from that of another" (p. 424), he also noted that variation does exist in the thickness of the epithelium, in the ratio of supporting cells to receptors, and in the number of cilia per receptor.

Washburn (1967) has recently stated that:

[In the anterior cranial fossa] the two frontal bones may meet in the midline, or they may be separated by the ethmoid . . . in primates if the ethmoid is large with a broad contact with the sphenoid, the animals have a well-developed sense of smell, usually vibrissae. . . . When the frontal bone of one side meets the frontal of the other, the animals are visually oriented (pp. 369–370).

This is a dangerous generalization, since, for instance, the frontal bones in man generally make no contact posterior to the cribriform plate of the ethmoid, this plate being in very broad contact with the jugum of the sphenoid bone. However, it is the case that, in all non-hominoid higher primates, catarrhine and platyrrhine, in which the writer has had the opportunity to examine the morphology of the anterior cerebral fossa, the frontals make contact both anterior and posterior to the cribriform plate, or the margin of the depression within which it lies. Among the lemurs, on the other hand, including *Archaeolemur*, the cribriform plate makes direct contact with the sphenoid posteriorly.

Insofar as this sutural configuration, with the exceptions noted above, appears to correlate perfectly with the overall organization of the olfactory system, and particularly the size of the cribriform plate, it provides further evidence that *Archaeolemur* possessed all the attributes of the “strepsirrhine” nasal condition: labial vibrissae, a moist, naked rhinarium bound to the gums, and a naked philtrum. An additional strong suggestion that this was the case is provided by the relatively highly vascularized condition of the anterior surfaces of the maxillae and premaxillae.

AUDITION

The most striking features of the external cranial base in *Archaeolemur* (as, indeed, of all lemurs with the exception of *Archaeoindris*, *Palaeopropithecus*, and *Megaladapis*) are the inflated auditory bullae. It is generally accepted that the bulla serves to protect the organs it contains, but this is clearly no explanation of bullar hypertrophy.

In a study of Saharan mammals, F. Petter (1953, 1961) noted that among gerbils a correlation exists between bullar enlargement and population density. In populations or species of *Meriones* whose density is low, the bullae tend to be larger than among high density groups. Experimental studies by Legoux, Petter, and

Wisner (1954) revealed that species of *Meriones* with larger bullae produced considerably greater cochlear microphonic responses in the range between about 500 and 4000 Hz. Thus individuals belonging to the more sparsely distributed groups are presumably able to hear more attenuated sounds, and therefore to communicate over greater distances. Legoux, Petter, and Wisner suggested that this greater auditory acuity in forms with large bullae is achieved through the decrease in damping of the tympanic membrane which results from the increased volume (and proportionally lowered resistance) of the air in the middle ear cavity.

Whereas among lemurs there is no demonstrable relationship between population size and bullar enlargement (admittedly, the more solitarily inclined cheirogaleines have relatively larger bullae than do other lemurs, but as van der Klaauw [1931] pointed out, there tends to be an inverse relationship between body and bullar size among all mammals; while the equally solitary *Daubentonia* E. Geoffroy has relatively small bullae), the latter part of Legoux, Petter, and Wisner's argument would indeed apply to these animals, as the mechanical consequences of increased bullar size are inescapable. It is clear, however, that more experimental evidence is required before the precise significance of bullar size among these animals can be evaluated.

The external morphology of the temporal lobe in *Archaeolemur* is extremely close to that in *Indri*, and nothing exists to suggest any meaningful difference in the auditory area between the two forms.

In short, examination of the external morphology of the brain and of the structure of the cranial sensory organs in *Archaeolemur* reveals that the level of sensory, and, indeed, overall neural organization, in this animal was no more “advanced” than that of the living indriines. Radinsky (1970) has noted, in AMNH 30007, one feature of the brain in which *Archaeolemur majori* does appear to be unusually specialized: the complexity of the coronal gyrus. In his specimen this area is broad, and is crossed by a pair of secondary sulci. The primary somatic representation of the face was probably situated in this area; its elaboration might imply an increase of tactile sensitivity in the face of this animal. Alternatively, Radinsky suggested that this complexity may represent an allometric

development. However, although BM M9965 belongs to a larger species than does Radinsky's specimen, such elaboration is lacking on its endocast; but, as has been pointed out, there is evidently a great deal less sulcal detail in this endocast than in that of AMNH 30007.

HADROPITHECUS

Piveteau (1956) has published the only description of an endocranial cast of *Hadropithecus*. This cast (unfortunately one apparently without much detail), lacks, like that of BM 9965, impressions of secondary sulci in the coronal gyrus. Insofar as can be told, the brain of *Hadropithecus* resembled that of *Archaeolemur edwardsi* more closely than it did that of *A. majori*, but its external morphology could not be said to differ greatly from that of either.

For want of sufficient material, particularly hemisected crania, the internal nasal structure of *Hadropithecus* is unknown, although radiographs of the Tsiravé cranium show the nasal fossa to have been of similar proportions to that of *Archaeolemur*, if perhaps slightly abbreviated posteriorly, and with a somewhat higher choanal passage. It would, in any event, be surprising to discover any significant differences between the two genera in this region.

The ear regions of *Hadropithecus* and *Archaeolemur* are likewise similar in most respects, the

most striking difference lying in the deepening of the auditory bullae in the former. This phenomenon would seem to be more plausibly associated with a change in the growth pattern of a morphogenetic field affecting the entire lower portion of the cranium than to any specific functional change allied to audition, although, following the arguments of Legoux, Petter, and Wisner, an increase in auditory acuity might be expected to follow from the increase in the volume of the bullae.

The orbits in *Hadropithecus* are still more frontated and convergent than are those of *Archaeolemur*, a change which has had an effect on the form of the frontal sinus, on the breadth of the face, and on the configuration of the anterior temporal fossa. In concert with the elevation of the brain, the frontal sinus has enlarged, especially dorsoventrally, even relative to *Archaeolemur edwardsi*, and has moved forward and concentrated most of its volume anteriorly, taking with it the anterior fibers of temporalis. This anterior shifting of temporalis may have been responsible to some degree for the anterior rotation of the anterior and lateral margins of the orbits, but it seems likely that the increased frontation and convergence of the orbits was in itself adaptive. This would particularly have been the case if the inference, made later, that *Hadropithecus* was heavily dependent on the use of its hands in feeding is correct.

ECOLOGICAL RELATIONSHIPS OF THE ARCHAEOLEMURINES¹

WALKER (MS) HAS DEMONSTRATED that in its postcranial skeleton *Archaeolemur* possesses many of the features listed by C. Jolly (MS) as characterizing terrestrial cercopithecoid monkeys, and has also adduced a number of other characteristics strongly suggestive of terrestrial quadrupedalism. Among these features are the following. In the humerus: high and prominent greater tuberosity, small brachialis flange, small and backwardly displaced medial epicondyle, poorly rounded capitulum, and wide olecranon fossa. In the ulna: posteriorly and medially inclined olecranon process, deep proximal radial facet, high coronoid process and transversely compressed styloid process. In the femur: anterior convexity of the shaft. Only in the scapula does *Archaeolemur* fail to show features associated with terrestriality among cercopithecoids.

The postcranial skeleton of *Hadropithecus* is much more poorly known than that of *Archaeolemur*, but those elements which we do have are in general very similar to those of this genus, although Walker considered that their relative gracility and elongation indicates a greater commitment to terrestriality. It is very interesting in this context that, as Lamberton ("1937" [1938]) has pointed out, the forelimb of *Hadropithecus* was probably longer than the hindlimb. Among highly terrestrial primates, such a configuration is unique (C. Jolly, MS) to the Pleistocene relatives (subgenus *Simopithecus* [Andrews]) of the present-day gelada baboon, *Theropithecus* I. Geoffroy. This animal is perhaps the most terrestrially committed of all cercopithecoid monkeys.

This comparison is especially significant because, from a strictly morphological standpoint, *Theropithecus* and *Hadropithecus* share many cranial characteristics whose common possession appears to reflect adaptation to similar ecological niches. Many of these features likewise characterize early hominids, and Jolly (1970a) has

utilized them in constructing a model of hominid differentiation. Jolly has summarized these features in tabular form, and table 10 represents a modification of his table to include those features of *Hadropithecus* pertinent to this adaptive complex.

Most of the cranial peculiarities of *Theropithecus* relative to *Papio* Erxleben, which probably approximates fairly closely its ancestral form, may be ascribed to the diet and feeding behavior of this animal. *Papio*, an extremely adaptable form, appears basically to be a woodland- or deciduous forest-dwelling type. Although today *Papio* is widespread in open-country habitats, where it has been most extensively studied, the present open environments of many populations of *Papio* appear largely to be artefacts of human interference. There is strong evidence that the Pleistocene *Theropithecus* was widespread in open, treeless areas, while *Papio* preferred a more wooded habitat (C. Jolly, MS). The present environments of *Papio* and *Theropithecus* are therefore somewhat atypical as far as the conditions in which their feeding adaptations evolved are concerned.

Papio, living in deciduous forests or seasonal woodlands, is thus required to possess a more plastic, adaptable, type of feeding behavior, involving the exploitation of food sources both in the trees and on the ground, than is *Theropithecus*, whose sustenance is entirely derived from terrestrial sources. The studies of Crook (1966, 1967; Crook and Aldrich-Blake, 1968) on the surviving populations of *Theropithecus* in the High Semyen of Ethiopia have revealed that these animals exist on a diet of the blades, seeds, and rhizomes of grasses, supplemented with ground-living arthropods, the leaves of low shrubs, and the bulbs of small plants. All these food items are small, most of them are relatively tough, and as they are obtained at or near ground level, they are generally gritty. These items are conveyed to the mouth via the hands usually while the animal is in a sitting position and require no incisal preparation.

The most striking adaptations to such a diet in the gelada lie in its dentition. The incisors are small (although they are not reduced to a degree

¹This section was written before the author had seen the article by Jolly (1970b). While we are in substantial agreement as regards our ecological inferences, our biomechanical conclusions differ because of Jolly's acceptance of a lever action of the mandible.

TABLE 10
COMMON CHARACTERISTICS OF EARLY HOMINIDS, *Theropithecus*, AND *Hadropithecus*
(Modified from Jolly, 1970)

	Hominids	<i>Theropithecus</i>	<i>Hadropithecus</i>
Cranium and Mandible			
Foramen magnum basally displaced	X	—	—
Articular fossa deep	X	—	X
Fossa narrow, post-glenoid process appressed to tympanic	X	X	X
Post-glenoid process long and stout	—	X	X
Basi-occipital short and broad	X	X	X
Mastoid process present	X	X	—
Temporal origins set forward on cranium	X	X	X
Ascending ramus vertical	X	X	X
Mandibular corpus robust in molar region	X	X	X
Premaxilla reduced	X	X	X
Dental arcade narrows anteriorly	X	X	X
Dental arcade V-shaped; massive "simian" shelf	—	X	X
Teeth			
Incisors small	X	X	X
Canine relatively small	X	X	X
Male canine "feminized"; little canine sex dimorph.	X	X	X
Cheek teeth markedly crowded mesiodistally	X	X	X
Cheek teeth with deep and complex enamel invagination	—	X	X
Cheek teeth with thick enamel	X	—	X
Wear on cheek teeth flat, not inclined buccolingually	X	—	X
Wear on teeth rapid, producing steep wear gradient	X	X	X

comparable with those of *Hadropithecus*), and although in extant *Theropithecus* large canines are retained in the males, in some of the large Pleistocene representatives of the genus the canines were relatively much smaller. The molars are high crowned, with tall cusps, and are larger than those of *Papio*. They become rapidly worn, and thus present a steep wear gradient from front to back. When worn, these teeth show alternating ridges of enamel and dentine. Unlike the molars of *Hadropithecus*, they decrease in size anteriorly. In association with this dentition, the gelada possesses deep maxillae and a robust mandible.

The resemblances of the dental system of *Hadropithecus* to that of the gelada are at once apparent, and are in themselves sufficient to suggest a close similarity between the two animals in diet and feeding behavior. It can be stated with fair assurance that *Hadropithecus* fed by conveying gritty and probably relatively small particles to its mouth with its hands, and grinding them powerfully.

Incisal and canine reduction were probably related to the virtual redundancy of these teeth

in this kind of feeding, although social factors may also have played a role in the reduction of the canines. The mechanisms of this reduction may well have been those adduced by Jolly (1970a) to explain the reduction of the incisors in *Theropithecus*: a "somatic budget effect," related to physiological economy, and the "Oppenheimer effect" by which, although dental size is determined genetically, alveolar size is partly a function of usage. A large tooth occupying an alveolus that is too small because it lacks the exercise that would promote its full development would be a functional liability. There is, in *Hadropithecus*, no apparent specialized explanation of canine (or, in the case of the lower dentition, caniniform) reduction such as is the case, for instance, among the hominids (Pilbeam, 1970), since although the lower caniniform was morphologically suited to use as a shearing premolar, this function was absent in *Hadropithecus*.

Among hominids, reduction of the canine has been ascribed by many authors to the redundancy of a dental weapon subsequent to the adoption of tool use. A variety of lines of evidence

make it clear that this hypothesis is untenable, and the presence of greatly reduced canines in *Hadropithecus* provides yet another argument against it. Lamberton ("1937" [1938]) tried to explain canine reduction in *Hadropithecus* by introducing a related suggestion which has also been applied to hominids: "Peut-être . . . ces Lémuriens suppleaient-ils, par l'intelligence et la ruse, à la faiblesse de leurs armes défensives, ce qui expliquerait le grand développement de leur boîte cervicale" (p. 18). The size and morphology of the brain of *Hadropithecus* shows, however, that such a suggestion is highly implausible. Canine reduction has occurred in a number of primate lines and is presumably to be explained differently in each one. If a specific common element is involved, it lies almost certainly in the masticatory mechanism; but, as implied above, such an element may not exist.

Molarization of the posterior premolars and molar expansion and complication in *Hadropithecus* were without doubt due to the need to increase the available dental grinding surface per unit body weight, and to lengthen the functional life of these teeth in the face of the exceptional wear imposed by an abrasive diet of the type suggested. Further evidence for a tough, abrasive diet lies in the extreme mesio-distal packing of the grinding teeth of *Hadropithecus*. This is largely a result of "mesial drift," apparently a compensatory mechanism for the loss of interproximal tooth substances. The name "mesial drift" is something of a misnomer; as Moss and Picton (1967) have shown, teeth tend to migrate in the direction in which they are inclined upon eruption. Thus the premolars of *Macaca* migrate distally. The loss of approximal dental material is caused by the movement of adjacent teeth relative to one another, and the degree of such wear seen in *Hadropithecus* indicates that powerful chewing, under which such wear is greatest, was taking place. This in turn indicates a tough diet. In *Archaeolemur* the decrease in cheek-tooth length through life is less severe.

The features of the cranium and mandible listed by Jolly as indicating a functional proximity between the gelada and early hominids are apparently somewhat less directly associated with terrestrial "graminivorous" feeding than are those of the dentition, and may in some cases be explained by functional hypotheses

other than those which Jolly provided, since this author's analysis of skull structure depends on the assumption that the jaw acted as a lever. Thus in *Theropithecus*, as in *Hadropithecus*, the vertical orientation of the ascending ramus of the mandible and the forward migration of the origin of the temporalis relative to the condition in *Papio* are correlated with the shortness of the animal's face rather than being due, as Jolly suggested, to increasing the moment arm of the masseters around the jaw joint and adding the pull of the temporalis to that of the masseters.

As entirely different masticatory systems are involved in *Hadropithecus* and *Theropithecus*, detailed functional comparisons between the two cannot freely be made, despite many morphological similarities, except in terms of the elements most specifically common to both, i.e. the teeth and their immediate supporting structures. As stated, however, these resemblances are so suggestive that it is difficult to avoid the conclusion that *Hadropithecus* and *Theropithecus* have adapted to similar ecological situations, albeit in very different ways. Whether or not the apparent elongation of the forelimbs of *Hadropithecus* indicates that this animal, like *Theropithecus*, generally foraged from a sitting position, remains obscure.

If *Theropithecus* and *Hadropithecus* were descended respectively from forms resembling modern *Papio* and *Archaeolemur*, as in each case seems likely, can any useful parallels be drawn between *Papio* and *Archaeolemur*? Since neither of these animals is as highly specialized as *Hadropithecus* or *Theropithecus*, and since they are descended from radically different stocks, one would expect any parallels to be much more tenuous than in the cases just discussed. This is precisely the situation. Basic cranial design differs greatly between these two animals, as between *Hadropithecus* and *Theropithecus*, and, again, the closest (almost the only) direct morphological similarities lie in the dentition. Such dental similarities are most striking in the incisal region, although the lateral incisors of *Archaeolemur* are much reduced relative to those of *Papio*, and are, in fact, most reminiscent of those of the predominantly frugivorous *Pongo* Lacépède. The great development of the central incisors in *Archaeolemur*, from an almost certainly highly reduced ancestral condition, appears somewhat unaccountable in view of the form and function of its premolars, which the animal might very

reasonably have used to prepare food in a manner analogous to incisal biting in higher primates. The premolars were evidently as well equipped as the incisors to perform almost any incisal function aside from grooming, which the incisors of *Archaeolemur* were patently not adapted to do. It might be speculated that the premolars of *Archaeolemur* evolved as they did, from a not altogether different prior condition, precisely to fulfill such functions; grooming teeth, such as the archaeolemurine ancestor probably possessed, are generally unsuited to any other function.

Possibly the large incisor teeth of *Archaeolemur* were used in cropping, in dealing with extremely large food objects, or, most likely, for scraping the internal surfaces of hard-skinned fruits. Modern lemurs generally reduce food items by inserting them manually between the premolars, which are used to slice them; this habit is presumably attributable, at least in part, to their possession of grooming incisors, and may well explain the morphology of their premolars.

With what vegetable materials might the highly specialized premolars of *Archaeolemur* have been equipped to deal? Such items as stems, twigs, and hard-skinned fruits are obvious possibilities, but in the cases of the first two of these one would expect to find greater wear on the molars than actually occurs, due to the necessity of strong comminution of such tough, fibrous substances prior to ingestion. One might also expect to find rather larger molar teeth than either species of *Archaeolemur* possesses. On the other hand, if the materials dealt with by the premolars were the thick outer skins of soft-centered fruits, these objections would be met, since pulpy fruits require little dental preparation prior to swallowing. A similar observation may be made of the ubiquitous tamarind, or *kily* pod (*Tamarindus indica*); A. Jolly (1966) has observed that lemurs gain nutrition not from the seeds themselves, which are generally excreted whole, but from their covering membranes. Although the tough outer husk of the *kily* pod presents no substantial obstacles to *Lemur* or *Propithecus*, whose masticatory apparatuses are far less robust than was that of *Archaeolemur*, an animal of archaeolemurine size would need to

process large quantities of pods to extract any substantial proportion of its nutritional requirements.

The molars of *Archaeolemur* are reminiscent of those of *Papio* and other cercopithecoid monkeys in showing a bilophodont condition. The fact that the molars of *Archaeolemur* decrease in size posteriorly, whereas the reverse occurs in *Papio*, merely reflects the difference in the preferred bite point and in the overall mechanics of the jaws. Bilophodonty has been evolved independently in many different lines of mammals, including, besides those under discussion, the deinotheres, listriodontid pigs, and tapirs. All these animals are known to be, or are inferred on the basis of strong evidence to have been, browsing types. Unfortunately, bilophodonty in itself suggests no more than this broad adaptive category. Colobine monkeys, however, possess higher, more pointed cusps and transverse lophs on their molar teeth (Pilbeam, *in* Pilbeam and Walker, 1968) than do cercopithecines, probably in correlation with their leaf-eating habits; the lower, blunter cusps and lophs of cercopithecines presumably reflect their more generalized, more frugivorous diet. The condition seen in *Archaeolemur* molars is most reminiscent of that of cercopithecines, and may suggest that this animal existed on a predominantly frugivorous diet.

It seems reasonable to suppose, at any rate, that *Archaeolemur* was dietarily more generalized than *Hadropithecus* and that in diet, as less certainly in preferred habitat, *Hadropithecus* was to *Archaeolemur* as *Theropithecus* is to *Papio*. Unfortunately, the known distributions of the two Malagasy genera do not clarify the situation, as both have been found in environments as dissimilar as those represented by Ampasambazimba, in the damp forested interior, and Andrahomana, in the dry south of the island.

In conclusion, it can unequivocally be said that the present findings support Lamberton's statement that: "Un régime alimentaire différent [between *Hadropithecus* and *Archaeolemur*] a amené une station habituelle différente et produit aussi beaucoup d'autres spécialisations, notamment dans la denture" ("1937" [1938], p. 44).

RELATIONSHIPS WITHIN THE INDRIIDAE

FROM THE FOREGOING descriptions and discussion, it is clear that the archaeolemurines are very closely related to the extant indriines, particularly *Propithecus*. It is also clear that *Palaeopropithecus* and *Archaeoindris* are extremely distinct from *Indri*, *Propithecus*, and *Avahi*, yet these two genera have invariably been classified within the Indriinae, while the archaeolemurines have invariably been classified separately from this subfamily.

It is difficult to avoid the conclusion that this taxonomy has been based purely on the teeth, however much other characteristics may have been discussed. The extant indriines, *Palaeopropithecus* and *Archaeoindris* share the same dental formula, and their molar and premolar teeth are very similar, although M_1^1 and M_2^2 in *Palaeopropithecus* and *Archaeoindris* are relatively somewhat elongated. The incisors of *Palaeopropithecus* (none of *Archaeoindris* are known) do not form a dental comb, but their size and morphology indicate derivation from such a condition. In short, the dentitions of these two animals (and likewise their mandibular morphology) are strongly reminiscent of those of the living indriines, far more so than are those of *Hadropithecus* and *Archaeolemur*. But on almost every other count, the degree of similarity between these groups are reversed. In the structure of the ear region, for instance, *Palaeopropithecus* and *Archaeoindris* are widely divergent from the general lemuroid condition, the bullae, as in *Megaladapis*, having become drastically

reduced, and the ectotympanic forming a long, ossified, tubular external auditory meatus. Other cranial differences from the extant indriines do not require enumeration here; suffice it to say that they are sufficiently strong to have led Gregory (1915) to characterize *Palaeopropithecus* as "gross and swinelike . . . degraded" (p. 440) when compared with *Propithecus*. Walker (1967) has concluded that the postcranial skeleton of *Palaeopropithecus* (that of *Archaeoindris* is unknown) indicates an arm-swinging, hanging mode of progression, which finds its closest living analogue in the quadrumanous orangutan.

All available evidence, then, points to the fact that *Archaeoindris* and *Palaeopropithecus* are morphologically at least as distinct from the living indriines as are the archaeolemurines; this is expressed in the provisional classifications given on pp. 98–100. The precise relationships between the Indriinae, Archaeolemurinae, and Palaeopropithecinae are conjectural; presumably the last two groups sprang from an indriine ancestor, but the relative times of divergence of the two groups are uncertain. Almost everything about the Archaeolemurinae (particularly *Archaeolemur majori*) bespeaks a relatively recent divergence from the Indriinae; of the Palaeopropithecinae the reverse applies. A case might be made for raising the three subfamilies just discussed to the familial level, and regarding the Indriidae as presently constituted as of superfamilial status; however, a more conservative judgment is provisionally preferred here.

CLASSIFICATION OF LOWER PRIMATES

Order Primates

- †Suborder Palaeoprosmii
- †Infraorder Plesiadapiformes
 - †Superfamily Plesiadapoidea
 - †Family Plesiadapidae
 - †Subfamily Plesiadapinae
 - †Subfamily Saxonellinae
 - †Family Carpolestidae
 - †Superfamily? Plesiadapoidea *incertae sedis*
 - †Family Paromomyidae
 - †Family Picrodontidae
 - †Family Microsyopidae

†Extinct taxa.

- †Subfamily Uintasoricinae
- †Subfamily Microsyopinae
- Suborder Prosimii
- Infraorder Lemuriformes
- †Superfamily Adapoidea
- †Family Adapidae
- †Subfamily Adapinae
- †Subfamily Notharctinae
- Superfamily Lemuroidea
- Family Lemuridae
- Subfamily Lemurinae
- Subfamily Cheirogaleinae
- †Subfamily Megaladapinae
- Family Indriidae
- Subfamily Indriinae
- †Subfamily Archaeolemurinae
- †Subfamily Palaeopropithecinae
- Family Daubentoniidae
- Infraorder Lorisiformes
- Superfamily Lorisioidea
- Family Lorisidae
- Subfamily Lorisinae
- Subfamily Galaginae
- Infraorder Tarsiiformes
- Superfamily Tarsioidea
- Family Tarsiidae
- Subfamily Tarsiinae
- †Subfamily Microchoerinae
- †Superfamily Tarsioidea? *incertae sedis*
- †Family Anaptomorphidae
- †Subfamily Anaptomorphinae
- †Subfamily Omomyinae

PROVISIONAL CLASSIFICATION OF LEMUROIDEA

- Superfamily Lemuroidea
- Family Lemuridae
- Subfamily Cheirogaleinae
- Cheirogaleus*
- C. major*
- C. medius*
- Microcebus*
- M. murinus*
- M. coquereli*
- Phaner*
- P. furcifer*
- Subfamily Lemurinae
- Lemur* (*Lemur*)
- L. catta*
- L. fulvus*
- L. macaco*
- L. mongoz*
- L. rubriventer*
- L. variegatus*
- †*Lemur* (*Pachylemur*)
- †*L. insignis*

†Extinct taxa.

- Lepilemur*
- L. mustelinus*
- L. ruficaudatus*
- Hapalemur*
- H. griseus*
- †*H. simus*
- †Subfamily Megaladapinae
- †*Megaladapis*
- †*M. madagascariensis*
- †*M. grandidieri*
- †*M. edwardsi*
- Family Indriidae
- Subfamily Indriinae
- Indri*
- Indri indri*
- Propithecus*
- P. verreauxi*
- P. diadema*
- Avahi*
- A. laniger*
- †*Mesopropithecus*
- †*M. pithecoides*
- †*M. globiceps*
- †Subfamily Archaeolemurinae
- †*Archaeolemur*
- †*A. majori*
- †*A. edwardsi*
- †*Hadropithecus*
- †*H. stenognathus*
- †Subfamily Palaeopropithecinae
- †*Palaeopropithecus*
- †*P. ingens*
- †*Archaeoindris*
- †*A. fontoynonti*
- Family Daubentonidae
- Daubentonia*
- D. madagascariensis*
- †*D. robusta*

†Extinct taxa.

Lamberton ("1937" [1938]) stated his belief that: "Il nous semble . . . logique de penser qu'*Archaeolemurs* et *Hadropithèques* sont des rameaux issus d'un tronc commun encore hypothétique et dont le développement s'est longtemps poursuivi côte à côte" (pp. 43-44).

Two of Lambertson's points require discussion here. First, although it is strictly true that the common ancestor of *Archaeolemur* and *Hadropithecus* is unknown, it is not difficult to guess at its nature. Second, a relatively recent divergence of the two genera, possibly within the latter half of the Pliocene, is not improbable.

Detailed examination of indriid cranial structure strongly suggests a morphological sequence as follows: *Propithecus*: *Mesopropithecus* (particu-

larly the gracile species): *Archaeolemur majori*: *A. edwardsi*: *Hadropithecus*. It is not suggested that these animals form an evolutionary sequence, but it is not implausible, especially in the light of Walker's (1967) belief that *Mesopropithecus* was an arboreal quadruped, that they approximate to one, each animal in the series representing a more conservative condition than does its successor. This hypothesis has been tested within the Archaeolemurinae by the technique of Trend Surface Analysis.

The computer-drawn deformation grids in figure 38 show the result of this analysis, using 26 reference points, on the side views of *Archaeolemur majori*, *A. edwardsi*, and *Hadropithecus*. Several clear trends are evident through this

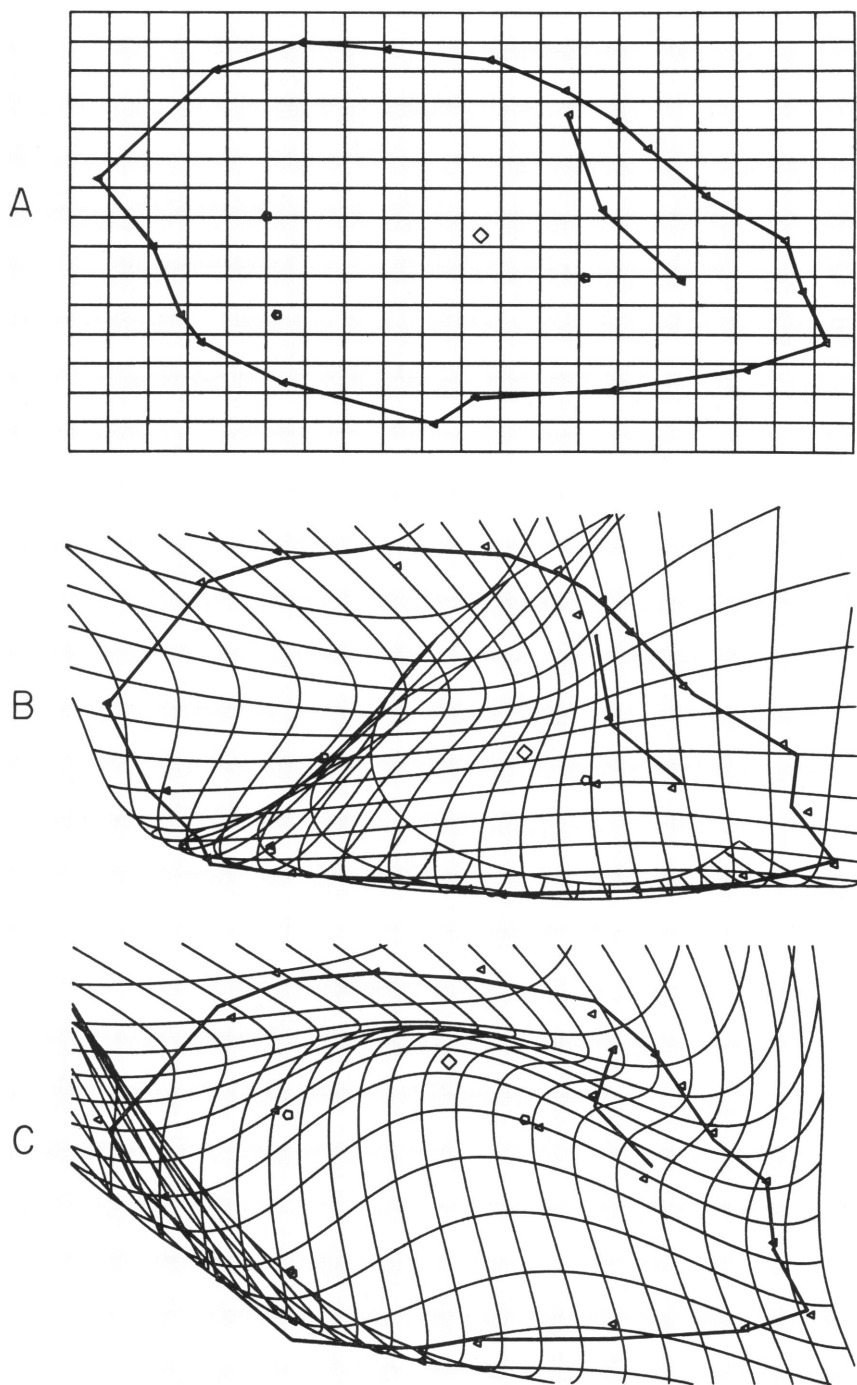


FIG. 38. Computer-drawn transformation grids of side views of the three archaeolemurine species. A. *Archaeolemur majori*, with basic cartesian grid superimposed (power 1). B. *Archaeolemur edwardsi* deformed to fit *A. majori* (power 5). C. *Hadropithecus stenognathus* deformed to fit *A. majori* (power 5). Deformation is indicated by the grids; the cranial outlines are merely for reference.

sequence. The facial profile becomes more vertical, largely in consequence of the swelling of the frontal sinus (and of anterior dental diminution in *Hadropithecus*); the sagittal crest, absent in *A. majori*, becomes more pronounced from *A. edwardsi* through *Hadropithecus*; the lower part of the face becomes deeper; the maximal height of the cranial vault is shifted posteriorly; the anterior root of the zygoma is pulled down (and in *Hadropithecus* also anteriorly), whereas the posterior root is dropped, giving a more horizontal arch; the orbits are moved relatively forward and rotated to a more vertical position; and the back of the skull becomes progressively less rounded, reflecting the greater development of the nuchal crest and surrounding areas.

In basal view (not illustrated) the overall trend is less clear-cut, almost entirely because the cranial base is slightly broader in *A. majori* than *A. edwardsi*, although the cranium of *Hadropithecus* is by far the broadest based. There is a progressive narrowing of the muzzle anteriorly, although the difference between *Archaeolemur edwardsi* and *Hadropithecus* is by far the more marked, while there is a clear trend toward widening of the occipital region, and some elongation in the posterior part of the skull base throughout the series.

The deformation grids thus demonstrate the plausibility of the morphological sequence suggested within the Archaeolemurinae, the only forms tested.

PARALLELISMS BETWEEN THE ARCHAEOLEMURINAE AND HIGHER PRIMATES

THE VIEW HAS PERVADED much of the literature on the Archaeolemurinae, particularly that part of it in English, that these animals were more "advanced" than other Malagasy prosimians. This idea was stated as early as 1896 by Major, who, as we have seen, at first believed *Archaeolemur* to have been a Malagasy monkey; but it received its most elaborate treatment at the hands of Standing (1908a), who propounded the thesis that the discovery of the subfossil primate fauna of Madagascar rendered artificial the separation of prosimians and higher primates into separate suborders of Primates. The lemurs, Standing believed, were the products of "retrogressive evolution" in isolation, which had robbed them of many characteristics present in the "Ape-like"¹ common ancestor of the lemurs and the Anthropoidea.

By way of summary, it may be useful to examine the extent to which parallelisms may in fact be detected between the Archaeolemurinae and the higher primates.

Clark (1959) has provided the most succinct recent account of the characteristics generally used to distinguish prosimians from higher primates. Such characters of the skull include reduction of the snout region, together with restriction of the nasal cavities; flexion of the cranial base and recession of the facial skeleton beneath the braincase; forward rotation of the orbits; enlargement of the entocarotid artery; appearance of the ethmoid in the medial orbital wall; postorbital closure; disappearance of a prominent auditory bulla and the formation of a tubular ossified external auditory meatus (except in Platyrrhines); and ventral migration of the foramen magnum.

In almost none of these characteristics do the archaeolemurines resemble higher primates. In the general structure of the ear region and in temporal arterial (and venous) circulation these animals do not depart from the general lemuroid condition; *contra* Major (1901) there is no os planum in the medial orbital wall (although this element is apparently present in some cheirogaleines); postorbital closure is absent. The

¹Standing used this term indiscriminately to describe all higher primates.

snout remains large (even, relatively speaking, in *Hadropithecus*, if the forward expansion of the upper face is considered); and the nasal cavity is capacious. The cranial base, as in other lemurs, shows no central kyphosis, and the foramen magnum is less ventrally rotated than that of living indriines (this is probably a postural correlate, although one applying only within the Prosimii). The recession of the tooth rows beneath the braincase (*sensu lato*; not beneath the brain) in *Archaeolemur* presumably reflects the extreme length of the dental arcade in this animal, and in *Hadropithecus*, with its shorter tooth rows, its derivation from a form similar to *Archaeolemur*.

Dental characteristics enumerated by Clark include spatulate incisors and quadritubercular molars; however, quadritubercular molars are present in living indriines as well as in *Archaeolemur*, although they are admittedly very different in form and function from those of catarrhines. The dental system is the feature of the archaeolemurines most reminiscent of those of higher primates, having adapted toward a powerful masticatory mode, although, as we have seen, it arrived at this condition via a different route.

The prosimian, and particularly indriine, affinities of the brain of *Archaeolemur* are very clear. Clark listed the following features as characterizing the higher primate brain: great expansion and convolution of the cerebral hemispheres; the pattern of sulcal development; marked reduction of the olfactory centers and expansion of the visual areas; elaboration of the cerebellum; eversion of the lateral geniculate nucleus. Many authors appear to have been beguiled by the longitudinal arrangement of the cerebral sulci in *Archaeolemur*, since this is the pattern found in higher primates, in contrast to the more radial sulcal dispositions found, for instance, in *Lemur*. However, this longitudinal pattern is also characteristic of *Indri* and *Propithecus*, and, as we have seen, there is no evidence to suggest that the brain of *Archaeolemur* represented any advance over the indriine condition. The relatively small olfactory areas in the brain of *Archaeolemur* are no further

reduced than are those of *Indri*; although the olfactory bulbs in this latter animal are somewhat reduced compared with those of one or two platyrrhine genera, they are nevertheless large relative to those of most platyrrhines and all catarrhines.

The cranial sensory organs of higher primates are characterized by Clark as follows: possession of a differentiated macula in the center of the retina; reduction of the external ear; disappearance of a naked rhinarium; and reduction of the turbinal elements in the nasal cavity. If my earlier inferences regarding the eye and rhinarium are correct, then the archaeolemurines showed the typical prosimian condition in these respects. The condition of the ear region leaves no doubt as to the animals' auditory organization, and the turbinates are known to have been complex.

Examination of the postcranial skeleton of *Archaeolemur* and *Hadropithecus* leaves no doubt as to the lemuroid affinities of these animals, but, as Walker has shown, the limb elements are in many respects modified toward the condition seen in highly terrestrial catarrhine monkeys. The situation relative to the postcranial skeleton appears to be precisely analogous to that of the masticatory apparatus; the archaeolemurines, from an entirely different starting point, evolved, like some catarrhine monkeys, into terrestrially adapted browsers (*Archaeolemur*, *Papio*), or grazers (*Hadropithecus*, *Theropithecus*). The fact that adaptation to presumably similar ecological niches took very different routes in the two groups (more so in the skull than in the postcranial skeleton) appears to be very largely a result of the difference in their ancestral forms. The principle has been well stated by Lewontin (1969): "It is not true . . . that all the results of evolution are different from each other because the forces of natural selection were different. Many are different from each other because the starting conditions were different" (p. 41).

Why, then, did the lemurs, which appear to have occupied a range of ecomiches not altogether dissimilar to those occupied by catarrhines, not evolve toward a condition more reminiscent of the higher primates? Cartmill (1972) implied that this was due to the failure of the ancestral

Malagasy prosimians to develop an extensive apical interorbital septum, resulting in the maintenance of a close contact between the braincase and the nasal cavity. This, Cartmill believed, meant that orbital reduction accompanying the shift from a nocturnal to a diurnal activity pattern would have resulted in an enlargement of the olfactory fossa at least equivalent to that of the braincase.

This explanation is unsatisfactory in that it is purely anatomical, and therefore takes no account of possible selective pressures other than those propelling the posited shift in activity rhythm, and assumes, without strong supporting evidence, that both are necessary correlates of reduced orbital size. The principal differences between lemurs and higher primates lie in the organization of the nervous system and in the qualities of the sensory organs housed by the skull. Cerebral expansion among the ancestral higher primates was surely the result of selective pressures toward increased intelligence, and the primary differences in the sensory organs of a shift in the balance between olfaction and vision. The reasons for cerebral expansion in higher primates are unlikely to be explicable purely in terms of an apparently unrelated morphological change which took place at a patently prosimian level of organization.

Increase in intelligence is primarily a matter of extending the ability to react positively and inventively to novel situations. If the ecological setting of ancient Madagascar did not provide any adaptive value in this, then it would not be surprising to find even the most specialized of the lemurs possessing a prosimian level of neural organization, although some extant lemurs are admittedly more encephalized than others. Perhaps isolated Madagascar, with its very restricted mammalian fauna, failed to provide an impetus toward a more advanced level of organization for precisely those reasons which permitted an extensive lemuroid adaptive radiation. The relative smallness of the island undoubtedly had a part to play, also; initial advances toward the catarrhine evolutionary condition probably took place widely over Eurasia and Africa.

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