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**CRANIA AND DENTITIONS OF ARCHAOLEMURINAE
(LEMUROIDEA, PRIMATES)**

by

Ian Tattersall

**A Dissertation Presented to the Faculty of the
Graduate School of Yale University in Candidacy
for the Degree of Doctor of Philosophy**

1971

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Abstract

Until relatively recently some sixteen lemuroid genera existed on Madagascar; due to the intervention of man, only ten survive today. Sites of recovery of subfossil lemuroids are widely distributed over the island; available C¹⁴ dates range from 2,850 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 primary objects in view: to determine to what extent they were, as has been frequently claimed, "advanced" relative to other lemuroids; to elucidate their ecological relationships, and to explain, as far as possible, their cranial architecture in functional terms.

The study indicates that the archaeolemurines were not advanced over the general indriid condition in their neural or peripheral sensory organisation; 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 Old World higher primates in their masticatory apparatus, but analysis shows this resemblance 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, especially 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 pterygoïd muscles as a couple acting around the mandibular insertion of the sphenomandibular ligament, while during lateral motion 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 particularly the dentitions, of the archaeolemurines, indicate that these animals represent an adaptive radiation closely paralleling that of the large terrestrial African monkeys. Archaeolemur appears to have been a browser similar to the common baboon Papio, while Hadropithecus represents a highly specialised grazer reminiscent of the gelada baboon, Theropithecus.

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PART ONE: GENERAL

INTRODUCTION

Isolated on the island of Madagascar for upwards of 50 million years, the lemuriform primates underwent a wide adaptive radiation. The modern Malagasy lemur fauna gives a distorted picture of the extent of this adaptive radiation, since during the last one thousand or so years many genera have become extinct. Of the extinct groups, Archaeolemurinae, in particular, has been regarded as greatly advanced relative to extant forms. This study was undertaken 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 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, doomed to failure. 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 which studies of living primates will, hopefully, provide in the future.

Inferences made in this report as to the possible ecological relationships of the archaeolemurines are based purely on morphology. Another possible approach to this problem lies in the fact that the sudden removal of a substantial proportion of the total lemuroid fauna must have left unoccupied a large number of the ecological niches available in Madagascar. Unfortunately, personal observation and the reports of J.-J. Petter (1962a, b) and A. Jolly (1966)

suggest that Parkinson's law could well be rephrased in this context to read "animals expand to fill the ecological space available to them". The apparent general lack of niche specificity and competitive exclusion among Malagasy lemurs suggests that far more, and more detailed, observations of lemur ecology than are presently available will be required before vacant niches can be identified, if, indeed, this is at all possible. The problem is, of course, exacerbated by the large-scale destruction of the natural vegetation of Madagascar which has taken place since the advent of man on the island, and which at the present time threatens the extinction of the entire native Malagasy mammalian fauna.

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ABBREVIATIONS

The following abbreviations have been used in the text and tables:

A. M.	Académie Malgache, Tananarive
V.N.H.M.	Naturhistorisches Museum, Vienna
A.M.N.H.	American Museum of Natural History, New York
B. M.	British Museum (Natural History), London

n	- sample size
\bar{x}	- mean
S.D.	- standard deviation
Max. length	- maximum length of cranium
Facial l.	- facial length (nasion to alveolare)
Bizy. w.	- maximum width of the cranium across the zygomae
W. p/o con.	- minimum frontal breadth at the post-orbital constriction
Max. zyg. ht.	- maximum height of the zygomatic arch
Max. nuch. w.	- maximum width of occiput
L. for. mag.	- maximum length of foramen magnum in the sagittal midline
W. for. mag.	- maximum breadth of foramen magnum perpendicular to sagittal plane
Nas. ht., br.	- maximum nasal height, breadth
Orb. ht., br.	- maximum orbital height, breadth
L. pg1. proc.	- greatest vertical dimension of the postglenoid process
Bas.-alv.	- basion to alveolare
Bas.-nas.	- basion to nasion
Nas.-t'row	- perpendicular distance from nasion to the alveolar margin

ORIGIN, ISOLATION AND EXTINCTION OF THE SUBFOSSIL MALAGASY LEMUROIDS

It is generally recognised that the Malagasy lemuroids are descended from a group, or groups, of early Tertiary African prosimians, possibly related to the Holarctic family Adapidae. If the lemuroids are in fact diphyletic, it seems likely that the division is between Cheirogaleinae and the other lemurs; this group possesses a number of characteristics not shared by 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). Moreover, Charles-Dominique and Martin (1970) have demonstrated the close similarity in social behaviour between Microcebus and Galago demidovii. Cartmill (in press) 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 Lepilemur (particularly in the dentition) suggests that, if this is indeed the case, the cheirogaleines and lemurines could not be descended from a common ancestor peculiar to 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 lorisiform, not lemuriform, affinities. (McInnes, 1943; Simpson, 1967). In the absence of direct paleontological evidence, it is necessary to rely on comparative osteological evidence in deciding between a monophyletic or a polyphyletic origin of the Malagasy primates, and this evidence is equivocal. For the moment it seems most reasonable to regard such cheirogaleine characteristics as those noted above as secondary specialisations, and to retain the conventional classification of the extant lemurs on the assumption that this group of animals was monophyletically derived. It is quite clear, however, that this question is far from having been resolved, and that it is unlikely to be so until the appropriate paleontological evidence is acquired.

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 makes this certain. Opinions differ, however, as to precisely where the two were adjoined. Thus DuToit (1957) believes that Madagascar broke away from the mainland in the area now occupied by the Miocene islands of Zanzibar and Pemba. Walker (1967a) prefers an alternative location off the coast of present-day Mocambique, "with modern Cap St. André in a position some 70 miles upstream from the mouth of the Zambezi River and modern Ampanihy in the position of Lorento Marques" (p. 479). This latter arrangement permits the alignment of the major fault patterns of Madagascar, and Tanzania

and Mocambique. Assuming a constant rate of drift and a period of drift lasting from the late Cretaceous to the Miocene, Walker has estimated a drifting rate of one mile per 100,000 years. Thus by the early Eocene the minimum width of the Mocambique Channel would have been 50 miles; by the early Oligocene, 150 miles. The present minimum width of the channel, 250 miles, was obtained by the middle Miocene.

The evidence for possible land-bridging subsequent to the rifting-apart of Madagascar and Africa is not strong; certainly, bridging of the Mocambique Channel could not have occurred subsequent to the earliest Tertiary (contra Terminer and Termier, 1960). Walker concludes that the odds against the entry into Madagascar of the ancestral lemuroid stock, either across a land bridge, or by a "sweepstakes route" (probably rafting) subsequent to the middle Eocene at latest, are impossibly long; to this writer the possibility of any primate invasion of the island after the earliest Eocene seems remote.

In isolation, the Malagasy lemuroids underwent a wide adaptive radiation, involving until recently some sixteen genera, of which only ten presently survive. Much has been written in attempts to explain this large-scale extinction, and most contributions espouse one or 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 south-west of the island (e.g. Lamberton, 1934c; Mahé and Sourdat, in press); these authors,

noting that most of the deposits represent the remains of ancient, now-dry lakes, believe 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. Since 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 watercourses 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 a result of 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 (1967b). 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 which cannot be identified with any extant Malagasy mammals.

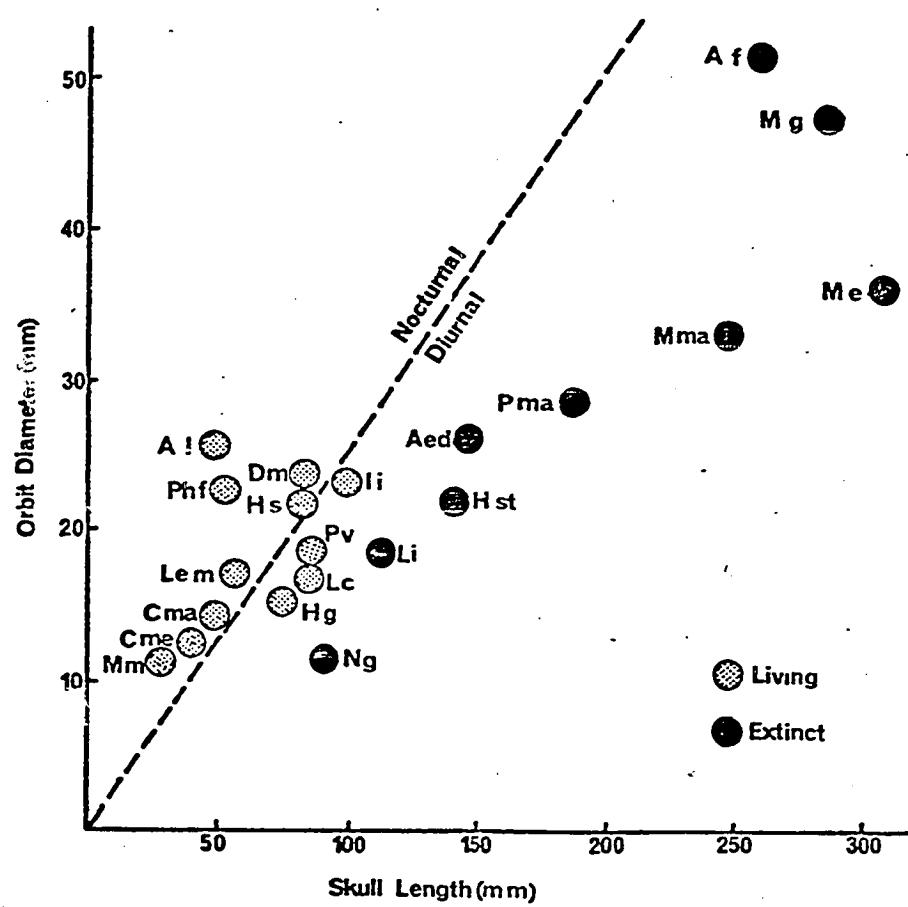
Walker (1967b) has more thoroughly investigated the agency of man in the destruction of the Malagasy fauna. He notes archaeological evidence of the contemporaneity of man and the subfossils at the sites of Taolambiby and Andrahomana, and reports

Figure 1

**Division between nocturnal and diurnal Malagasy lemuroids
as reflected in orbital size. (From Walker, 1970b).**

Abbreviations:

Aed	<u>Archaeolemur edwardsi</u>
Af	<u>Archaeoindris fontoynonti</u>
A1	<u>Avahi laniger</u>
Cma	<u>Cheirogaleus major</u>
Cme	<u>Cheirogaleus medius</u>
Dm	<u>Daubentonias madagascariensis</u>
Hg	<u>Hapalemur griseus</u>
Hs	<u>Hapalemur simus</u>
Hst	<u>Hadropithecus stenognathus</u>
Ii	<u>Indri indri</u>
Lc	<u>Lemur catta</u>
Li	<u>Lemur insignis</u>
Lem	<u>Lepilemur mustelinus</u>
Me	<u>Megaladapis edwardsi</u>
Mg	<u>Megaladapis grandidieri</u>
Mma	<u>Megaladapis madagascariensis</u>
Mm	<u>Microcebus murinus</u>
Ng	<u>"Neopropithecus" globiceps</u>
Pma	<u>Palaeopropithecus maximus</u>
Pv	<u>Propithecus verreauxi</u>
Phf	<u>Phaner furcifer</u>



that the latter locality has yielded subfossil bones bearing traces of cutting and burning; one Archaeolemur majori cranium, (B.M. M 7374), 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 to extant lemurs, and has suggested that they were all diurnal (except, presumably, Daubentonias robusta, whose cranium is not known), on the basis of the size of their orbits (see Fig. and accompanying caption). In addition, while all extant lemurs are arboreal, the archaeolemurines were terrestrially adapted. Thus we find that large, diurnal forms, those presumably most vulnerable to human predation, are extinct, while 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 1,000 or 1,500 B.P. at most. The most recent absolute date on a subfossil-bearing deposit is 1,000 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 wonderful fauna.

THE 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 which cannot be stratigraphically correlated, and which lie within modern, active, drainage systems (Walker, 1967). Mahé (1965) has classified these sites into three categories:

1. Marshes in volcanic areas (e.g. Morarano and Ampasambazimba).
2. Coastal marshes (on the south-west coast, e.g. Bevoha, Itampolo).
3. Caves (in the cliffs near Fort-Dauphin: Andrahomana).

As Walker has pointed out, however, there is little to be gained by adopting such a classification because of the isolated and fortuitous nature of the sites.

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 their nature can be gleaned from the literature. Recent surveys have been made of some sites (Walker, 1967; Raison and Verin, 1968; Mahe 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).

The most recently discovered of the subfossil sites, having come to light in 1961 when a farmer accidentally uncovered the first subfossil. Mahé assigns 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 tater 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 Amparihindro 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 meters.

Unfortunately, no complete list is yet available of the fauna recovered at Amparihindro, but Archaeolemur, Palaeopropithecus, Lemur (Pachylemur) and Lemur s.s. are represented.

AMPASAMBAZIMBA

In the province of Miarinarivo, 1.5 km. south-west of the village of Tsarazaza. 49° 25' E., 21° 05' S.; 1010 m. in altitude

(Walker, 1967). This site is the only one on which there is any extensive literature (Raybaud, 1902; Jolly and Standing, 1904; Grandidier, 1905; Standing, 1907; Fontoynont, 1908; Perrier de la Bathie, 1927; Lenoble, 1940; Walker, 1967). Both Raybaud and Standing published stratigraphic sections of the site.

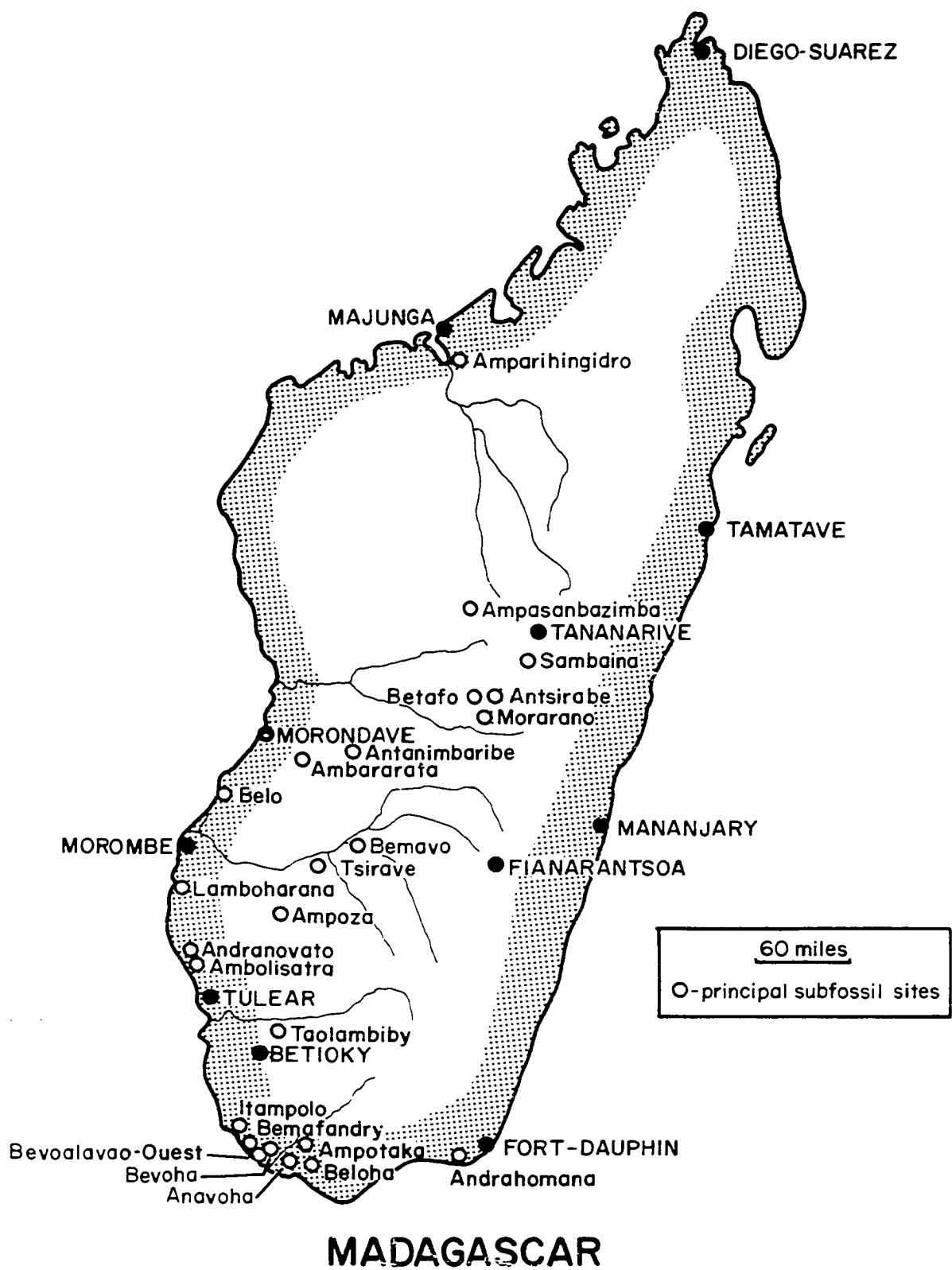
Ampasambazimba forms part of the Lake Itasy area, a region abounding in dormant volcanic cones from which radiate extensive lava streams. As Standing described the site:

"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.

Figure 2
Subfossil sites of Madagascar



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." (1907, p. 63).

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

"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 débris, 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..." (p. 63, 65).

Walker (1967) has summarised 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." (p. 433-4).

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 subfossil Malagasy lemuroids as the contemporaries of extant species in other parts of the island." (p. 71). Walker notes that samples from Ampasambazimba have been submitted for radiocarbon dating, but results are not yet available.

Perrier de la Bathie (1927) analysed a collection of fruits and seeds made by Lamberton 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). One wonders whether the word "occidentales" might represent a misprint for "orientales",

the fauna from Ampasambazimba, containing Indri and Avahi, has an eastern flavour. 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

<u>Archaeoindris fontoynonti</u>	<u>Avahi laniger</u>
<u>Palaeopropithecus maximus</u>	<u>Indri indri</u>
<u>Archaeolemur edwardsi</u>	<u>Cheirogaleus</u> sp.
<u>Hadropithecus stenognathus</u>	<u>Propithecus</u> sp.
<u>Megaladapis grandidieri</u>	<u>Lemur s.s.</u> sp.
<u>Mesopropithecus pithecoides</u>	<u>Hapalemur griseus</u>
<u>Lemur (Pachylemur) insignis</u> ¹	<u>Lepilemur mustelinus</u>

Other mammals:

<u>Cryptoprocta feros</u>	<u>Plesiorycterus madagascariensis</u>
<u>Cryptoprocta spelea</u>	<u>Hippopotamus lemerlei</u>
<u>Galictis</u> sp.	<u>Centetes</u> sp.
<u>Pseudailurus edwardsi</u>	

AMBOLISATRA

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

¹ L. (P.) jullyi of other authors; the two "species" are here regarded as conspecific.

Although this site has been known since 1865, when Alfred Grandidier found the first remains of extinct Malagasy mammals there, very little is known of Ambolisatra. Walker, who visited the site in 1965 reported (Walker, 1967) 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

Megaladapis edwardsi

Palaeopropithecus maximus¹

Lemur (Pachylemur) insignis²

Archaeolemur sp.

Other mammals

Hippopotamus lemerlei

Potamochoerus sp.

Sus sp.

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

² L. (P.) jullyi of other authors.

AMPOZA

47° 00' E., 24° 79' S. according to Walker (1967); approximately 44° 35' E., 22° 20' S. according to 1:500,000 map (Institut Géographique National, Tananarive, 1963). 620 m. above sea level. The site lies 3 km. north of the village of Ampoza, some 22 km. east of Ankazoabo, on a river variously named the Ampoza or Sakavanaka. C¹⁴ dated at 1910 ± 120 years B.P. (Mahé and Sourdat, in press).

Ampoza has been worked by Lamberton (1925), and White (1930) who collected large quantities of subfossil vertebrate material there. It was also visited by Walker (1967), who has provided the most comprehensive existing account of the site, although he notes that detailed geological mapping is still required.

The river flows in a westerly direction, towards its confluence with the Ampanihy river, across a series of sandstone strata which dip gently towards the east, cutting a step-like 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 notes that the large collections of lemuroid remains made there by White give a false impression of the composition of the fauna represented at Ampoza, since while several hundredweights of bones of Crocodilus, Hippopotamus and Testudo 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 meters, at the bottom of the fossiliferous beds.

The fauna from Ampoza includes:

Primates

Archaeolemur edwardsi

Megaladapis edwardsi

Megaladapis madagascariensis

Palaeopropithecus maximus

Lemur (Pachylemur) insignis

Propithecus verreauxi

Others

Hippopotamus lemerlei

Aepyornis sp.

Mullerornis sp.

Crocodilus niloticus

Testudo grandidieri

ANAVOHA

One of the sites in the Lower Menarandra valley, south of Ampanihy on the boundary between the Préfectures of Tuléar and Fort-Dauphin. C^{14} 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, 1934c, 1936a, c), Walker (1967) 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) 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 meters thick.

Lamberton was mystified by the heavy concentrations of bones of an enormous variety of animals in these deposits, and to account for this 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 recognise 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 maximus¹
Archaeolemur majori
Hadropithecus stenognathus
Propithecus verreauxi
Lemur (Pachylemur) insianis

Other mammals

Hippopotamus sp.
Hypogeomys sp.
Centetes sp.

ANDRAHOMANA

Cave site situated about 35 km. W.S.W. of Fort-Dauphin, on the south-eastern 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 (1967); the two accounts are very similar.

According to Walker:

"The cave is formed by the gouging of a series 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.

¹ P. ingens of Lamberton (1932).

The collapse of blocks between adjacent sink-holes 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 twenty metres. 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	Others
<u>Archaeolemur majori</u>	<u>Aepyornis</u> sp.
<u>Hadropithecus stenognathus</u>	<u>Centetes</u> sp.
<u>Megaladapis madagascariensis</u>	<u>Cryptoprocta ferox</u>
<u>Megaladapis edwardsi</u>	<u>Cryptoprocta spelea</u>
<u>Lemur (Pachylemur) insignis</u>	<u>Crocodilus niloticus</u>
<u>Cheirogaleus</u> sp.	<u>Testudo grandidieri</u>

ANDRANOVATO

Site on west coast somewhat north of Ambolisatra; bears same relation to coast as does Ambolisatra (Walker, 1967).

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 Jully (1899). Marsh site probably
of similar origin to Ampasambazimba, close to the town of
Antsirabé about 170 km. south of Tananarive on R. N. 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 cotié'res." (p. 36).

BELOHA

Situated slightly to the east of the Lower Menarandra
valley, Beloha is the administrative centre of the district.
Fossils described as coming from here are probably in fact
derived from one or other of the Lower Menarandra sites, most
likely Anavoha.

BEMAFANDRY

Lower Menarandra site near the village of Bemafandry to the west of Bevoha. C^{14} dated at 1980 ± 90 and 2060 ± 150 years B.P. (Mahé and Sourdant, in press).

Situated in the middle of the vast Sadaona series of sand dunes, close to the coast, this site apparently formed much as did those at Itampolo described by Mahé and Sourdant (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 Antsirabe on R.N. 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 some 10 km. west of the Menarandra estuary. According to Mahé and Sourdant (in press) the site consists of two fossiliferous deposits similarly formed, evidently in a manner analogous to Itampolo.

BEVOHA

Lower Menarandra site to west of the river. C^{14} dated at 2160 ± 110 years B.P. (Mahé and Sourdant, 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 this site; for faunal list and other information see entry on Anavoha.

ITAMPOLO

2-3 km north of Itampolo village on the southwest coast, a short distance inland from the Baie de Sapaly. C^{14} dated at 2290 ± 90 years B.P.; also at 980 ± 200 years B.P. (Mahé and Sourdant, in press).

Discussed briefly by Walker (1967) and at greater length by Mahé and Sourdant (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 Sourdant describe 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-grey in colour.

60 - 90 cm.: a clay-sandy layer quite distinct from that above, brownish in colour, 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 colour.

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. C^{14} dated at 1220 ± 80 and 2350 ± 120 years B.P. (Mahé and Sourdant, in press).

Excavated by Grandidier, Lamberton and White; in origin appears to be similar to Ambolisatra and many other sites, i.e. patches of alluvial deposits behind sand dunes (Walker, 1967). Grandidier records that bones are discovered at depths of less than 200 cm., and complains 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. 13).

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

Only identified as "les gisements de la région de Manombo" (Lamberton, 1933, p. xxxiii). Manombo is an administrative centre about 50 miles north of Tuléar on the estuary of the Manombo river. According to Lamberton, the sites consist of dried-up marshes.

Since Lamberton describes 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 maximus¹

Archaeolemur majori

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

MORARANO

Located near the village of Morarano, some 20 km. due east of Betafo. Central plateau site; marsh deposit in volcanic region, c.f. Ampasambazimba. Excavations by Lamberton in 1919 produced remains of Archaeolemur, Megaladapis and Palaeopropithecus (Lamberton, 1919).

¹ P. ingens of other authors.

SAMBAINA

Central plateau site, some 34 km. north of Antsirabé on R.N. 7. Worked by Lamberton from mid-October to mid-November, 1927. According to Lamberton (1927) the site lies on a broad plain in the neighbourhood of a mineralised 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 four meters, 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

49° 90' E., 26° 30' S., (Walker, 1967), approx. 44° 30' E., 23° 40' S. (1:500,000 map, Institut de Géographie, Tananarive, 1963); 200 m. above sea level. C¹⁴ dated at 2290 ± 90 years B.P. (Mahé and Sourdat, in press). 20 km. east of Betsiboka.

This site has been surveyed by Walker (1967) and by Raison and Vérin (1968), with similar results. According to Walker, Taolambiby:

"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" (p. 438, 444).

Walker provides 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-coloured 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 interprets 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 Sourdant say 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, though by how much remains debatable, since Mahé and Sourdant do not state the exact provenance of their sample, and the rate of deposition is unknown. Walker states that a sample from the black sands has been submitted for C¹⁴ dating; the result of this test should resolve the problem.

The primate fauna of Taolambiby includes:

Archaeolemur majori

Palaeopropithecus maximus¹

Lemur (Pachylemur) sp.

Lemur (s.s.) sp.

Propithecus verreauxi

Lepilemur mustelinus

Cheirogaleus sp.

¹ P. ingens of other authors.

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). 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, p. xxxii).

Crocodiles, turtles and hippopotamus dominate the Tsiravé fauna; the lemurs are represented by Hadropithecus stenoqnathus, Archaeolemur majori, Lemur (Pachylemur) insignis, Daubentonia robusta, and "quelques os des grands lemuriens".

TSIHOMBE

Lower Menarandra site. See entry for Anavoha.

PART TWO: ARCHAOLEMURINAE

ARCHAEOLEMUR

History of Study

Although the first subfossil lemur to be brought to scientific attention was the type specimen of Megaladapis madagascariensis (Forsyth Major, verbal communication to the Royal Society, June 15, 1893, published 1894), the first such specimen to be described in print was an incomplete calvaria (B.M. M 4874) of a subadult Archaeolemur majori (Major, 1893) 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 a 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 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 and consisting of the facial portion of a skull (B.M. M 7075) and a left dentary (B.M. M 7072). 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 B.M. M 4874, which he had left unnamed four years earlier, Major (1897) applied 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 B.M. M 7374), 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 G. 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* on account 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 (1900b) felt it necessary to review current knowledges of subfossil Malagasy primates. While not formally proposing 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, B.M. M 7374, which he had himself 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 (1902b) formally to synonymise 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. 591).

In 1905 appeared the first large-scale monograph on the Malagasy lemurs (Grandidier, 1905). Although at the beginning of this work Grandidier

formally synonymised 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 to 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" (p. 135-6). 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 Archaeolemuri_nae, distinct only at this taxonomic level from 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 north-west 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 recognise that the Malagasy prosimian fauna represents an isolated radiation derived from an early Tertiary African primate stock.

Between 1903 and 1909 Herbert Standing (Jully and Standing, 1904; Standing, 1903, 1904, 1905, 1907, 1908, 1909) 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 1907, in which he described all subfossils then known from Ampasambazimba in a comprehensive monograph which contained for the first time a diagnosis of subfamily Archaeolemurinae, and in which was emphasised the individual variation present in the series of ten 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 (A.M. 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 specialised (i.e. parallel) nature of the "simian" characteristics of Archaeolemur, but chose himself an alternative hypothesis, in accord with the interpretations of Forsyth 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 specialised" (p. 103).

In the wide-ranging and discursive 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." (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'!" (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 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 posses higher primate characteristics in the lacrymal 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." (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. W. K. 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 Indrisidae and the Anthropoidea" (p. 440-1). He accepted, however, the affinities of Archaeolemur with Indriinae, and incorporated Standing's classification of Archaeolemur within Indriidae in his own scheme.

Despite the fact that Charles 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 quotes elsewhere, had long before demonstrated the invalidity of the distinction, and had been followed by such authorities as Gregory 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 (Lamberton, 1937a), Lamberton figured, without fully describing, a complete restoration of the skeleton of A. majori, and in the same year (1937b), 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, (1939a), Lamberton, in the course of a discussion of the possible evolutionary relationships of the lemurs, wrote: "Pour les Archaeolemuridae, ils ont du se detacher 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 (1939c) Lamberton more fully described the osteology of the foot of Archaeolemur as then known. He also (1939d) 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. Discovering that while extant prosimians possessing extra teeth normally have them in the form of

premolars, higher primates are prone to possess supernumerary molars, Lamberton asked: "Faut-il rappeler que, par leurs molaires quadrituberculées, les Archaeolemurs se rapprochent des Simiens?" (p. 154). He also remarked that: "il ne semble pas déraisonnable de penser que l'origine [of fossil lemurs] doive être recherchée très loin dans le passé et il est possible que les ancêtres aient eu 4 molaires." (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, Lamberton 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 platyrhinus, 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 respectively by platyrhine and catarrhine phases, the entire sequence ultimately

derivative from an aquatic condition. Later, in an equally enormous contribution, (Sera, 1950), Sera 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 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; 1907) 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. 172). Nevertheless, Clark (1959) was led to conclude that "the brain of Archaeolemur has a remarkably pithecid appearance, though the resemblances to the brain of a monkey are offset by the poor development of the frontal lobes." (p. 249-50).

Following Edinger's studies of 1917 and 1942, Lamberton (1949-50) published some observations on the relationships between hypophyseal

development and body size in a variety of subfossil lemurs. He found that, in the case 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" (p. 34), a situation unique among the fossil lemurs. Lamberton's final contribution appeared in 1956, 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 towards 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 (1967), 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

History of Study

The initial remains of Hadropithecus stenognathus, cranially, at least, the most interesting of the extinct Malagasy lemurs, 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 V.N.H.M. 1934 IV 1/1. Hill (1953) errs 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, dafur spricht, das der Unterkiefer einem weiblichen Thiere angehörte." (p. 256).

Shortly thereafter, Lorenz (1901) figured and further described this mandible, together with a photograph of the first of only two crania of the genus known (V.N.H.M. 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, 1902), when he reviewed all known material of the genus (for many years to be known only from Andrahomana), synonymised Pithecodon sikorae with Hadropithecus stenognathus,

and described and figured the contents of a further consignment of fossils from Sikora, including 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 with Lorenz's 1901 opinion as to the close relationship of Hadropithecus and Archaeolemur, and had discussed their dental similarities and differences, although in this 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 (1902b), 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 (1907) and later to W. K. Gregory (1915) to diagnose Archaeolemurinae, containing Archaeolemur and Hadropithecus, as a subfamily of 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 Hadropithecinae as a separate subfamily within Indriidae.

The major monograph on Hadropithecus is that of Lamberton (1937). In this, Lamberton 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 stenoognathus. In the following year, 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). However, as the comparative measurements given by Lamberton, and those reported here, show, the size differences between the two specimens are not striking, while the Vienna individual, although much younger than that from Tsiravé, is dentally adult.

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 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 (Lamberton, 1931) 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 courrent et grimpent avec beaucoup d'agilité." (1937, p. 44).

In 1950 Sera, running true to form, posited an aquatic habitat for Hadropithecus; six years later Lamberton (1956) 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 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 (1967) studied the postcranial skeleton of Hadropithecus and concluded:

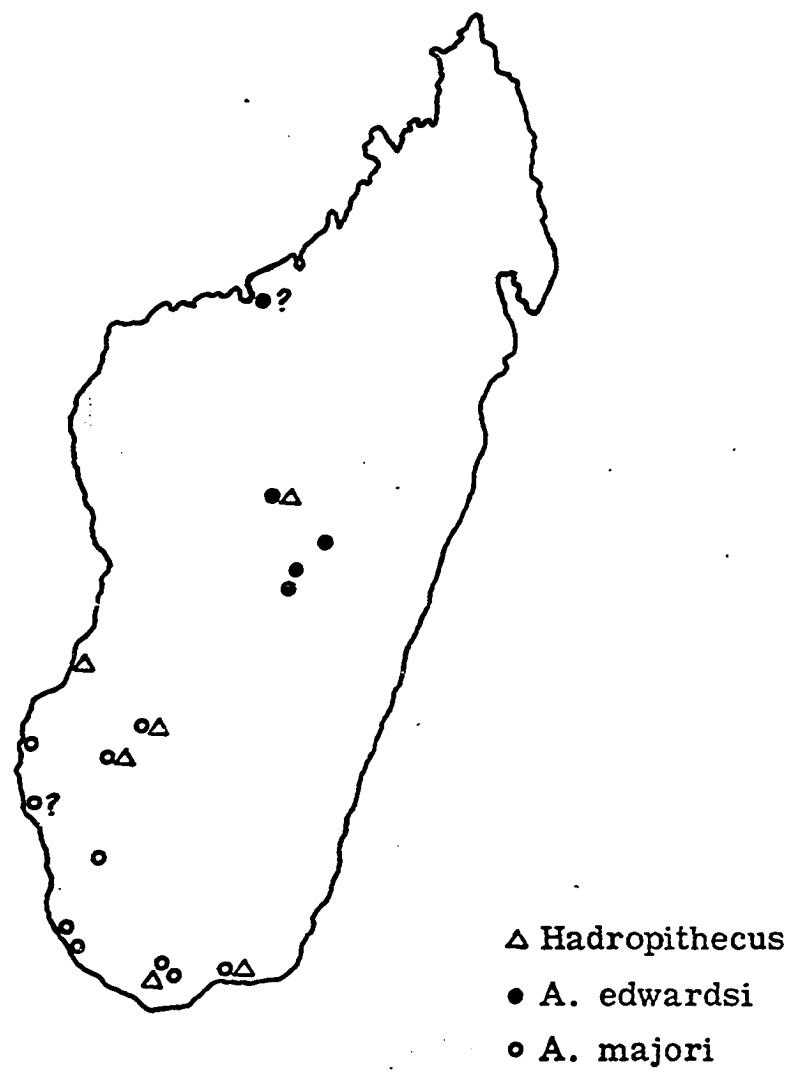
"What elements we have of Hadropithecus show the same features as Archaeolemur, but on the whole the bones are more gracile and elongated. Probably Hadropithecus was to Archaeolemur as Erythrocébus is to Papio today; Hadropithecus and the patas monkey being more slender, longer-limbed creatures, more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

DISTRIBUTION AND TAXONOMY OF ARCHAEOLEMURINAE

It is highly 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 consist 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 Fig. 3 is therefore doubtless incomplete even as far as known material is concerned, besides the fact that not all areas of the island have been sampled.

A fairly clear picture of the distribution of species 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, since to this writer's knowledge there are no complete Archaeolemur crania or calvaria known from this site. The single cranium of Archaeolemur from Amparihingidro is identified in the Muséum of the Académie Malgache as an individual of A. majori, but is probably better viewed as of A. edwardsi. If this identification is correct, Amparihingidro is the only coastal site to have yielded A. edwardsi,

Figure 3
Distribution of the archaeolemurines



the species being otherwise confined to the central plateau.

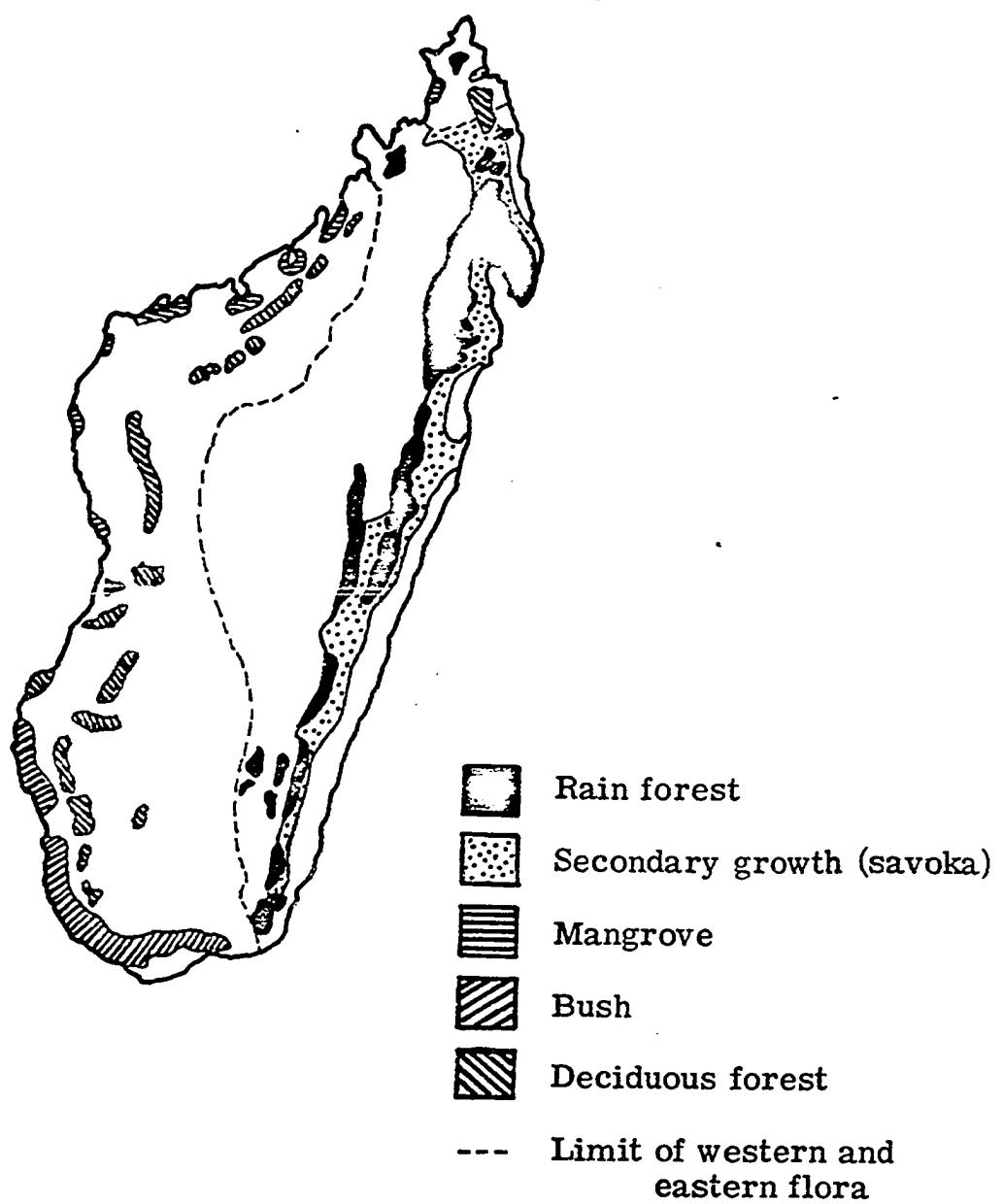
A. majori is found widely in the south and south-west of the island.

Since the advent there of man Madagascar has become largely deforested in consequence of land-clearance by burning. At the present time only some 7% 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 Véritin, 1970), some broad inferences may be made. Fig. 4 shows the present distribution of vegetal types in Madagascar.

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 south-west coast were probably originally covered by deciduous forests which flourished in a drier, more seasonal climate than that of the center, while 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 Mandrary today. The belief that aridification

Figure 4
Present-day distribution of vegetation
in Madagascar (after Battistini and
Véritin, 1967).



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

Hadropithecus stenoognathus, 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 the niche occupied by Hadropithecus was evidently much more limited than that of Archaeolemur, speciation seems less likely.

Because some recent authors continue to recognise 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	Tsiravé
Ampoza	
Andrahomana	
Belo-sur-Mer	
Lower Menarandra	

Archaeolemur edwardsi

Ampasambazimba
Antsirabé
Morarano
Sambaina

Archaeolemur majori

Ampoza	Lower Menarandra
Andrahomana	Manombo
Bemafandry	Taolambiby
Itampolo	Tsiravé
Lamboharana	Belo-sur-Mer

Archaeolemur ?sp.

Ambolisatra
Amparihingidro

MORPHOLOGICAL DESCRIPTION

Archaeolemur majori

General description of cranium.

In comparison with that of its congener, A. edwardsi, the skull of this animal 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 of the cranium 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 thirty degrees, and in relation to the plane of the palate are dorsally directed by about the same amount. The frontal and malar bones partake about equally in their formation; there is no post-orbital 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 anteriorly

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 lacrymal foramen, which is situated in the orbital margin and which is bounded by the lacrymal 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 this, the palate is primarily of maxillary formation, the maxillary-palatine suture originating posterior to the last molar, and travelling 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 post-palatine 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 fronto-malar suture. The malar flares considerably, in consequence of which the angle of the long maxillo-malar 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 postero-medial 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 lacrymal bone, variable in shape from triangular to rectangular, and bounding the posterior border of the relatively large lacrymal 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 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 from 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 (1931-6) a narrow strip of parietal intrudes anteriorly into the frontal bone, to the level of the supra-orbital lines, bilaterally. The

Table 1

Archaeolemur majori: cranial dimensions (mm.)

	\bar{x}	S.D.	n
Max. length	130.6	5.7	17
Facial l.	48.2	3.4	16
Bizy. w.	96.4	5.1	12
W. p/o con	32.2	2.5	16
Max. zyg. ht	13.6	1.6	14
Palate l.	48.3	2.1	15
Palate w. at M ¹	23.5	1.4	17
Max. nuch. w.	60.6	3.0	17
L. for. mag.	15.6	1.0	16
W. for. mag.	17.4	1.7	16
Nas. ht.	18.9	1.3	7
Nas. b.	18.1	1.3	16
Orb. ht	28.6	1.7	16
Orb. b.	24.6	1.2	16
L. pgl. proc.	11.1	1.1	9
Bas - alv.	109.7	6.5	16
Bas - nas.	88.1	4.7	15
Nas - t'row	43.7	2.4	16

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 centre one-third of the moderately-developed nuchal ridge to meet the sagittal suture, while 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 post-mastoid 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, semi-flattened 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 characterised 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 fronto-nasal foramina. The maxillary sinus is small, and lies just anterior to the sphenopalatine foramen, invading the root of the zygomatic arch. Since all specimens examined have 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 around 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 around 10 mm; its superior, antero-superior

and postero-superior borders are formed in the temporal bone, while 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 antero-inferior 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 squamsum only in one part, viz. anteriorly to the stylo-mastoid foramen. Ontogeny therefore teaches us that the annulus of the adult is not a secondarily detached part of the bulla." (p. 987-8).

The post-glenoid foramen opens into the postero-internal aspect of the postglenoid process, and abuts onto the antero-superior 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 (associated anteriorly with the orbital venous foramen).

The petrous process of the bulla is not very strongly developed, as it is, for instance, in Megaladapis, though 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 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 stapedial 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, while 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 forarm, 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 nine, ten and eleven. 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 will be found under the discussion of Hadropithecus.

Slightly anterior and internal to the mastoid rugosity, and directly posterior to the external auditory meatus, lies the small

stylo-mastoid foramen which, besides transmitting the stylo-mastoid artery and the auricular branch of the vagus nerve, also provides the external orifice of the facial (Fallopian) canal, which conducts 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 nearly 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 Indriinae, and arches backwards in a continuous, very gentle, curve towards 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 postero-inferior 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 towards 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 centre of P_3 . Only extremely infrequently is there any trace whatsoever of a mental spine. 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 this profile bulges anteriorly to varying extents. The mylohyoid line is well marked in many specimens, 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 always present at mid-depth of the mandible below P_3 ; 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 will be found under the section dealing with myology.

For dimensions of the cranium and mandible, see Table 1.

Permanent dentition

The dental formula of Archaeolemur, 2.1.3.3, differs from 2.0.3.3, 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 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 (1938) would seem to suggest, the dental formula is 2.1.2.3. 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 I_2 and P_2 , and between I^2 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 a mechanical phenomenon, as it is in the case of some other primates, but 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 labio-lingually than mesiodistally; in profile the labial border of the tooth is smoothly rounded. Labially the enamel layer of the tooth is relatively thick, though not as 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

Table 2

Archaeolemur majori: dimensions of upper dentition (mm.)

	\bar{x}	S.D.	n
B. I ¹	5.3	0.9	10
L. I ¹	8.1	0.8	10
B. I ²	3.6	0.8	14
L. I ²	5.4	0.7	14
B. C	7.2	0.8	17
L. C	9.2	0.9	17
B. P ²	8.2	0.8	21
L. P ²	9.7	0.8	21
B. P ³	8.0	0.7	23
L. P ³	9.7	0.7	23
B. P ⁴	10.0	1.2	23
L. P ⁴	8.3	0.8	23
B. M ¹	9.2	0.7	23
L. M ¹	8.1	0.6	23
B. M ²	8.5	0.6	22
L. M ²	7.2	0.4	22
B. M ³	8.0	0.5	20
L. M ³	6.3	0.8	20

Table 3
Archaeolemur majori: dimensions of lower dentition (mm.)

	\bar{x}	S.D.	n
B. P ²	9.2	0.9	16
L. P ²	9.7	0.8	16
B. P ³	7.8	0.9	18
L. P ³	9.4	0.6	18
B. P ⁴	8.5	0.8	19
L. P ⁴	8.9	0.6	19
B. M ¹	8.3	0.7	21
L. M ¹	8.2	0.5	21
B. M ²	8.1	0.6	21
L. M ²	7.7	0.5	21
B. M ³	7.3	0.6	20
L. M ³	7.1	0.6	20

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

p²-4

The premolars embody the most specialised 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 possession 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, though 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. P^4 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 towards 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 towards the gingival border; however, the basal swelling is more pronounced on this side, giving the impression of decreased slope.

The posteroexternal extremity of P^3 fits into the angle of the L in such a way that the parastyle-paracone-mesostyle crest of P^4 is confluent with the longitudinal shearing surface of P^3 . Microscopic examination of the shear surfaces of the premolar, 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 cuspules, rapidly removed by wear. Such cuspules 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 M^1 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, antero-superiorly sloping cingulum. Buccally, 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 postero-internally from the metacone and hypocone.

M^2 is essentially similar to M^1 , 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 bucco-lingually compared to M^1 , and the lingual cingulum tends to be less strongly developed.

M^3 is smaller and more circular (occasionally triangular) in outline compared to 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 towards the lingual side than is that of M^2 .

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 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 conves laterally. The distribution of enamel is as on the upper incisors: thick enamel labially and laterally; very thin enamel lingually and medially.

—

Not present if the lateral procumbent tooth is interpreted as an incisor.

P₂₋₄

The anterior lower premolar is a stout, 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 protostyloid 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 P_3 , and continuous with it.

M₁₋₃

M_1 and M_2 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 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 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.

Archaeolemur edwardsi

Cranial morphology

Somewhat larger in linear dimensions (some 6-7% 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, while 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 lacrymal foramen lies within the orbital margin; rather, it is marginal to the orbit, as in A. majori, the anterior and posterior lacrymal crests marking the respective limits of the orbital margin.

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 fronto-malar suture. Anteroinferiorly the sinus communicates with the nasal cavity through large, oval, bilaterally-paired fronto-nasal 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 maxillo-malar 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.

Table 4

Archaeolemur edwardsi: cranial dimensions (mm.)

	\bar{x}	S.D.	n
Max. l.	147.0	4.0	17
Facial l.	55.0	2.2	16
Bizy. w.	108.4	3.3	7
W. p/o con	35.2	5.6	16
Max. zyg. ht.	15.2	1.1	17
Palate l.	53.9	2.0	15
Palate w. at M ¹	26.5	1.5	17
Max. nuch. w.	66.6	2.0	16
L. for. mag.	17.1	1.5	15
W. for. mag.	18.6	1.6	16
Nas. ht.	20.9	3.1	10
Nas. br.	21.5	1.7	14
Orb. ht.	31.1	1.9	16
Orb. br.	25.8	1.4	16
L. pgl. proc.	10.7	1.4	5
Bas. - alv.	121.3	3.7	16
Bas. - nas.	97.7	4.1	15
Nas. - t'row	50.2	2.8	16

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 supra-orbital lines are strongly marked and continuous with the sharp lateral edge of the post-orbital bar. They curve postero-medially to meet the midline somewhat anterior to the coronal suture, where they become confluent with the strong sagittal crest. This latter crest is invariably present, even in those cases (such as A. "platyrhinus", A.M. 311024) where 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 its lies a distinct mastoid rugosity.

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

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, refer to Table 4.

The mandible

The lower jaws of A. majori and A. edwardsi are extremely similar in morphology, and can overlap in terms of 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 individuals since the ranges of dental size in the two species overlap. In A. edwardsi the diastemata between I^2 and 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, refer to Tables 5 and 6.

Table 5

Archaeolemur edwardsi: dimensions of upper dentition (mm.)

	\bar{x}	S.D.	n
B. I ¹	8.3		1
L. I ¹	8.4		1
B. I ²	5.5		2
L. I ²	5.8		2
B. C	7.9	0.5	5
L. C	10.7	1.1	5
B. P ²	9.4	1.0	8
L. P ²	11.1	0.6	8
B. P ³	8.7	0.8	9
L. P ³	10.9	0.6	9
B. P ⁴	11.8	0.9	9
L. P ⁴	9.1	0.6	9
B. M ¹	10.7	0.5	9
L. M ¹	9.2	0.5	9
B. M ²	10.0	0.5	9
L. M ²	7.9	0.5	9
B. M ³	8.3	0.5	7
L. M ³	7.1	0.4	7

Table 6

Archaeolemur edwardsi: dimensions of lower dentition (mm.)

	\bar{x}	S.D.	N
B. P ²	9.7	0.6	17
L. P ²	10.7	0.7	17
B. P ³	8.2	0.7	18
L. P ³	9.9	0.8	18
B. P ⁴	9.0	0.7	18
L. P ⁴	9.7	0.6	18
B. M ¹	9.2	0.7	18
L. M ¹	9.3	0.5	18
B. M ²	8.8	0.6	17
L. M ²	8.8	0.5	17
B. M ³	8.2	0.5	17
L. M ³	8.0	0.6	17

Hadropithecus stenognathus

General description of cranium

The following description is based on the almost complete cranium found by Lamberton at Tsiravé in 1931, and now in the collections of the Académie Malgache. This individual differs in some ways from the Andrahomana cranium, V.N.H.M. 1934 IV 1; these differences will be discussed following the formal description of the Académie Malgache specimen.

The general foreshortening and broadening of the skull of *Hadropithecus* as compared to that of *Archaeolemur* is at once evident in the comparison of major dimensions. While the maximum cranial length of Tsiravé *Hadropithecus* is 141.8 mm, somewhat less than the mean of seventeen 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 orthognathism 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 towards 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 post-orbital constriction. The supra-orbital 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 frontated and convergent than those of Archaeolemur; the malar bones are therefore more widely flared laterally, and are 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 maxillo-malar suture is oriented much as it is in Archaeolemur. The orbits are almost circular, the vertical dimension barely exceeding the lateral one. The inter-orbital distance (15.8 mm) is slightly less than is usual in A. edwardsi. Lamberton (1937) 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

Table 7

Hadropithecus stenognathus: cranial dimensions (mm.)

	Tsiravé	Andrahomana
Max. length	141.8	128.2*
Facial l.	51.2	45.0*
Bizy. w.	114.5*	108.0*
W. p/o con.	21.8	24.4*
Max. zyg. ht.	18.7	15.1
Palate l.	54.3	
Palate w. at M ¹	26.9	23.8
Max. nuch. w.	66.9	63.8
L. for. mag.	16.8	18.4
W. for. mag.	17.8	18.4
Nas. ht.	19.1	
Nas. br.	20.0	15.8*
Orb. ht.	29.0	
Orb. br.	27.0	26.4
L. pgl. proc.	12.0	13.0
Bas. - alv.	110.2	100.0
Bas. - nas.	94.8	88.0
Nas. - trow	53.6	50.3

* denotes a reliably estimated dimension

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 maxillo-premaxillary sutures in the Tsiravé individual, and damage to this region in V.N.H.M. 1934 IV 1, renders impossible determination the extent of the premaxillæ 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 that 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 post-palatine 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 post-orbital 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 antero-posterior 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 to the mean of 15.2 mm for seventeen A. edwardsi. The arch is oriented more obliquely than in Archaeolemur because its posterior root is raised relative to the anterior one. The temporo-malar 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 splanchnocranum 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 of the sub-glenoid 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 anterior inferior 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 point on the malar, and the alveolar border, is in the Tsiravé specimen about 13.0 mm. as compared to 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 this 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 latter (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 post-mastoid foramina lie in these latter portions. A pronounced median vermis separated 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), and the occipital condyles are likewise similar in morphology and position to those of Archaeolemur. The extent of the supra-occipital portion of the occipital bone is obscured in the Tsiravé individual because of sutural obliteration; in the Andrahomana specimen it is comparable to that in Archaeolemur, although posteriorly it is slightly more flared, since 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 to that in Archaeolemur, in that 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, is 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 was 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 groove. The 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 (presumably it conducted the auricular branch of the facial nerve). Within this orifice also lies the opening of the canal of the chorda tympani, which ran along the petro-tympanic 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 post-glenoid foramen, anterior and lateral to the dorsal border of the external auditory meatus, is comparable in size to 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 post-glenoid process, and the interior of the postglenoid foramen; Lamberton (1941) has termed their anterior orifices "perforations ectoglenoïdiennes".

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. Yet more lateral lies 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 laterally 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 latter 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 stapedial artery, which passed between the legs of the stapes above the oval fenestra and penetrated the endocranum after passing across the epitympanic recess; and an entocarotid, which travelled 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 very 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 of 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 travelled 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 (petro-squamous) 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 petro-squamous 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) 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. V.N.H.M. 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) and subsequent authors. The nasal bones are, however, rather more salient in V.N.H.M. 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 proportionately to its length (respectively, the cephalic indices are 85.6 [V.N.H.M. 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 V.N.H.M. 1934 IV 1 show similar curves of Spee.

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) that:

"les differences...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 if anything even more striking than those existing in the cranium. The following description will be based on younger material, particularly V.N.H.M. 1934 IV 2/1a and b, because it is generally better preserved; differences apparent in older specimens will be 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 broader 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 V.N.H.M. 1934 IV 2/la, 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 toothrow lies in front of the anterior border of the ascending ramus, a reflection of their relatively longer faces.

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 V.N.H.M. 1934 IV 2/la, 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 accomodating 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 is 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, V.N.H.M. 1934 IV 1 probably had only a single large foramen at mid-depth of the corpus, below the rear of the caniniform, while in V.N.H.M. 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 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.

Age-changes in the mandibular morphology of Hadropithecus are most pronounced in the angular region. Given the very small sample sizes it is naturally 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, V.N.H.M. 1934 IV 1/1, with its left-side counterpart V.N.H.M. 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 rugoise, 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 V.N.H.M. 1934 IV 1/1 - 2, since 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: 2.1.3.3. No known specimen of Hadropithecus possesses the diastemata between I_2 and P_2 and I^2 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 M^1 (the latter described from the isolated B.M. M 7869) is based on a beautifully-preserved subadult maxilla, V.N.H.M. 1934 IV 2, while the sole upper incisor (I^2) is known from the Tsiravé cranium. The lower premolars and molars are described from V.N.H.M. 1934 IV 2/1a, the lower incisors from the Tsiravé mandible, V.N.H.M. 1934 IV 1/1 and IV 3.

Dental dimensions are given in Tables 8a and b.

Table 8a

Hadropithecus stenognathus: dimensions of upper dentition (mm.)

	\bar{x}	S.D.	n
B. I ¹	3.7		1
L. I ¹	-		
B. I ²	2.1		1
L. I ²	6.3		1
B. C	-		
L. C	-		
B. P ²	7.8	1.5	3
L. P ²	9.4	1.0	3
B. P ³	7.2	0.5	4
L. P ³	9.7	1.1	4
B. P ⁴	14.2	1.0	4
L. P ⁴	9.3	1.0	4
B. M ¹	12.8	0.4	5
L. M ¹	10.9	1.1	5
B. M ²	12.3	0.3	4
L. M ²	10.0	0.8	4
B. M ³	8.6	1.0	4
L. M ³	7.8	1.7	4

Table 8b

Hadropithecus stenognathus: dimensions of lower dentition (mm.)

	\bar{x}	S.D.	n
B. P ²	5.9	0.6	4
L. P ²	8.2	1.3	4
B. P ³	7.7	1.4	5
L. P ³	10.2	1.4	5
B. P ⁴	11.0	0.6	8
L. P ⁴	11.7	2.7	8
B. M ¹	10.9	1.2	12
L. M ¹	12.2	0.7	13
B. M ²	11.7	0.8	14
L. M ²	11.9	0.8	15
B. M ³	10.0	1.0	10
L. M ³	10.6	0.2	10

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 neighbour. 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 to 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 somewhat 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 towards the

alveolar margin of the tooth. Lingually, there is a relatively distinct paracone, with a blade-like parastyle and mesostyle travelling 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 P^4 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, but its parastyle and mesostyle are distinct cusps closely approximated but slightly lingual to it. The protocone is morphologically similar to, but is much larger than, that of P^3 , 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.

M^1-3

The upper molars are remarkably broad and high-crowned, and decrease in size from front to back. The only completely unworn M^1 known to the writer is B.M. M 7869, 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 protocone, 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.

M^2 is built on the same plan as M^1 , but is somewhat shorter mesiodistally; its internal cingulum is generally slightly reduced compared to that of M^1 .

M^3 is greatly reduced, and is 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

I_{1-2}

The only unworn incisor of Hadropithecus known is the erupting I^2 in V.N.H.M. 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 V.N.H.M. 1934 IV 1/1 and in the Tsiravé mandible, is essentially

similar but is yet 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 not unreminiscent of, the upper canine. Λ-shaped in lateral profile and laterally compressed, the tooth consists of a central pillar coinciding with the apical axis of the Λ; 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 crest turns buccally at its anterior extremity, and the posterior crest turns lingually at its posterior extremity; posteromedially there lies a small cingulum. P₂ and P₃ are closely approximated, and their blades are longitudinally aligned.

P₄ 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 P₃, 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.

M₁₋₃

The lower molars approximate to mirror images of the upper ones, and decrease in size posteriorly. In M₁ the metaconid and entoconid are lobular, as are the paracone and metacone of M¹, 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, 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, though 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.

RELATIONSHIPS WITHIN 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 always been classified within 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 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 extant indriines do not require enumeration here; suffice it to say that they are sufficiently strong to have led Gregory (1915) to characterise Palaeopropithecus as "gross and swinelike...degraded" (p. 440) when compared with Propithecus. Walker (1967b) 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 orang-utan.

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 in Tables 9 and 10. The precise relationships between Indriinae, Archaeolemurinae and Palaeopropithecinae are conjectural; presumably latter both groups sprang from an indriine ancestor, but the relative times of divergence of the two groups are uncertain. Everything about Archaeolemurinae (particularly Archaeolemur majori) bespeaks a relatively recent divergence from Indriinae;

Table 9. Classification of lower primates

ORDER PRIMATES

Suborder Palaeoprosimii*

Infraorder Plesiadapiformes*

Superfamily Plesiadapoidea*

Family Plesiadapidae*

Subfamily Plesiadapinae*

Subfamily Saxonellinae*

Family Carpolestidae*

Superfamily ? Plesiadapoidea incertae sedis*

Family Paromomyidae*

Family Picodontidae*

Family Microsyopidae*

Subfamily Uintasoricinae*

Subfamily Microsyopinae*

Suborder Prosimii

Infraorder Lemuriformes

Superfamily Adapoidea*

Family Adapidae*

Subfamily Adapinae*

Subfamily Notharctinae*

Family Omomyidae*

Superfamily Lemuroidea

Family Lemuridae

Subfamily Lemurinae

Subfamily Cheiogaleinae

Family Indriidae

Subfamily Indriinae

Subfamily Archaeolemurinae*

Subfamily Palaeopropithecinae*

Family Daubentonidae

Family Megaladapidae*

Infraorder Lorisiformes

Superfamily Lorioidea

Family Lorisidae

Subfamily Lorisinae

Subfamily Galaginae

Infraorder Tarsiiformes

Superfamily Tarsioidea

Family Tarsiidae

Subfamily Tarsiinae

Subfamily Microchoerinae*

Superfamily Tarsioidea? incertae sedis*

Family Anaptomorphidae*

* indicates extinct taxa

Table 10. Classification of Lemuroidea

Lemuroidea	Indriidae (cont'd)
Lemuridae	Palaeopropithecinae*
Cheirogaleinae	Palaeopropithecus*
Cheirogaleus	P. maximus*
C. major	Archaeoindris*
C. medius	A. fontoynonti*
Microcebus	Megaladapidae*
M. murinus	Megaladapinae*
M. coquereli	Megaladapis*
Phaner	M. madagascariensis*
P. furcifer	M. grandidieri*
Lemurinae	M. edwardsi*
Lemur (Lemur)	Daubentoniidae
L. catta	Daubentoniiinae
L. fulvus	Daubentonina
L. macaco	D. madagascariensis
L. mongoz	D. robusta*
L. rubriventer	
L. variegatus	
Lemur (Pachylemur)*	* indicates extinct taxa
L. insignis*	
Lepilemur	
L. mustelinus	
L. ruficaudatus	
Hapalemur	
H. griseus	
H. simus*	
Indriidae	
Indriinae	
Indri indri	
Propithecus	
P. verreauxi	
P. diadema	
Avahi	
A. laniger	
Mesopropithecus*	
M. pithecoides*	
M. globiceps*	
Archaeolemurinae*	
Archaeolemur*	
A. majori*	
A. edwardsi	
Hadropithecus	
H. stenoqnathus	

of Palaeopropithecinae the reverse applies. A case might be made, on grounds of probable econiche, for raising the three subfamilies just discussed to the familial level, and regarding Indriidae as presently constituted as of superfamilial status; however, a more conservative judgement is preferred here.

Lamberton (1937) stated his belief that:

"Il nous semble...logique de penser
qu'Archaeolemur et Hadropithèques
sont des rameaux issus d'un tronc
commun encore hypothétique et dont le
développement s'est longtemps poursuivi
côte à côte." (p. 43-44).

Two of Lamberton'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 (particularly 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

the light of Walker's (1967a) 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 Archaeolemurinae by the technique of Trend Surface Analysis.

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 co-ordinate system is superimposed on a two-dimensional image of the specimens, co-ordinates on the X and Y axes can be given each of the points. If X_{ha} is the X co-ordinate of point h on specimen a, and X_{hb} is the co-ordinate 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 calculated 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.

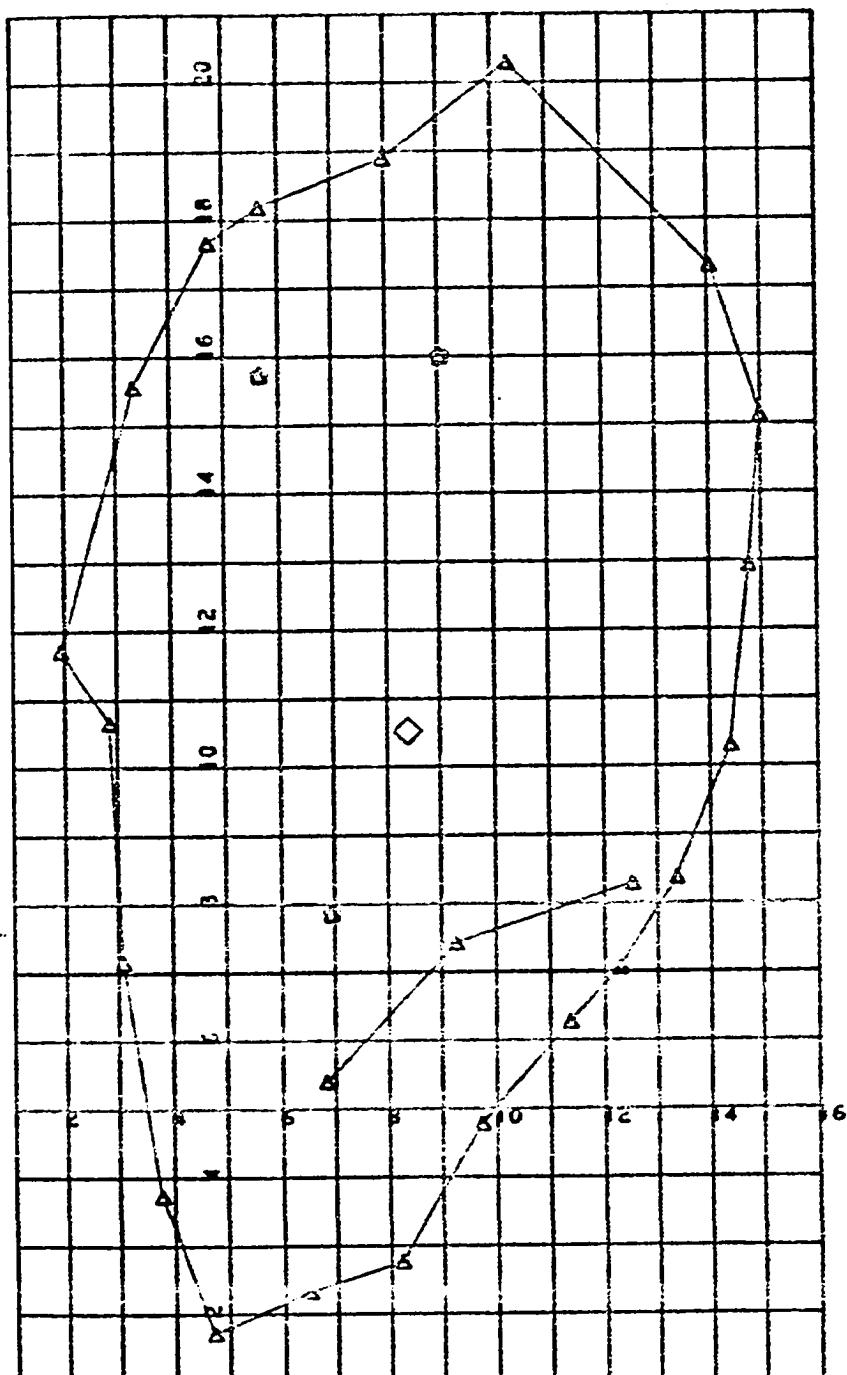
The ability of the polynomial to express the displacement of any given homologous point is a function of the power of the polynomial, and the number of homologous points used. The concepts involved can best be understood if the system is viewed as a topological model with the horizontal position of a 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 ($Z_{Xh} = \alpha_1 + \alpha_2 X_{ha} + \alpha_3 Y_{ha}$, where $\alpha_1 - \alpha_3$ 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 best it can. However, if the power of the polynomial is increased it is possible to describe the additional complexity exactly. The number of points which 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 co-ordinate 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 co-ordinate points of the grid lines are fed into the polynomial which 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 polynomial for the trend in Y to determine the new Y co-ordinate. 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 to figure a.

The computer-drawn deformation grids in Figures 5a, b and c 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 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), while the posterior root is dropped, giving a more horizontal arch; the orbits are moved relatively forward and rotated to a

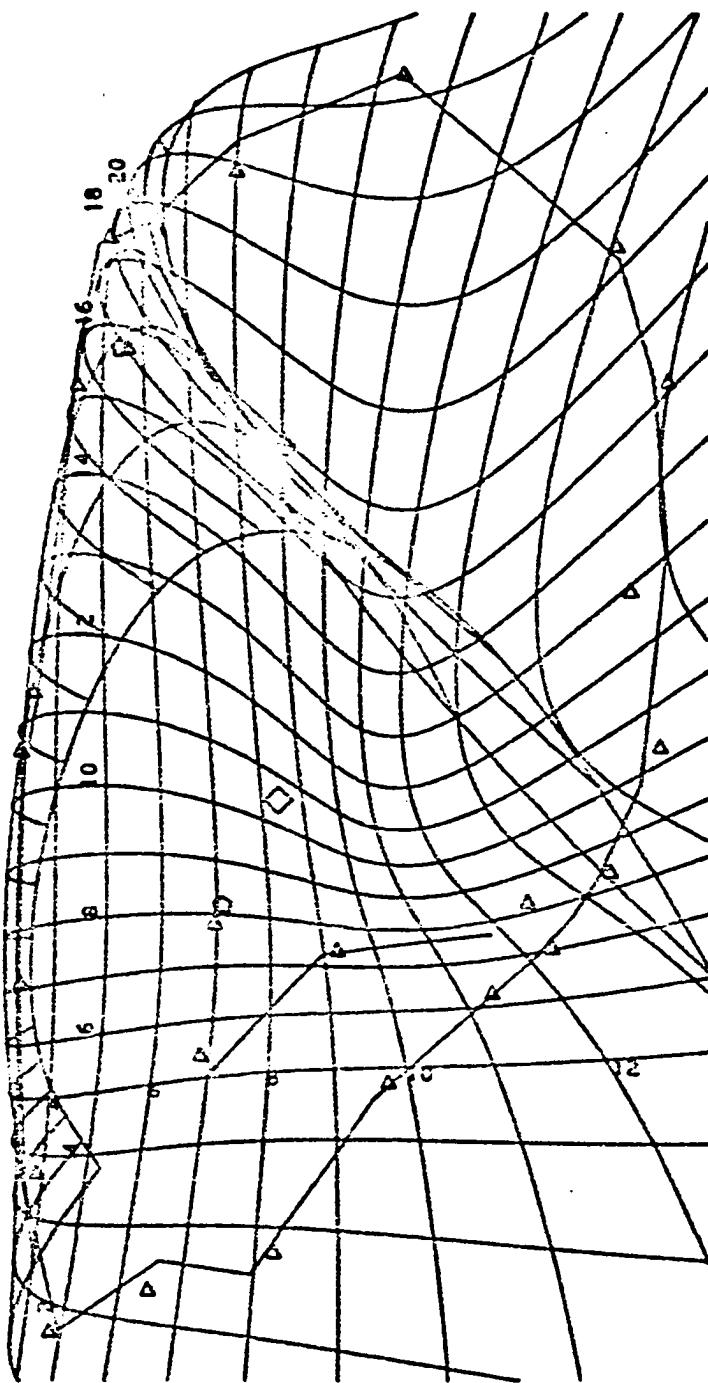
Figure 5a
Computer-drawn side view of the cranium of
Archaeolemur majori, with basic cartesian
grid superimposed.



A. MAJORI SIDE
POWER 1
PERCENT FIT IN X 0.00
PERCENT FIT IN Y 0.00

Figure 5b

Side view of Archaeolemur edwardsi, deformed
to fit A. majori.

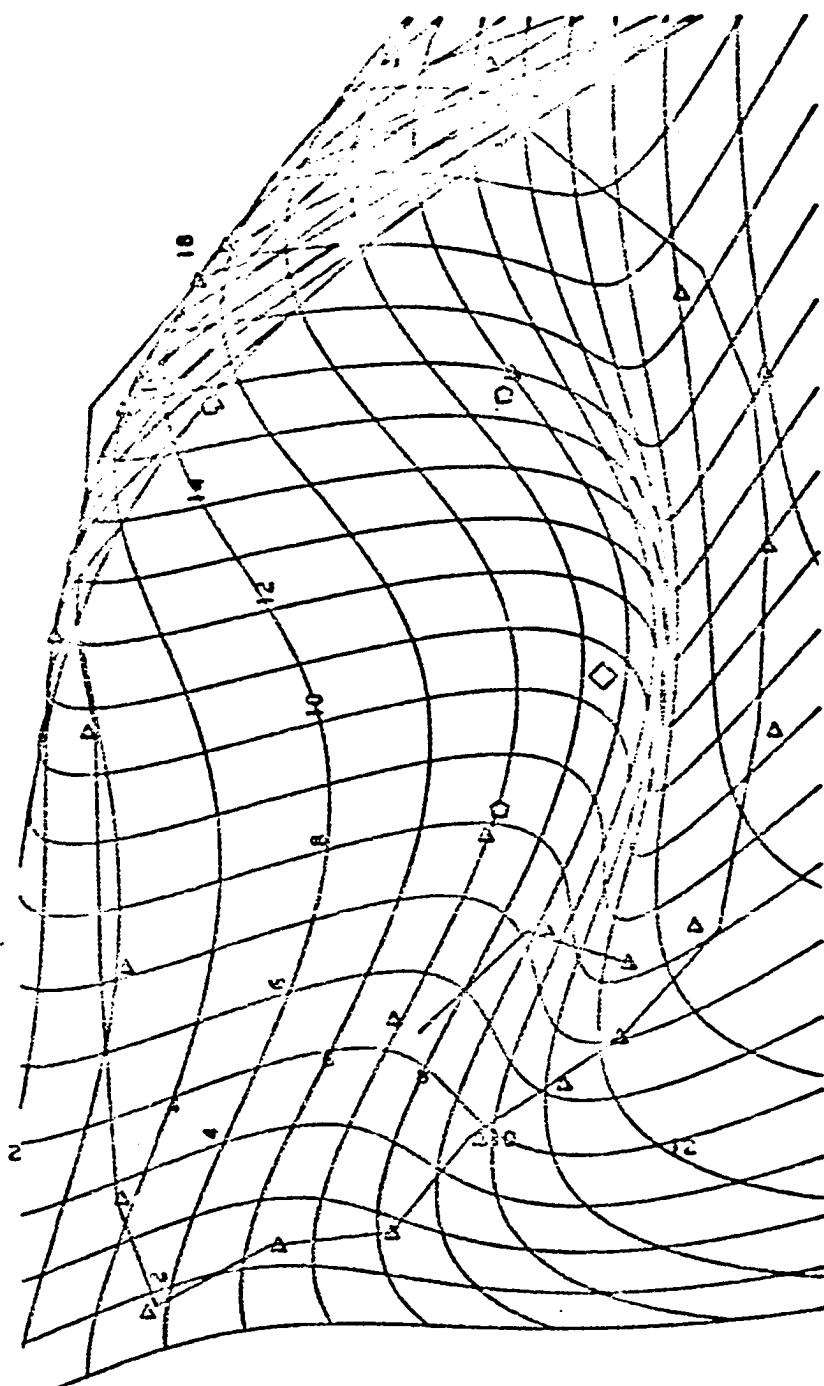


A. EDWARDSI SIDE
POWER 4
PERCENT FIT IN X 77.67
PERCENT FIT IN Y 57.83

14

Figure 5c

Side view of Hadropithecus (Tsiravé cranium)
deformed to fit A. majori.



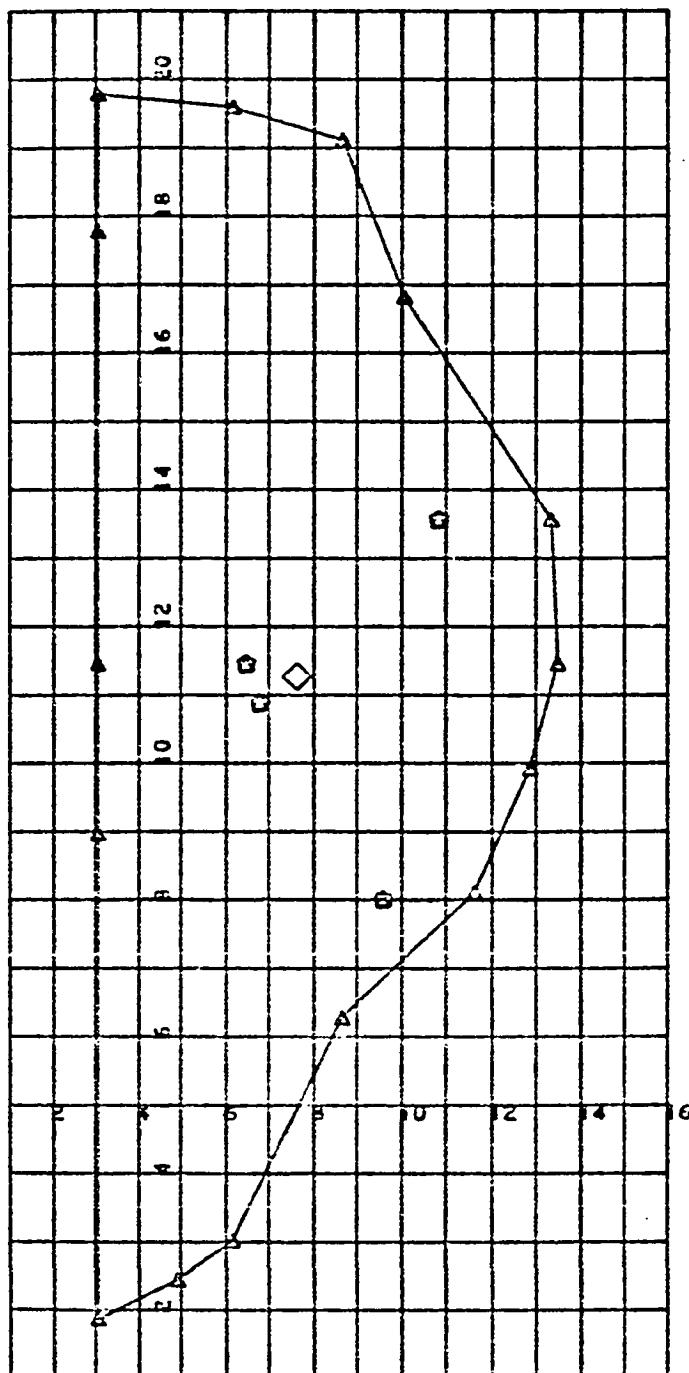
14

HADROPITHECUS SIDE
POWER 4

PERCENT FIT IN X 89.91
PERCENT FIT IN Y 86.87

Figure 6a

Computer-drawn ventral view of the cranium
of Archaeolemur majori, with cartesian grid
superimposed.

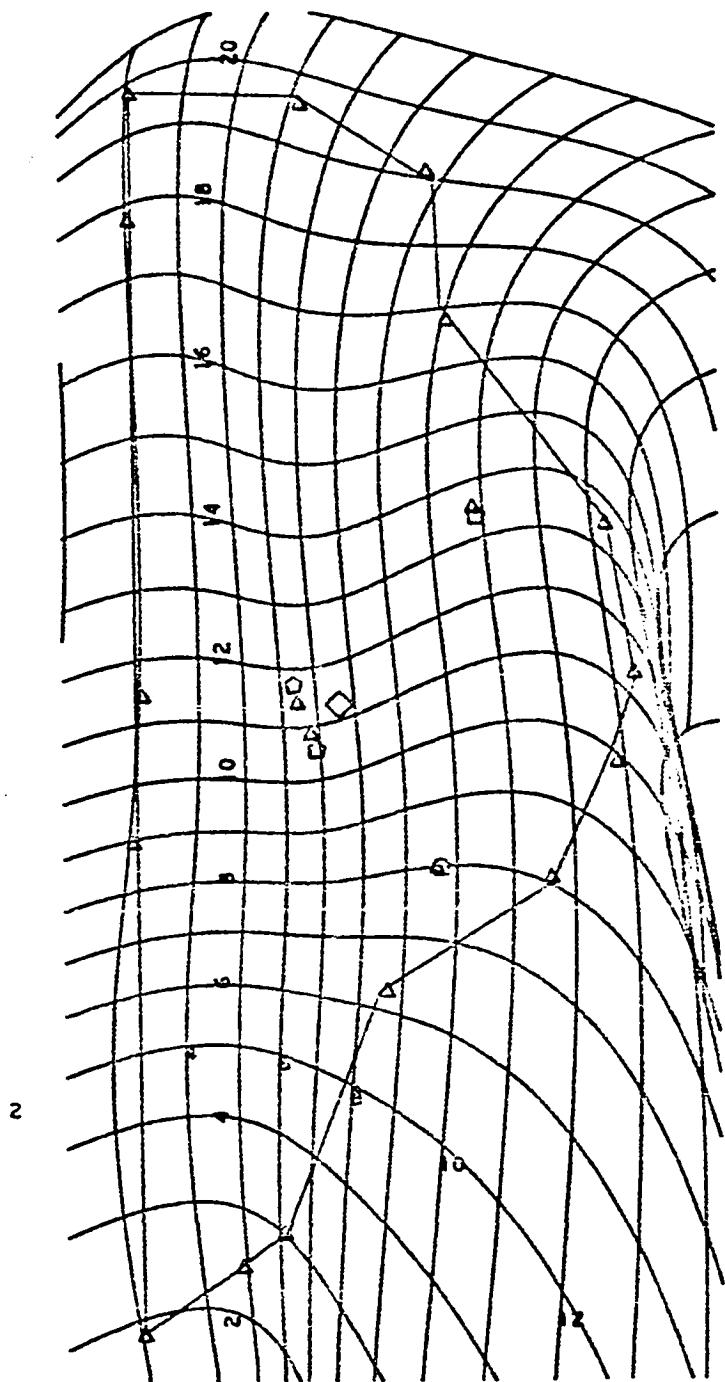


14

A. MAJORI BASE
POWER 1
PERCENT FIT IN X 0.00
PERCENT FIT IN Y 0.00

Figure 6b

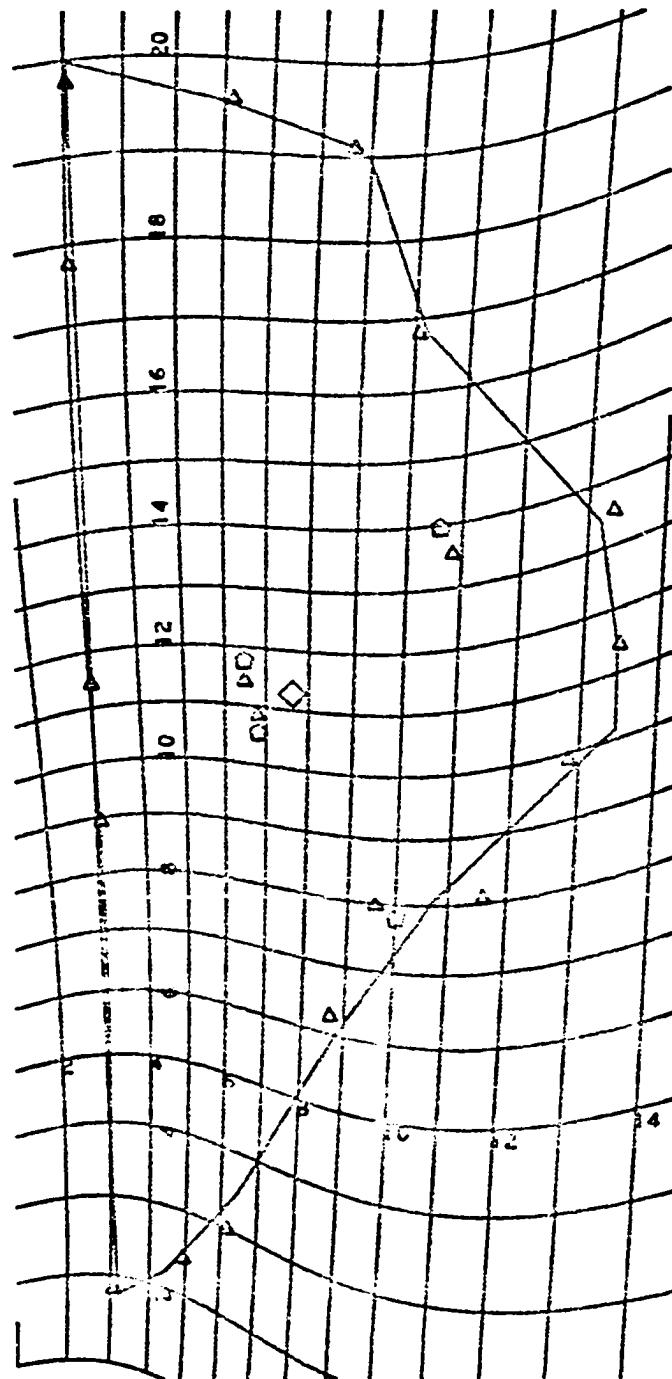
**Ventral view of Archaeolemur edwardsi,
deformed to fit A. majori.**



A. EDWARDSI BASE
POWER 4
PERCENT FIT IN X 86.18
PERCENT FIT IN Y 58.42

Hand drawing.

Figure 6c
Hadropithecus (Tsiravé cranium) deformed
to fit A. majori.



16

HADROPITHECUS BASE
POWER 3

PERCENT FIT IN X
PERCENT FIT IN Y

66.79
54.53

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 (Figures 6a, b and c; 21 points), 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 towards 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 Archaeolemurinae, the only forms tested.

MYOLOGY

Archaeolemur (figures 7 - 14)

Although the genotype plays a basic role in the determination of skeletal form, full skeletal development is also a function of the development and activity of the attached muscles. Certainly, as Scott (1957) has pointed out, considerable uncertainty still exists regarding the role of muscle action in the determination of the final form of skeletal parts such as the cranium and facial skeleton; nevertheless, a useful amount of information concerning the influence of cranial musculature on skull form can be gained 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 on the skull to provide 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 will be discussed later.

Masticatory musculature

M. temporalis

The degree of development of this muscle represents one of the most striking distinctions between Archaeolemur majori and A. edwardsi, the most prominent result of the relative hypertrophy of temporalis in the latter form being the almost invariable presence of a sagittal crest. Although sagittal cresting has been claimed to have taxonomic significance (see discussion by Holloway, 1962), the trend during the past two decades has been to regard this characteristic as being purely functionally determined,

as a result of temporalis development. Weidenreich (1941) early pointed out that temporalis development does not appear to exert any influence on the basic form of the skull, but is correlated with the presence of such superficial features as nuchal and sagittal crests. This view was elaborated by later workers such as Washburn (1947), Scott (1954, 1957; Brash, McKeag and Scott, 1956) and Riesenfeld (1955). Scott has described the ontogenetic migration of the temporal lines and the formation of a sagittal crest as follows:

"The temporal ridges develop where the facia covering the temporal muscle is attached to the fibrous outer layer of the periosteum. Along the line of union of the two fibrous layers, the underlying cellular osteogenetic layer of the periosteum forms a bony ridge. As the muscle migrates upward and backward with growth, the bony ridge moves before it by a process of resorption and redeposition of bone until, in the male gorilla or baboon, the two ridges come together along the middle line above the sagittal suture. Here the fasciae covering the temporal muscles of the two sides of the skull meet and run together to the underlying bone, forming a two-layered fibrous septum between the muscles. Ossification extending into this fibrous septum produces a mid line sagittal crest."

(1957, p. 217-8).

More recently, however, Hoyte and Enlow (1966) have pointed out that basic to such an interpretation lie the propositions that the inner and outer

bony tables of the skull are not functionally integrated, that cranial superstructures such as sagittal crests are functionally related only to the outer bony table, and that the inner table alone is affected by brain growth. The work reported by Enlow (1963, 1968), Enlow and Harris (1964) and Hoyte and Enlow (1966) suggests, however, that these assumptions may not, in theory, at least, be justified. It was found, for instance, that the temporalis in the developing guinea-pig is initially restricted to the parietal bone. At this stage the parietal is separate from the interparietal, whose outer surface is depositional, and whose endocranial aspect is resorptive. At a later stage the parietal and interparietal fuse, and the temporalis origin extends on to the interparietal area, becoming bordered by a low sagittal crest at the midline. As the interparietal becomes covered by temporalis fibers, the external surface of the bone, previously accretional, becomes resorptive, while the inner surface, previously resorptive, becomes depositional. The encroachment on to the interparietal of the temporalis is the only mechanical factor to have changed during this phase of development; the change in nature of the bone surfaces is interpreted as indicating the functional integration of the inner and outer tables of calvarial bone. The entire thickness of bone, from cortex to cortex, therefore responds to stress. This conclusion is totally at variance with that of Moss and Young (1960), who state that:

"Within a given calvarial bone we may differentiate three functionally independent components: an outer table, a diploe, and an inner table." (p. 281).

This latter point of view has been implicit or explicit in the work of a large number of students (see references in Moss and Young, (1960; see also Klatt, 1949; Hofer, 1953, 1965, 1969; Scott, 1963). Although it is of course impossible to say with any certainty in the absence of more experimental work, the contradiction between the views espoused by Moss and Young on the one hand, and by Hoyte and Enlow on the other, may be more apparent than real, since the former view has been taken by workers primarily concerned with cranial development on a more or less gross level, while Hoyte and Enlow's investigations were concerned with histological changes.

It is in any case well known that bone is in a constant state of flux, continuously undergoing accretion and resorption which under normal conditions balance out. In addition, the work of Bélanger and others (see Krook, et al, 1970, and references therein) has shown that bone resorption is achieved not only through osteoclasia, a surface phenomenon, but also by osteolysis, or resorption within the bone, a process depending on the action of more or less deeply situated mature osteocytes. Moreover, osteolysis has been shown to be the primary agent of bone resorption, whether normal or pathological, and to form an integral part of the process of "bone flow", a concept rejected by Enlow (1963) on the grounds that "because bone is hard, it cannot grow and increase in mass by internal expansion of existing tissues". More recent work, however, particularly that of Bélanger (Bélanger and Migicovsky, 1963; Bélanger et al, 1963) has demonstrated that bone flow does indeed occur, is a continuing process, and is, in fact, the primary agent of bone remodelling. Compact bone is formed on the surface of the haversian

canals, and flows outwards to be resorbed through osteolysis in the peripheral lamellae, while cancellous bone is formed on the surface and flows inwards to be similarly resorbed in the deepest portion of the bone. This process is most plausibly interpreted as an adaptation for the avoidance of bone failure through fatigue. In view of this it is imperative, since bone remodelling is a continuous process, to distinguish clearly between remodelling which takes place for mechanical or physiological or genetic reasons. It may be that in the case of the infant guinea-pig the change from resorption to deposition on the endocranial surface of the interparietal as the temporalis becomes associated with the external aspect of this bone is related to the necessity to maintain the balance between deposition and resorption in the bone as the outer surface becomes resorptive, rather than directly due to mechanical stresses resulting from muscle attachment.

This interpretation depends on the possibility of a relationship between resorption in the outer bony table and muscle attachment, a proposition difficult to demonstrate causally rather than empirically, and one running counter to the long-established dogma that muscles attach only to periosteal, depositional bone surfaces. However, as Hoyte and Enlow have shown, muscles may attach not only to depositional but also to resorptive surfaces. Indeed, beneath a single muscle there may lie adjacent areas of deposition and resorption whose boundaries correspond to no change in muscle structure or fiber direction, and which cannot, therefore, be explained in purely mechanical terms. Muscle attachment is maintained throughout surface resorption because this is not, as widely held, an indiscriminately destructive process during which all cells and intercellular matrix disappear; those fibers within the bone matrix which are continuous

with the connective tissue framework of the attaching muscle remain undisturbed during the periosteal resorption associated with endosteal growth.

It follows, then, that the development of bony processes is not merely a function of muscle growth and size, but that it takes place as part of a broader process of bone remodelling. As Hoyte and Enlow put it: "there is a regular and alternating sequence of resorption and deposition as both the surfaces of the parent bone and of the process shift in the direction of growth, irrespective of muscle attachment of fiber direction" (p. 208). It is obviously erroneous to assume that muscle tension or presence invariably stimulates merely local osteogenesis and the consequent development of localized bony processes.

Although we lack at present a convincing comprehensive model of the controlling mechanism of bone development, it is clear that both genetic (evolutionary) and mechanical (ontogenetic) factors play vital parts. The experimental data of Washburn (1947) show, for example, that the temporal lines and sagittal crest depend on the presence of temporalis, and that normal nuchal cresting results from full development of both temporalis and of the long muscles of the neck. On the other hand, Fell (1956) has demonstrated that the sternal keel of the chick, a feature closely analogous functionally to the primate sagittal crest, will form to some extent when the bone is grown in vitro, with no muscles attached. Similar results of in vitro bone growth have been reported by Crelin and others (see references in Crelin, 1969). Additionally, it is well known that abnormal forces, i.e. those which the bone is presumably not genetically programmed to withstand, induce rapid resorption.

It therefore seems reasonable to invoke bone form as an example of the genetic "reaction norm", whereby a genotype is potentially capable of producing a variety of phenotypes, depending on the environment. In this case, the environment of the bone, the muscles and connective tissue surrounding and attaching to it, is also to some extent a product of the genotype. In spite of the lack of the model referred to earlier, enough is known on a purely empirical level to allow us to identify the gross effects of muscular development on skeletal form, and to reconstruct the myology of extinct vertebrates, at least those not too remote from living forms, with reasonable accuracy. Thus it is possible to say, for instance, that temporalis development is legitimately identifiable as the factor responsible for one of the most distinctive suites of differences between the two species of Archaeolemur.

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 postero-medial aspect of the postorbital bar. In most cases this area of origin extends almost as far along the postorbital bar as the fronto-malar 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 towards 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 ridge which runs postero-dorsally up the parietal from around the point of intersection of the fronto-parietal suture with the squamous suture. If projected antero-inferiorly, 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 anterior and posterior moieties of the temporalis in Archaeolemur; Møller (1966) has shown that in man the separately innervated anterior and posterior portions of temporalis are functionally distinct. The anterior temporalis acts to elevate the mandible, while the posterior fibres work to retract it.

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. the posterior and dorsal portion of the arch, 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 10.0mm 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 orbital process of the frontal. Minimum thickness appear 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, while 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

Figure 7

Muscle attachment areas on the cranium of Archaeolemur
edwardsi. Lateral view.

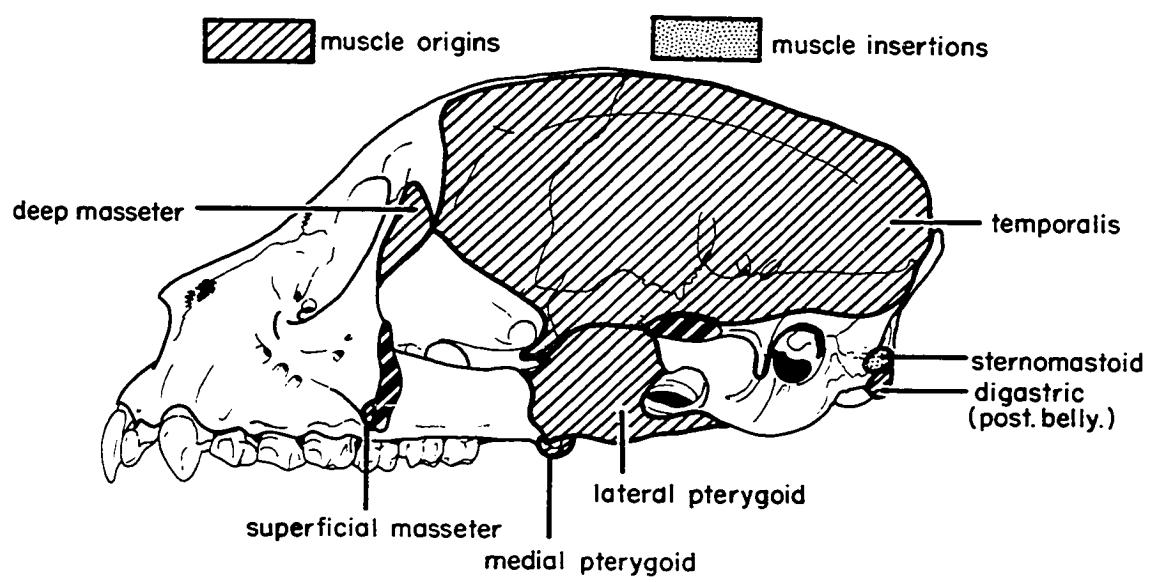
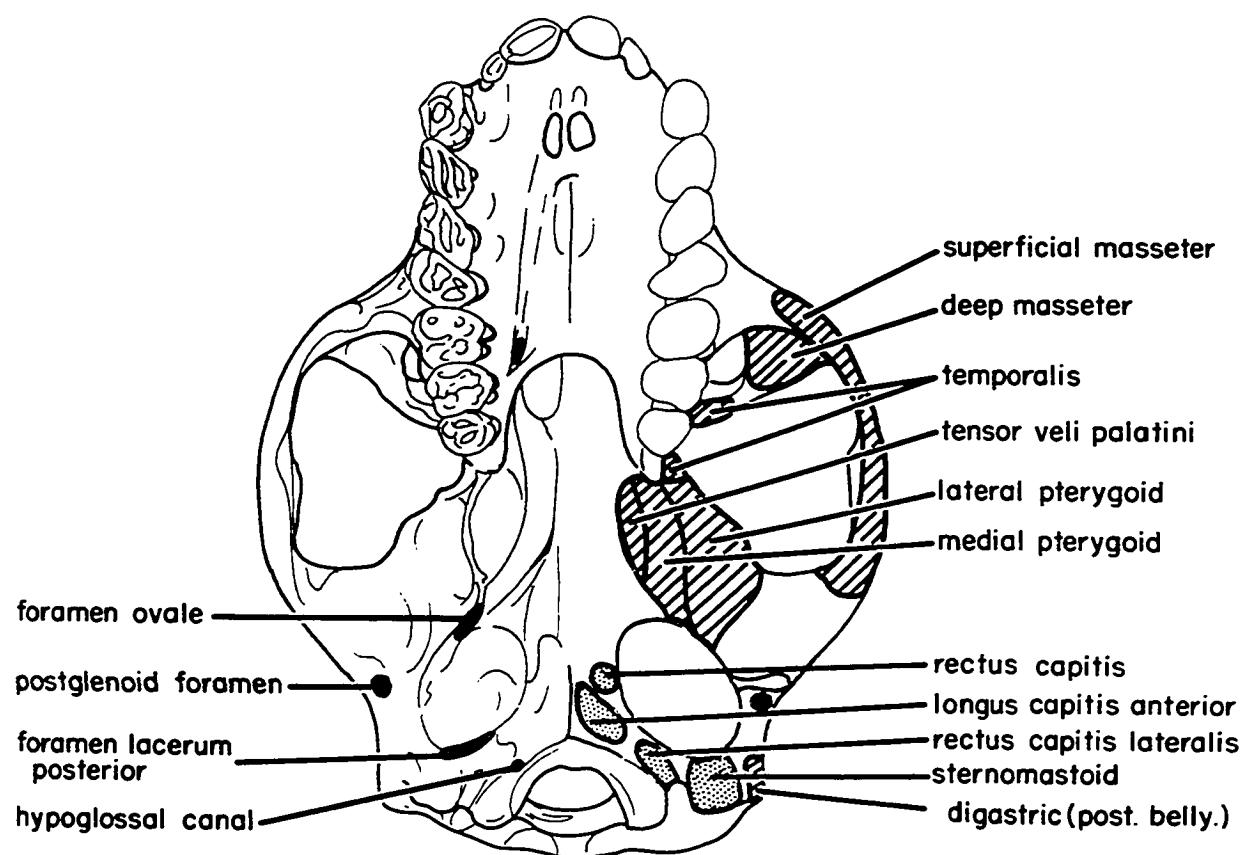


Figure 8

Muscle attachment areas on the cranium of Archaeolemur
edwardsi. Ventral view.

 muscle origins  muscle insertions



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 temporo-malar 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 temporo-malar suture.

The superficial masseter inserted broadly over the lateral surface of the rounded mandibular angle, posterior and ventral to the massesteric 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, the cresting marks the confluence of the tendons of insertion of the superficial masseter and internal pterygoid muscles.

As Avis (1961) has shown, the persistence of the angular process is dependent on the functioning of both of these muscles. In the rat, the experimental animal used by Avis, the superficial masseter proved to be the muscle which exerted the dominant influence upon angular formation, although total resorption of the process only takes place in the absence of both muscles. Bilateral removal of the superficial masseter severely impeded the animals' ability to approximate their incisors.

Avis was impressed by her observation that "prosimians, both fossil and modern, share with the rat well-developed front teeth and shallow jaws with an angular process" and believed that therefore "the bone-muscle complex should function in much the same manner" (p. 58). She suggested that the procumbent incisor teeth of prosimians represent a feeding adaptation analogous to that of "modern sheep, cattle and deer" (p. 59), thereby reviving the old controversy over the function of the prosimian dental comb (see, for instance, Stein, 1936; Roberts, 1941), and concluded that the angular process developed to increase the protraction component of the attached muscles in jaw movement at the expense of the component of elevation. In this view, angular development among prosimians is correlated inversely with jaw depth; the falseness of such an assumption is quite evident when Avahi, or indeed, any indriine, is considered. And as Buettner-Janusch and Andrew (1962) have clearly demonstrated, the dental comb is a grooming, not a feeding, adaptation.

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

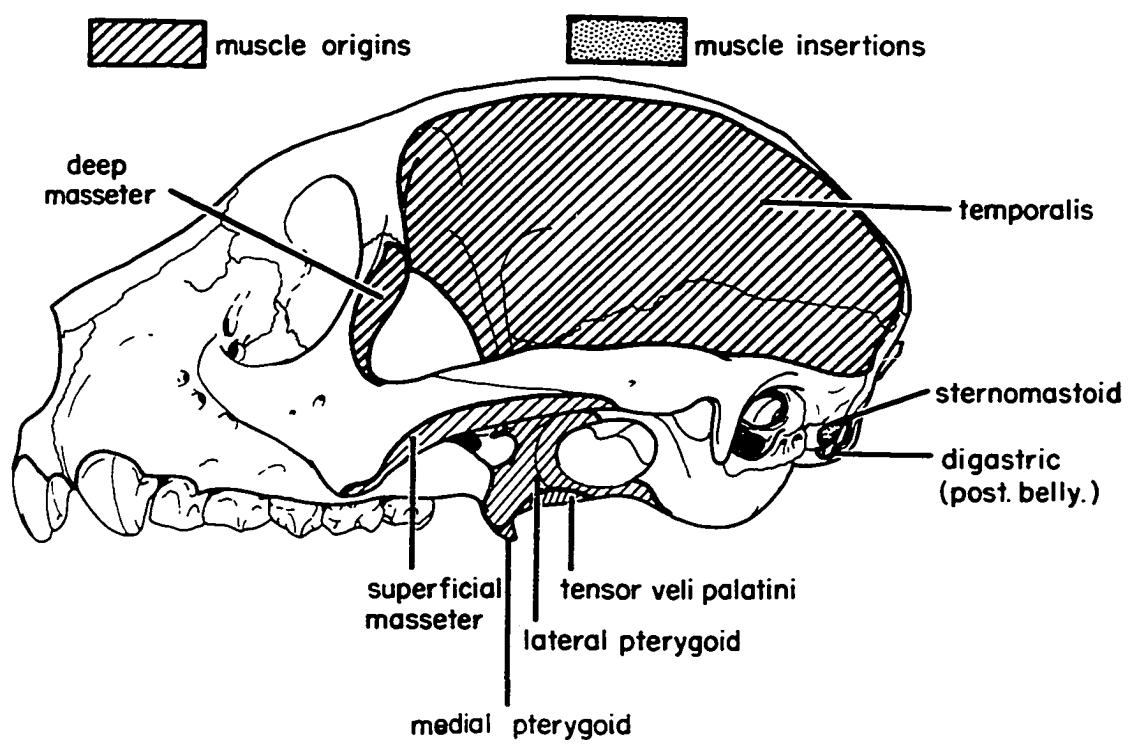
A. majori apparently did not differ materially from the larger species in massteric arrangement, although the area of origin of the deep masseter is generally less well marked.

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 is oriented slightly medially,

Figure 9

Muscle attachment areas on the cranium of Archaeolemur
majori. Lateral view.



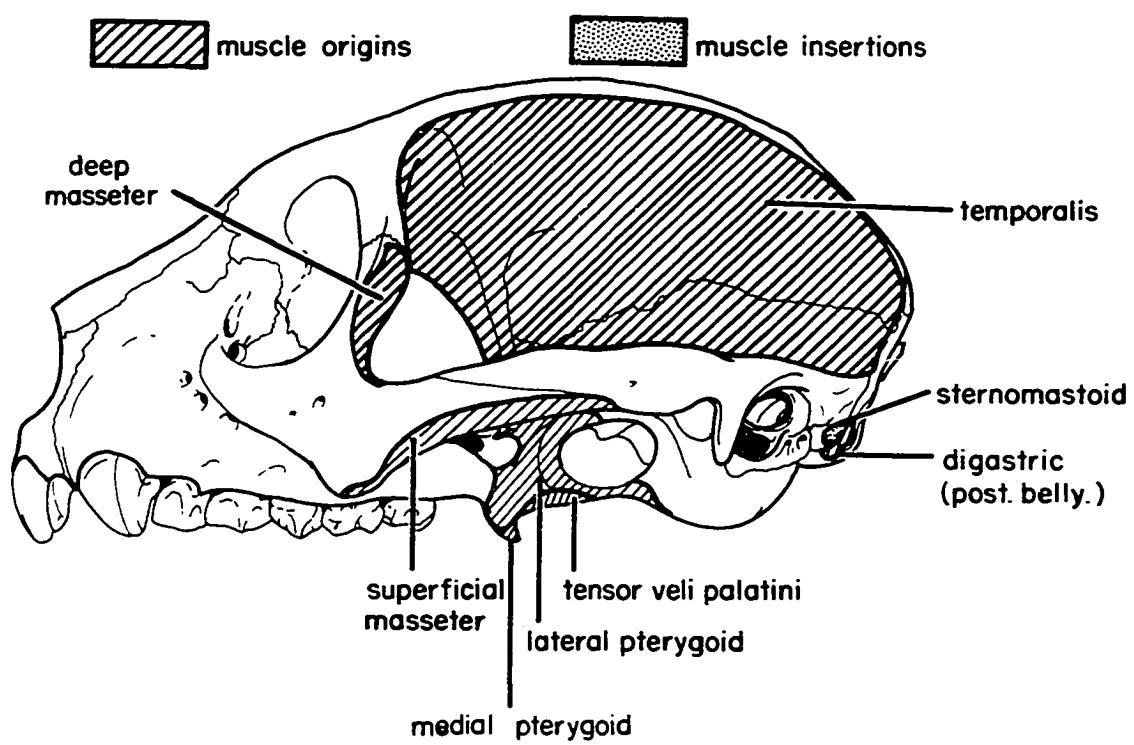
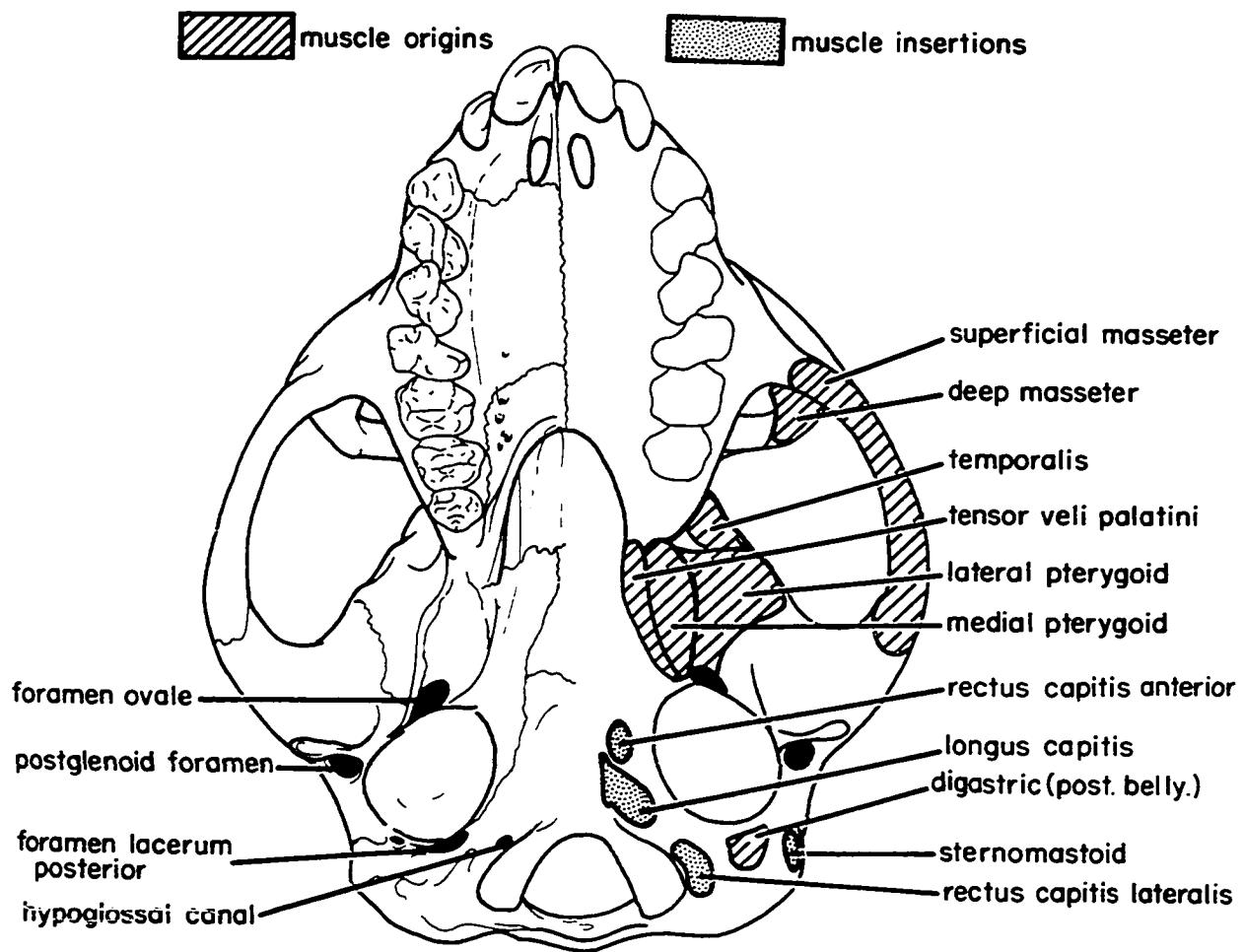


Figure 10

Muscle attachment areas on the cranium of Archaeolemur
majori. Ventral view.



providing a maximal area for origin of the medial pterygoid. Gill and Grant (1966) describe this muscle in a variety of mammals as attaching not only to the medial surface of the lateral pterygoid plate but also to a small area of its lateral surface adjacent to its ventral border. A similar occurrence may be indicated in some specimens of Archaeolemur by a small rugosity, common to both surfaces of the lateral pterygoid plate, in the region of the lamina joining the plate to the petrous process of the bulla. This can remain no more than a suggestion, however, since this region has rarely escaped damage during fossilization. The origin of the medial pterygoid 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 gonal area is strongly rugose, the primary features of this 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 infratemporal 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. Since 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 P_3 to the anterior limit of the anterior process, slightly posterior to M_3 . A tuberosity at midlehgth 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 fposterior bullar wall. While the surfaces of origin of the anterior

Figure 11

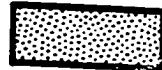
Muscle attachment areas on the mandible of Archaeolemur.

Medial and lateral views.

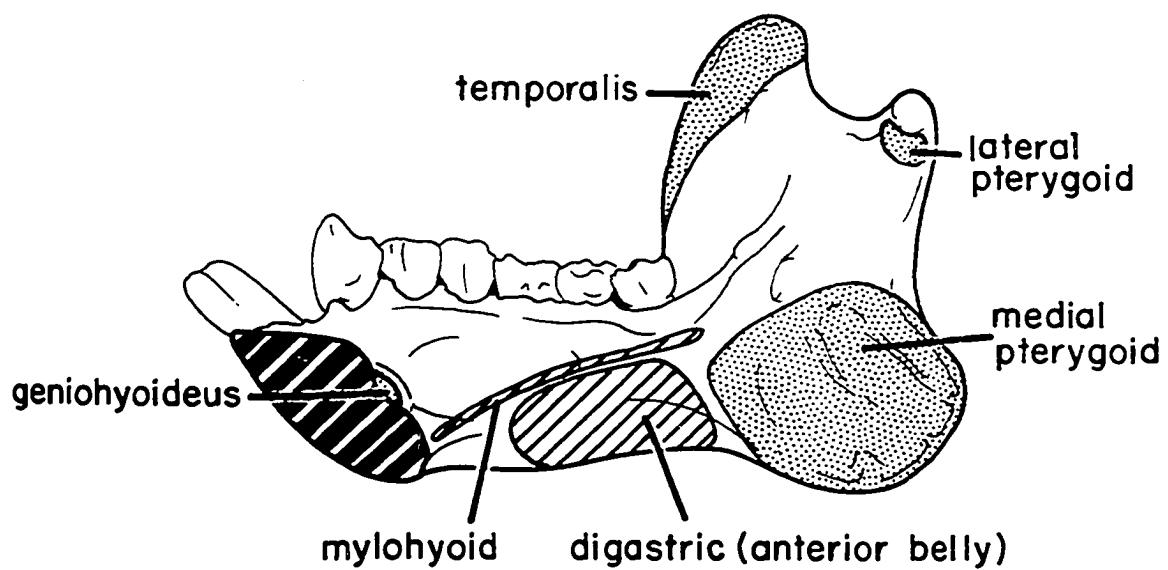
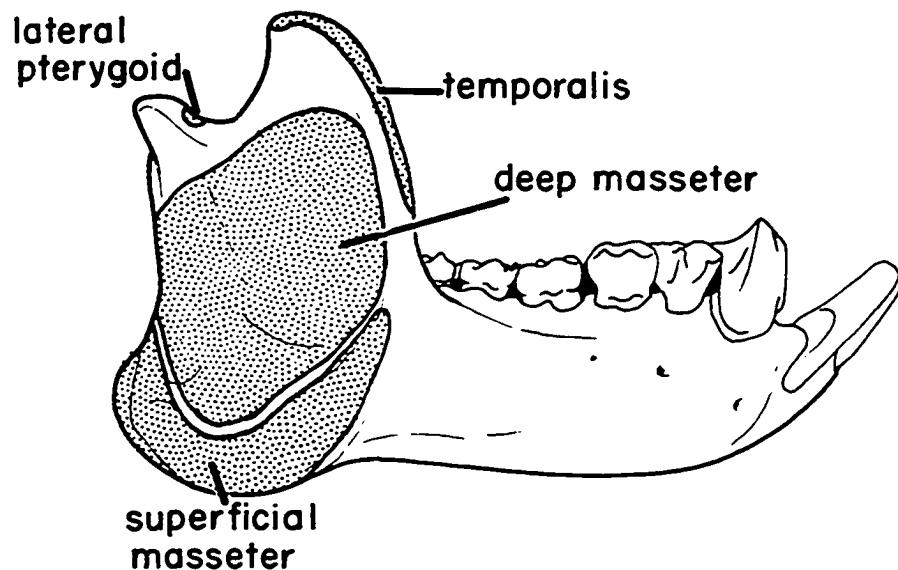
Based on A. majori (B. M. M 7374); there is no significant difference between the species.



muscle origins



muscle insertions



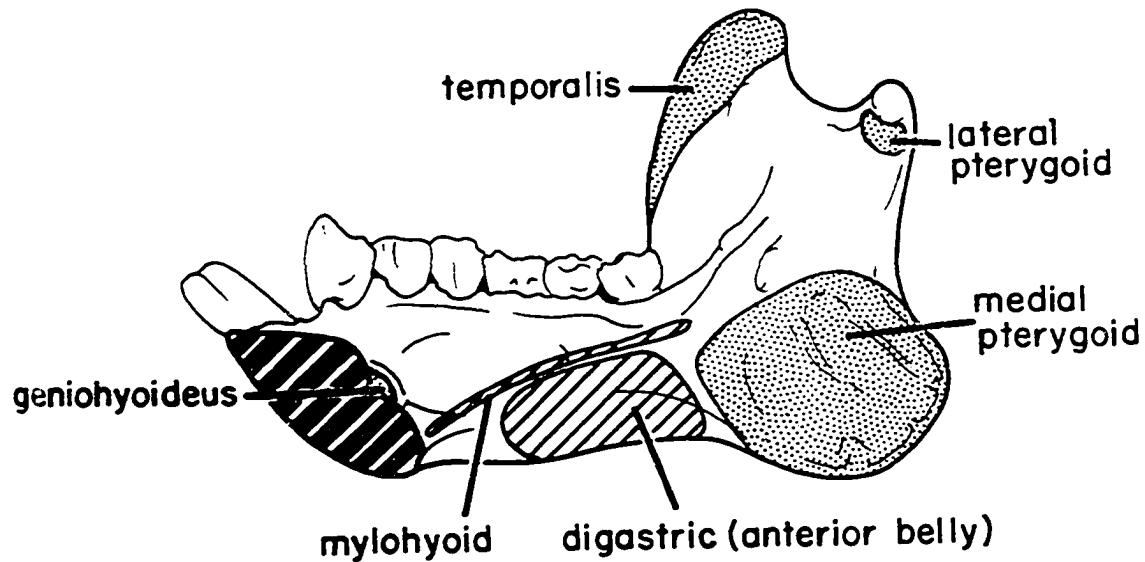
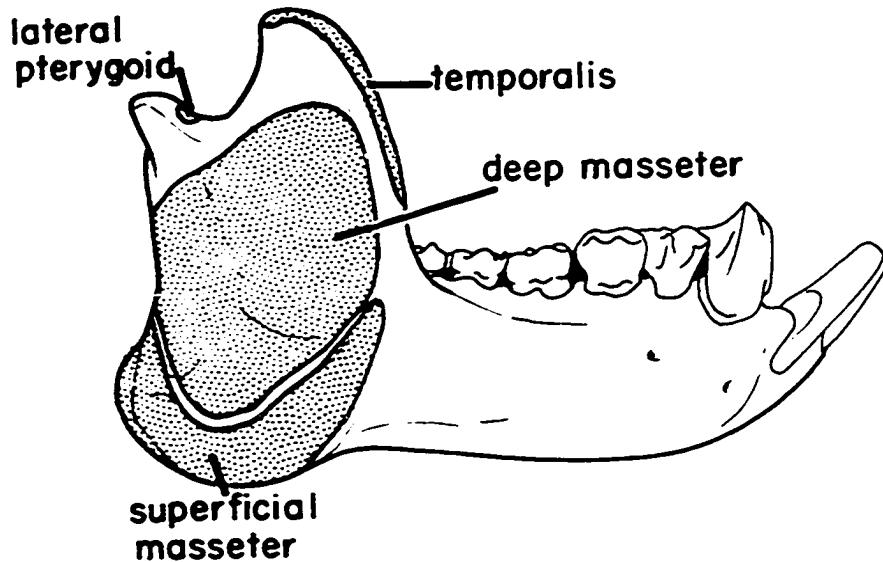
belly of the muscle are relatively of about the same size in both species of Archaeolemur, there is a considerable difference in the size of the paroccipital process; the area of origin of the posterior belly of the digastric in A. majori is commonly in the region of 30.0 mm^2 , while the figure in A. edwardsi is generally around $65.0 - 70.0 \text{ mm}^2$, although there is some intra-species variation.

Muscle action

Anatomists have traditionally inferred the functions of individual muscles by reference to their average lines of action: a reasonably accurate process when isolated muscles are under consideration. But muscles rarely if ever act in isolation, and when the effects of the contraction of a complex of muscles are considered, it is desirable to know not only the power exerted by each muscle of the complex relative to the others at every phase of movement, but also the firing sequence and duration of contraction of the muscles involved.

A more viable approach to the understanding of muscle function is provided by the technique of electromyography, in which the electric "action potential" accompanying muscle contraction is directly measured. Unfortunately, electromyographic analyses of the masticatory system have been almost completely confined to humans, although the investigations of Moyers (1950), Carlsöö (1952), Woelfel et al (1960), Ahlgren (1966) and Møller (1966) have made the characteristics of this system well known in man. Elevation of the human mandible is effected by the combined action of the temporalis, masseter and medial pterygoid, while the lateral pterygoid and digastrics act in mandibular depression. The digastrics

 muscle origins  muscle insertions



may also serve as retractors of the lower jaw. Lateral movements result from contraction of the ipsilateral masseter and temporalis together with that of the contralateral medial, and to some extent lateral, pterygoid. Protrusion of the mandible appears to be a function of both pterygoids and the superficial masseter, while the temporalis, digastrics and possibly the deep masseter, effect retraction.

The pattern of muscular contraction during mastication depends largely upon the nature of the material being chewed. Thus, while it is generally found that during the chewing of gum the ipsilateral temporalis contracts slightly earlier than the contralateral temporalis and both masseters, all these muscles tend to fire simultaneously when peanuts are chewed. The role of postural muscle of the jaw is played by temporalis, both the anterior and posterior fibers of which are continuously active, albeit at a low level, during normal standing. Møller (1966) has suggested that the firing of the anterior and posterior parts of the temporalis are under strictly separate functional control, as is also implied by their separate innervation. At maximum gape, when the digastrics, which invariably act bilaterally, are at the peak of their activity, temporalis aids the temporomandibular ligament in resisting dislocation of the temporomandibular joint. The masseters are most active at the point when the molars come into centric occlusion. The medial pterygoids contract most strongly during simple protraction of the jaw; unilateral contraction produces contralateral movement. The lateral pterygoid plays the major role in initiation of mandibular depression, and is also concerned with protrusion and movement in a contralateral direction.

Muscle function in Archaeolemur can be inferred only from visual inspection of the lines of muscle action, and from the presumed movements of the mandible as reflected by dental wear. The arrangement of the muscles, however, does not depart markedly from that in Homo. Temporalis was the most strongly developed muscle in Archaeolemur, its posterior portion probably having exceeded its anterior part in bulk. The posterior temporalis was situated to act as a strong mandibular retractor, while the anterior temporalis was primarily an elevator; the most anterior fibers, those originating on the postorbital process of the frontal, were mechanically capable of producing a small degree of protrusion.

Unilateral temporal contraction would have produced ipsilateral adduction.

The superficial masseters, contacting together, would have produced elevation, and possibly protrusion, of the lower jaw; unilateral firing would have produced rotation around the ipsilateral condyle and consequent ipsilateral adduction during elevation, although this lateral movement would have been reversed when occlusion began to guide the course of the teeth. The deep masseter was a powerful elevator of the jaw, acting at its greatest mechanical advantage when the teeth came into occlusion. The oblique course of the malar-temporal suture of the zygomatic arch in A. majori, and its horizontal orientation in A. edwardsi, are probably explicable in terms of resistance to the forces exerted on the zygomatic arch during contraction of the masseters, since the suture was oriented perpendicularly to the mean line of action of these muscles at the point of occlusion, when they were presumably exerting their maximum power. The wide bowing of the zygomata, especially in the larger species, is probably due as much to the provision of additional lateral orientation

for the masseters and medial pterygoid as to the accommodation of the large temporal muscle; the infratemporal and temporal fossae of many mammals contain fat pads which probably perform a spacing function.

The medial pterygoid was situated to act as a powerful elevator, and, to a lesser extent, retractor, of the mandible. Unilateral contraction would have produced a contralateral movement, rotation being around the contralateral condyle. The average line of action of this muscle was virtually identical, in the sagittal plane, to that of the masseters. The lateral pterygoid was well placed to act in mandibular protrusion, and also to stabilize the temporomandibular joint during posterior movement of the condyle; Möller (1966) has shown that this muscle fires irregularly during elevation of the lower jaw in man, a movement involving condylar retraction.

Hadropithecus

Masticatory musculature (Figs. 12, 13, 14).

M. temporalis

Temporalis in Hadropithecus is still more 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, V.N.H.M. 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 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

Figure 12

Muscle attachment areas on the cranium of Hadropithecus
stenognathus. Lateral view.

Based on the Tsiravé skull.

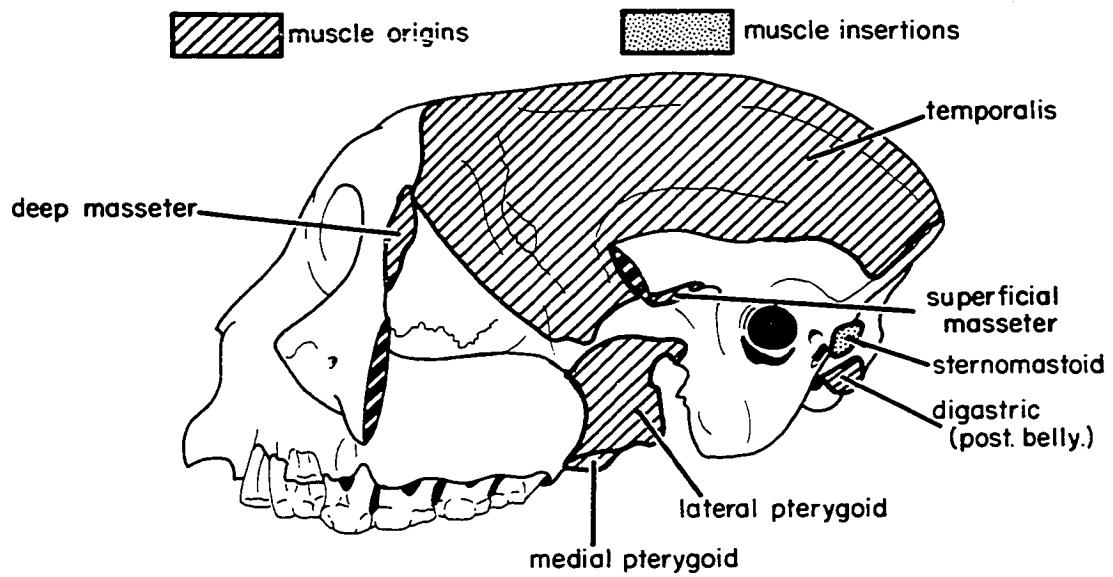
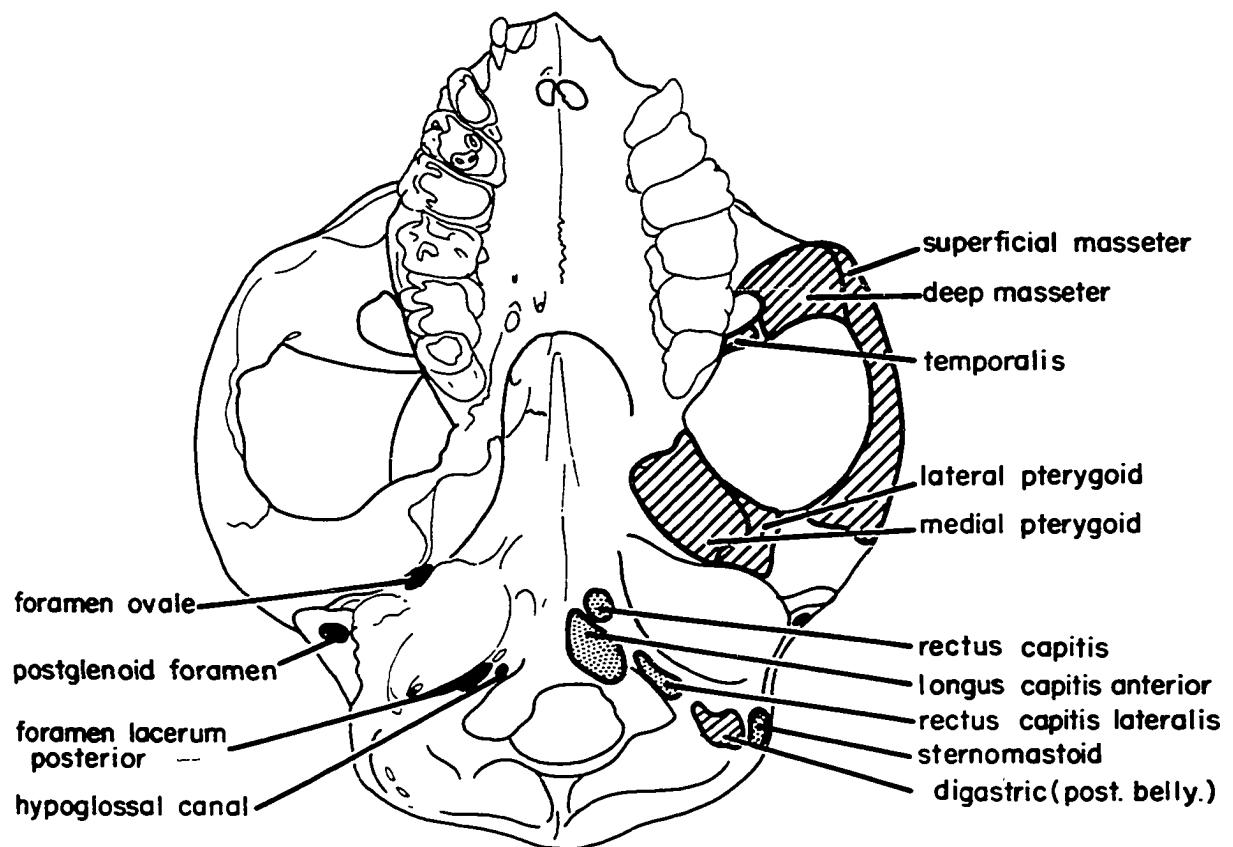


Figure 13

Muscle attachment areas on the cranium of Hadropithecus
stenognathus. Ventral view.

Based on Tsiravé cranium.

 muscle origins  muscle insertions



tubercle, level with the back of P^4 . 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. Since no complete mandibular gonal 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 further dorsally than in Archaeolemur 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.

Figure 14.

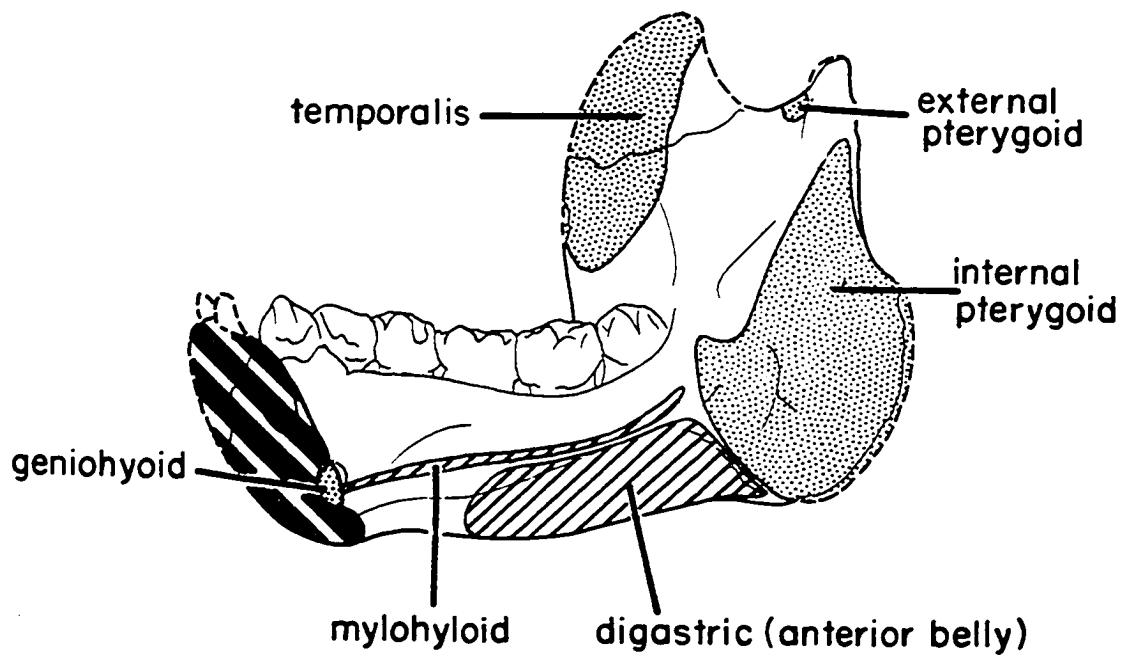
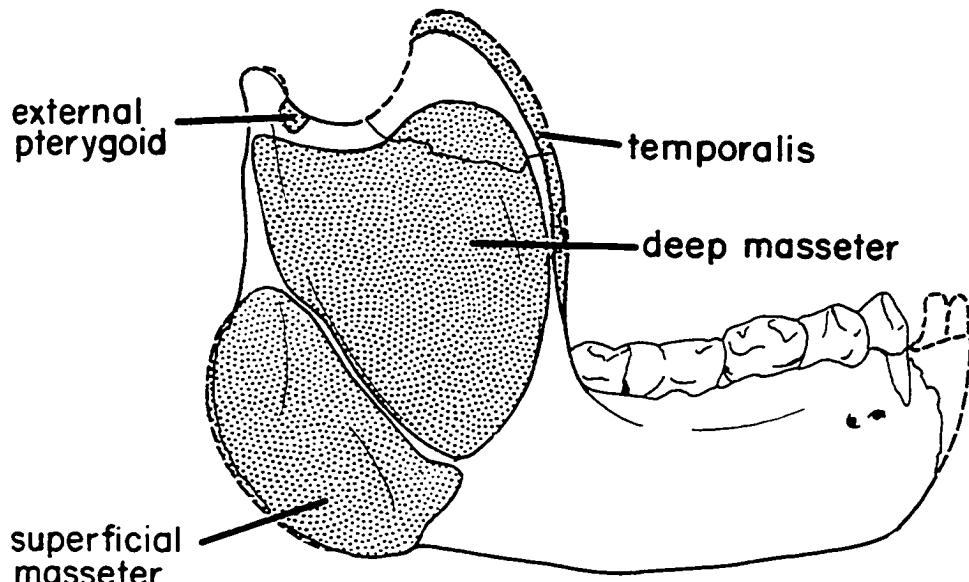
Muscle attachment areas on the mandible of Hadropithecus
stenognathus. Ventral view.



muscle origins



muscle insertions



In concert with the general deepening of the ventral part of the cranium in Hadropithecus, the pterygoid plates are considerably enlarged dorsoventrally compared to 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 cocontact 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 midpoint 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 proportionately 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.

Muscle action

In broad terms the actions of the muscles just discussed were the same as those of their counterparts in Archaeolemur. The significance of the more precise aspects of muscle disposition will be discussed latter.

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; Butler and Mills, 1959; Mills, 1955, 1963, 1964, 1966; Welsch, 1967a, b; Jenkins, 1969; Crompton and Hiiemäe, 1969a; Crompton and Sita-Lumsden, 1970) and mandibular movements (Mills 1966, 1967; Crompton and Hiiemäe, 1969a, b, 1970), as well as providing indices of age in individual animals (Welsch, 1967a, b). Although, as Crompton and Hiiemäe (1969a, b, 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, 1969, 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. 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, since 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 twenty or thirty times 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 to 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 upwards

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 (Hiemae and Jenkins, 1970), Crompton and Hiemae believe (pers. comm.) 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 salience 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 Hiemae for Didelphis, the critical phase again being the power stroke, which striations on the incisal surfaces suggest was produced by 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 upwards 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 specialised condition of this dental region to have arisen among the primates since the Paleocene. As we have seen, P^2 , P^3 and the anterior portion of P^4 are laterally compressed and aligned to produce a single shearing blade which works against a similar blade formed from P_2 , P_3 and the anterior part of P_4 . 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 apices move against the troughs formed at the contacts of successive teeth in the opposing row. The posterior shearing surface of P_2 moves against the anterior surface of P^2 , the anterior surface of P_3 against the posterior surface of P^2 , and so forth. This pattern of shear is slightly modified in the case of P^4 and P_4 because of the molarisation of the posterior moieties of these teeth. The development in P^4 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 protostyloid 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 very clearly marked, and are continuous along the entire series. They are set at about 45° 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 backwards 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 to 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 to that obtained on cusps of the molar teeth.

Although there is a good deal of individual variation in this, 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 as 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 utilising information gathered from a number of individuals, a process which reveals that mandibular movement during the power stroke was upwards 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_4^4 and M_1^1 respectively. Similarly, the combined anterior and posterior foveae of P_4 and M_1 move across the protocone of P_4^4 . 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_1^1 , the hypoconid of M_1 across the central fovea of M_1^1 , 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}^1 , the central fovea of M_2 across the protocone of M_2^2 , the hypoconid of M_2 across the central fovea of M_2^2 , the posterior-anterior foveae of M_{2-3} across the hypocone of M_2^2 , the protoconid of M_3 across the posterior-anterior foveae of M_{2-3}^2 , the central fovea of M_3 across the protocone of M_3^3 , and the hypoconid of M_3 across the central fovea of M_3^3 . 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. The wear facets made by this contact are believed by Welsch (1967a), following the terminology of Mills (1955), to have been formed during a "lingual phase" of occlusion; this phase occurs when the mandibular teeth move beyond the position of centric occlusion, and the mouth begins to open; Welsch (1967a, b) states that the buccal phase serves a cutting function, while during the lingual phase food is squashed. However, as indicated above,

the wear facets referred to by Welsch occur at the end of the power stroke, when the teeth are in centric relation and the mandible is symmetrical around the midline. Crompton and Hiemae (1970) have discussed the definition of the concepts of centric relation and centric occlusion; in the case of Archaeolemur they are broadly synonymous because the animal is not fully anisognathic.

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 towards 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 upwards 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 to 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 an abrasive 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 a 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 backwards 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

This 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 which 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 concludes 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, p. 658-9).

MacConaill 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 inter-condylar space. This arc is so small relative to the circle's diameter 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, while 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.

From the delicate structure of the postglenoid process in Archaeolemur it may be inferred that mastication produced no very large posteriorly-directed reaction at the joint.

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, while almost none of those which do exist are striated. Virtually all the evidence of mandibular movement from this source which may be gained from material available to the writer for microscopic examination comes from M¹ of V.N.H.M. 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 levelled 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, while 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 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 V.N.H.M. 1934 IV with V.N.H.M. 1934 IV 2/1a and 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°. That of L₁₂ is approximately horizontal, as is that of its opponent in the upper jaw. Since the incisors in the type mandible V.N.H.M. 1934 IV 1/1 conform to the latter type of wear, (L₁-₂, RI₁ in the Tsiravé mandible represent an occlusal anomaly. Unlike the case in Archaeolemur, there are no striae on the facets to indicate the plane of movement. The degree to which the incisors are worn, however, indicates that, compared to the posterior teeth, they were little used. In the Tsiravé cranium, for instance, while

Figure 15

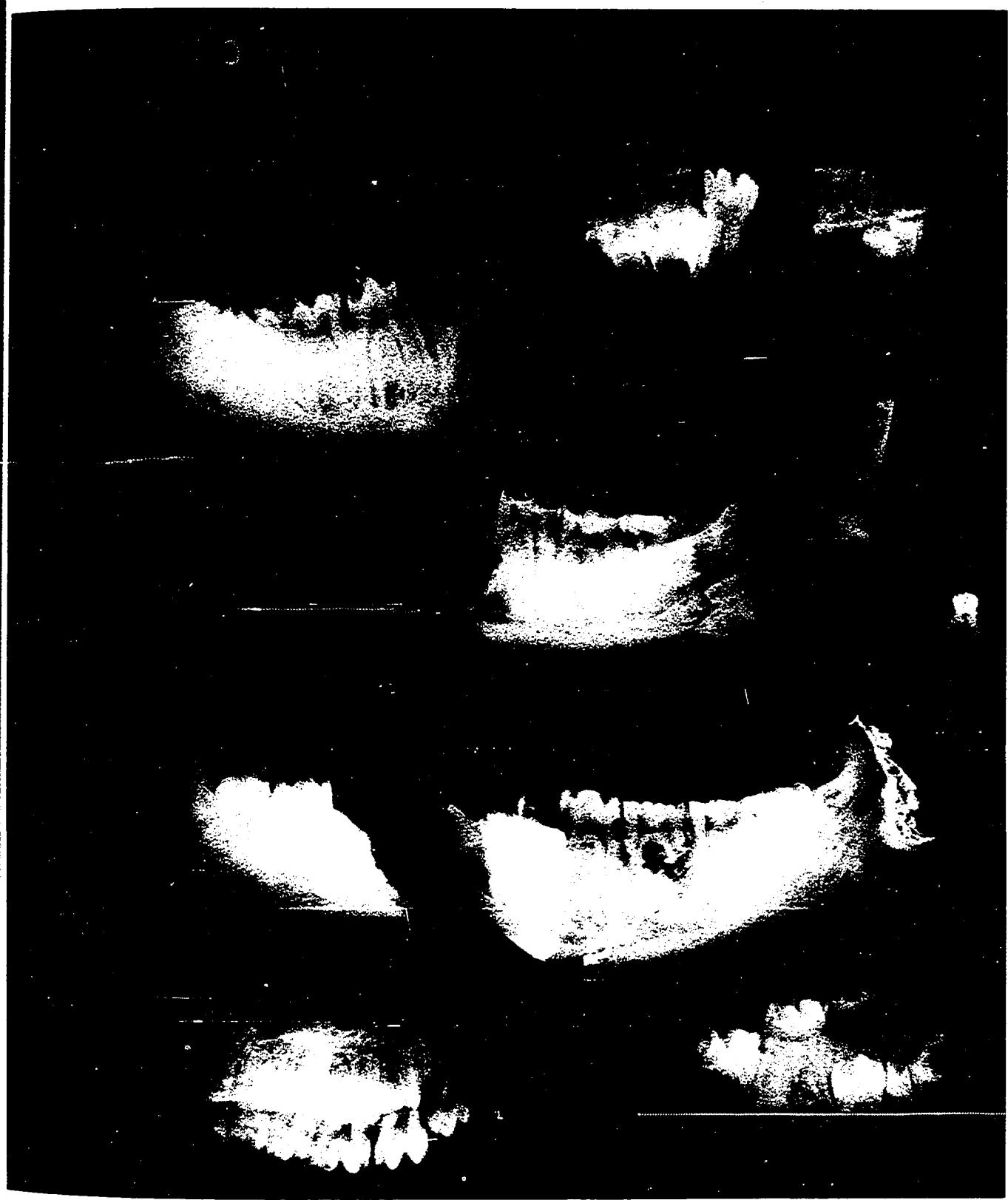
Hadropithecus stenognathus: radiographs of maxillary and mandibular specimens in the collections of the Naturhistorisches Museum, Vienna.

Top row (left to right): V. N. H. M. 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



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M^1 is almost totally worn out, and the other cheek teeth show very considerable wear, the relatively less hypodont 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 V.N.H.M. 1934 IV 1/1, the incisors show very little wear indeed, no more than the amount required to produce the initial breach of their relatively thin enamel. This is not necessarily a phenomenon related to the dental eruption sequence; in the subadult V.N.H.M. 1934 IV 3, the permanent lateral incisor is almost as advanced in its eruption as is M_2 (see radiograph in Fig. 15).

In young adult Hadropithecus the post-incisor anterior dentitions formed morphological units very similar to those of their homologues in Archaeolemur; the canine and anterior premolar above, and P_{2-3} 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 p^3 , and the paraconid crest of P_4 also form part of this shearing series, but the medial portion (protocone crest) of p^3 , and the remainder of P_4 , 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 towards hypodonty and the maximisation of the available grinding surface. Occlusion during the power stroke appears to have been as follows: the metaconid lobe, and then the protoconid, of P^4 passed across the closely-approximated posterior and anterior transverse crests of P^3 and P^4 respectively, while the posterior longitudinal crest of P_4 passed across the median transverse crest of P^4 . The paraconid crest and protoconid-metaconid crest of M_1 passed across the mesostyle and posterior transverse crest of P^4 , and the anterior transverse crest of M^1 , respectively. The entoconid-hypoconid crest of M_1 passed through the laterally-open central fovea of M^1 , and the hypoconulid (posterior transverse) crest of the same tooth and the paraconid crest of M_2 passed over the rear of the hypocone-metacone and posterior transverse crests of M^1 . 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 genus showing intermediate stages of wear, but the type specimen, V.N.H.M. 1934 IV 1/1, in which wear is advanced, although by no means as 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, though 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; V.N.H.M. 1934 IV 3 and 4a show (see radiographs in Figure 15) 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 V.N.H.M. 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 molarised.

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. The curve of Spee itself would make good mechanical sense if some degree of anteroposterior movement were involved in mastication (vide Elephas, Loxodonta); greater pressure is applied in the region of contact if two surfaces are inclined relative to the direction in which one is moving against the other, and to the force moving it. The pattern of advanced wear observed in the Tsiravé Hadropithecus might be held to support an interpretation of its dental function involving anteroposterior movement. The teeth of the mandible are more heavily worn than are those of the maxilla, and are less evenly worn; P_4 and M_1 are the most heavily worn of the mandibular teeth. This might be somewhat surprising in an animal depending solely on lateral jaw motions, since P_4 probably erupted at about the same time as the much more lightly worn M_3 , but would be easily explicable if this tooth represented the primary pressure-point in the lower part of a system were the pressure-point shifted above but remained relatively constant below, as would be the case, at least to a limited extent, if the mandible did indeed move antero-posteriorly. Predominance of anteroposterior movement would also explain the lack of shearing wear on the premolars.

However, the Vienna skull, though young, shows the reverse relation of wear on the upper and lower teeth, while the heavy wear of P^4 and M^1 in the Tsiravé cranium is more plausibly attributed to the animal's preference of this area as a primary

bite-point, while the wear-facets also point to a predominantly lateral movement of the mandible.

In no specimen of Hadropithecus is it possible to ascertain the position of the condyles with the teeth in centric occlusion with perfect precision, since 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, while the variation in direction of the buccal striae discussed earlier provides faint evidence that in Hadropithecus chewing motions were somewhat less specialised than in Archaeolemur.

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 only too well aware that the muscular contents of the temporal and infratemporal 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.

Incisal biting in Archaeolemur, and presumably also in Hadropithecus, was achieved by symmetrical bilateral retraction of

the condyles, combined with elevation. Quite evidently, the muscles primarily involved in the retractive component of this movement were the temporals, and in particular their posterior portions. We have seen in Archaeolemur edwardsi that a bilateral dorsal expansion of the nuchal crests between their sagittal and mastoid margins indicates an enlargement of the part of the posterior temporalis attaching in this area. A line drawn posterodorsally from the point of approximation of the upper and lower incisors and passing through the tip of the coronoid process roughly bisects this part of the temporalis.

Gingerich (1971, ms) has recently proposed that the force produced by temporalis will be entirely transmitted to such a bite-point if the condyle is permitted to translate posteriorly over a well-lubricated, effectively friction-free surface during muscular contraction, since the only points at which the mandible contacts the cranium are at the food and at the condyle. This is only the case, of course, if the sliding plane along which the condyle moves is parallel to the force producing the motion, thus eliminating any reaction force as the condyle moves over the glenoid surface. In Archaeolemur this condition is largely satisfied since the posterior part of the temporal articular surface is inclined slightly dorsally towards the postglenoid process. During condylar retraction by the action of the posterior temporalis the temporomandibular joints were stabilized by the external pterygoid, whose direction of contraction was directly antagonistic to that of the posterior temporalis.

Elevation of the jaw was accomplished by the interaction of all the adductor muscles, probably in a manner analogous to the role played by these muscles in elevation during premolar shear and molar grinding, as discussed later.

A similar pattern of incisal action appears to have applied in the case of A. majori, the depressions in the parietals adjacent to the occipital and temporal bones evidently having played the same role as the enlargement of the nuchal crests in A. edwardsi. In Hadropithecus, too, this mechanism was operative, although in consequence of facial shortening and deepening in this animal the bulk of the posterior temporal muscles was shifted forward to the most posterior portion of the sagittal crest.

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; Turnbull, 1970), 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 backwardly-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 of the system's having 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 temporo-mandibular joint, it follows that the anterior adductor muscles (the masseters and the medial pterygoid; as Figure 16 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 some 40% 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%. 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 which 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 that the temporomandibular joint of mammals is the only articulation lined with fibrocartilage, rather than hyaline cartilage. While 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 operation of the archaeolemurine mandible as a lever would have produced a resultant force at the dentition oriented tangent to the arc of adduction. Such a force would have resolved into two components: a vertical force, and an anteriorly directed one, which would have placed the palate in tension. Bone, although strong in compression, is weak in tension, and tensile forces must be resisted by a great increase in bulk and modification of the internal structure of the bone. There is no evidence whatever in the archaeolemurine (or, indeed, in any other mammal examined) that the palate was designed to resist tension.

The key to the operation of the masticatory system in Archaeolemur and Hadropithecus lies in the structure of the facial skeleton. 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 represents 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 the post-orbital bar, and by a strong trabecular structure, clearly visible in radiographs of B. M. M 9965 (Figure 21), which runs from the region of the hamulus of the palatine 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 facial region of Archaeolemur is therefore ideally structured to resolve compressive forces, particularly those directed towards its apex. The foregoing explanation of facial structure also reinforces the interpretation of the frontal sinus as a "dead" space between bony structures related to stress transmission or other functions.

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

Figure 16

Orientations of the masticatory muscles in Archaeolemur edwardsi.

Abbreviations:

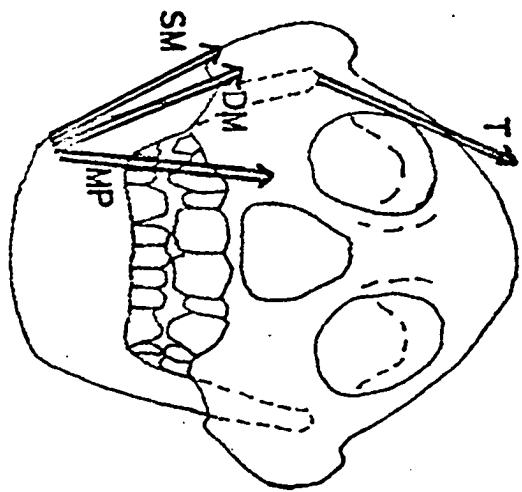
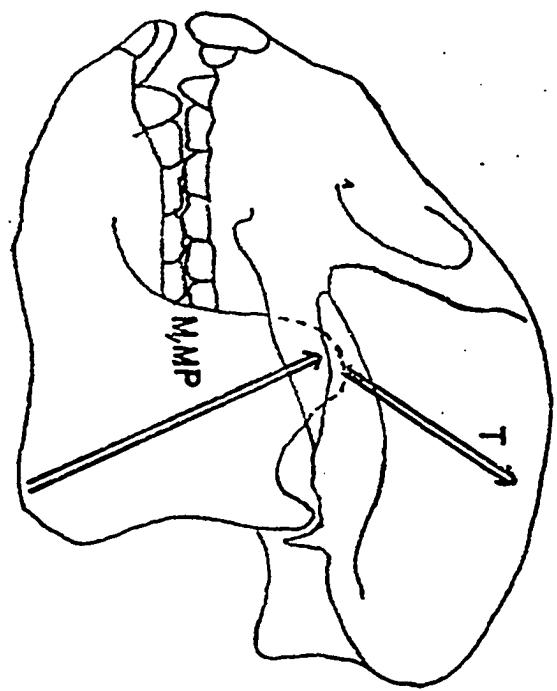
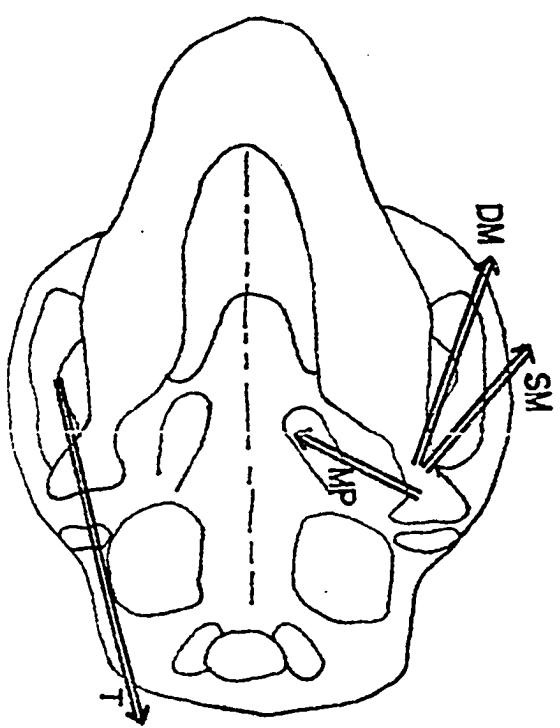
T Temporalis

M,MP Masseters + medial pterygoid

SM Superficial masseter

DM Deep masseter

MP Medial pterygoid



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 orthognathic 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; David (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 (Figure 15); the roots of the teeth of Archaeolemur are puny compared to 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. Pneumatisation 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 pneumatisation (Figure 15). 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.

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 force at the jaw joint (Figure 18). The jaw may be maintained in equilibrium during biting if the moments of force in all directions around the bite-point sum to zero, i.e. if the resultant force is equal and opposite to the forces acting at the teeth to produce it. The mandibular mechanics change slightly at different bite-points along the jaw, but the jaw 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. Since 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

Figure 17

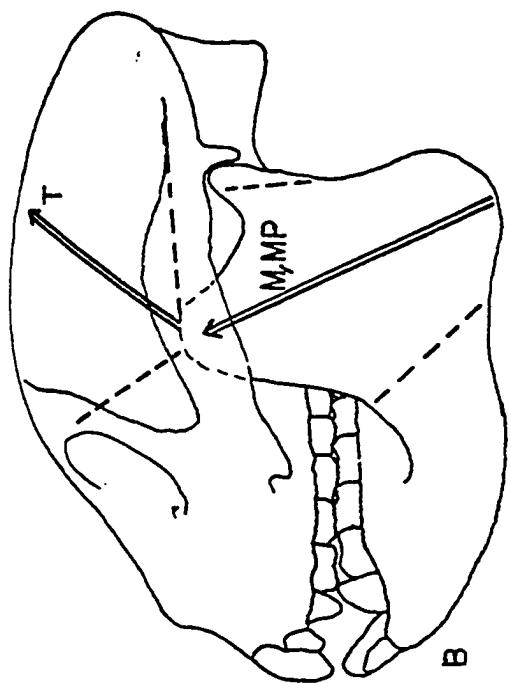
Orientations of the mandibular adductor muscles in:

- A. Propithecus verreauxi
- B. Archaeolemur edwardsi
- C. Archaeolemur majori
- D. Hadropithecus stenognathus

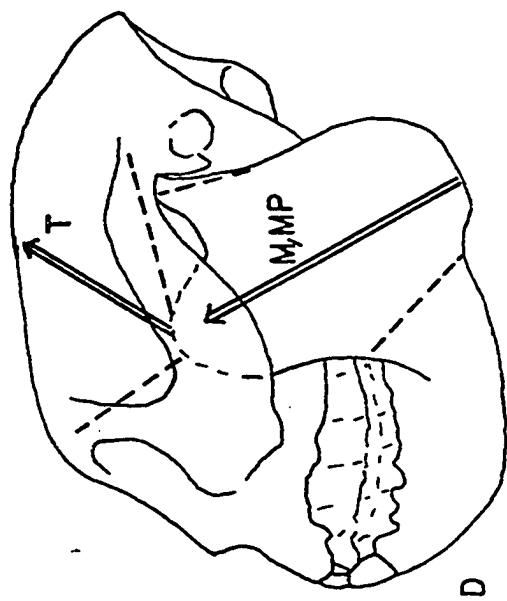
Abbreviations:

T Temporalis

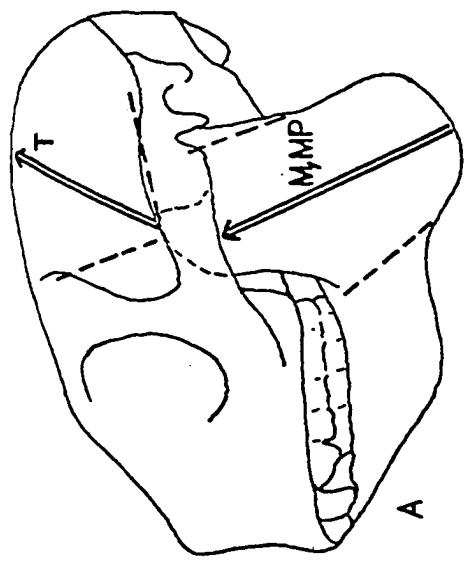
M,MP Masseters + medial pterygoid



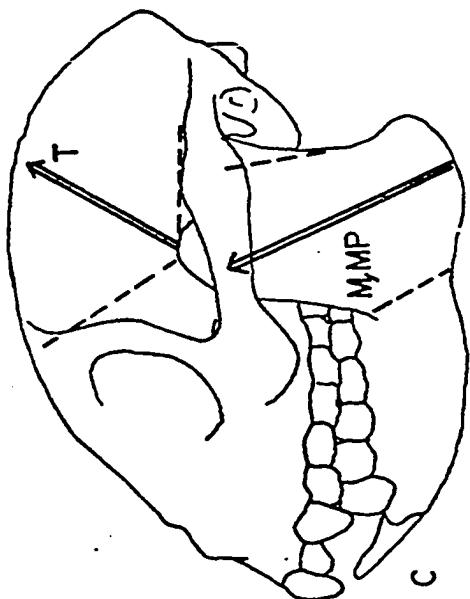
A



B



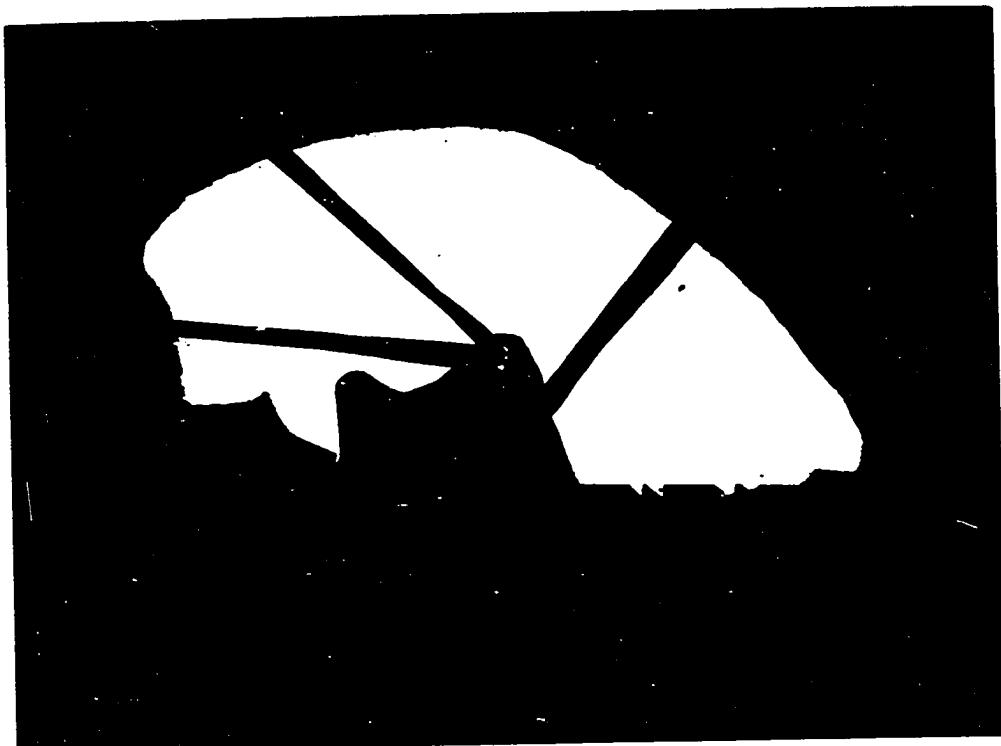
C



D

Figure 18

Model of the mandible of Archaeolemur edwardsi, demonstrating how the jaw can be held in equilibrium during mastication with no resultant force at the temporomandibular joint. The model is suspended only by elastic bands representing the adductor muscles and the resultant (occlusal) force, and is shown in equilibrium at two different bite points.



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, since 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.

If the bite-point is moved further 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 proportionately 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 advantageousness 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 postulated above, the resultant force at the dentition remains constantly directed, towards 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 rotatory 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 nearly 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 which 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 Fig. 16 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 17). There is one extremely important difference, however. Living indriines possess an unfused mandibular symphysis. The work of Crompton and Hiiemäe (1969, 1970; Hiiemäe, pers. comm.) 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, existing 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 (which should, incidentally,

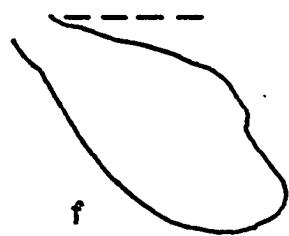
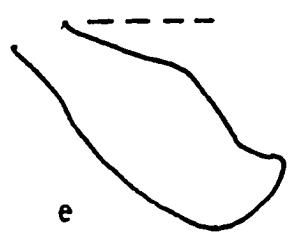
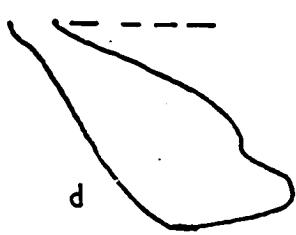
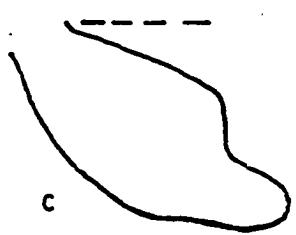
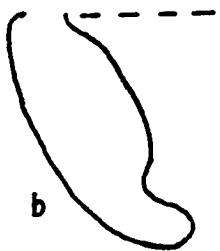
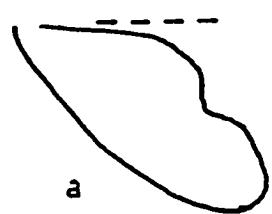
sound the final death-knell of the use of symphyseal morphology as a taxonomically useful characteristic). In Figure 19 symphyseal cross-sections of Hadropithecus and Archaeolemur are compared with those of a number of gorillas.

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 an extremely strongly buttressed symphysis, characterised in particular by the possession of a strong inferior transverse torus.

Goodman (1968) 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

Figure 19

Sympyseal cross-sections of (a) Archaeolemur (A. majori, B. M. M. 7374), and (b) Hadropithecus (reconstruction, based on V. N. H. M. 1934 IV 1/1) compared with (c - f) similar sections of the mandibles of four adult individuals of Gorilla gorilla.
c - f from Goodman (1968).



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 19), while the forces developed in this area of the mandible during contralateral temporalis contraction would have been very much of the sort Goodman describes.

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 towards 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 towards 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 Indriinae and Archaeolemurinae was already relatively highly specialised towards the modern indriine condition. If this were indeed the case, subsequent evolution of a line adapting as the archaeolemurines did would have been strictly channelled.

THE BRAIN AND CRANIAL SENSORY ORGANS AS DETERMINANTS OF SKULL FORM

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 channelled, 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, summarised 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 outwards 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 point 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 induced 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 well 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, pneumatisation 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 recognises, was to emphasise 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 unpneumatised vertebrate cranial bone rarely exceeds more

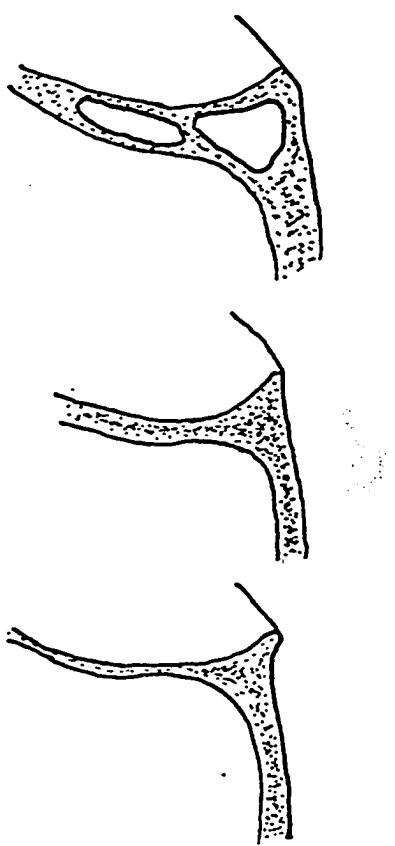
than a few millimeters, even in the largest animals. The only exception to this known to the writer occurs in the case of the "dome-headed" pachycephalosaurid dinosaurs, among males of which the thickness of compact bone above the cranial cavity reached as much as nine inches in a two-foot-long skull. This remarkable condition has, however, been convincingly shown by Galton (1970, 1971) to have had a specific 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 discordance 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. The pneumatisation of cranial bone as a spacing mechanism is well instanced by Figure 20, taken from a textbook on orbital anatomy, and illustrating a normal series of variations in the spatial relations of the orbit and anterior cranial fossa in man. As the distance separating the two functional units increases, the dividing bone at first thickens, and then pneumatises.

Figure 20

To show pneumatisation as a result of the separation of functional components in the skull. The figures represent three normal human variations in the relations of the orbit and the anterior cranial fossa. As the functional components move apart, the bone at first thickens, then pneumatizes.

After Whitnall, 1921.



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, anteroposterior 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 fronto-malar 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 over 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 already 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 supra-orbital line. In the absence of the frontal sinus, the superior part of the post-orbital 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% larger on average than that of the more gracile A. majori (the mean neurocranial volume of nine A. edwardsi crania is 121.5 cm³; that of six A. majori is 98.6 cm³ ≈), but which is only some 6-7% larger in mean cranial length, possesses frontal sinuses whose volume may surpass that of those of A. majori by as much as 250%. 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

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

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 sinusial development, and that this condition is a correlate of the possession of a small brain and large, forwardly-shifted masticatory muscles. The maxillary sinus presumably 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 reinvestigated 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 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 sinusial 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.

Figure 21

Radiographs in lateral view of Hadropithecus (above; the Tsiravé skull) and Archaeolemur edwardsi (B. M. M 9965).

Hadropithecus courtesy of Dr Roger Saban.



It would appear, 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, B.M. M 9965 (Figure 23). Most of the information derived is shown in the figure. The endocranial volume of this individual is estimated to be approximately 136 cm². 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 (A.M.N.H. 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

Figure 22

Lateral view of endocranial cast of Archaeolemur
edwardsi, B. M. M 9965, showing tentative identification
of cerebral sulci.

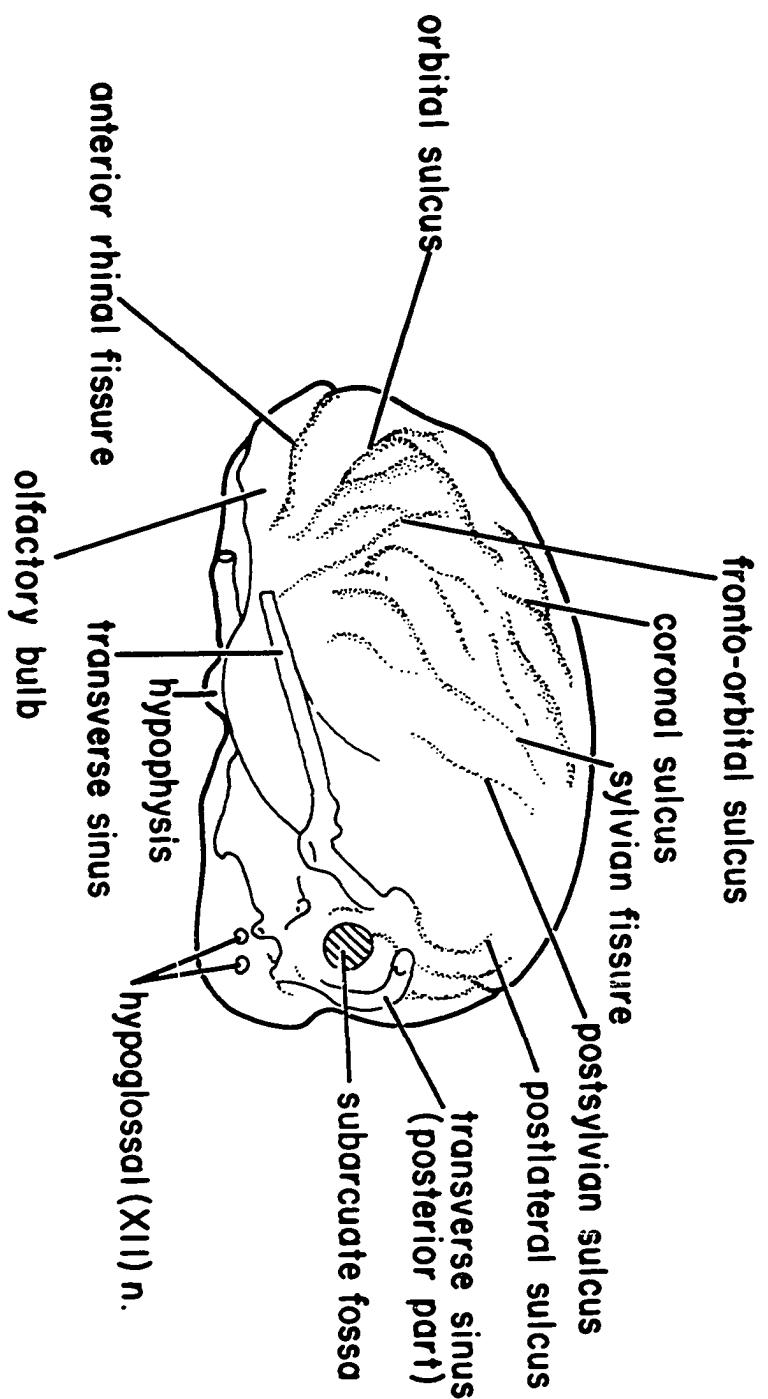
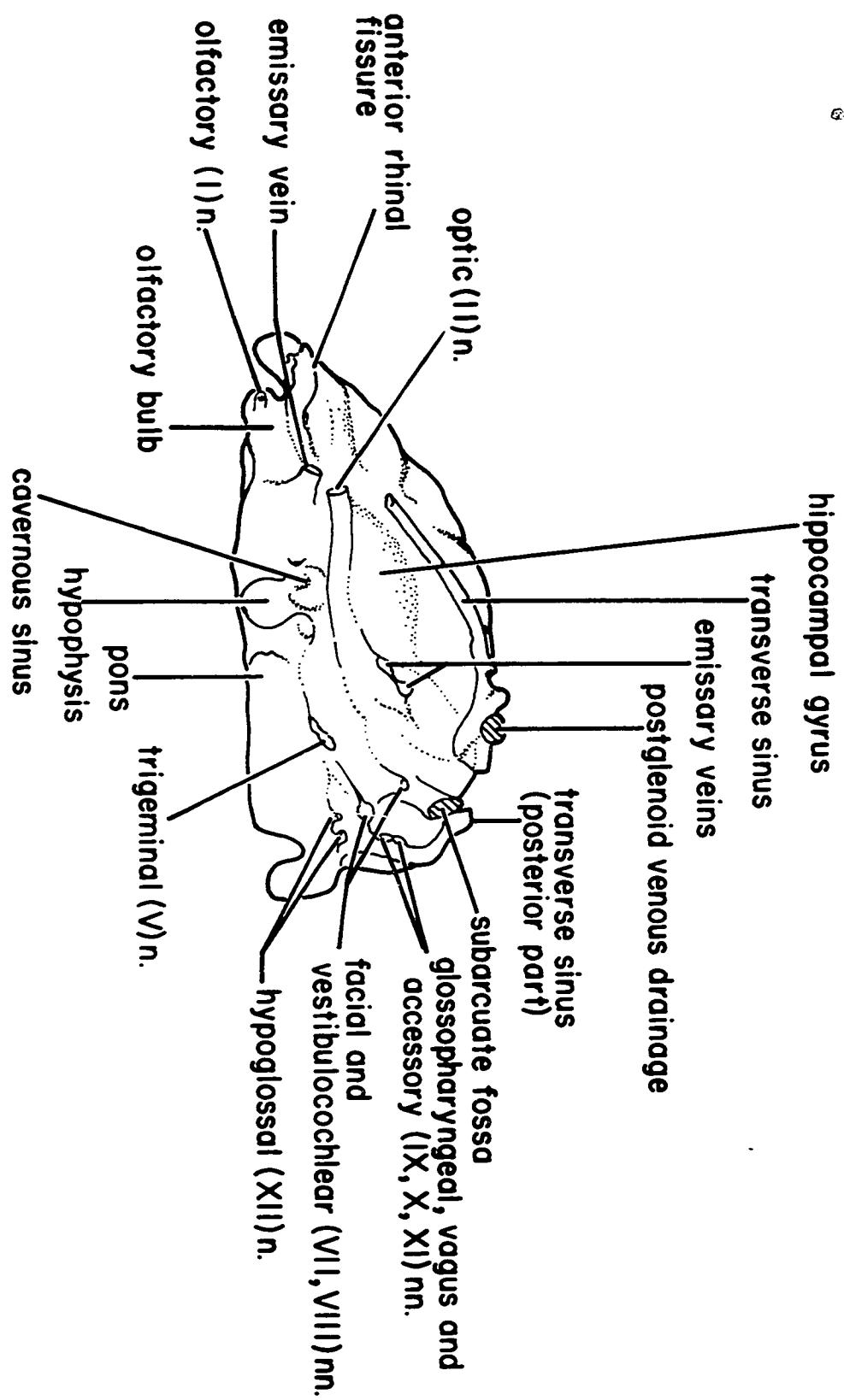


Figure 23

Ventral view of endocranial cast of Archaeolemur
edwardsi (B. M. M 9965), showing cranial nerves.



frontal lobes between his endocast of A. majori and living indriines to the larger size and smaller orbital impressions of Archaeolemur; in B.M. M 9965, 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 forwardly directed orbits than do other prosimians (both more "convergent" and more "frontated", in the terminology of Cartmill [in press]); since 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 erectness during rest and locomotion. Possibly it is correlated with feeding or some other non-locomotory activity.

Radinsky (1968) has suggested that among indriines the proportions of the frontal lobes, which in this group are consistently broader than among 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 inter-orbital 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 dorso-lateral orbital margins. Avahi, on the other hand, shares this feature only to a limited extent, although this is probably due to the fact that,

as a smaller animal and as 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 relative 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 post-orbital 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 dorso-lateral margins of the orbit. The orbits of Archaeolemur are, however, rather more closely approximated than are those of Propithecus and Indri (more so compared to 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 inter-orbital breadth. Propithecus, with relatively the least approximated orbits, has in dorsal view the most rounded anterior contour of the brain (Hill, 1953; Fig. 157). A. 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 Indriidae. Lemur, for instance, has narrow frontal lobes coupled with a broad inter-orbital space. Nevertheless, within 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.

Unfortunately, the area of the visual cortex, whose superficial exposure would have been limited anyway, is obscured on the endocast of B.M. M 9965 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 post-orbital closure. Standing (1908) who, as we have seen, believed in a close relationship between the lemurs and higher primates, attempted to explain the absence of post-orbital closure in Archaeolemur and other subfossil lemurs as follows*:

"In the various families of Monkeys the frontal postorbital 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 brain-case.....

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. 47).

* In 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.

The inadequacy of this explanation for the absence of post-orbital closure is at once apparent when Tarsius 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 post-orbital 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, while 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 post-orbital 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 first suggested by Collins (1921) in connection with the post-orbital bar. According to this hypothesis, closure would serve to insulate the eye from the movements of the musculature in the temporal and infratemporal fossae. Such an interpretation accords well with the fact that the retina in prosimians appears to be 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.

In the words of the latter:

"Failure to develop a fovea in the higher primates (ceteris paribus) would result in a thickening, greater than that found in prosimians, of the retina in the visual region. This would further necessitate increased vascularisation of this area. The combination of thickening of the retina and increased vascularization of this area would almost certainly result in some reduction of visual acuity." (Wolin and Massopust, 1970; p. 26).

The fovea, then, is a correlate of advanced retinal organization; possibly the relationship of stability of the eye to visual acuity is not as 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 early anthropoidea or their immediate ancestors to isolate the eye from the heaving mass in the temporal fossa, while 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, since higher primates are not notably more acrobatic or swift in their locomotion than are many groups of prosimians.

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 to those of some platyrhine 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 B.M. M 9965; 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 naso-frontal fenestrae. In Piveteau's specimen there appears to be a very small sphenoid sinus, but there is no evidence of such a feature in B.M. M 9965.

According to Piveteau (1948), the maxillo-turbinal 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) state that the maxillo-turbinal is doubly-rolled in Lemur, while in other prosimians the element consists merely of a single scroll. It seems unlikely that the maxillo-turbinal of Archaeolemur was doubly-rolled. The functional significance of the maxillo-turbinal is at present hypothetical; Scott (1954, 1958) has suggested a thermoregulatory function of the inferior turbinate processes, particularly the maxillo-turbinal, and relates 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 maxillo-turbinal" (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.

Since 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) has 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 notes 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.

In the absence of better information, then, it seems reasonable to assume, in the light of the evidence of nasal fossa architecture and of the external morphology of the brain, that Archaeolemur possessed a level of olfactory acuity comparable to that of Indri or Propithecus.

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."

(p. 369-370).

This is a dangerous generalisation, since, for instance, the frontal bones in man 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 platyrhine, 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 exception noted above, appears to correlate perfectly with the organisation of the olfactory system, and particularly with the size of the cribriform plate, it provides additional 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 vascularised condition of the anterior surfaces of the maxillae and premaxillae.

The most striking features of the external cranial base in Archaeolemur (as, indeed, of all lemurs with the exception of Archaeolindris, Palaeopropithecus and Megaladapis) is 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. The problem of bullar function is one which has attracted a variety of imaginative theories; for instance, Zavattari (1938a, b), noting that bullar inflation is characteristic of many desert-living mammals, proposed that, in view of the fact that silence is a major characteristic of the desert, the hypertrophied bulla, projecting strongly ventrally from the skull base, was developed to permit an animal to apply the ear region directly to the ground.

In this way, vibrations transmitted through the earth could be picked up and conducted directly through bone. Such a system would, moreover, remain operative while the animal was in a normal sleeping posture.

Also studying 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 Legouix, 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 4,000 Hz. Thus individuals belonging to more sparsely distributed groups are presumably able to hear more attenuated sounds, and therefore to communicate over greater distances. Legouix, Petter and Wisner suggest 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 proportionately lowered resistance) of the air in the middle ear cavity.

While 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 Daubentonias has relatively small bullae), the latter part of Legouix, Petter and Wisner's argument would indeed apply to these animals, since the mechanical consequences of increased bullar size are inescapable. It is clear, however, that more experimental evidence will be 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 organisation, in this animal was no more "advanced" than that of living indriines. Radinsky (1970) has noted, in A.M.N.H. 30007, one feature of the brain in which Archaeolemur majori does appear to be unusually specialised: 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 located in this area; its elaboration might imply an increase of tactile sensitivity in the face of this animal. Alternatively, Radinsky suggests that this complexity may represent an allometric development. However, although B.M. M 9965 belongs to a larger species than does Radinsky's specimen, such elaboration is lacking on its endocast;

but, as has already been pointed out, there is evidently a great deal less sulcal detail in this endocast than in that of A.M.N.H. 30007.

The ratio of brain to body size has been widely used as an index of "encephalisation", or degree of advancement in neural organisation. The most sophisticated of such studies, for instance the works of Stephan and his co-workers (see Stephan and Andy [1970] and references therein) have used serially-sectioned brains of a wide range of primates and other mammals to compare the volumes of the various brain components relative to each other and to those of other forms, but, surprisingly, little information appears to be available on simple brain volume: body weight ratios among prosimians, although such ratios provide the only possible approach to the evaluation of relative brain size in fossil forms. In the case of fossil species, of course, the procedure is rendered extremely approximate by the necessity of estimating body size.

An attempt has been made here to compare the brain volume (98.6 cm^3 ; mean of six individuals): body weight relationship in Archaeolemur majori with the same relationship in various other prosimians and higher primates. Unfortunately, in no case has it been possible, for want of data, to compare brain volume and body weight in a single individual, which renders the procedure even more approximate since both of these characteristics are notoriously variable. A further restriction has been that, although brain volumes have been measured (by filling the braincase

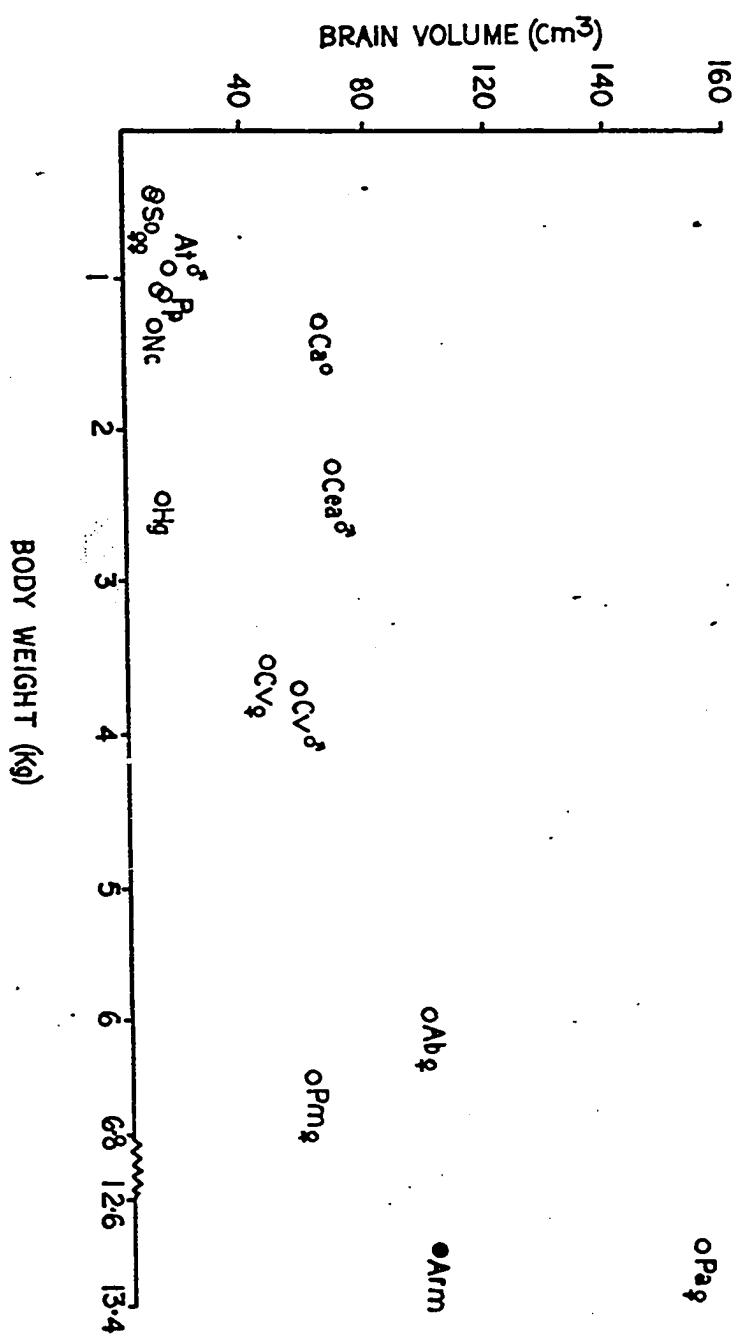
Figure 24

Brain volume plotted against body weight:

Archaeolemur majori and a variety of extant
primates (see text).

Abbreviations:

Ab	<u>Ateles belzebuth</u>
Arm	<u>Archaeolemur majori</u>
At	<u>Aotus trivirgatus</u>
Ca	<u>Cercopithecus aethiops</u>
Cea	<u>Cebus albifrons</u>
Cv	<u>Colobus verus</u>
Hg	<u>Hapalemur griseus</u>
Nc	<u>Nycticebus coucang</u>
Pa	<u>Papio anubis</u>
Pm	<u>Presbytis melalophos</u>
So	<u>Saguinus oedipus</u>



with lead shot, and measuring the volume of shot required to fill it) in a wide variety of primates, data on body weight are entirely lacking for many forms; for instance, there is no record of body-weight available in the literature for any indriine, which is particularly unfortunate because these animals are generally regarded as being the most highly encephalised of modern prosimians.

Lamberton's reconstruction of an almost complete associated skeleton of A. majori shows this animal to have been, post-cranially as in its skull, about the size of a female baboon, and its body weight has therefore been estimated as about 130 kg. Body weights of comparative species have been taken, where available, from Napier and Napier (1967); where a size-range is given, a median value was chosen. Brain volumes and body weights have been plotted against each other in Figure 24, which does reflect the well-known trend towards an absolute increase, but relative decrease, in brain volume with increasing body weight (whereby, for instance, adults of Saimiri, the squirrel monkey, possess relatively larger brains, compared to body weight, than that of man [Schultz, 1969]). The figure also demonstrates the well-known circumstance that prosimians are in general less highly encephalised than are higher primates. Most importantly to the present enquiry, it shows that, compared to a higher primate (a female Papio anubis) of similar body size, Archaeolemur majori possessed a far smaller brain. The closeness of Archaeolemur to other prosimians would probably have been more strikingly demonstrated

had data on body weight made it possible to include extant indriines; three measured specimens of Propithecus verreauxi possessed cranial volumes of 24.0, 26.0 and 39.0 cm³, and one of Indri indri measured 35.0 cm³, which would almost certainly suggest a greater degree of encephalisation than that of other prosimians, although not one comparable to that of any of the catarrhines measured.

Although Figure 24 represents only the roughest of approximations, it does indicate that Archaeolemur majori did not possess a degree of encephalisation in any way greater than that of its closest living relatives; it possessed, in fact, a brain similar in size to that of a platyrhine monkey, Ateles, whose body weight is probably well under half of its own. It is unfortunate that presently available data do not permit a more refined analysis.

Hadropithecus

Piveteau (1956) has published the only description of an endocranial cast of Hadropithecus. This cast (unfortunately one which apparently lacks much detail), lacks, like that of B.M.N.H. 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 in any significant respect 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 Legouix, 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 as well as 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.

Hadropithecus is remarkable for the complete absence of maxillary sinuses. This is probably due to the necessity for strong bony buttressing of the maxillary dentition.

CRANIAL FLEXION

Two aspects of cranial flexion: central kyphosis (or lordosis) of the basicranium, and angulation between splanchnocranum and neurocranium, have long formed a focus of attention among (particularly German) morphologists. Indeed, Hofer (1952) has based his classification of skull types solely on the latter characteristic. The types distinguished by Hofer which are represented among the primates are the following:

1. **Klinorhynchia:** the facial skeleton is directed ventrally with respect to the cranial base.
2. **Orthocrany:** the long axes of the facial and basicranial skeletons are in longitudinal alignment.
3. **Airorhynchia:** the facial skeleton is directed dorsally with respect to the plane of the cranial base.
4. **Klinocrany:** the cranial base and facial skeleton are both flexed ventrally around their junction.

The developmental mechanisms responsible for splanchnocranial-neurocranial angulation have been reviewed by Scott (1953, 1954, 1958), who has identified the agent responsible for the downward and forward growth of the upper facial skeleton as the skeleton as the nasal septal cartilage, which during ontogeny pushes the maxillae out and down, permitting growth at the facial

sutures. In forms possessing long snouts, the forward component of growth exceeds the ventral component; in orthognathous animals the reverse applies. A more recent and more detailed examination of this phenomenon by Enlow (1966) has revealed that during facial growth in monkeys the downward-growing maxillary arch is entirely depository in nature, while in humans the anterior part of this arch is resorptive. Decreased prognathism therefore results in the case of the latter, because while the downward component of growth is maintained, the forward component is not.

Although this mechanism provides a developmental basis for the shortening of the face in Hadropithecus relative to Archaeolemur, it does not explain the adaptive significance of craniofacial angulation. Both Hadropithecus and Archaeolemur show a slight tendency towards klinorhynchy, as do other lemuriformes; the reasons for this are not necessarily related to those producing basicranial flexion, since this generally occurs posteriorly about the sella turcica. No general model for flexion or the lack of it of the facial skeleton about the pre-sellaric basicranial axis has been proposed, although individual explanations have been adduced in a few extreme cases (e.g. for the klinocrany of Tarsius [Spatz, 1968], and for the pronounced klinorhynchy of Daubentonia [Radinsky, 1968]).

Starck (1965) has proposed that slight klinorhynchy represents a primitive condition, and from its general presence among the lemurs, which comprise a wide variety of adaptive types, this would

appear to be the case. Among the subfossil lemurs (apart from, presumably, only Daubentonia robusta, whose cranium is unknown), only Megaladapis demonstrates any marked departure from the pattern of slight klinorhynchy, and a special explanation may be adduced in its case, too. Walker (1967) has shown by analysis of its postcranial skeleton that Megaladapis possessed a mode of locomotion similar to that of the Australian phalangerid marsupial Phascolarctos, the koala bear. This animal is specialised for clinging to vertical supports. Phascolarctos shares with Megaladapis a variety of cranial characteristics, those of most concern here being airorhynchy and an almost completely posteriorly-oriented foramen magnum. This last condition, particularly, is surprising in animals characterised by truncal erectness, but both features can be related to a feeding complex.

Phascolarctos, and, more particularly, Megaladapis, is a heavy, robust animal, far less acrobatic than the indriines, and prone to crop food material with its teeth, rather than plucking it with its hands. Since the hands are primarily engaged in supporting the heavy body during feeding, it would appear to be highly adaptive to maximise the range within which food is accessible to the anterior part of the mouth. The combination of airorhynchy and a backwardly-directed foramen magnum would appear to provide a functional extension of the neck precisely for this purpose. The 90° of flexion required to provide a horizontal orientation of the skull base is provided by flexion in the cervical vertebral column. This might also furnish an explanation for the extreme elongation of the face in Megaladapis,

a condition which superficially seems maladaptive in an animal which clung to vertical supports. It would also go some way towards explaining the long diastemata in the maxillary and mandibular tooth-rows, and the loss of the upper incisors and their presumed replacement by a horny pad; both of these features are characteristic of cropping animals.

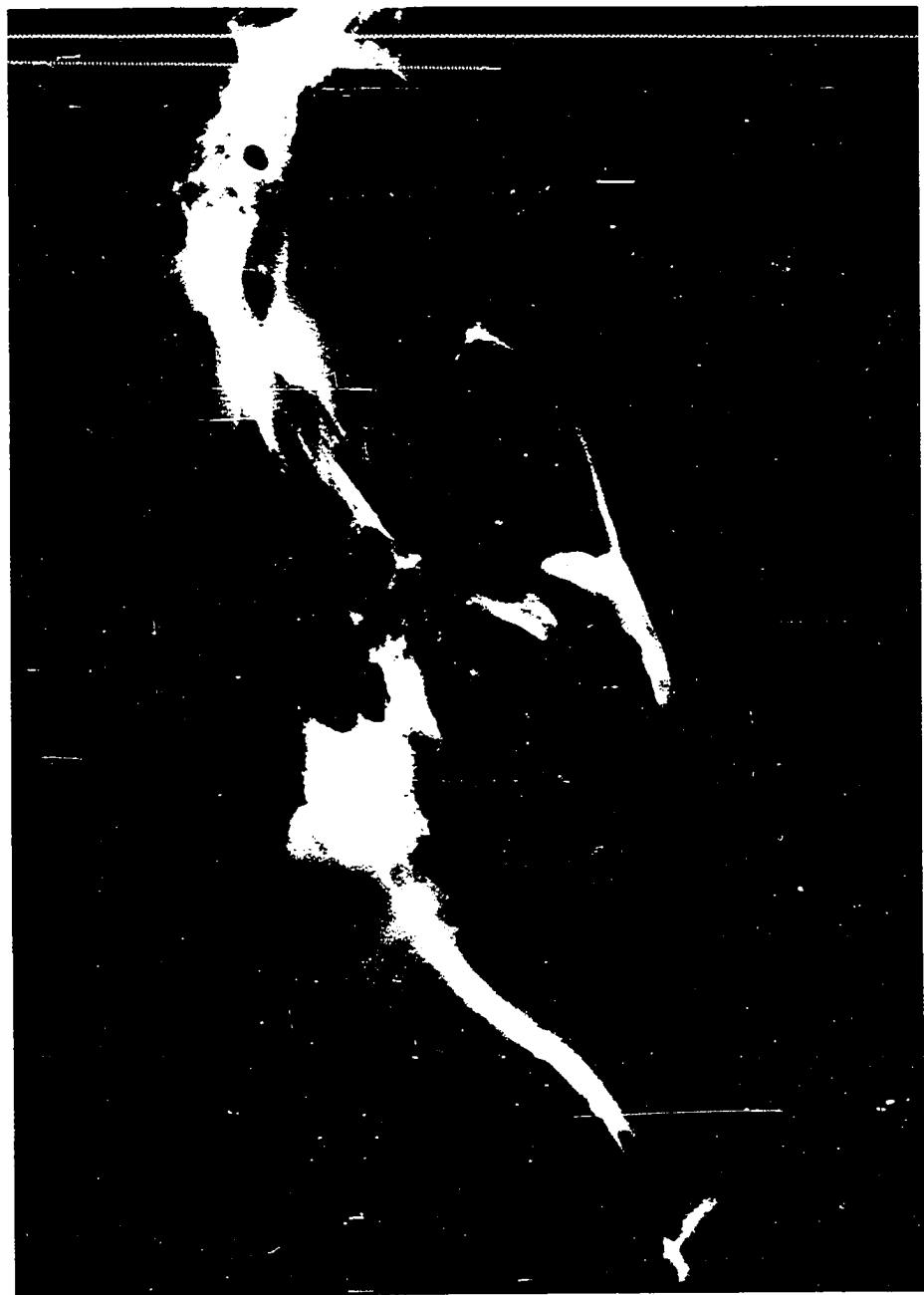
The broad developmental basis for basicranial flexion in mammals is fairly well understood; flexion occurs as result of differential growth at the basicranial synchondroses relative to the development of the bones of the cranial vault. Basicranial kyphosis is a consequence of excessive growth of the membranous bones of the skull roof compared to the growth of the cartilaginous bone of the basicranium; basicranial lordosis is a result of the reverse. By excising the spheno-occipital synchondrosis in infant rats, DuBrul and Laskin (1961) induced the following changes in the crania of experimental animals as compared to controls:

In lateral view:

1. A general shortening and rounding of the skull.
2. Increased curvature of the skull roof.
3. Ventral migration of the nuchal crest.
4. Ventral and rostral rotation of the nuchal plane around inion.
5. Downward and forward movement of the occipital condyles.
6. Posterior rotation of the ventral margin of the cribiform plate.

Figure 25

Radiograph of cranium of Megaladapis edwardsi in lateral view, showing airorhynch condition of the skull.



7. Formation of pronounced kyphosis of the skull base around the hypophyseal fossa.

In basal view:

8. Ventral and anterior movement of the foramen magnum, bringing it beneath the cranial base.
9. Marked shortening of the cranial base.
10. Forward crowding of the auditory bullae, and an increase in the angle between their long axes.

This suite of changes resulted in a more primate-like skull, but also in one reminiscent of those of a number of mammals which have adopted an upright posture. Indeed, DuBrul and Laskin invoked postural erectness as an explanation of basicranial flexion. Under their hypothesis, kyphosis develops to maintain a functional, horizontal orientation of the facial skeleton as the vertebral column becomes vertical. The great populariser of this view was Weidenreich (1924, 1934, 1941), whose initial exposition of it was endorsed by Dabelow (1929), who went so far as to suggest that the expansion of the human brain was a result of flexion which had occurred in response to the adoption of upright posture. But at the same time he suggested that as some animals possessing truncal erectness show lordosis of the skull base, the response to upright posture would only take the form of kyphosis if the orbits were already convergent, since in this case the anterior portion of the skull would of necessity have to flex downwards to achieve the proper facial orientation. Dabelow realised, however, that posture could not serve as a universal explanation of central kyphosis, since owls, despite having an

upright posture and convergent eyes, show basicranial lordosis.

Scott (1958), in perhaps the most extreme variation of the postural view, suggested that:

"the failure of the human face to alter its foetal developmental relationship to the cranium initiated the establishment of fully upright posture and ... this ... was responsible for the later phenomenal development of the human brain." (1958, p. 346-7).

By 1931, however, Dabelow had virtually reversed his argument on the aetiology of basicranial flexion. A pupil of Bolk, and evidently much influenced by the latter's "fetalisationstheorie", Dabelow had found basicranial kyphosis in the foetal stages of animals which never acquire an upright posture, and in later ontogenetic stages of which the flexion is lost. He therefore proposed that bending of the cranial base resulted from disproportionate expansion of the cerebral cortex as compared with the brain stem.

Biegert (1957, 1963) adopted a similar position to Dabelow's. Biegert noted that, if a series of primate skulls is aligned with the cerebral surface of the pre-sellar base held horizontal, the following trends correlate with an increase in central kyphosis:

1. an increasingly horizontal orientation of the nuchal plane;
2. a forward movement of the foramen magnum; and
3. a slight rostral shift of the occipital condyles.

He attributed the flexion to a "rolling-up" of the neurocranium, and rejected the proposition that any of the associated characteristics could be due to upright posture:

"Comparative investigations, considering the entire organisation of the organism, conclusively show that between the manner of locomotion on the one hand, and the occipital condyle position, the orientation of the foramen magnum and the condition of the base of the skull on the other hand, no causal relationship whatever exists. The kind of locomotion of fossil primates can be determined only from the condition of the post-cranial skeleton." (1963, p. 121).

The case of Megaladapis, just discussed, provides striking corroboration of this last assertion.

Biegert, recognising practical objections to a scheme linking the degree of cranial base kyphosis solely to neocortical enlargement, admits certain modifying influences, primary among which is the size-relationship between masticatory apparatus and neurocranium:

"A masticatory apparatus which is large relative to the brain reduces the rolling-up of the neurocranium...compared with the brain the masticatory apparatus is affected to a greater degree by an increase in body-size...Differences in skull topography, therefore, can be expected

in consequence of differences in body-size alone." (1963, p. 122).

However:

"This principle can be circumvented if a specialised expansion of the neopallium... or a specialised reduction of the masticatory apparatus occurs." (1963, p. 122-3).

Similarly, the disposition of the orbits plays a role in determining the condition of the skull base. If the eyes are large relative to the neurocranium, and are also closely approximated, then:

"The planum sphenoideum approximates in its position and form the niveau of the orbital roofs. The pre-sellar basal skull becomes elevated in its entirety, with a predominant elevation of its anterior portion." (1963, p. 127).

Dabelow's hypothesis, with Biegert's modifications, comes far closer to being a valid explanation of basicranial flexion than does the postural theory. Although in the case of Archaeolemurinae both models might be admissible the latter

is vitiated by Indriinae, whereas the former is not.

Neither Archaeolemur nor, insofar as can be told from available radiographs, Hadropithecus, shows any more than a very slight central kyphosis; the brains of these two animals, as we have seen, show no cerebral expansion over the condition seen in extant indriines. What we see in the archaeolemurines is probably a very generalised condition, despite the expansion of their musculature (although this expansion is probably not "specialised" in Biegert's sense), departures from which may be explained in terms of special functional requirements, for instance brain expansion.

ECOLOGICAL RELATIONSHIPS OF THE ARCHAEOLEMURINES

Walker (1967a) has demonstrated that in its postcranial skeleton Archaeolemur possesses many of the features listed by C. Jolly (1963) as characterising 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 terrestrialism 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 considers that their relative gracility and elongation indicates a greater commitment to terrestriality. It is very interesting in this context that, as Lamberton (1937) has pointed out, the forelimb of Hadropithecus was probably longer than the hindlimb. Among highly terrestrial primates, such a configuration is unique (C. Jolly, 1965) to the Pleistocene relatives (subgenus Simopithecus) of the present-day gelada baboon, Theropithecus.

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 characterise early hominids, and Jolly (1970) has utilised them in constructing a model of hominid differentiation. Jolly has summarised these features in tabular form, and Table 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, 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, 1965). Since the present environments of Papio and Theropithecus are therefore somewhat atypical as far as the conditions in which their feeding adaptations evolved are concerned, it is important to recognise this.

Table 11. Common Characteristics of early hominids, Theropithecus and Hadropithecus. (Modified from Jolly, 1970).

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

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 since 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 comparable with those of Hadropithecus), and while 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 resemblance 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 (1970) 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 which is too small because it lacks the exercise which would promote its full development would be a functional liability. There is, in Hadropithecus, apparently no specialised 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) tried to explain canine reduction in Hadropithecus by introducing a related suggestion which has also been applied to hominids:

"Peut-être...ces Lémuriens suppléaient-ils, par l'intelligence et la ruse, à la faiblesse de leurs armes défensives, ce qui expliquerait le grand développement de leur boite 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 probably does not exist.

Molarisation 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 mesiodistal 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 since, 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 far 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 provides.

Gingerich (1970, ms) has recently proposed that the primary component of occlusal force in Papio (and this model would apply as well to Theropithecus) is provided by the contraction of the ipsilateral temporalis, which exerts a force tending to translate the condyle backwards. Since (subject to the conditions mentioned earlier) a sliding condyle exerts no reaction force at the jaw joint,

this system is mechanically highly efficient. In Theropithecus, therefore, 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 those of Papio are correlated with the shortness of the animal's face rather than being due, as Jolly suggests, to increasing the moment arm of the masseters around the jaw joint and adding the pull of the temporalis to that of the masseters.

Since 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 them both, i.e. the teeth and their immediate supporting structures. As already remarked, 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 specialised 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, but, 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. 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 extremely different prior condition, precisely to fulfil such functions, since grooming teeth, such as the archaeolemurine ancestor probably possessed, are totally unsuited to any other function.

Possibly the large incisor teeth of Archaeolemur were used for cropping, or for dealing with larger food-objects for coping with which the premolars possessed insufficient clearance. Modern

lemurs generally reduce food items in the first instance by inserting them manually, from the side of the mouth, between the premolars, which are then used to cut them. This is presumably because they possess grooming incisors.

With what kinds of vegetable material might the highly specialised premolars of Archaeolemur have been equipped to deal? Such items as stems, twigs and hard-skinned fruits are obvious possibilities, but in the case of the first two of these, one would expect to find greater wear on the molars than actually occurs, due to the need for strong comminution of such tough, fibrous substances prior to ingestion. One would 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 preparation prior to swallowing. Another type of vegetable product of which the same observation might be made is the tamarind, or "kily" pod (Tamarindus indica), which is a dietary staple of the lemurs in the gallery forest at Berenty, in the south of Madagascar (A. Jolly, 1966). However, the tough outer husk of the kily pod does not appear to present any obstacle to Lemur or Propithecus, whose masticatory apparatuses are much less robust than was that of Archaeolemur.

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, while 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 lops 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 lops of cercopithecines presumably reflect their more generalised, more frugivorous diet. The condition seen 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 generalised 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, since 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 Lambert'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, p. 44).

PARALLELISMS BETWEEN ARCHAEOLEMURINAE
AND HIGHER PRIMATES

The view has pervaded much of the literature on 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 (1908), 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" * common ancestor of the lemurs and Anthropoidea.

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

* Standing used this term indiscriminately to describe all 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 the cheirogaleines); post-orbital closure is absent. The 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 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 archaeolemurines most reminiscent of those of higher primates, having adapted towards a powerful masticatory mode, although, as we have seen, it arrived at this condition via a very different route.

The prosimian, and particularly indriine, affinities of the brain of Archaeolemur are very clear. Clark lists the following features as characterising 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 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 to those of one or two platyrhine genera, they are nevertheless large relative to those of most platyrhines and all catarrhines.

The cranial sensory organs of higher primates are characterised 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 organisation, and the turbinals 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 towards the condition 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."

Why, then, did the lemurs, which appear to have occupied a range of econiches not altogether dissimilar to those occupied by catarrhines, not evolve towards a condition more reminiscent of the higher primates? Cartmill (in press) implies 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 believes, 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 organisation of the brain 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 towards 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 organisation.

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 specialised of the lemurs possessing a prosimian level of neural organisation, although some extant lemurs are admittedly more encephalised than others. Perhaps isolated Madagascar, with its very restricted mammalian fauna, failed to provide an impetus towards a more advanced level of organisation 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 towards the catarrhine evolutionary condition took place widely over Eurasia and Africa.

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PLATE SECTION

PLATE 1

Lateral view of articulated cranium and mandible
of Archaeolemur majori (B. M. M. 7374;
Andrahomana). Below: stereophotograph of same.
Natural size.

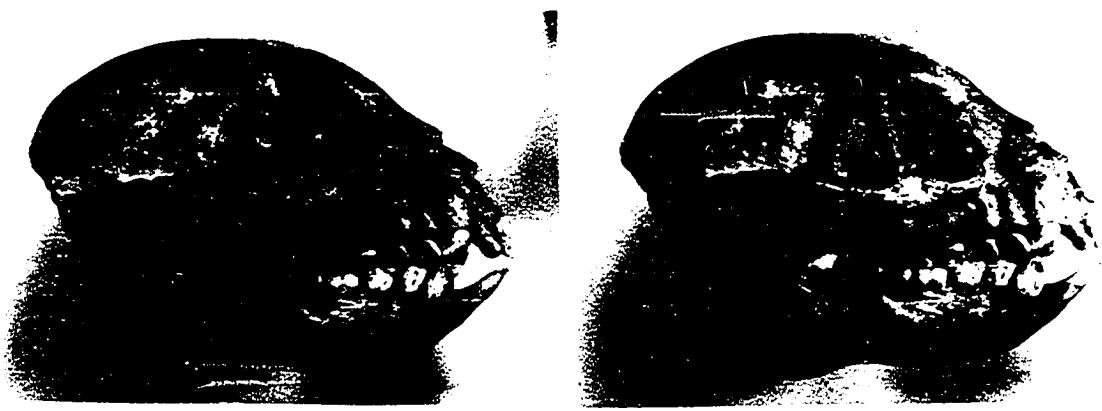


PLATE 2

Lateral view of articulated cranium and
mandible of Archaeolemur edwardsi (B. M.
M. 9909 and 9910; Ampasambazimba).

Below: stereophotograph of same.

Natural size.

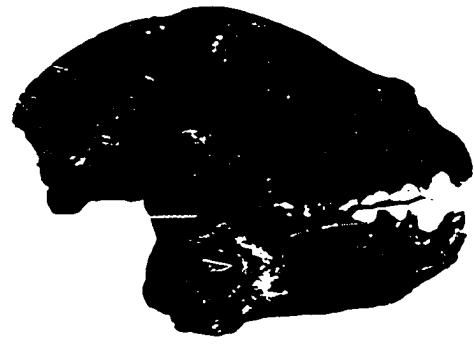


PLATE 3

Above: lateral view of cranium of Archaeolemur majori (A. M. 311027; Tsiravé).

Below: lateral view of cranium of Archaeolemur edwardsi (B. M. M 9965; Ampasambazimba).

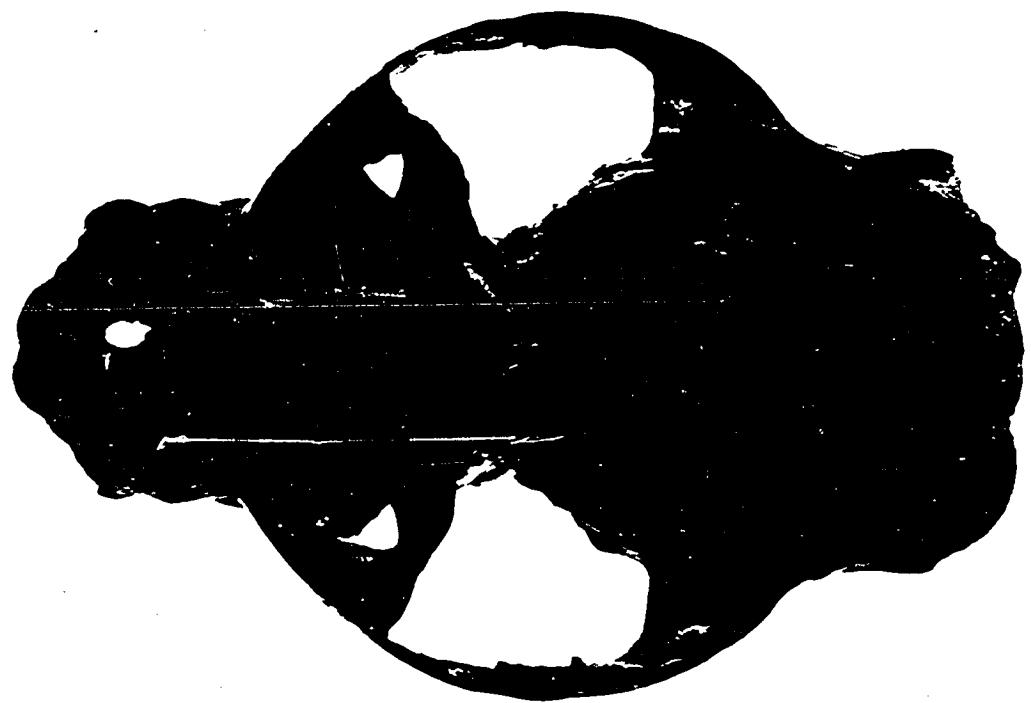
Natural size.



PLATE 4

Above: dorsal view of cranium of Archaeolemur majori (A. M. 311027; Tsiravé).
Below: dorsal view of cranium of Archaeolemur edwardsi (B. M. M 9909; Ampasambazimba).

Natural size



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PLATE 5

Above: ventral view of cranium of Archaeolemur majori (A. M. 311027; Tsiravé).

Below: ventral view of cranium of Archaeolemur edwardsi (B. M. M 9909).

Natural size.

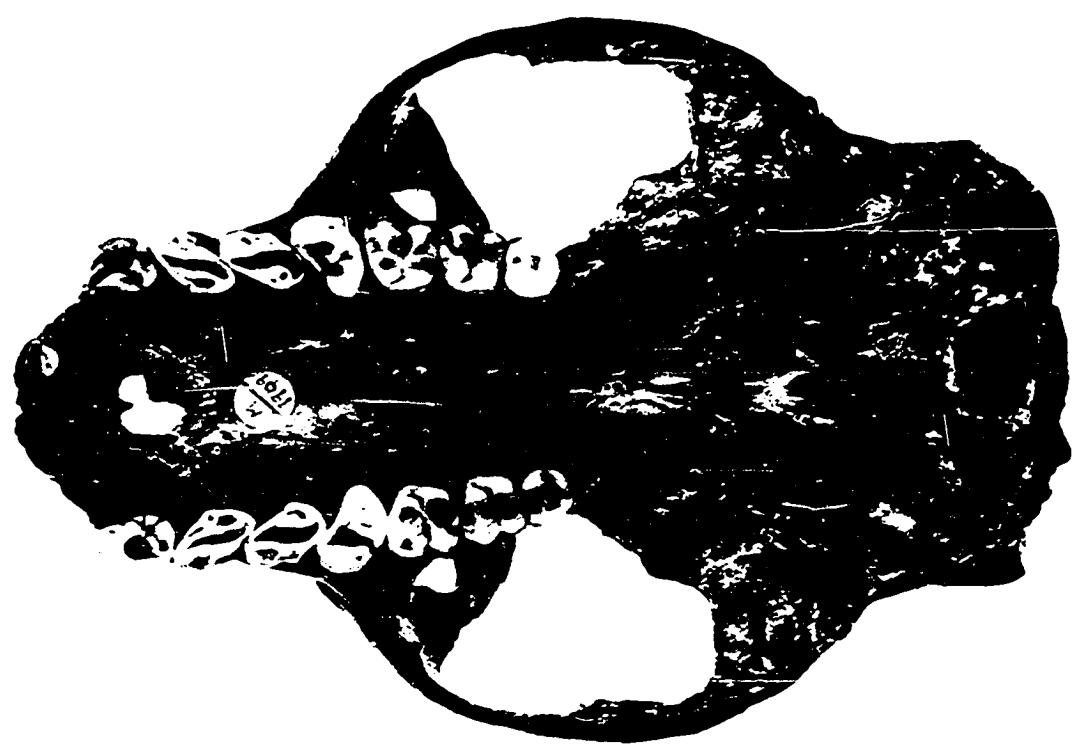


PLATE 6

Facial views of the three archaeolemurine species.

Above left: Hadropithecus stenoqnathus (the
Tsiravé cranium; A. M. uncat.).

Above right: Archaeolemur edwardsi (B. M. M
9909; Ampasambazimba).

Below: Archaeolemur majori (A. M. 311027; Tsiravé).

Not to scale



PLATE 7

Lateral (above) and medial (below) views of
the mandible of Archaeolemur majori (B. M.
M. 7374; Andrahomana).

Natural size.

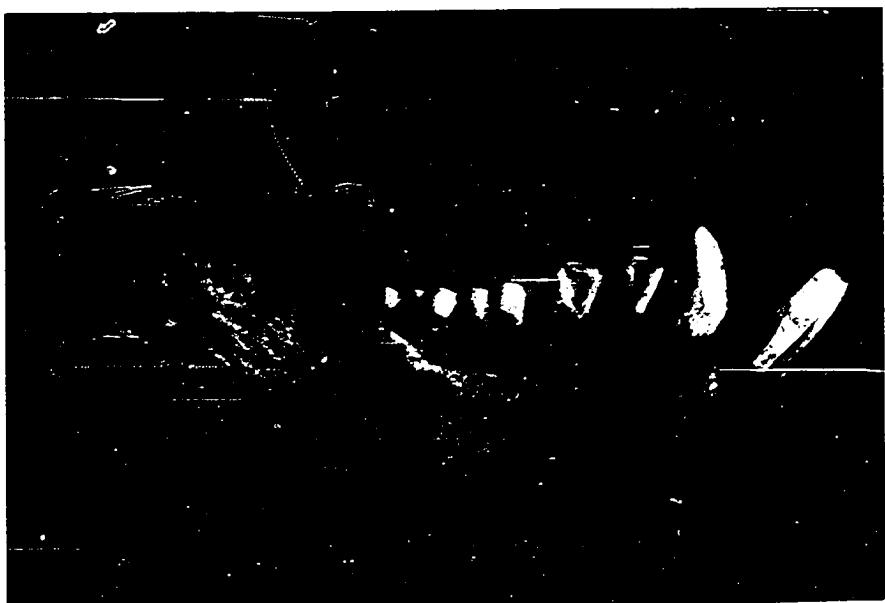


PLATE 8

Above: lateral view of auditory region of
the Tsiravé cranium of Hadropithecus
stenognathus (A. M. uncat.).

Below: ventral view of the auditory region
of Archaeolemur majori; most of the bulla
has been broken away (A.M.N.H. 30007).

Stereophotographs; not to scale.



PLATE 9

Comparison of the mandibles of Archaeolemur
and Hadropithecus (dorsal view).

Left: Archaeolemur sp. (probably A. majori;
A. M. uncat., no provenance).

Right: Hadropithecus stenognathus (V.N.H.M.
1934 IV 1/1 and 1/2; Andrahomana).

Natural size.



PLATE 10

Lateral view of the Tsiravé cranium and mandible
of Hadropithecus stenoqnathus, articulated.

(A. M. uncat.). Natural size.

Below: stereophotograph of same.



PLATE 11

The two crania of Hadropithecus stenognathus
in lateral view.

Above: the Tsiravé cranium (A. M. uncat.).

Below: the Andrahomana cranium (V. N. H. M.
1934 IV 1).

Both natural size.



PLATE 12

The two crania of Hadropithecus stenognathus
in dorsal view.

Above: The Tsiravé cranium (A. M. uncat.).

Below: The Andrahomana cranium (V. N. H. M.
1934 IV 1).

Both natural size.

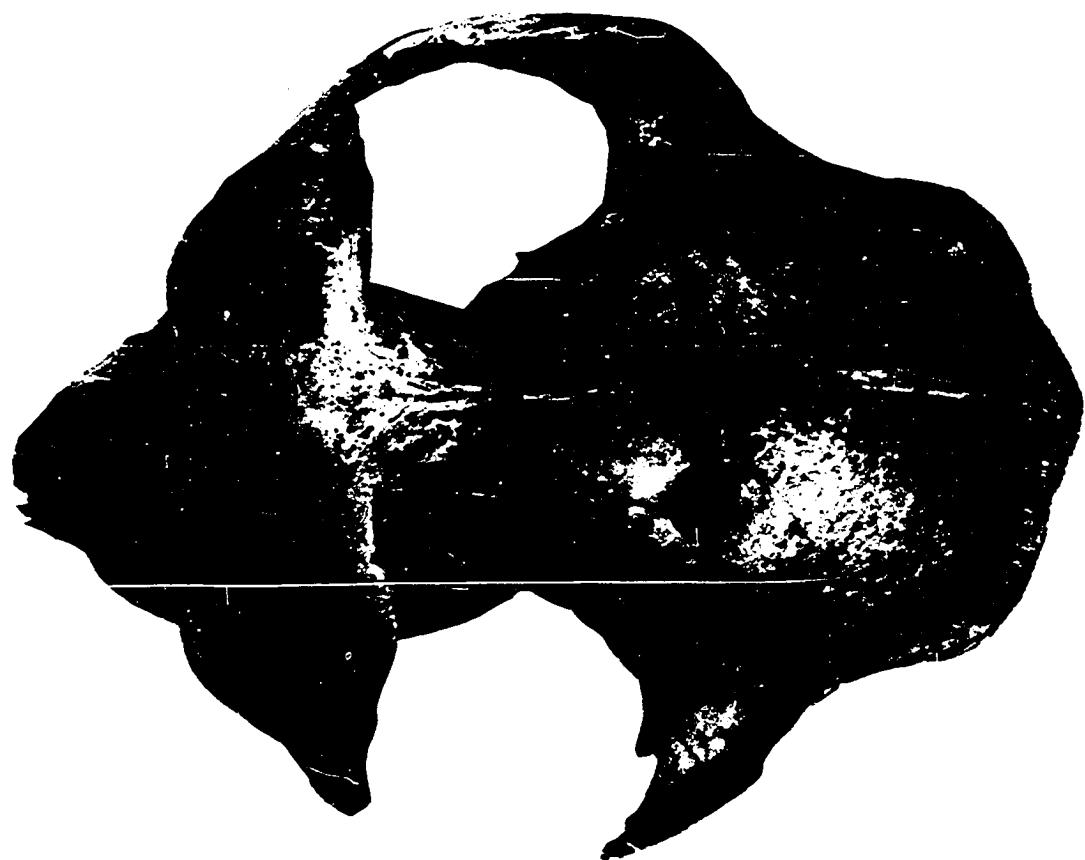


PLATE 13

The two crania of Hadropithecus stenognathus
in ventral view.

Above: the Tsiravé cranium (A. M. uncat.).

Below: the Andrahomana cranium (V. N. H. M.
1934 IV 1).

Both natural size.



PLATE 14

Stereophotographs of maxillary specimens of
Hadropithecus stenoognathus.

Above: V. N. H. M. 1934 IV 4a and 4b (Andra-
homana).

Center: V. N. H. M. 1934 IV 2 (Andrahomana),
occlusal view.

Below: V. N. H. M. 1934 IV 2 (Andrahomana),
lateral view.

All natural size.

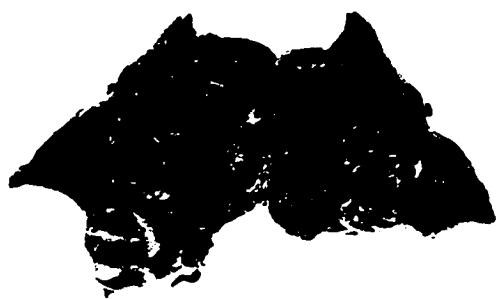
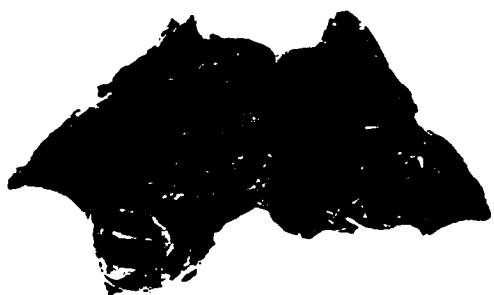


PLATE 15

Mandibular specimens of Hadropithecus stenognathus.

Above left: the Tsiravé mandible (A. M. uncat.).

Above right: V. N. H. M. 1934 IV 1/1 (Andrahomana).

Below (left pair): Stereophotograph of V. N. H. M.
1934 IV 3 (Andrahomana).

Below (right pair): Stereophotograph of V. N. H.
M. 1934 IV 2/1a (Andrahomana).

All natural size.

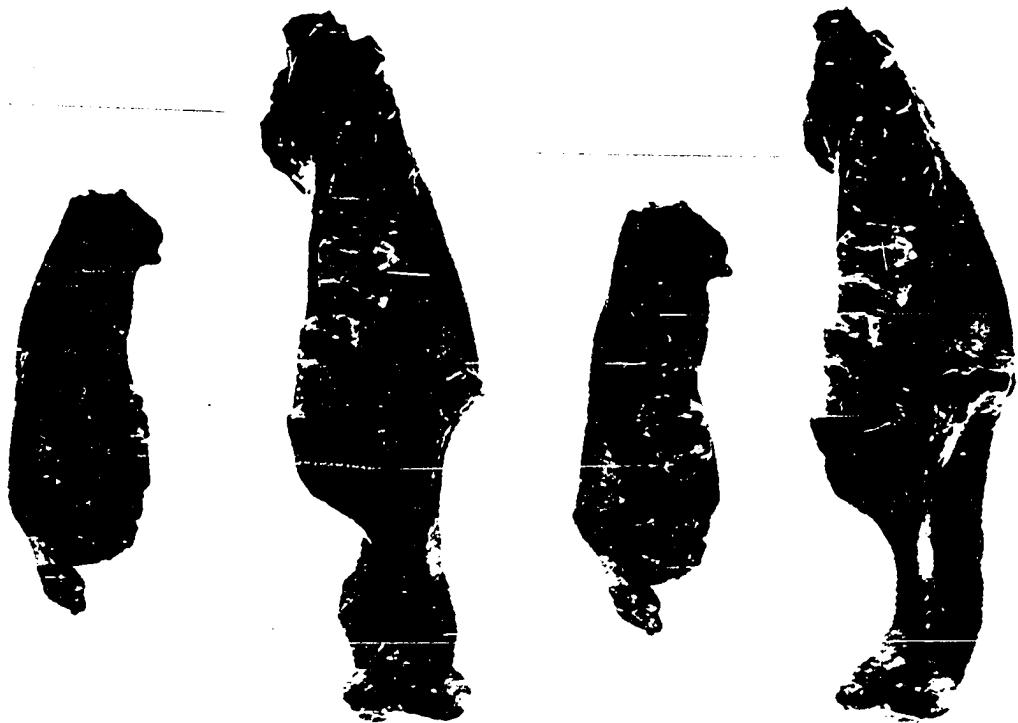
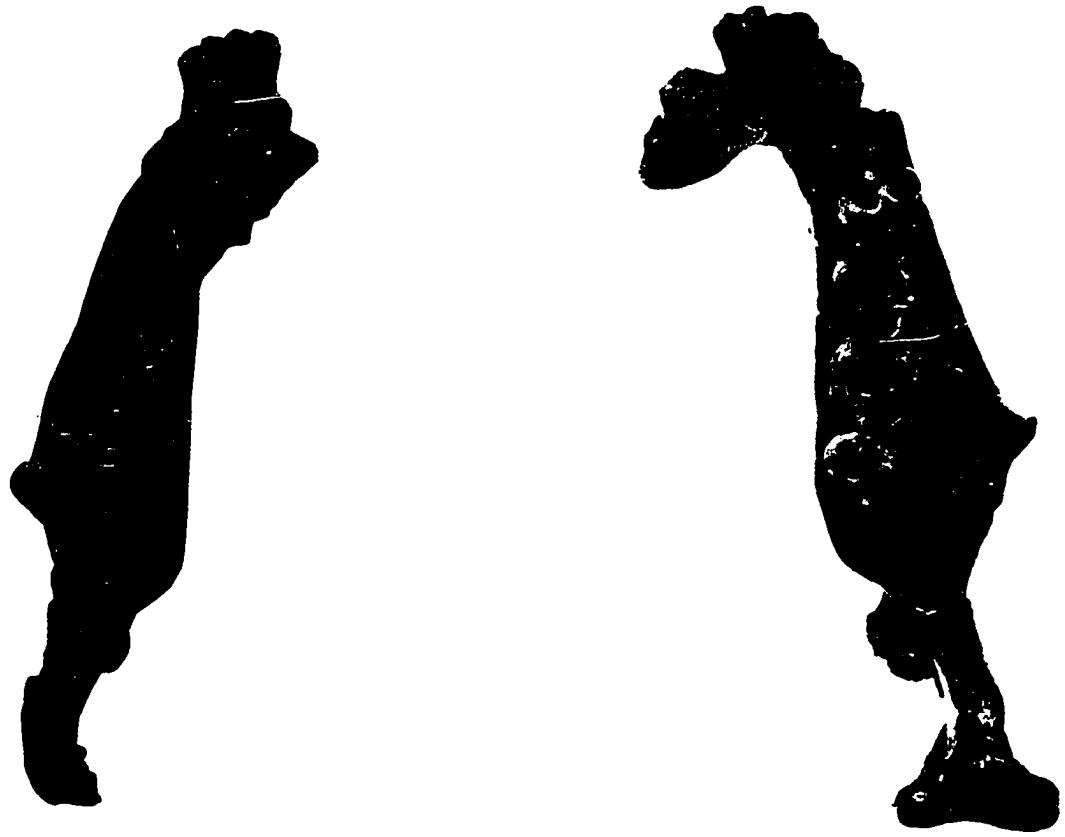


PLATE 16

Lateral views of the three most complete
mandibular specimens of Hadropithecus
stenognathus.

Above: the Tsiravé mandible (A. M. uncat.).

Center: V. N. H. M. 1934 IV 1/1 (Andra-
homana; the holotype of the genus and species).

Below: V. N. H. M. 1934 IV 2/1a (Andra-
homana).

All natural size.



PLATE 17

Medial views of the three most complete
mandibular specimens of Hadropithecus
stenognathus.

Above: the Tsiravé mandible (A. M. uncat.).

Center: V. N. H. M. 1934 IV 1/1 (Andra-
homana).

Below: V. N. H. M. 1934 IV 2/1a (Andra-
homana).

All natural size.

