REVIEW LECTURE

ADAPTIVE RADIATION AND BEHAVIOUR OF THE MALAGASY LEMURS

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[Plates 34 to 38]

The systematic distribution of behavioural characters in lemurs can be analysed using the same techniques as for anatomical characters, without considering physiological mechanisms. Behaviour and structure are usually interdependent (functional morphology), so it follows that behavioural features probably evolve hand-in-hand with morphology. Behavioural and morphological characters generally exhibit the same patterns of systematic distribution, though it is not yet clear whether evolution typically operates through selection of inherited behaviour patterns, or through indirect canalization of behaviour which is dependent upon particular structures.

The extant Malagasy lemurs and their recent subfossil relatives must be considered together as an integrated lemur fauna, which has undergone great reduction over the last few thousand years. The lemurs appear to form a natural group with the Afro-Asian loris/bush-baby group, certain Miocene lorisoids from East Africa ('*Progalago* group') and the Eocene Adapinae (Northern Europe) and Notharctinae (North America). This natural group can be referred to as the Strepsirhini. Simpson's classification (1945) implies that these Strepsirhines are closely related to the Tupaiidae (tree-shrews), and to the fossil Anagalidae and Plesiadapidae. Inclusion of these groups in the Order Primates is regarded here as superfluous, and discussion is restricted to the Strepsirhini, as defined above. It is suggested that the Malagasy lemurs and the Afro-Asian bush-babies and lorises had a common origin in Africa (lemur/loris stock), and that this ancestral stock had an earlier common origin with the Adapinae and Notharctinae of the Northern continents.

The geographical distribution of the lemurs within Madagascar is examined, and seven basic zones of species distribution are identified. Each of these zones has distinctive climatic and vegetational characteristics which can be expressed on a 'climagramme' incorporating Emberger's pluviothermic quotient. Major physical barriers can be recognized along all of the boundaries between the present distribution zones. A model is suggested, in which climatically and physically demarcated zones of this kind can operate as agents for geographical isolation and speciation. Occasional emigration from zone to zone could produce a dynamic situation in which ecological competition between closely related species would favour a pattern of adaptive radiation with individual species becoming increasingly specialized for distinct ecological niches.

In order to discuss the origin of the ancestors of the Malagasy lemurs, the relationship between Madagascar and other land-masses is examined. Although most authors agree that emigration from Africa has provided the main basis for biological invasion of Madagascar, there has been some controversy about the pattern of spatial relationships between Madagascar and Africa over time. Some authors (notably Simpson (1943) and Millot (1952)) have favoured a 'stable continents' hypothesis, and this has led to a concentration of interest on the Northern continents as the seat of Primate evolution. One outcome of this has been the suggestion that lemurs and lorises are separately derived from Northern European Adapinae. New geophysical evidence indicates that the 'stable continents' hypothesis is virtually untenable, and that continental drift theory provides the only coherent explanation of terrestrial evolution. This shifts the emphasis on Primate evolution to the Southern continents (notably Africa), and it seems likely that the lemurs and lorises had a common ancestry in Africa during the early Tertiary (for which no fossil evidence is available). One further consequence of drift theory is the observation that the Mozambique Channel has probably increased in width throughout the Tertiary, and that emigration of mammals to Madagascar from Africa has become increasingly improbable.

Having established that Madagascar was probably invaded by a very small number of ancestral lemur species, which subsequently underwent adaptive radiation within the island, the systematic distribution of behavioural characters among living forms is examined. Attention is given to annual and daily patterns of activity, nesting patterns, diet (and some correlated dental features), locomotion (and some skeletal features), reproduction and social behaviour. In each case, it is shown that the Mouse Lemur group (Cheirogaleinae) and the Indri group (Indriidae) are internally cohesive in their characteristic behaviour patterns. The True Lemur group (Lemurinae) exhibits a wide range of behavioural adaptation, which is paralleled by equivalent morphological diversity. Behaviourally, the Aye-aye (*Daubentonia*) is as distinct as it is in morphological terms.

By a process of induction, it is established that the behaviour of the ancestral lemurs was probably quite similar to that now exhibited by some Cheirogaleinae (particularly *Microcebus*), although living species in this group exhibit a number of probable specializations away from the ancestral condition. This conclusion is not surprising, since the Cheirogaleinae are also the least specialized of the lemurs in morphological terms. However, it is significant that the same ancestral pattern can be deduced for the loris/bush-baby group. Thus, the common ancestor of the Southern Strepsirhini (lemurs + lorises) was probably a small omnivorous form feeding primarily on insects, fruit and sap. The sap would have been gathered with the 'tooth-scraper' in the lower anterior dentition. There was probably a weakly developed spatial system of social organization, with central males of a population nucleus having access to females (a small number to each male), and peripheral males living on the fringe of each population. Competition between males would have provided a basis for selective mating and migration of peripheral males between population nuclei would have ensured exogamy. Extension of Walker's (1967) exemplary study of prosimian locomotion shows that the ancestral lemur/loris probably exhibited hindlimb dominated locomotion based on a grasping function of the extremities (primarily developed in the pes). The ancestral lemur/loris was probably nest-living, giving birth to – and caring for – a small number of well-developed infants after a relatively long period of gestation. There is some evidence that this ancestral form was nocturnal in habits, and it seems likely that the ancestral species which invaded Madagascar would have had a well-developed seasonal pattern of activity. Arboreal adaptation, the attachment to a nest, the small body size, and the ability to survive an adverse period of poor food supply (e.g. on the basis of fat reserves) would have fitted the early lemurs for a period of chance emigration across the Mozambique Channel on natural rafts of vegetation. Such rafts could have been formed from trees and other vegetation torn from forests lining rivers (e.g. the River Zambesi) on the east coast of Africa.

Since the common ancestor of the lemurs and lorises was not very far removed from the ancestral Primate stock, many of the characters listed above must have been to some extent developed in the earliest Primates. This provides further evidence for the hypothesis that tree-shrews, anagalids and plesiadapids are quite separately derived from the ancestral Eutherian mammal stock, and that these three groups have no specific relationship to the Order Primates.

INTRODUCTION

The primary aim of this paper† is to integrate comparative data on the behaviour of the extant Malagasy lemurs with certain information on their morphology, ecology and geography. In so doing the attempt is made to draw some tentative conclusions about their evolution. The approach is essentially pragmatic; no attention is paid to mechanisms of causation and control of behaviour. The procedure used is fundamentally the same as that followed in classical comparative anatomy: a preliminary stage of *description* is followed by theoretical *interpretation* of the systematic distribution and variation of individual, species-specific components ('characters'). When this procedure is applied to behaviour, however, certain difficulties arise. The major difficulty is inherent in the description of behavioural 'characters', since this involves consideration of processes, rather than structures, so that it is impossible to store the actual observed material in collections for future reference. (Still photographs, film records and tape-recordings provide a partial – and extremely time-consuming – solution to this problem). Observations of behaviour should also ideally be made under natural conditions, since species-typical behaviour patterns are fully meaningful only under those conditions and since it is unlikely that an animal will exhibit a complete, unimpaired behavioural repertoire under an appreciably different set of conditions. In particular, interpretation of the *evolution* of behaviour must be made with respect to a set of natural environmental conditions, since the survival value of each

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† An expanded version of the lecture given on 9 April 1970, incorporating observations from a subsequent field visit in September/October 1970 and including reference to a number of essential new publications.

behaviour pattern is relevant to particular aspects of the animals's environment (e.g. climate, food, shelter, predation pressure, locomotor substrate, etc.). It must be remembered, however, that environmental features may have changed following the evolution of particular behaviour patterns, and that the present environment may not provide all the answers to questions regarding evolution of the behavioural repertoire of an animal species.

Thus, general field studies of behaviour under natural conditions are particularly valuable. In view of the difficulties of recording behavioural events, confirmation of the observations of previous authors is in itself desirable. A good general description of the behaviour of the Malagasy lemurs under natural conditions has been provided by Petter (1962*a*, *b*, *c*), and the field study leading to this present publication (July to December 1968) was conducted in order to confirm and extend Petter's accounts in various respects. Thirteen of the 19 recognized species of Malagasy lemurs (see p. 308) were observed at some time during the field study, permitting behavioural observations of a very general kind, and a detailed study was made of the behaviour of the Lesser Mouse Lemur (*Microcebus murinus*) (Martin 1972). The Lesser Mouse Lemur was selected as a subject for study because the nocturnal lemurs have been relatively little studied, and because this species seems to have retained a large number of primitive morphological characteristics. Recent publications have provided fairly detailed accounts of the behaviour and ecology of a number of individual lemur species, and there is now sufficient information to provide a provisional synthesis. Detailed information is provided by the following sources:

Charles-Dominique & Hladik (1971): Sportive Lemur (*Lepilemur mustelinus*)
Jolly (1966): Ringtail (*Lemur catta*) and Sifaka (*Propithecus verreauxi verreauxi*)
Petter & Petter-Rousseaux (1967): Aye-aye (*Daubentonia madagascariensis*)
Petter & Peyrieras (1970): Gentle Lemur (*Hapalemur griseus*)
Petter, Schilling & Pariente (1971): Fork-crowned Lemur (*Phaner furcifer*) and Coquerel's Mouse Lemur (*Microcebus coquereli*)

A word should be said about interpretation of the systematic distribution of behavioural characters. Complex problems arise because of the integration of endogenous mechanisms (with an hereditary basis) and mechanisms permitting direct accommodation to environmental factors (e.g. through conditioning). Few people would deny that there is *some* genetic contribution to behaviour (be it only in broad determination of the structure of the nervous system), and presumably nobody would claim that all behaviour is immediately genetically controlled. But problems arise in establishing the manner in which hereditary factors and the environment interact to produce each behavioural character. On the one hand, it has been claimed by Lorenz (1965) that some observable behavioural characters ('innate motor patterns') do not require plastic adaptation to the environment during the development of the individual animal, since the process of adaptation has taken place during evolution of the species. This does not necessarily imply that the natural environment does not participate in individual development of any given behavioural character; but the behavioural end-product should be the same in all members of each age/sex class of a species. It is the species-typical *end-product* which has been subjected to natural selection. This position has been criticized by Lehrman (1953) on the grounds that it is impossible to exclude the participation of learning processes in the development of any given behaviour pattern, and it has become fashionable to regard 'innate motor patterns' as dubious extreme cases on a spectrum running from totally fixed behaviour patterns to those which are essentially plastic. The net result of this controversy has been a drawn-out, and somewhat unrewarding, discussion about the meaning of the term 'innate' and its usefulness in description and interpretation of behaviour. However, until we know far more about the operation of neurophysiological mechanisms underlying overt behaviour, analyses of the term 'innate' cannot be particularly fruitful.

The position taken by Lorenz on comparative behavioural studies is best illustrated by the following quotation (Lorenz 1950: p. 237):

> 'With the discovery of phyletic homology of behaviour patterns the study of behaviour may be said to have grown out of the purely idiographic stage of its development and to have reached the second systematic stage. This discovery was of the greatest importance in several respects. Not only could innate behaviour patterns be used as very valuable and certainly very welcome new taxonomic characters in ascertaining the phyletic relations between allied forms, but the special form of certain innate behaviour patterns became accessible to a causal explanation based on the understanding of their phyletic origin. Both of these facts, though certainly important enough in themselves, attain an even greater secondary importance by proving the great independence of the behaviour patterns in question, as *particulate elements* of behaviour. Thus not only the well-tried method of comparative morphology became applicable to the study of behaviour, but it also became possible to *isolate* a very distinct physiological process as an independent constituent of behaviour and to study it separately, in a legitimate departure from the otherwise obligatory method of correlative analysis on a broad front. Therefore, physiological analysis followed closely on the heels of the comparative and systematic study of the elementary process in question.'

One can thus distinguish between the comparison of behavioural components with a view to considering their evolution (the 'comparative anatomy' of behaviour in Lorenz's words) and inference of the physiological basis of these components. It is interesting to note that comparative anatomists have rarely concerned themselves with the physiological basis for the development of observable morphological characters, in so far as there is a clear correlation between evolutionary proximity and anatomical similarity. Early investigators in the field of comparative behaviour (such as Heinroth and Whitman) drew attention to a correlation between the systematic distributions of species-specific behavioural characters and species-specific anatomical characters, and this point has been repeatedly confirmed in recent years. It is therefore reasonable to assume that at least some behaviour components are dependent upon evolutionary modification and determination, in the same way as morphological characters. The main controversy about evolutionary interpretations of behaviour patterns has centred around interpretation of the ontogenetic basis of behaviour, involving *induction* from the observed facts. However, it is sufficient for the following analysis to note that species-typical patterns of behaviour do exist, and that these patterns (at least in some cases) exhibit the same systematic distribution as anatomical characters. If the latter have been determined by evolution through natural selection, then the same must apply (directly or indirectly) to behavioural characters with the same systematic occurrence.

From this pragmatic standpoint, it is sufficient for consideration of behavioural evolution within a group of animals (e.g. the Malagasy lemurs) to establish, through careful observation, the typical behavioural characters of each species and then to examine the distribution and variation of these characters among the living species.

It could be argued that all members of a species, in a given environment, might ultimately develop the same behaviour pattern through an entirely plastic process of learning taking place separately within each individual, and that the resulting similarity between individuals arises because there is an optimal solution to a particular requirement in that environment. In some cases, this possibility can be excluded by isolating animals of that species from the apparently 'necessary' environmental conditions. (Hence the value of combining captive studies with field studies). However, as a general rule, there is no reason why the distribution of particular behaviour patterns should coincide with the distribution of anatomical characters, if the latter are subject to genetic control and the former are not. One would expect such plastic behaviour of animal species to be far more rapidly adaptable (and thus far more variable between species and subpopulations of a species) than anatomical characters, whose modification is presumably dependent upon chance emergence of favourable mutations. Experience shows, however, that many behavioural features show the same small degree of variability between species, and between subpopulations of a species, as that exhibited by morphological characters. In the Malagasy lemurs, this has proved to be the case with locomotor patterns, nesting habits, maternal care, basic elements of social behaviour and patterns of spatial distribution.

As a modification of the 'behavioural plasticity' argument, it could be maintained that behaviour is actually plastic, but directly contingent upon morphology and/or physiology, and that behaviour patterns show the same kind of systematic distribution as anatomical and physiological characters for this reason, and not because the behavioural components themselves are directly subject to the same, slow rate of modification through natural selection. It is difficult to exclude this possibility, and for present purposes this is not really necessary, since it is still permissible to discuss the change of behaviour through time, as closely related species would exhibit behavioural similarities contingent upon their morphological similarities. In either case it can be assumed that morphological similarities between fossil and living forms indicate behavioural similarities. In recent years, increasing attention has been paid to *functional morphology*. It is, for example, far more rewarding to consider the evolution of locomotion in a particular animal group in terms of morphology and behaviour, rather than simply in terms of one of these aspects, as has latterly been admirably illustrated by a thesis referring to the evolution of locomotion in Malagasy lemurs (Walker 1967*a*). In such a case, it is obvious that morphology and behaviour are interdependent.

Overall, it would appear to be permissible to discuss the evolution of behaviour in a group of animals, such as the Malagasy lemurs, provided that attention is paid to morphology, as far as possible. In the first place, it should be established that the distribution of behavioural characters approximately follows that of morphological characters, and, secondly, functional morphological aspects must be adequately considered. As a final point, it is essential to remember that our only concrete evidence of evolution over long periods of time is provided by the fossil record, and that functional morphological interpretation of fossil evidence thus provides the only source of corroboration of hypotheses based on analysis of the behaviour and/or morphology of living forms.

Zoological relationships of the Malagasy lemurs

The Madagascar lemurs have attracted particular attention because of their position within the Order Primates (lemurs, lorises, tarsiers, monkeys, apes and man). Quite apart from their intrinsic interest, interpretations of behavioural evolution in the lemurs are of special value in that they can provide information about the very early stages of Primate evolution, for example with respect to locomotion, maternal behaviour and social organization (see p. 301).

In any modern classification of the Primates, the attempt is made to represent probable evolutionary relationships in addition to providing a useful reference scheme. Although the various classifications which have been proposed differ in detail, there is general agreement about the division of the living Primates into six 'natural groups' which are distinguished geographically as well as morphologically:

(1) Lemurs (Madagascar)
(2) Bush-babies and Lorises (Africa + Asia).
(3) Tarsiers (South-East Asia)
(4) New World Monkeys (South America)
(5) Old World Monkeys (Africa + Asia)
(6) Apes and Man (Africa + Asia)

The differences between alternative modern classifications of the Primates are essentially due to differences in opinion about evolution within the Order, and it is hoped that this article will provide additional information towards clarification of this aspect of Primate classification.

The majority of authors follow, to a greater or lesser extent, the classification given by Simpson (1945), in which the Malagasy lemurs are included in the Infra-Order Lemuriformes in the following arrangement:

Infra-Order: LEMURIFORMES

Super-family 1	TUPAIOIDEA
Family	Tupaiidae (tree-shrews)
Family	Anagalidae†
Super-family 2	LEMUROIDEA
Family	Plesiadapidae†
Family	Adapidae†
Family.	Lemuridae
Family	Indridae
Super-family 3	DAUBENTONIOIDEA
Family	Daubentoniidae

† Fossil group.

It is important to note that Simpson places the loris/bush-baby group in a separate Infra-Order – the Lorisiformes – and that the tarsiers are placed in a third group of the same rank (Infra-Order Tarsiiformes). The three Infra-Orders (Lemuriformes, Lorisiformes, Tarsiiformes) together form the Sub-Order Prosimii, and all of these Primates are commonly referred to as *prosimians*, in distinction from the *simians* (monkeys, apes and man) placed by Simpson in the Sub-Order Anthropoidea.

It has been suggested elsewhere (Martin 1967, 1968*a*), that the similarities between living tree-shrews (Tupaiidae) and Primates are based exclusively on retention of ancestral placental mammal characteristics and the convergent development of certain features in the two groups, such that there is no justification for including the tree-shrews within the Order Primates.

Further, it has recently been stated with some conviction (van Valen 1960, 1965; McKenna 1963) that there is no specific relationship between the fossil Anagalidae and the tree-shrews, and that the anagalids cannot reasonably be included in the Order Primates. Accordingly, the 'Super-Family Tupaioidea' probably represents an inappropriate, heterogeneous inclusion within the Order Primates. Much further work is necessary to establish the true relationship) of the tree-shrews; but it is quite clear that the tree-shrews should not be included in the Infra-Order Lemuriformes, since this implies that there is a closer relationship between tree-shrews and lemurs than between lemurs and the loris/bush-baby group. There is new evidence Charles-Dominique & Martin 1970) indicating that the lemurs and the loris/bush-baby groups are far more closely related than has generally been supposed (figure 1), and a suitable classification should indicate this close relationship, rather than implying that the tree-shrews are close relatives of the lemurs. Another unfortunate feature of Simpson's classification is the implication that the Aye-aye is less closely related to the other Malagasy lemurs than are the bizarre fossil Plesiadapidae.

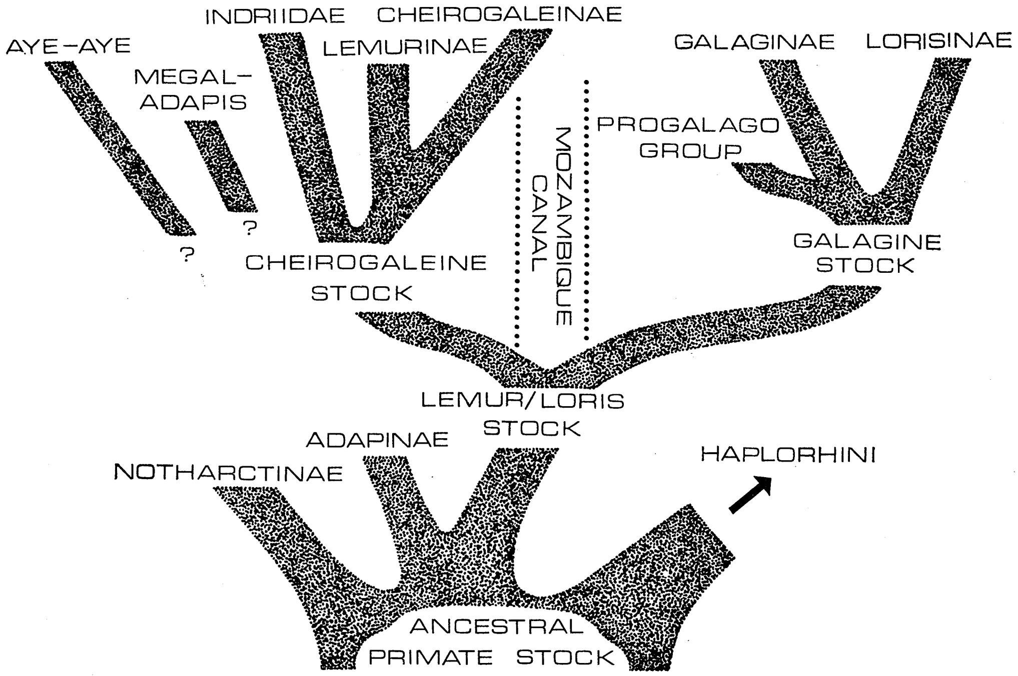


Figure 1. Diagram indicating possible evolutionary relationships between the Malagasy lemurs, the Afro-Asian lorisoids and the Eocene Adapidae (modified from Charles-Dominique & Martin 1970).

Another point of contention concerns the relationship of the tarsiers to the lemurs and lorises on one hand, and to the simians (monkeys, apes and man) on the other. As noted above, Simpson places the tarsier with the lemurs and lorises in the Sub-Order Prosimii, whilst Hill (1953) distinguishes between the Grade Strepsirhini (lemurs + lorises) and the Grade Haplorhini (tarsiers + simians). The balance of morphological evidence indicates that there *was* an initial dichotomy (figure 2) in the evolution of the Primates, justifying Hill's major division of the Order. In line with this view, it is sufficient in the following account to consider the living Strepsirhini (lemurs + lorises) and closely associated fossil forms in order to discuss the evolution of the Madagascar lemurs from the Primate stock. Conversely, an overall view of evolution within the Strepsirhini is sufficient to permit direct extrapolation back to the ancestral Primate stock. As far as the fossil forms are concerned, there are three well-known groups which seem to be unquestionable relatives of the living Strepsirhini: the relatively recent Malagasy subfossil lemurs, the Miocene lorisoids (*Progalago* group) from East Africa and the (essentially) Eocene Adapidae (incorporating the sub-family Adapinae of Northern Europe and the sub-family Notharctinae of North America). In all of these cases, the fossils indicate a sufficient number of Primate characters to place their systematic status beyond reasonable doubt. In the case of the Adapidae and the Miocene lorisoids, there are a number of clear-cut characters indicating a relationship to the Strepsirhini rather than to the Haplorhini; in the case of the subfossil lemurs, their occurrence on Madagascar itself indicates a specific relationship to the extant lemurs.

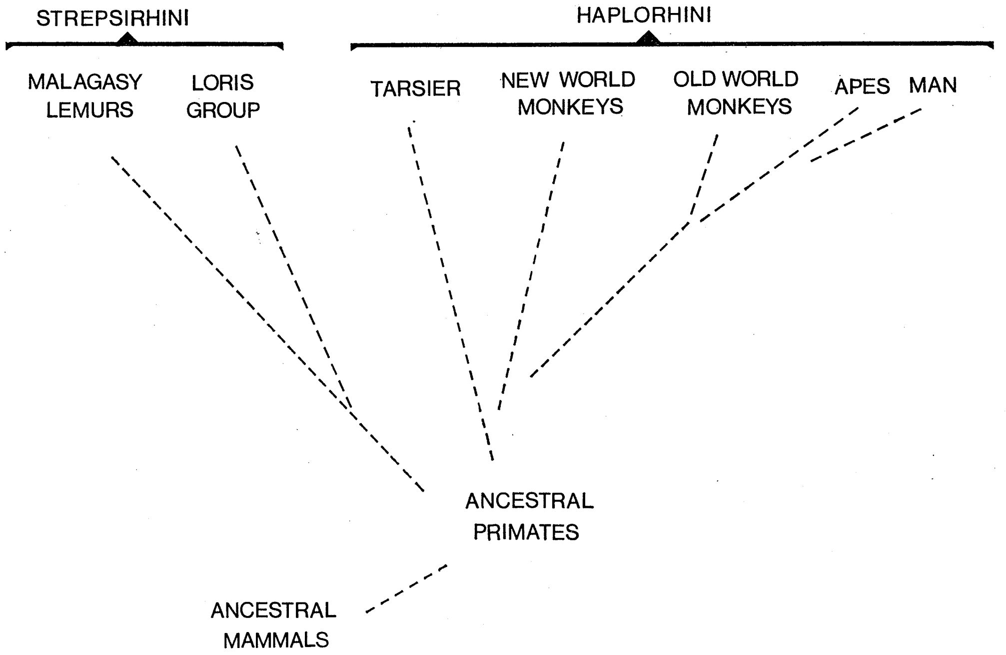


FIGURE 2. Outline diagram of the probable relationships between the six main groups of living Primates.

Since it would be premature to suggest a new formal classification without extensive discussion of morphological characters, a simple schema (figure 3) will be used here for easy reference to broad zoological relationships within the Strepsirhini. In view of the present confused situation concerning Primate classification, it should be emphasized that this schema is primarily *descriptive* at this stage (hence the heavier reliance on common names). Some of the groupings are convenient for reference purposes, but not necessarily taxonomically valid.

It will be noted that no attention is paid to relatively poorly known fossil forms, such as the Plesiadapidae, which are frequently included in the Order Primates. These essentially fragmentary fossils have been included in the Order primarily on the basis of molar tooth morphology, and without exception they exhibit peculiar modification of the anterior dentition. Since virtually all other recorded cranial characteristics of these fossils (e.g. in the orbital and auditory regions) are incompatible with a cohesive concept of evolution of the Primate skull, their classification within the Order Primates is of questionable value. Even if these fossils do eventually prove to have a tenuous ancestral relationship to Primates, they will have to be classified as extremely aberrant side-branches, since they must have evolved away from the ancestral Primate condition with remarkable rapidity. They certainly have little relevance to the evolution of the Strepsirhini as defined above, and cannot meaningfully be classified with the Malagasy lemurs.

The basic raw material discussed in this paper – that is, the *ensemble* of the Malagasy lemurs– is represented by 19 extant species (12 genera) and 14 identified subfossil species (seven exclusively subfossil genera). The latter were probably thriving 2000 years ago, and some seem to have survived until historical times (Walker 1967*a*). Several lines of evidence indicate that the extinction of the subfossil species (many of which were larger and probably more diurnal in habits than the extant forms) coincided with the late arrival of human settlers on the island (Lamberton 1934, 1939; Walker 1967*b*). As Walker has pointed out, this recent date of extinction of the subfossil lemurs indicates that the extant and subfossil species together once represented an integrated fauna. Standing (1908, p. 71), one of the earlier investigators of the subfossils, stated: 'One may at any rate from the biological point of view regard all these subfossil Malagasy lemuroids as the contemporaries of extant species in other parts of the island.' It follows from this that the extant Madagascar lemurs are not fully representative of the previously balanced faunal situation. Extinction of the subfossil species must have liberated previously occupied ecological opportunities so recently that the surviving lemur species cannot have evolved appreciable new adaptations to exploit them. The most that can have happened in the short period available is that the ecological niches of the surviving species have been expanded or shifted through minor modifications (e.g. in diurnal activity pattern, preferred habitat, dietary spectrum, etc.). This possibility dictates caution in interpretation of present ecological and geographical distribution limits in the extant lemur species, and it is obvious that a detailed study of the evolution of the Malagasy lemurs must include adequate reference to the subfossil forms.

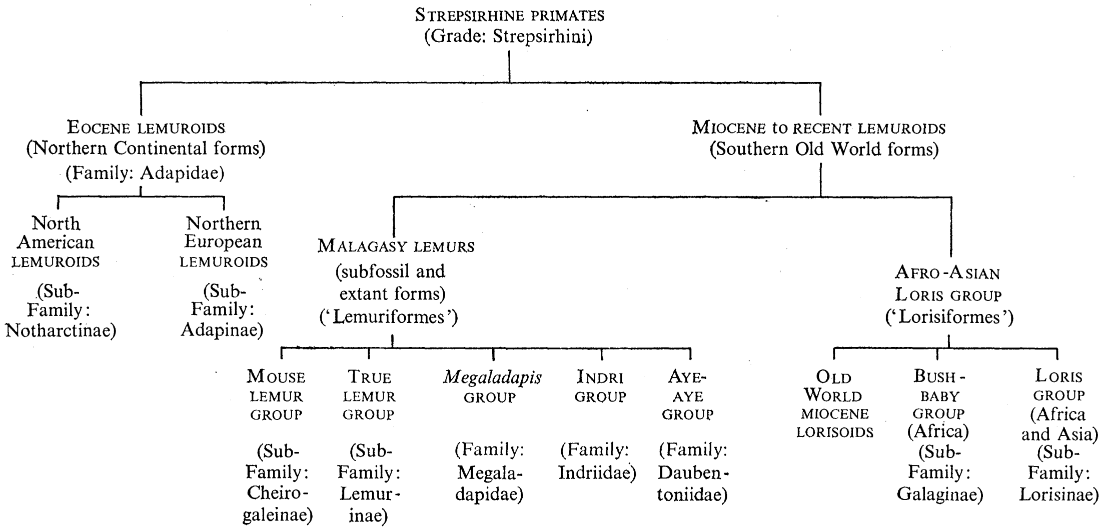


FIGURE 3. Hierarchical reference scheme for the main groups of Strepsirhine Primates.

Caution must also be exercised because of the geographical distribution of the main sites which have yielded subfossil lemur material (figure 4). If this distribution pattern is compared with the map indicating the seven major zones of occurrence of extant lemur species (figure 6*a*, p. 307), it can be seen that subfossil material has been derived almost exclusively from only two of these zones (W_2, CP), and that no subfossil material has been taken from three zones (W_1, N and E_2). Very little material has been gleaned from the remaining two zones (NW and E_1). In view of this, it is to be expected that investigations in the five poorly known zones could well

Figure 4. Map showing the main sites yielding subfossil lemur material (after Lamberton 1934, 1937 and Walker 1967*a*). *Key*:

Towns

1. Tananarive
2. Tamatave
3. Majunga
4. Diego Suarez
5. Morondava
6. Fort Dauphin

Fossil sites

A. Ampasambazimba
B. Sambaina
C. Antsirabe
D. Betafo
E. Morarano
F. Antanimbaribe
G. Ambararatra
H. Belo
I. Bemavo
J. Tsirave
K. Ampoza
L. Lamboharana
M. Andranovato
N. Ambolisatra
O. Taolambiby
P. Itampolo
Q. Bevoha
R. Ampotaka
S. Anavoha
T. Andrahomana
U. Mananjary
V. Amparihingidro
W. unnamed locality

lead to the discovery of many more subfossil species, though these are likely, at least in many cases, to be species of genera which are already known. Bearing this in mind, the list of extant and subfossil Malagasy lemurs used for this discussion must be regarded as incomplete (see table 1).

Although the recent Malagasy lemur fauna must thus be regarded as incompletely known, it is still valuable to speculate about the evolution of the lemurs on Madagascar, since this group provides us with one of the neatest examples of adaptive radiation within the Primates. Further, if it is true that the evolution of the lemurs has essentially taken place within Madagascar, we are presented with a situation which is virtually a closed system.

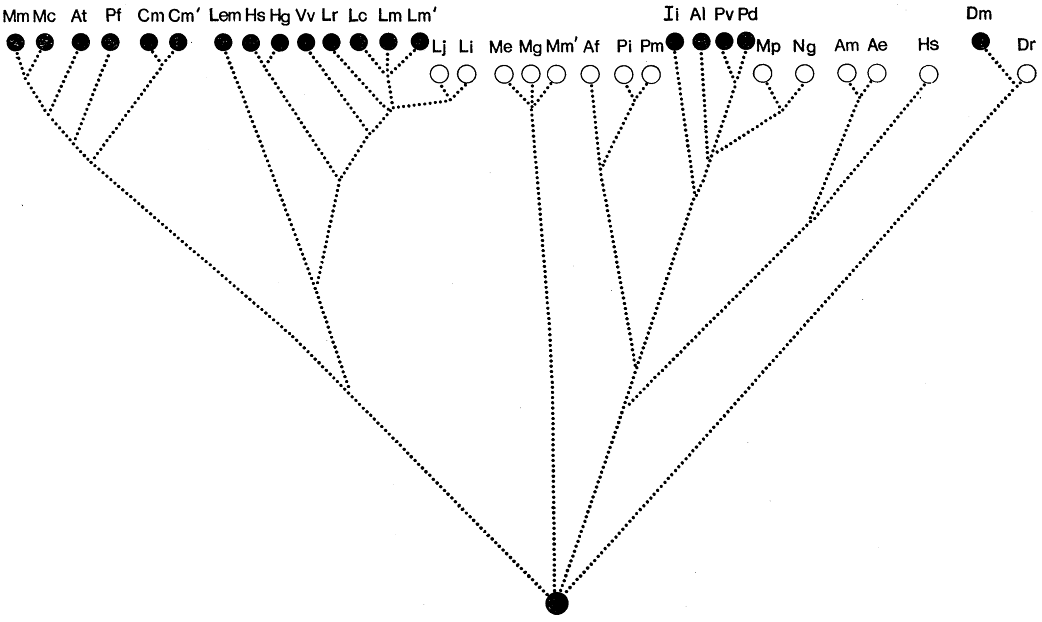
In order to discuss the adaptive radiation of the lemurs, it is useful to have some reference diagram giving an approximate guide to their likely evolutionary relationships (as determined primarily on morphological grounds). Figure 5 provides a 'resemblance diagram' indicating approximate degrees of morphological affinity between the extinct and living species, and thus suggesting an extremely rough idea of possible evolutionary relationships. This resemblance diagram incorporates Lamberton's (1939) views on the relationships of the subfossil lemurs, and it is in general accordance with the overall Malagasy lemur classification provided by Walker (1967*a*) and summarized (with some modification) in table 1.

TABLE 1. PROVISIONAL LIST OF SUBFOSSIL AND EXTANT LEMUR SPECIES

extant species	subfossil species
1. Mouse Lemur group	
Microcebus murinus† (Mm)	
M. coquereli (Mc)	
Cheirogaleus medius† (Cm)	
C. major (Cm′)	
Phaner furcifer† (Pf)	
Allocebus trichotis (At)	
2. True Lemur group	
Lemur catta (Lc)	
L. rubriventer (Lr)	
L. mongoz (Lm)	
L. macaco (incl. *L. fulvus*) (Lm′)	
	L. jullyi (Lj)‡
	L. insignis (Li)‡
Varecia variegata (Vv)	
Hapalemur griseus† (Hg)	
H. simus (Hs)	
Lepilemur mustelinus† (Lem)	
3. Indri group	
Indri indri (Ii)	
Propithecus verreauxi† (Pv)	
P. diadema (Pd)	
Avahi laniger† (Al)	
	Mesopropithecus pithecoides (Mp)
	Neopropithecus globiceps (Ng)
4. Archaeolemur group	
	Archaeolemur edwardsi (Ae)
	A. majori (Am)
	Hadropithecus stenognathus (Hs)
5. Palaeopropithecus group	
	Palaeopropithecus ingens (Pi)
	P. maximus (Pm)
	Archaeoindris fontoynonti (Af)
6. Megaladapis group	
	Megaladapis edwardsi (Me)
	M. grandidieri (Mg)
	M. madagascariensis (Mm′)
7. Aye-aye group	
Daubentonia madagascariensis (Dm)	*Daubentonia robusta* (Dr)

† May represent more than one species. ‡ Probably best allocated to the genus *Varecia*.

It is important to note that the broad relationships indicated in the diagram are in concordance with the distribution of behavioural characters in the living forms and the occurrence of some presumed behavioural features (e.g. locomotor adaptations) in the subfossil forms. The diagram also underlines the fact that – at present – nothing whatsoever is known of the fossil history of the Malagasy lemurs on Madagascar prior to recent times (i.e. not before 10000 years ago). Thus, comparative morphology is virtually subject to the same constraint as comparative behavioural study in this instance: the pattern of evolution must in both cases be deduced from comparison of (and extrapolation from) recent forms. Establishment of the ancestral characters of lemurs is accordingly dependent upon a process of logical extrapolation



lance diagram for living and subfossil lemur species (abbreviations listed in
may be taken as a very rough guide to evolutionary relationships.

from the characteristics of living forms, though the correctness of such inferences must ultimately be assessed on the basis of fossil discoveries. For the moment, one can only note with regret that, apart from the existence of some unquestionable Miocene lorisid remains in Africa and the occurrence of well-known (but somewhat distantly related) Eocene Strepsirhines in Northern Europe and North America, little is known about the fossil history of the Lemur and Loris groups.

ZOOGEOGRAPHICAL ASPECTS OF MALAGASY LEMURS

1. *Distribution within Madagascar*

Although various distribution maps have been provided for the extant lemurs (Hill 1953; Petter 1962*b*; Walker 1967*a*), there is still a basic lack of detailed information on the occurrence of the individual species in those regions which still have forest cover. At present, one can do no more than follow the existing distribution maps, correcting them wherever detailed data have become available. In general, the maps provided by Petter and Walker are reliable, and broadly agree with observations made during the author's field study, thus permitting discussion of the major characteristics of lemur distribution patterns. On this basis, Madagascar can be divided into seven main zones (figure 6) which, in various combinations, broadly accord with the distribution patterns of all species and subspecies for which sufficient data is available (table 2 indicates the occurrence of the extant lemur species in each of these zones). Although these zones provide only an approximate indication of the present distribution limits of the lemurs, the correlation is good enough to permit discussion of speciation patterns. It is not necessary that a given geographical race, subspecies or species should occur *throughout* one or more of these zones; nor is it essential that distribution patterns should exactly coincide with these zones, as we are concerned with a dynamic system. In discussing geographical speciation, it is sufficient to consider barriers to emigration which may operate both imperfectly and intermittently.

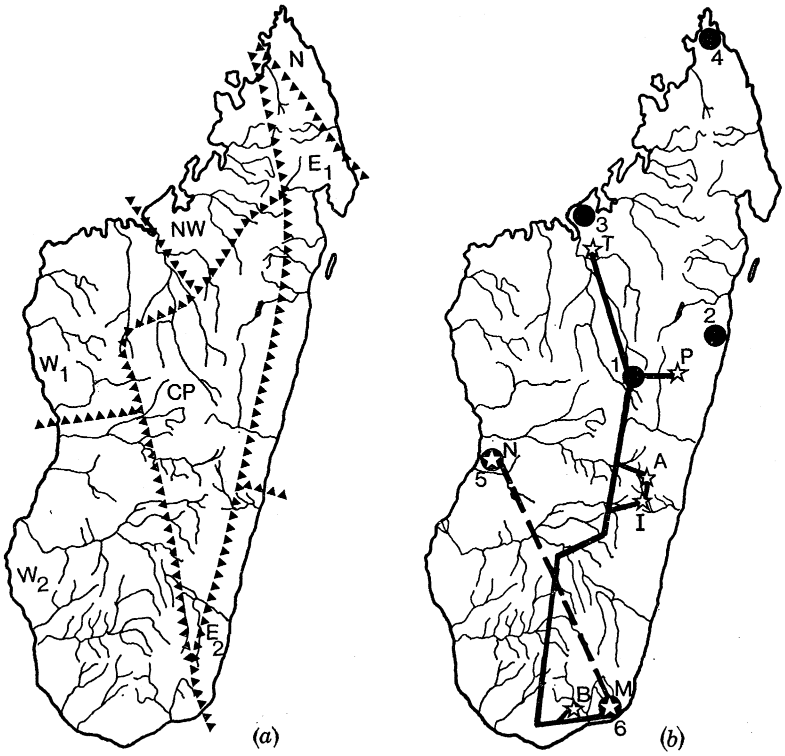


FIGURE 6. Maps showing (*a*) seven main areas of lemur distribution (see text) and (*b*) the areas visited by the author in 1968. *Key* (6*b*):

1. Tananarive
2. Tamatave
3. Majunga
4. Diego Suarez
5. Morondava
6. Fort Dauphin

Study areas:
A. Ambohimanga-du-Sud
B. Berenty (de Heaulme Estate)
I. Ifanadiana
M. Mandena (near Fort Dauphin)
N. Analabe (de Heaulme Estate, near Morondava)
T. Ampijoroa (near Tsaramandroso)

It is obvious from a comparison of table 2 with figure 6 that the main demarcation in distribution is between species occurring in the east coast zones (E_1+E_2) and those occurring in the four other coastal zones (N, NW, W_1, W_2). The central plateau (CP) is largely deforested, and there is therefore little information on distribution within this area. In the east coast area, some species occur in E_1 but not E_2, whilst all species found in E_2 are apparently also found in E_1. On the western coastal area, the situation is somewhat more complex. W_2 contains at least one species which does not occur in other areas; there are some species apparently shared only by W_2 and W_1, and there are some species which occur in W_1, NW and N, but not in W_2. The situation becomes even more complex if subspecies (as now recognized) are taken into account. For example, *Propithecus verreauxi verreauxi* occurs in W_2, *P. v. coronatus*+*P. v. deckeni* occur in W_1, and *P. v. coquereli* occurs in NW. This pattern would be understandable, were it not for the fact that *P. v. verreauxi* and *P. v. coquereli* are morphologically closer to one another than either is to the geographically intermediate *P. v. coronatus*/*P. v. deckeni* population (Kaudern 1915; author's personal observations). All of this indicates that the four west coast zones (N, NW, W_1 and W_2) are essentially distinct from one another. Some species (e.g. *Microcebus murinus*, *Lepilemur mustelinus*, *Hapalemur griseus*, *Avahi laniger*) which appear to be island-wide, according to present classifications, in fact include quite distinct east and west coast 'subspecies' which may well prove to be separate species on closer examination. It seems that the east and west coast zones, which are largely separated by the central plateau zone, have provided the basic division underlying the speciation of the lemurs, with the various eastern and western subzones providing further subdivision. In view of this, it is surprising that Paulian (1961) should have stated that geographic speciation in Madagascar has probably played a minor role, with *sympatric speciation* providing the main basis for diversification of the lemurs in Madagascar. However, Paulian was doubtless led to this conclusion by the apparent lack of coincidence between distribution limits of the lemurs and the limits of vegetational and climatic zones in some cases, and by the fact that some of the species subgroups in the major distribution zones can be easily hybridized in captivity (e.g. *Lemur macaco* and *Propithecus verreauxi* geographical subspecies). Since this is a crucial point, it should be examined in more detail.

TABLE 2. PROBABLE OCCURRENCE OF EXTANT LEMUR SPECIES IN THE SEVEN MAJOR ZONES (FIGURE 6*a*)

	areas of occurrence						
species	E_1	E_2	CP	N	NW	W_1	W_2
†*Microcebus murinus*‡	+	+	?	+	+	+	+
M. coquereli	–	–	?	?	?	+	+
†*Cheirogaleus medius*‡	–	–	?	+	+	+	+
C. major	+	+	?	–	–	–	–
†*Phaner furcifer*‡	+	?	?	?	?	+	+
Allocebus trichotis	+	?	?	?	–	–	–
†*Lepilemur mustelinus*‡	+	+	?	+	+	+	+
†*Hapalemur griseus*‡	+	+	?	+	+	+	+
H. simus	?	?	?	?	?	?	?
†*Lemur catta*	–	–	?	–	–	–	+
†*L. rubriventer*	+	+	?	–	–	–	–
†*L. mongoz*	–	–	?	+	+	+	–
†*L. macaco*	+	+	?	+	+	+	+
†*Varecia variegata*	+	?	?	–	–	–	–
†*Avahi laniger*‡	+	+	?	+	+	+	+
†*Propithecus verreauxi*‡	–	–	?	+	+	+	+
P. diadema	+	+	?	–	–	–	–
†*Indri indri*	+	–	?	–	–	–	–
Daubentonia madagascariensis	+	–	?	–	–	–	–

† Species observed by the author at some time in the field (13 out of 19).
‡ May contain a number of distinct species.
+ = probably occur there.
? = insufficient data.
– = probably absent.

Extensive studies of the flora of Madagascar, particularly by Humbert (1927, 1955, 1965), show that climatic factors are closely correlated with a clear-cut pattern of geographical plant speciation. This has been illustrated particularly clearly in a recent publication by Morat (1969). On the basis of the geographical occurrence of soil types, major climatic zones and plant types, Humbert provided a basic subdivision of Madagascar into phytogeographic zones (figure 7), and this has acted as a foundation for most subsequent zoogeographic studies in Madagascar. It can be seen at once that there is not complete agreement between the distribution patterns of plant groups (figure 7) and the major zones of lemur distribution (figure 6*a*).

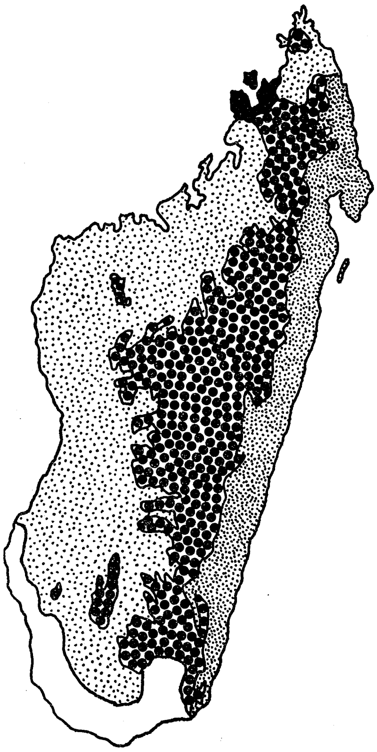


FIGURE 7. Map showing Humbert's phytogeographic zones (1965).

Key:	
heavy stippling	Eastern Domain
fine stippling	Western Domain
white area	Southern Domain
black spots	Plateau Domain
black area	Sambirano Domain

Although there is agreement in the basic division between east coast rain-forest and other, dryer forest areas, there is no striking correlation between the botanical subdivision of the west coast areas and the lemur distribution zones. There is, for example, no local group of lemurs adapted to live exclusively in the semi-arid forest zone (characterized by Didiereaceae and Euphorbiaceae) in the south and extreme south-west. Nevertheless, it is important to note that climatic conditions form an ideal gradient situation down the entire west coast zone, and that the plants and the lemurs may each be responding to different threshold values in the gradient from relatively wet, deciduous forest conditions in the north to semi-arid conditions in the south. The primary climatic factors concerned (minimum and maximum temperatures; annual rainfall) are illustrated in figures 8*a* to 8*d*, largely following the data provided by Humbert & Cours Darne (1965) and by Morat (1969).

Measurements of annual rainfall and daily temperatures can only provide extremely general

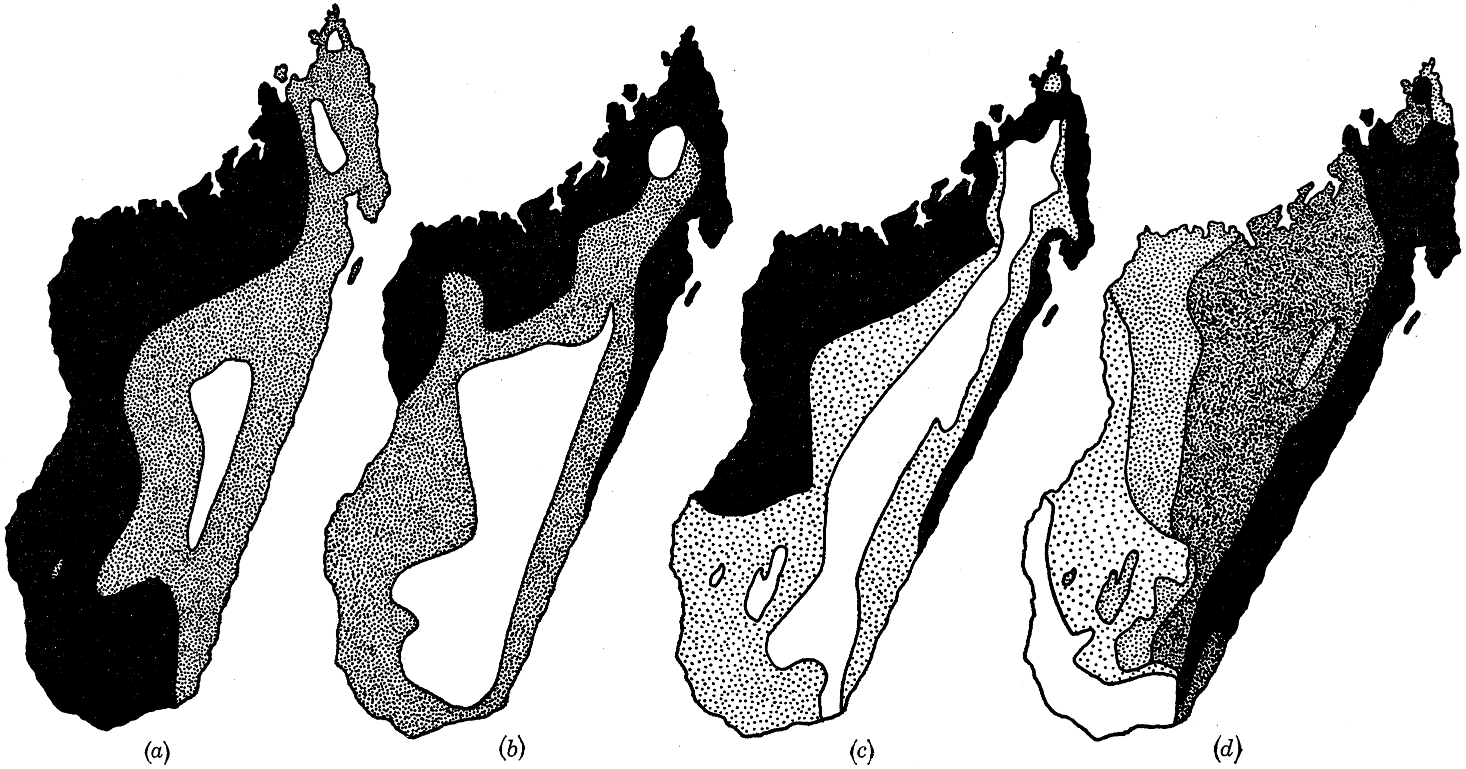


FIGURE 8. Maps showing temperature and rainfall distributions in Madagascar.

(a) Mean of temperature maxima for hottest month (data from Morat 1969)

white area	22–27 °C
stippled area	27–32 °C
black area	32–37 °C

(b) Mean of temperature minima for coldest month (data from Morat 1969)

white area	6–11 °C
stippled area	11–16 °C
black area	16–21 °C

(c) Mean average daily temperature of coldest month (data from Humbert 1965)

white area	below 15 °C
stippled area	15–20 °C
black area	above 20 °C

(d) Total annual rainfall (data from Humbert 1965)

white area	below 600 mm
light stippling	600–1000 mm
medium stippling	1000–1500 mm
heavy stippling	1500–2000 mm
black area	above 2000 mm

information about macroclimatic characteristics, as has been pointed out by Morat. As far as rainfall is concerned, consideration of the annual total rainfall (figure 8*d*) gives no idea of the seasonality of such rainfall, and no distinction is made between areas where rainfall is heavy but sporadic and areas where there is mild, yet continuous rain. Analysis of ambient temperatures can be conducted in various ways; but it is not yet clear which aspects of daily and annual temperature variations are crucial in determining plant and animal distribution patterns. Morat considered the mean of the temperature maxima (M) for the hottest month (figure 8*a*) and the mean of the temperature minima (m) for the coldest month (figure 8*b*), whilst Humbert was primarily concerned with the daily mean temperature for the coldest month (figure 8*c*). All three measurements are illustrated here, as any one of them could relate to a limiting factor under certain conditions.

Following Emberger's analysis of the relationship between plant distribution and climate in the Mediterranean area, Morat (1969) applied the concept of the *pluviothermic quotient* to the phytogeography of Madagascar, using the following formula:

$$\text{pluviothermic quotient } (Q_T) = \frac{P\,(N/365)}{2([M+m]/2)(M-m)} \times 100.$$

When this quotient is plotted against corresponding values of m for different areas of Madagascar, a convenient diagram ('climagramme') is obtained, illustrating regional relationships between total annual rainfall (P mm) and the mean temperature maxima and minima (M °C for the hottest month and m °C for the coldest month, respectively). Morat improved upon Emberger's original formula by incorporating the correcting factor $N/365$, which gives some indication of seasonal rainfall distribution, in that the number of rainy days (N) per year is included in the formula.

The pluviothermic quotient is plotted against minimum temperature values (m), since this factor has been empirically recognized as a vital one limiting the distribution of various plant communities. It seems likely that this factor is also important in limiting the distribution of various mammal groups, especially since they are dependent upon maintenance of a high, constant body-temperature, and since energy expenditure will depend upon the difference between the body-temperature and the external temperature throughout the year.

Morat used the resulting Madagascar 'climagramme' to study the regional delimitation of various plant groups, and came to the conclusion that the diagram is extremely useful for portraying the division of Madagascar into '*bioclimatic stages*' corresponding to zones of plant distribution. In fact, the four bioclimatic zones indicated by Morat accord well with the seven major zones of lemur distribution indicated in figure 6*a*. Figure 9 shows Morat's climagramme adapted so that the seven major lemur distribution zones are represented by different symbols. It can be seen that there is a fairly clear distinction between the northern section of the rain-forest (zone E_1; black squares), the central plateau area (zone CP; open triangles) and the dry forest of the south-west and the south (zone W_2; open circles). The southern section of the rain-forest (zone E_2; open squares) overlaps to some extent with the northern rain-forest area and the central plateau, whilst the north-west coastal region comprising areas W_1, NW and N (black circles, circle + dot and circle + triangle, respectively) represents a block in which the climate is generally similar in its broad outlines. Over and above this, the distinctions between these various areas generally follow Morat's division into perhumid, humid, subhumid and semi-arid bioclimatic stages.

As Morat has clearly emphasized, this climagramme can only give a very coarse indication of climatic variation in Madagascar, and its main justification lies in the consistency of climatic type throughout the island. All areas show a summer maximum and a winter minimum in rainfall, and similar annual patterns of temperature and day-length variation. Thus, although the climagramme does not take into account features such as local soil characteristics, a general comparison of macroclimatic parameters is possible. On the basis of this diagram and the maps in figure 8, the seven main lemur distribution zones can be characterized as follows:

E_1: essentially coastal dense, evergreen forest. Very high annual rainfall, with rain fairly evenly spread throughout the year. Temperature relatively high during the austral winter; moderate temperatures during the austral summer (i.e. little annual variation in average daily temperature).

E_2: essentially coastal evergreen forest. Moderately high annual rainfall, with rain fairly evenly spread throughout the year. Temperature relatively low during the austral winter;

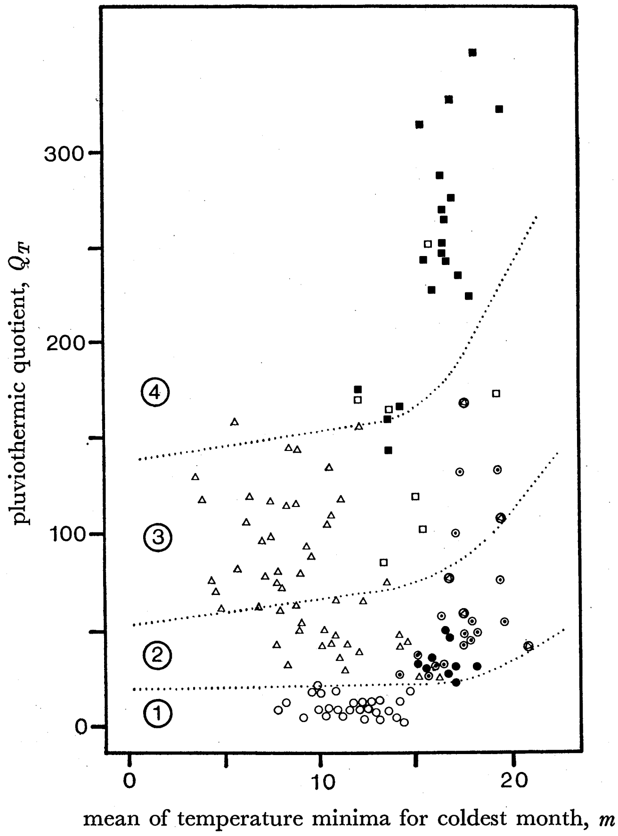


FIGURE 9. Adaptation of Morat's pluviothermic diagram for Madagascar, to distinguish the seven main lemur distribution zones. See Morat (1969) for the basic climatological data.

lemur distribution zones (figure 6*a*):

E_1	black squares	N	circle + triangle
E_2	open squares	NW	circle + spot
CP	open triangles	W_1	black circle
		W_2	open circle

climatic subdivisions:

1. semi-arid zone
2. subhumid zone
3. humid zone
4. perhumid zone

moderate temperatures during the austral summer (i.e. quite marked annual variation in average daily temperature).

CP: high altitude evergreen forest. Moderately high annual rainfall, with rain fairly evenly spread throughout the year. Temperature quite low during the austral winter; low to moderate temperatures during the austral summer (i.e. slight to marked annual variation in low average daily temperature).

N, NW, W_1: essentially coastal forest (evergreen for m values below 14 °C and deciduous for m values above 14 °C). Moderately high to moderate annual rainfall, with marked seasonality. Temperature relatively high during the austral winter; high temperatures during the austral summer (i.e. quite marked annual variation in average daily temperature).

W_2: semi-arid, xerophytic forest (dense dry deciduous type or bush). Low annual rainfall, with marked seasonality. Temperature relatively low during the austral winter; high temperatures during the austral summer (i.e. extremely marked annual variation in average daily temperature).

This breakdown shows that each of the areas shown in figure 6*a* has its own climatic characteristics, though areas N, NW and W_1 differ only in the level of annual rainfall. The other areas are distinct in several features, including vegetational characteristics, and there is obviously a broad climatic and botanical basis for the demarcation of the seven major lemur distribution zones. Morat's analysis of the *bioclimatic stages* would appear to dispel the doubts expressed by Paulian (1961) as to the relationship between lemur speciation and the existence of climatic and vegetational zones. Furthermore, recognition of an adequate climatic and botanical zonation underlying present lemur distribution patterns removes the necessity for postulating sympatric speciation.

It should be reiterated that, although the climatic and botanical zones might provide the basis for lemur speciation in Madagascar, it should not be expected that the distribution patterns of all lemur species should coincide exactly with these zones at any time. Evolution is a dynamic process, and it is quite conceivable that some species may still be confined to the zones where their reproductive isolation has occurred, whilst others have passed the phase of genetic isolation and are beginning to spread into other areas. For example, *Lemur catta* seems to be confined to zone W_2, whilst the widespread species *Lemur macaco* (generally recognized as incorporating several subspecies) may be in the process of expansion and speciation.†

On theoretical grounds, it is now generally accepted that most speciation occurs through geographical isolation. The crucial stage is the separation of one originally interbreeding species population into two or more subpopulations which remain separate long enough for the emergence of barriers to interbreeding between them (emergence of separate biological species). In accordance with this view, it is not sufficient that Madagascar should be subdivided into distinct climatic zones; there must be physical barriers of some kind which can effectively isolate subpopulations for periods of time sufficient for speciation to occur. Without such barriers, one would expect no more than cline-formation in Madagascar, with each species forming a continuously interbreeding chain around the island.

Figure 10 (following Walker 1967*a*) gives an extremely simple picture of the physical contures of Madagascar. The most important feature is the presence of an elevated central plateau, which can effectively isolate animal and plant groups on the coastal areas. (The low temperatures typical of the central plateau may have prevented their colonization by species which can

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† A recent paper by Albignac *et al.* (1971) provides a useful survey of *Lemur macaco* subspecies hybrids.

exist on the coasts.) The net effect would be the formation of coastal populations existing as 'wreaths' around the central plateau. The vast majority of the extant lemur species are restricted to the coastal forests, and it is not clear to what extent the central plateau (now largely deforested) was originally occupied by lemurs. Presumably, any populations which did occupy the plateau forest were adapted for the very low winter temperatures.

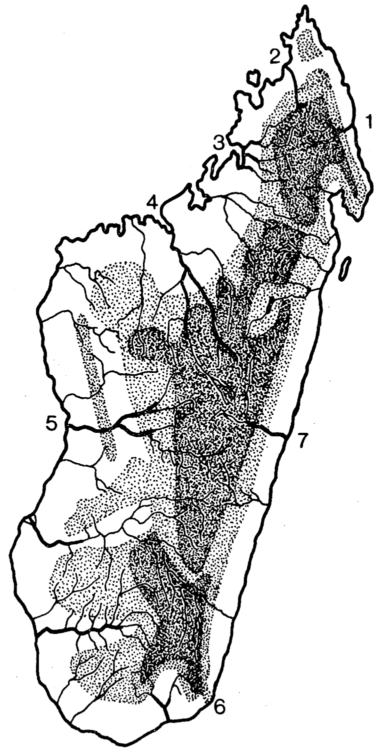

FIGURE 10. Map showing broad outlines of physical relief in Madagascar.

white area	0–300 m altitude
light stippled area	300–900 m altitude
heavy stippled area	900 m altitude and above

Major physical barriers (partly in agreement with Walker 1967*a*):

1. River Bemarivo
2. River Mahavavy
3. Antsohihy river complex
4. River Betsiboka
5. River Tsiribihina
6. Anosy hill-chain
7. River Mangoro

Assuming that some lemur populations, at least, existed as wreaths around the central plateau, it is easy to imagine that the presence of fairly large rivers could have subdivided such populations into subpopulations with a low level of inter-migration and inter-breeding. Figure 10 indicates various rivers and some elevated land areas which could have been involved in the subdivision of lemur populations at various times. The Rivers Mahavavy and Bemarivo in the north could have contributed to the isolation of zone N (figure 6*a*); the complex of rivers in the Antsohihy area and the River Bestiboka could have isolated zone NW, and the River Tsiribihina could have isolated zone W_1 from zone W_2. In the south-east, the Anosy chain of hills could well have isolated zone W_2 from zone E_2. Finally, the River Mangoro on the east coast may have served to isolate zone E_2 from zone E_1 at various times in the past. Although the present size of various rivers may give some idea of the existence of barriers between populations, there are a number of complicating factors. In the first place, extensive deforestation of the central plateau (probably over the last two millenia) has doubtless radically altered the nature of these rivers. Secondly, it must be remembered that the pattern of rivers in Madagascar may have undergone modification and fluctuation over the past 60 million years. Lastly, the question of seasonal variation in river flow (more important in the south-west than on the east coast) must be considered in evaluating the importance of rivers as barriers to inter-breeding. In view of these restrictions, all that can be said at the moment is that there appears to be a general coincidence between major rivers and the apparent barriers to distribution in extant lemurs. This observation is sufficient to permit discussion of a model for speciation of the lemurs. In those instances where a major physical barrier coincides with a marked climatic and botanical barrier (e.g. between the northern and southern sectors of the west coast), the combined effect may be to reduce movement between subpopulations to a minimum. An animal on one side of the combined barrier would generally be a member of a population adapted to a particular set of climatic and vegetational factors, and chance passage across the physical barrier would be offset by the reduced chances of survival in the adjacent climatic/vegetational zone. In cases where a physical barrier did not coincide with a climatic/vegetational boundary, any appreciable level of emigration across the barrier would lead to spread of the species, without speciation. One can therefore view Madagascar as consisting of a number of separate climatic zones, separated by barriers to emigration, at least as far as the lemurs are concerned. Any lemur species existing in one of the zones would tend to expand, by chance emigration, to other zones. If emigration were a rare event, the product would be a number of non-interbreeding populations (species) inhabiting the various zones. Each species would be adapted to the climatic and vegetational peculiarities of its zone of occupation.

Conversely, the existence of vegetational and/or climatic variation in the absence of physical barriers would not necessarily lead to speciation. For example, the south-west dry forest zone (W_2; figure 6*a*) contains two quite distinct forest types – dry deciduous forest and semi-arid bush characterized by peculiar Didiereaceae and Euphorbiaceae – and distinct gallery forest vegetation lining the various rivers. Despite these marked vegetational subdivisions and the existence of a fair degree of climatic diversity, there does not seem to have been any speciation of the lemurs in the different habitats. In the south (e.g. Amboasary area), various lemur species (e.g. *Lepilemur mustelinus*, *Lemur catta*, *Propithecus verreauxi*, *Microcebus murinus*) are apparently able to colonize with equal ease the xerophytic bush areas and the lush green gallery forest, and there is no evidence of subdivision into morphologically distinct subspecies or races. Certainly there is no evidence of sympatric speciation.

It is important to note that many of the lemur genera indicated in figure 5 include a small number (two to six) of extremely similar species which are likely to have diverged from their parental species quite recently. Unless the basic subdivision of Madagascar (pp. 306 to 308) into major faunal zones has changed radically through recent multiplication of such zones, this implies that there must be a continual process of replacement of networks of similar species throughout the island. For example, the geographical species *Cheirogaleus medius* and *C. major* are unlikely to have diverged more than a few million years ago. This must mean either that the two distinct zones now occupied by these two species were originally occupied by one island-wide species population, or that the genus *Cheirogaleus* has recently expanded and speciated to occupy these two zones. It could be argued that one of the two zones now occupied by *Cheirogaleus* species remained unoccupied for a vast period of geological time (tens of millions of years); but it seems more likely that these zones were occupied by other species (now extinct) before the evolution of the genus *Cheirogaleus*, rather than by one *Cheirogaleus* species which abruptly gave rise to two daughter species after millions of years of existence as a single species. It is quite clear from figure 5 that the differences between adjacent genera are far greater than the differences between daughter species of a genus, implying that there is a discontinuity between the evolution of a genus and the radiation of that genus to give a small number of extremely similar species. This apparent discontinuity disappears if it is assumed that in the radiation of a genus there are successive waves of adaptation to a set of ecological niches separated by effective barriers to inter-breeding.

The most extreme case in figure 5 is provided by the Aye-aye (far right). It is difficult to imagine that this animal existed as a single species for 40 to 50 million years and then abruptly gave rise to two daughter species (*Daubentonia madagascariensis* and *D. robusta*) just a few million years ago. It seems far more likely that successive sets of Aye-aye species have occupied the different habitat zones of Madagascar throughout the history of evolution of the lemurs on the island. The two recent species are probably quite late derivatives from a single, interbreeding Aye-aye population which existed somewhere on Madagascar. As this species population spread (and subsequently became subdivided into two reproductively separate units), it must have replaced the previous Aye-aye species, which were presumably less adapted for survival in a competitive situation. This is an important insight, coming as it does from a virtually closed situation, since it means that successive populations of a basic animal type may compete with one another and thus favour ever-increasing refinement of features which provide incremental increase in survival value. This fact is significant, since it provides for an ecological concept of the genus and also explains the obvious tendency for animal species to evolve in fairly well-defined directions. *Evolution may progress not only by the selection of favourable mutations within a species population, but also by sequential replacement of reproductively distinct species populations.* At any time, two reproductively distinct species populations of recent ancestry may be in competition within a given ecological niche. Such competition may lead to narrowing of the ecological niches of the two species (e.g. in terms of spatial distribution or food preferences), such that competition is reduced, or it may promote extinction of one of the species. If the latter occurs, one species population is replaced by another which is better adapted to the particular ecological niche (and thus more specialized). If the former occurs, both species populations become more specialized, though this process need not be genetically anchored in the first instance.

This dynamic aspect of the evolution of the Malagasy lemurs is vital, since it means that we are confronted with an extremely complex situation. Some populations will be in the process of reproductive isolation (and hence geographically distinct), whilst others may be in the phase of post-speciation emigration and interaction with closely related species populations.

The concept of ecological competition between closely related species has been adequately established by Lack's studies of British passerines (1944) and of Darwin's finches on the Galapagos Islands (1947). In fact, the situation in Madagascar is quite similar to the situation in the Galapagos Islands, except that the barriers to migration are provided by rivers and climatic factors (rather than by expanses of sea), and that the closed system in Madagascar has probably operated for a far greater period of time than that in the Galapagos Islands. Lack (1947, p. 113) has pointed out that adaptive radiation of the Galapagos finches could only have occurred in the absence of other bird species which might have been more efficient at particular types of feeding, and the same could be said of the lemurs on Madagascar. It was also noted by Lack (1947, p. 114) that competition between the Galapagos finch species was itself an important factor in their radiation:

> 'It should be added that, though largely freed from competition with land birds of other types, some of Darwin's finches have come into competition with each other, and this, as considered later, has highly important evolutionary consequences.'

For example, *Geospiza difficilis* breeds on arid lowlands on three outlying islands of the Galapagos complex, but not on the central islands, where it is in competition with *G. fuliginosa*.

It has often been said that Madagascar is more a small continent than a large island; yet in terms of evolution Madagascar may be more like a closed group of (somewhat elastic) islands. The separation between the subzones of Madagascar probably provides the basis for speciation, whilst the possibility of emigration between these subzones provides the basis for subsequent specialization of new species. Gause (1934) has founded the concept that a given ecological niche cannot be fully shared by two or more species. Lack has extended this to show that ecological competition may provide one of the main foundations for habitat separation in birds. With the lemurs, it may well be the case that ecological competition has provided one of the main factors leading to the extensive radiation of this isolated group of Primates.

2. *Relationships between Madagascar and other land masses*

One of the main issues for any discussion of evolution within Madagascar centres around *emigration routes* for colonization and this particular aspect has evoked animated contributions from a succession of authors (e.g. see Millot 1952). As was pointed out by Simpson (1943). there are three fundamental hypotheses purporting to explain the past and present relationships between continents and thus the geographical framework for the dispersal and speciation of organisms: (1) the hypothesis of continental drift; (2) the hypothesis of trans-oceanic continents; (3) the 'stable continents' hypothesis. In fact, the choice between these hypotheses must ultimately depend upon geophysical evidence but, at various times in the past, biologists have nevertheless attempted to draw conclusions about continental relationships primarily from the distribution of living (and, in some cases, fossil) organisms. Simpson, for example, stated with conviction:

> 'The distribution of mammals definitely supports the hypothesis that continents were essentially stable throughout the whole time involved in mammalian history'.

Acceptance of this procedure reflects the long-established bond between biological evidence and theories of continental relationships. Wegener (1941) and Du Toit (1937) relied heavily on such evidence in establishing the early foundations of the theory of continental drift, and since that time biological evidence has been cited with equal vigour for and against this theory. In recent years, the hypothesis of trans-oceanic continents has largely disappeared from view, leaving a direct confrontation between the theory of continental drift and the 'stable continents' hypothesis. However, the (now obsolete) invocation of enormous trans-oceanic continents, purely in order to explain biological distribution patterns, is itself surely symptomatic of an inability to explain those patterns on the basis of stable continents.

Nowadays, the situation has entirely altered. Whereas resolution of geophysical relationships seemed in the past to be partially dependent upon interpretations of biological data, adequate geophysical data have now independently demonstrated the reality of the process of continental drift and have provided a firm, autonomous basis for discussing past relationships between continental independent land-masses and the progress of organic evolution. It has been demonstrated that there is a close correspondence between palaeoclimatic data and palaeomagnetic indicators of ancient latitudes for the major continents (Blackett 1961) and a subsequent symposium reviewing various geophysical arguments (Blackett, Bullard & Runcorn 1965) has shown that the overall evidence is overwhelmingly in favour of the theory of continental drift. More recently, computer analysis of the 'best geometrical fit' of the 500-fathom contours of the southern continental masses (Gilbert Smith & Hallam 1970) has demonstrated that the assembly of the southern continents ('Gondwanaland') obtained on this mathematical basis agrees closely with the various lines of geophysical evidence (e.g. stratigraphical data) and that the pattern of assembly is essentially similar to that which – in a simpler form – led Wegener and Du Toit to propose the drift theory in the first place. Unfortunately, it is still too early for the provision of detailed maps showing the mutual relationships of the continental land-masses at various times in the past; but eventually such maps should become available as a solid basis for discussion of past patterns of emigration of living organisms.

Since independent geophysical evidence has now upheld the formerly unpopular theory of continental drift, one must ask why authors such as Simpson (1943) and Millot (1952) were erroneously convinced that the distribution of mammals and other organisms conflicts with this theory. (This is important, since past discussions of the evolution of Primates – and specifically of the lemurs – have generally been based on the assumption that the continents have always been stable in position.) Two basic reasons for this error emerge: in the first place, it is generally agreed that the bulk of the initial rifting in the southern continental land-mass ('Gondwanaland') occurred in the Jurassic and Lower Cretaceous (e.g. see Gilbert Smith & Hallam 1970); so there is no real conflict with Millot's basic assumption (1952, p. 2) that Madagascar was a distinct island by the end of the Cretaceous. Since it is also generally agreed that this is the earliest date for the initial radiation of the Eutherian mammals, it is likely that direct continental connexions ('land-bridges') would have existed only in the very early stages of mammalian evolution (e.g. see Kurtén 1969). The main period of Eutherian mammal evolution (i.e. Palaeocene to Recent) coincides with the main period of gradual continental separation, during which oceanic barriers of continuously increasing dimensions would have been forming. This means that continental drift would have produced varying degrees of isolation of mammalian stocks, rather than facilitating direct emigration between the southern continents. Indeed, the rapid radiation of the Class Mammalia is doubtless a result of the early existence of ideal conditions for intermigration, isolation and speciation on separate land-masses. Hence, there is no qualitative difference between the theories of stable continents and continental drift as regards the evolution of mammals; in both cases, the major land-masses are recognized as separated by bodies of water. However, there is a *quantitative* difference in that some water barriers have gradually been increasing in extent with the progress of continental drift; a factor which would have been absent in a system involving stable continents. It is precisely this aspect which Simpson, Millot and other authors have omitted to consider, treating the discussion as a choice between two extremes – the existence of clear-cut land connexions or the presence of considerable oceanic barriers. Yet, with either theory, it seems highly likely that colonization of Madagascar by mammals would have occurred by chance rafting along the lines suggested by Millot. The difference between the two theories lies in the fact that continental drift would have gradually reduced the likelihood of such rafting throughout the greater part of the Tertiary period, whilst rafting between stable continents would have been equally unlikely at any time during the Tertiary, other things being equal. (Millot himself expressed concern that none of the African monkeys managed to reach Madagascar by rafting.) This fact is of prime importance for examination of the evolution of the Malagasy lemurs, since independent confirmation of the theory of continental drift indicates that Madagascar was probably occupied by a small number of ancestral species at a time when the island was still relatively close to the African mainland (Late Cretaceous–Early Eocene).

As a corollary to this, it is obvious that the earlier the separation of the island began to take place, the smaller the number of ancestral forms which can be reasonably postulated for each mammal group now represented on Madagascar. For the four main endemic groups of Madagascan mammals (lemurs, rodents, carnivores, insectivores) it can be said that the known representatives are closer to one another than to any extant related forms in Africa, or elsewhere. What cannot yet be decided, in the absence of reliable independent evidence, is how many different lines of lemurs, rodents, carnivores and insectivores originally colonized the island when the Mozambique Channel was narrower than it is today. Differences of opinion on the number of ancestral lines are largely responsible for differences in interpretation of the relationships of Malagasy mammals (e.g. see F. Petter (1961) on the rodents and G. Petter (1961) on the carnivores). It is generally recognized that each of these four main groups of Malagasy mammals comprises forms which exhibit a relatively primitive constellation of characters within the relevant Order. Specializations present in the individual species can in every case be reasonably attributed to evolution within Madagascar. Overall, the picture is one of a handful of ancestral mammalian forms crossing the Mozambique Channel at an early stage (e.g. in the Palaeocene) and subsequently diversifying within the island.

The second factor underlying the forthright condemnation of the theory of continental drift expressed by Simpson, Millot and other authors lies in the inherent reversibility of most zoogeographical arguments. As Simpson indicates (1943), the adherents of the drift theory are largely concerned with the situation in the southern continents, whilst adherents of the stable continent theory centre zoogeographical arguments on the northern hemisphere (an obvious outcome of the present configuration of the continental land-masses). Neither Simpson nor Millot seemed to have recognized that, in the absence of external evidence, either case can be put with equal conviction. For example, Millot (1952, p. 28) cites the great resemblance between the fossil fauna of the French 'Phosphorites de Quercy' (essentially Eocene) and the extant fauna of Madagascar as evidence that the ancestors of the Malagasy fauna (south) were once present in Europe (north). However, it could equally well be argued that the ancestors of both the northern European forms and the Malagasy forms were once present in Africa. Since there are apparently no suitable Early Tertiary deposits in Africa, it is unlikely that this question will ever be resolved by zoological evidence alone. All authors seem to agree nowadays that the lemurs of Madagascar must be derived from ancestral forms once represented on the African continent and if the colonization of Madagascar by lemuroid ancestors took place in the Early Tertiary, there must have been a thriving stock of lemuroids in Africa in the Palaeocene, or even earlier. On the one hand, disjunctive distribution of a biological group in the southern continents can be interpreted as a relict distribution following northern continental extinction in a previously world-wide group (hence 'disproving' the drift theory), whilst on the other hand occurrence of northern forms can be dismissed by supporters of the drift theory as a product of northerly emigration and specialization of offshoots from a pan-continental southern stock.

Without independent geophysical evidence, the theory of continental drift cannot be confirmed, or refuted, on the basis of late Mesozoic or Tertiary distribution patterns of plants and animals. The only firm biological evidence for continental drift is to be sought from the period when Gondwanaland was still an entire land-mass; that is, during the Triassic or still earlier. Even for these earlier times, it is essential to have detailed information on floral and faunal relationships in order to decide whether the southern continental forms are more closely related to one another than would be expected following separate derivation from a hypothetical pan-continental northern ancestral stock. It is, indeed, extremely fortunate that biologists can now take the theory of continental drift as a reliable starting-point for discussion of geographical correlates in evolution, thus avoiding this inherent reversibility of interpretation of distribution patterns.

Renewed examination of the process of Primate evolution on the basis of a well-established drift theory should provide a number of new insights. For example, it is commonly held (e.g. see Simons 1962) that the Afro-Asian 'Lorisiformes' and the Malagasy 'Lemuriformes' are quite separately derived from northern European lemuroids or their relatives. One consequence of this line of argument is the assumption that the lower jaw 'tooth-scraper' (p. 328) found in all living Lorisiformes and most recent (subfossil and extant) Lemuriformes has been independently developed in these two lines. This, despite the fact that it is not a simple transformation to alter completely the function of the lower canine (incorporated into the tooth-scraper of the lower jaw as an inclined incisiform tooth) and subsequently to modify the first lower premolar to act as a caniniform tooth. Nevertheless, this assumption was apparently supported for a while by the statement (Le Gros Clark & Thomas 1952) that the tooth-scraper was only weakly developed in *Progalago* of the African Miocene. Recently, Walker (1969) has demonstrated that the tooth-scraper was present in its characteristic form in the *Progalago* group, and accordingly one would expect to find in the Eocene precursors of these fossil Lorisiforms at least some indication of functional modification of the lower canine. In fact, the Adapinae and Notharctinae exhibit without exception perfectly typical mammalian lower canine teeth with erect, styliform incisors. This character alone excludes them from direct Eocene ancestry of the Lorisiformes and most of the Lemuriformes. As it happens, even those few subfossil or extant lemur species which lack the tooth-scraper (e.g. *Archaeolemur*, *Hadropithecus*, *Daubentonia*) have a dental array which can be derived from the common Strepsirhine pattern, including a tooth-scraper (see p. 331), and in most cases there is clear evidence of functional modification of the lower canine (e.g. *Archaeolemur*, *Hadropithecus*). Thus, it is perfectly logical to postulate a common ancestral stock for the Lemuriformes and the Lorisiformes in which the tooth-scraper was already developed, and this is one of the reasons for inclusion of such a hypothetical stock in figure 1. Since the living offshoots of this stock are now confined to the Southern land-masses (Africa + Madagascar, India, S.E. Asia), it is likely that the ancestral representatives were also present in the south (e.g. see McKenna 1967). The existence of such a stock in the early Tertiary of Africa would explain the relatively easy colonization of Madagascar and the development of the *Progalago* group in the African Miocene. On the other hand, the lack of suitable early Tertiary deposits in Africa would explain why no fossil traces of this hypothetical ancestral stock have been unearthed. The Eocene Adapinae and Notharctinae and the hypothetical lemur/loris stock probably shared a common ancestry at a much earlier stage, during the initial radiation of the Order Primates. Since many of the characters shared by these three groups are ancestral Primate characters, there is only slim evidence of a specific relationship between them; but such a relationship can perhaps be inferred. In the past, emphasis on northern continental evolution and lack of fossil material from the south has forced most authors (e.g. Simpson, Simons) to search for an ancestral Primate stock in the northern hemisphere. This probably explains why the Adapinae and Notharctinae have been regarded as direct ancestral forms and why such disproportionate attention has been given to the Plesiadapidae (Le Gros Clark 1962), Microsyopidae (Szalay 1969) and other groups with Palaeocene representatives. This, despite the fact that these latter forms – even accepting the dubious proposition that their molar teeth *are* specifically Primate-like – are cranially far more specialized than most living lemurs and lorises. The very fact that the relatively well known early Tertiary northern deposits seem to lack generalized early Primate material (other than optimistically allocated molar teeth) indicates that some of the earliest phases of Primate evolution could have occurred in the south. If this were the case, then the Adapinae and the Notharctinae probably represented peripheral northern representatives of an early southern Strepsirhine stock, with early Adapines probably providing the direct ancestors of the Notharctinae (as implied by McKenna 1967). According to this view, the African galagines and lorisines are the specialized remnants of a once generalized stock which gave rise to the lemurs of Madagascar, and shared an earlier common ancestry with the northern Eocene lemuroids. Thus, in discussing the evolution of the Malagasy lemurs, it is for most purposes sufficient to consider the radiation of the lemur/loris stock in isolation (figure 1; see also Charles-Dominique & Martin 1970). In the absence of evidence to the contrary, the fairly clear dichotomy between the extant Lorisiformes and Lemuriformes indicates that a very small number of ancestral lemur species succeeded in colonizing Madagascar in the early Tertiary. Subsequently, the gradual increase in width of the Mozambique Channel greatly reduced the probability of further emigration to the island and thus permitted adaptive radiation in Madagascar to occur as a virtually closed system. Over a wider front, this explains why the entire fauna and flora of Madagascar, whilst exhibiting various fundamental affinities with groups elsewhere (but mainly in Africa), exhibit an extremely high proportion of endemic species (approximately nine-tenths overall). On the balance of present evidence, the following basic assumptions can be made in discussing the evolution of the Malagasy lemurs:

(i) As part of the general process of continental drift, the Mozambique Channel gradually increased in width throughout the late Mesozoic and Early Tertiary, perhaps with some fluctuations due to changes in sea-level.

(ii) Most of the faunal and floral elements now represented in Madagascar can be regarded as essentially of African origin (as argued by Simpson (1943) and Millot (1952)).

(iii) Madagascar exhibits, and has probably exhibited throughout its history, sufficient geographical and climatic fragmentation into subzones to permit rapid diversification of any species which succeeded in establishing themselves on Madagascar.

(iv) Since a water barrier of some kind has probably surrounded Madagascar throughout the evolutionary history of the placental mammals, emigration of the latter to Madagascar probably occurred by chance rafting along the lines suggested by Millot, perhaps via intervening islands ('sweepstake routes' of Simpson) and probably through discharge of uprooted trees by the River Zambesi into the Mozambique Channel.

(v) Given the probable nature of vegetational rafts (uprooted trees and other forest debris) and the predominance of African faunal influences, East African arboreal mammals adapted to a climate similar to that prevailing in West Madagascar would have had the greatest chance of successful emigration to the island.

The only difficulty at the present time derives from a paucity of information on the exact geophysical relationships of Madagascar. Wegener and Du Toit differed in their views both on the original location of the island (alongside Mozambique and Tanzania, respectively) and on the sequence of separation of Africa, Madagascar and India. In Wegener's view, India broke away from Madagascar and Africa at an early stage, and Madagascar became definitively separated from Africa at some time in the early Tertiary. Du Toit, on the other hand, suggested that India and Madagascar broke away from Africa soon after the Jurassic and that an attachment between Madagascar, India and South America persisted until the late Cretaceous. But, as a rider to this, Du Toit was forced to propose a temporary re-union between Madagascar and Africa during the Oligocene, without explaining exactly how this would have occurred. In fact, there is fairly sound geophysical evidence for a major separation between India and Madagascar/Africa, in that there is a mid-oceanic ridge between these two continental blocks which could have acted as a source of sea-floor spreading. Further, Walker (1967*a*) has summarized the available evidence, which indicates on balance that Madagascar was originally joined to Mozambique rather than to Tanzania. Thus, Wegener's concept of the separation of Madagascar seems to be the more reliable. However, it is not yet clear *how* Madagascar was separated from Africa, since there is no well-established evidence of sea-floor activity between these two land-masses. For this reason, no firm conclusions can yet be drawn about the actual course of separation; it seems likely that some kind of water-filled rift existed between East Africa and Madagascar from a quite early date, but there is no clear information on the timing and uniformity of the process of establishment of the Mozambique Channel. When such information is available, it will be possible to examine in greater detail the history of possibilities for emigration between East Africa and Madagascar.†

THE SYSTEMATIC DISTRIBUTION OF BEHAVIOURAL CHARACTERS‡

1. *General activity*

One conspicuous feature of the Malagasy mammalian fauna as a whole is the preponderance of *nocturnal* species. The majority of the extant lemur species are typically nocturnal, and in the other three main groups of endemic Malagasy mammals (insectivores, rodents, carnivores) nocturnal activity is the general rule. This is one of the obvious signs of imbalance in the surviving Malagasy fauna: the larger lemur species are virtually the only endemic mammals typically active during the daytime. Table 3 shows the general distribution of nocturnal adaptation in the four main groups of extant lemur genera. This breakdown clearly shows that the majority (7 genera, 10 species) are nocturnal, whilst relatively few forms (3 genera, 6 species) are definitely diurnal in habits. Since all four lemur groups include nocturnal species, it seems likely that nocturnal activity was the ancestral pattern for the lemurs, particularly since the morphologically least specialized forms are all nocturnal (Mouse Lemur group). The Cheirogaleinae are also anatomically closest to the Afro-Asian Strepsirhini (Lorisinae/Galaginae) – and the latter are without exception nocturnal.

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† Walker's discussion of this topic has now been published (Walker 1972).

‡ Photographs illustrating various behavioural features of lemurs are grouped at the end of this article (figure 16, plates 34 to 38).

A major characteristic of the nocturnal Afro-Asian and Malagasy Strepsirhines is the possession of a membraneous tapetum lucidum behind the retina (e.g. see Wolin & Massopust 1970), which reflects an orange-red glow when the animals are observed by torch-light. Indeed, use of a headlamp to spot reflexions from the tapetum provides one of the basic methods for studying nocturnal Strepsirhini at night (Petter & Petter-Rousseaux 1964; Jewell & Oates 1969; Petter & Hladik 1970; Charles-Dominique 1971, 1972; Martin 1972). The development of a tapetum is generally regarded as an adaptation for nocturnal vision,† since an analogous structure is found in a number of other mammals which feed at night (e.g. some carnivores and ungulates), and since the clearly diurnal monkeys and apes lack such a membrane. It is therefore surprising to find that several of the diurnal and crepuscular lemurs also exhibit a tapetum.

Table 3. Characteristic periods of activity in the extant lemurs

(Based on Petter (1962*c*) modified by personal observations.)

	diurnal	crepuscular	nocturnal
Mouse Lemur group	—	—	*Microcebus* *Allocebus* *Phaner* *Cheirogaleus*
True Lemur group	*Lemur*		
	—	*Varecia* *Hapalemur*	*Lepilemur*
Indri group	*Indri* *Propithecus*	—	*Avahi*
Aye-aye	—	—	*Daubentonia*

A distinct reflected glow can be perceived with some *Lemur* species, *Hapalemur*, *Indri* and *Propithecus* (Pariente 1970; P. Charles-Dominique & C. M. Hladik, personal communication; author's personal observations). In most of these cases, the histological basis of a tapetum has been identified (Wolin & Massopust 1970). Sleeping-groups of these lemurs can easily be located at night with a headlamp, and it is difficult to distinguish nocturnal species from diurnal species without practice. The presence of this apparent adaptation for nocturnal vision in these diurnal and crepuscular forms provides further confirmation that the ancestral lemurs were nocturnal in habits.

Curiously, *Lemur macaco* subspecies, *L. rubriventer* and *Varecia variegata* do not exhibit a clearly identifiable tapetum, despite the fact that these species are generally more crepuscular than *Lemur catta*, *Indri indri* and *Propithecus verreauxi*. Pariente (1970) has shown that the former three species have heavy pigmentation of the ocular fundus, whereas Wolin & Massopust (1970) indicate that *Lemur macaco fulvus* may possess a histological layer representing a weakly developed tapetum. These two observations together indicate that there has been pronounced modification of an original tapetum in these three lemur species. However, the author has located *L. rubriventer* at night by means of reflexion from the eyes, so this difference is probably only quantitative, rather than qualitative. The reasons for this difference remain obscure.

The retention of the tapetum in some diurnal lemurs, despite their apparent behavioural adaptation to daytime activity, raises an important question. Since so many lemur species (at least 14) have recently become extinct, it is possible that these extant diurnal forms have quite

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† Pirie (1959) reports that the tapetum of *Galago crassicaudatus* incorporates riboflavin crystals and suggests two mechanisms whereby the tapetum might assist nocturnal vision in this species.

recently modified their activity patterns to fill vacant niches (remembering that separation is possible on a temporal, as well as spatial, basis). This may, in fact, have led to an increase in population of certain species which are now diurnal. In Ampijoroa (figure 6*b*) the author observed *Propithecus verreauxi coquereli*, *Lemur mongoz* and *Microcebus murinus* feeding upon the same food-source (kapok flowers and fruits) in temporal succession (diurnal: crepuscular: nocturnal). This indicates that there is some mechanism for mutual avoidance between species feeding on the same trees. It was also observed in Berenty that *L. catta* may occasionally feed during the night. This provides support for the assumption that the tapetum is an aid to nocturnal vision, and may also support the suggestion that some lemur species have recently modified their patterns of activity.

Walker (1967*b*) has demonstrated that the extant diurnal lemurs and the subfossil forms have smaller orbits (relative to cranial length) than the surviving nocturnal forms. Since the subfossil species are also the most specialized in cranial anatomy (with the exception of the surviving Aye-aye), it is probable that the subfossil forms were specialized for diurnal feeding on plants not extensively exploited by the nocturnal species (e.g. terrestrial vegetation), or for feeding upon plant foods which necessitated frequent movement from one tree to another.

It is also important to examine seasonal patterns of activity in the lemurs. Unfortunately, there is little information available on annual dietary patterns in the lemurs. However, the Cheirogaleinae do show a clear-cut seasonal pattern, in that the Dwarf Lemurs (*Cheirogaleus medius*, *C. major*) undergo a period of dormancy (equivalent to hibernation in northern latitudes) during the main part of the dry season. Dormancy in *Cheirogaleus* probably covers most of the period June to September, regardless of local forest conditions. It has been widely stated that *Microcebus murinus* is similarly dormant during this period; but field observations (Martin 1972) indicate that this is unlikely. Such statements are probably based on observations that Mouse Lemurs nest in groups in hollow trees and that *Microcebus* shares with *Cheirogaleus* the ability to store fat reserves in its tail. It has also been reported that *Microcebus murinus* will become torpid under certain conditions in captivity (Weidholz 1932). However, it is clear from Weidholz's discussion that such torpor does not provide evidence for dormancy (misleadingly called 'aestivation'), since it is primarily temperature-dependent. Torpor is not triggered by day-length reduction, lack of food, or desiccation. It is conceivable that Mouse Lemurs may enter a state of torpor under natural conditions when temperatures are remarkably low; but no evidence for this has yet been provided. It is interesting to note, however, that some of the Cheirogaleinae apparently exhibit imperfect control of body temperature in captivity (Bourlière & Petter-Rousseaux 1953; Bourlière, Petter & Petter-Rousseaux 1956).

As far as other lemurs are concerned, it can only be said that the species in most areas of Madagascar (figure 6*a*: areas W_1, W_2, NW and N) are subject to a marked dry season, and that their behaviour should be adapted to cope with an annual period of potentially restricted food-supply. Evidence for a period of poor food supply has been provided for *Lepilemur mustelinus* (area W_1) by Charles-Dominique & Hladik (1971).

2. *Nesting patterns*

All living lemur species rest in trees during periods of inactivity, sheltering in nests of some kind or in relatively dense foliage. The type of retreat used correlates closely with the pattern of activity: the nocturnal forms (*Avahi* excepted) have a nest of some kind (spherical leaf-nests, tree-hollows, tangles of vegetation), whilst the diurnal forms (and *Avahi*) simply rest in the forks of large branches. The two clearly crepuscular genera (*Varecia*, *Hapalemur*) are intermediate in the sense that the adults rest on open branches, whilst the babies are initially left in natural 'nests' provided by bundles of epiphytes and the like (Petter 1962*c*). This distinction correlates with a general tendency for the nocturnal and crepuscular forms to leave their offspring in nests or in foliage while foraging (see p. 343). Some of the nocturnal genera (*Microcebus*, *Allocebus*?, *Daubentonia*) construct spherical leaf-nests, wedged between ramifying branches, while the others generally make use of available hollows (*Cheirogaleus*, *Phaner*, *Lepilemur*). In the case of *Microcebus* and *Phaner*, both tree-hollows and leaf-nests can be used, according to local conditions.

The morphologically unspecialized Cheirogaleinae are essentially similar in that all genera use nests of some kind, and there is a remarkable resemblance between the spherical leaf-nests of the Mouse Lemur and those constructed by some *Galago* species (Charles-Dominique 1971, 1972). The fact that the aberrant Aye-aye builds a nest along the same basic lines (Petter & Petter-Rousseaux 1967) suggests that the ability to build spherical nests may be an ancestral Strepsirhine pattern. The use of tree-hollows, natural foliage cover, and even open branches, can be interpreted as a result of evolutionary loss of this ability, correlated with development of baby-carriage on the fur and the adoption of diurnal habits. Petter *et al.* (1971) report that *Phaner furcifer* makes use of unoccupied leaf-nests of *Microcebus coquereli*, and Petter (1962*c*) has reported finding two adult *Cheirogaleus major* in a leaf-nest. It is not certain whether *Phaner* and *Cheirogaleus* can construct leaf-nests themselves; but they certainly do make use of them.

The utility of a well-defined nest depends upon several factors. In the first place, nocturnal species are more vulnerable to visually oriented predators when resting during the daytime than are diurnal species resting at night. Secondly, the need for a nest – and the ease with which it may be found or constructed – varies inversely with body-size. The smallest lemurs (*Microcebus murinus*) probably require a nest for a number of reasons (e.g. thermoregulation), and they can locate or build a suitable retreat relatively easily. The largest lemurs, on the other hand, have fewer requirements for an established retreat, and they would be hard put to find or construct a hiding-place of adequate size. Thirdly, there is the question of requirements for reproduction (p. 343). Smaller species which do not carry the infant(s) on the fur (e.g. Cheirogaleinae) need a nest as a protected place to leave their offspring during foraging periods. Species which carry the infant(s) on the fur from birth onwards (e.g. Indriidae) have no such requirement. The same dichotomy is found in the Afro-Asian Lorisiformes: the Bush-babies (Galaginae) build or occupy nests in which they may leave the young, which are not usually carried on the fur. By contrast, the lorises and pottos (Lorisinae) do not build nests and carry their young on the fur most of the time. (N.B. This otherwise distinct separation between the Galaginae and the Lorisinae is obscured by the fact that most or all Lorisiformes exhibit 'baby-parking' during periods of nocturnal activity.) The special relationship between nest-building and infant-deposition links up with the first condition, in that babies left in a nest are more vulnerable during the daytime than during the night.

It has already been shown that the ancestral lemurs were probably nocturnal in habits, and since they were probably small in body-size as well (in view of the generally small size of early mammals), two conditions for nest-building were present in the ancestral stock. In the section on reproduction (p. 340), it is shown that there is a good case for nest-deposition of babies in early mammals (and hence in early Primates). Thus, it can be concluded that the early lemur inhabitants of Madagascar probably used nests of some kind. Once again, the Cheirogaleinae prove to have remained the least specialized among the extant lemurs. This particular character of nest-use provides a clear link between the Galaginae and the Cheirogaleinae (probably based on ancestral Strepsirhine characters). The Aye-aye, though specialized in many other respects, seems to have remained primitive in the retention of a nocturnal habit and the ability to construct a spherical leaf-nest. This is one of many cases of 'mosaic evolution' (i.e. independent specialization of characters) in the lemurs.

3. *Diet*

Petter (1962*c*) has pointed out that the surviving lemurs form a spectrum from omnivorous to specialized folivorous forms. The main groups of lemurs are once again internally consistent in their adaptations. The members of the Cheirogaleinae are more-or-less omnivorous, eating fruits and insects, whilst the Indriidae are frugivorous/folivorous. The Aye-aye is a specialized frugivore/insectivore, feeding upon a particular range of fruits and concentrating mainly on wood-boring grubs, which are attained by using the specialized rodent-like incisors and the filiform middle finger of the hand (Petter & Petter-Rousseaux 1967). As with the other features so far discussed, the Lemurinae exhibit the greatest diversity: The species of the genera *Lemur* and *Varecia* feed predominantly on flowers and fruits, whilst *Hapalemur* and *Lepilemur* are more-or-less folivorous. *Hapalemur* exhibits a general tendency to specialize on bamboo leaves (Petter & Peyrieras 1970), though fruits may be eaten on occasion, whilst *Lepilemur* appears to exhibit local specialization on the leaves (and sometimes flowers) of a few plant species. For example, Charles-Dominique & Hladik (1971) have reported that in the late dry season *Lepilemur mustelinus* in the semi-arid bush near Berenty (figure 6*b*) feeds heavily on two *Alluaudia* species, whilst in the adjacent (lusher) gallery forest it feeds mainly upon the leaves of the kily tree (*Tamarindus indica*). This spectrum of dietary preferences is the main indicator of ecological separation among the lemurs. Even though it is possible to find up to 10 sympatric species in some areas, differences in diet and times of feeding ensure that direct competition is usually lacking.

There are no obvious behavioural clues to the original dietary preferences of the lemur ancestors which colonized Madagascar, since the living forms exhibit such diversity. However, general considerations of the evolution of mammalian dental patterns provide a sound basis for interpretation. It is now generally accepted that the early placental mammals were essentially 'insectivorous' (i.e. consumers of small animal prey), and that the various mammalian Orders have gradually become specialized away from this condition – most lines tending towards an increased intake of plant food and a few tending towards concentration upon animal prey of various size-classes. Szalay (1968) has proposed that one of the major developments in the early evolution of the Primates was an 'increasing occupation of feeding on fruits, leaves and other herbaceous matter' and has pointed out that this trend would have been accompanied by a gradual shift from relatively simple teeth with sharp, high cusps (for piercing and shearing) to teeth with lower, more bulbous cusps supplemented by accessory conules.† Szalay also made the significant observation that the first steps in this direction would necessarily have been *behavioural* modifications, leading to subsequent morphological specialization.

All of the living lemurs consume a considerable proportion of plant food. This indicates that the ancestral lemurs had probably already evolved to some extent in the direction indicated by Szalay. Accordingly, the most primitive dietary pattern among the lemurs is represented by

† This trend was, of course, present in numerous mammal lines; the Primates were peculiar in that they generally followed this trend more *slowly* than other mammalian Orders. It is thus exceedingly difficult to identify early Primates purely on the basis of molar morphology.

mixed consumption of small animal prey (predominantly insects) and easily accessible plant products. Thus, the Cheirogaleinae have probably undergone less dietary specialization than the other lemurs; a fact which is reflected in the relatively primitive molar morphology of the Mouse and Dwarf Lemurs. The other groups of extant lemurs exhibit more complex molar teeth, and even the Aye-aye exhibits a number of specializations: the molar teeth are quadratic in form, although they are virtually devoid of surface detail on eruption (secondary reduction). Specialization upon plant food is generally accompanied by other behavioural and morphological specializations. Significantly, extremely specialized forms of locomotion (see p. 331) are found in those lemurs which consume relatively large quantities of leaves (Indriidae; *Lepilemur*; *Hapalemur*). There are also a number of modifications of behaviour and morphology directly associated with feeding activity. *Hapalemur* has a characteristic pattern of drawing elongated leaves through its mouth from one side to the other, holding the ends of each leaf with its hands. The green matter is chewed off with the cheek teeth, and the bare leaf petiole emerges on the other side of the mouth. *Lepilemur* shows even more pronounced modifications (Charles-Dominique & Hladik 1971; Hladik *et al.* 1971): this lemur browses directly on the leaves and flowers that form the major part of its diet, and restricts locomotion primarily to leaps necessary to visit a few branches each night. The alimentary tract has been vastly modified, such that the small intestine has been greatly reduced whilst the caecum and colon have been greatly expanded. *Lepilemur* is, in fact, poorly adapted for an exclusively folivorous diet, in that there is no appropriate specialization of the stomach for leaf-eating (cf. Colobinae of Africa and Asia). Direct digestion of the ingested matter is insufficient to provide the energy requirements of *Lepilemur*, and Hladik *et al.* (1971) have shown that this difficulty is overcome through the relatively simple mechanism of *caecotrophy*. Bacterial action in the caecum releases assimilable nutrients which are absorbed when the faeces are re-ingested during the diurnal resting period. Even with this mechanism, *Lepilemur* barely covers its energy requirements, and this explains why this lemur passes long periods of immobility even during its nocturnal phase of activity away from the nest (Petter 1962*c*; Charles-Dominique & Hladik 1971; personal observations). This provides a good example of the inherent fragility of species which evolve in the absence of pronounced competition (e.g. from well-adapted herbivores).

Examination of subfossil lemur species (other than those closely related to extant forms) shows that the molar teeth are generally quite complex. The only exception is *Megaladapis*, which has very simple upper molars of virtually tricuspid form; but in this large-bodied genus the great increase in surface area of the cheek teeth may to some extent compensate for a lack of surface complexity. *Archaeoindris* and *Palaeopropithecus* have rather more complex molar teeth, which are similarly quite large, and this indicates that they were better adapted for crushing food than those of *Megaladapis*. The most noticeable specializations of the cheek teeth are found in *Archaeolemur* and *Hadropithecus*. *Archaeolemur* exhibits quadritubercular teeth with the cusps combined to form two transverse ridges (bilophodonty). These teeth are superficially very similar to those found in Old World monkeys (Cercopithecinae and Colobinae). *Hadropithecus*, on the other hand, exhibits a less orderly arrangement of cusps organized on a modified quadritubercular plan. In both cases, it seems that there must have been extensive dental adaptation to cope with feeding behaviour similar to that of the African monkeys (extensive mastication of fruit and leaves?). In fact, a comparison of the dental patterns of *Archaeolemur* and *Hadropithecus* (Jolly 1970*b*) shows that there may be a functional dichotomy similar to that found between the Pongidae and the Hominidae (Jolly 1970*a*). Jolly interprets the similar dental specializations of *Hadropithecus* and the Hominids as an adaptation to 'small-object feeding', as opposed to feeding on relatively large plant food items (*Archaeolemur*; Pongidae). Walker (1967*a*) presents evidence indicating that both *Archaeolemur* and *Hadropithecus* were largely terrestrial, and it seems likely that *Archaeolemur* had feeding habits similar to those of terrestrial Cercopithecine monkeys, whilst *Hadropithecus* may have exhibited feeding behaviour similar to that of the gelada baboon (terrestrial feeding on small objects such as roots, grasses, etc.). There is certainly an undeniable pattern of cranial characters shared by *Hadropithecus*, the gelada and *Homo*, indicating a pronounced degree of functional convergence.

One can therefore trace several lines of specialization from an original insectivorous/frugivorous ancestral lemur stock, leading to varying degrees of concentration on fruit, flowers or leaves, and to reduction in the quantity of animal food consumed. Such specialization is correlated with changes in body-size, in that only the smallest lemurs can obtain sufficient insect food to cover an appreciable proportion of their energy requirements (cf. Charles-Dominique 1971). The larger lemur species are exclusively herbivorous, and this provides further evidence that the (generally large-bodied) subfossil forms fed upon vegetation.

In agreement with the general pattern, the most primitive feeding behaviour would seem to be that of *Microcebus murinus*. *Microcebus* has generally been described as mainly insectivorous, with a secondary preference for fruit. But it has now emerged (Martin 1972) that *M. murinus* has a broader diet than was originally supposed. Lesser Mouse Lemurs feed upon flowers and leaves, in addition to fruit, and they prey upon a number of small animals (spiders, small chameleons, tree-frogs, etc.) in addition to insects. Over and above this, it has now been observed that Mouse Lemurs feed upon sap exuding from lianes and tree-trunks (personal observations; P. Charles-Dominique & C. M. Hladik, personal communication). Since this broad (virtually omnivorous) diet correlates with an extremely primitive molar cusp pattern, it is highly likely that the ancestral lemurs were similarly omnivorous in habits.

Observations that some of the Cheirogaleinae feed upon sap and resins have recently uncovered a further tie between the African Galaginae and the Madagascar lemurs. Charles-Dominique (1971, p. 190) has reported that *Galago* species in Gabon generally include resins in the diet; indeed, some species (e.g. *G. elegantulus*) feed almost exclusively on these exudates. Following observations that *Microcebus murinus* frequently scores and licks tree-trunks and lianes, it was found that *M. coquereli* and *Phaner furcifer* rely even more upon this source of nutrients (Petter *et al.* 1971). In the case of *P. furcifer*, extensive specialization on sap, resins and flower secretions has occurred, and this dietary peculiarity apparently allows for exceptionally high population densities. Petter *et al.* have demonstrated that this specialized diet is matched by specialization of the anterior dentition and by special adaptation of the digestive tract (notably through great expansion of the caecum). Since similar dental specializations are present in the rare *Allocebus trichotis*, specialization on sap and resin-eating may have occurred in this species as well.

These observations underline the necessity to consider the *anterior dentition* (canines and incisors) as well as the cheek-tooth battery (premolars and molars) when discussing dietary adaptations. As already stated (p. 320), the Afro-Asian Lorisiformes and the Malagasy lemurs generally share a striking adaptation of the lower anterior dentition: The two canines and four incisors are styliform and almost horizontal, forming a 'tooth-scraper'. There has been a great deal of argument about the functions of this tooth-scraper. Roberts (1941) and Buettner-Janusch & Andrew (1962) state that the primary function of the tooth-scraper is that of grooming the fur, and this has been accepted by Simons (1962). Other authors – notably Avis (1961) – have maintained that the tooth-scraper has been developed as an adaptation for feeding, and that the grooming function is insignificant or completely lacking. There is no doubt that the tooth-scraper is used by many (if not all) lemurs and lorises for grooming; but this is probably a secondary function. Field observations have shown that the smaller-bodied Cheirogaleinae and Galaginae use the tooth-scraper to gather plant exudates, and it is likely that the horizontal arrangement of these anterior teeth has been primarily developed for scraping and prising. A. F. Richard (personal communication) has observed *Propithecus verreauxi* feeding extensively on bark, using prising actions of the modified tooth-scraper. Since the lower canines have (remarkably) undergone complete modification, a novel combination of selection pressures must be invoked to explain this as an early development in the ancestral lemur/loris stock:

(1) The early development of manual mobility in Primates alleviated the grasping functions of the anterior dentition (transfer of prehensile function from the snout to the hands).

(2) The partial switch to plant food reduced dependence upon trapping small animal prey with the anterior dentition.

(3) The radiation of the vascular plants provided new opportunities for sap-eating in addition to fruit- and leaf-eating. Licking of plant exudates could have preceded adaptations for scraping.

(4) Small-bodied mammals would have been less dependent upon canine teeth for defence against predators, relying instead upon rapid escape.

Given these factors, it is conceivable that the scraping function of the anterior teeth was more important for sap-eating species than the stabbing, prehensile function of the lower canine. Nevertheless, it is obvious that functional modification of the canine was only possible under exceptional conditions, since in many of the larger lemurs there has been secondary modification of the first lower premolar as a caniniform tooth. Thus, although it is not impossible that the Lorisiformes and the Lemuriformes independently produced a 'tooth-scraper', it seems superfluous to suggest such parallelism, particularly in view of the widespread occurrence of this structure in the southern Strepsirhini. As is stated by Walker (1969): 'The fact that the Miocene lorisoids of East Africa had a grooming-comb as developed as modern lemurs and lorisoids supports the idea that these two major groups could have shared a common ancestry in pre-Miocene times in Africa.'

The anterior dentition of some lemurs has also undergone modification in other respects. The upper incisors are generally relatively small, peg-like teeth, and the canine usually retains its typical mammalian form. However, in specialized leaf-eating forms the incisors are greatly reduced (*Hapalemur*) or entirely absent (*Lepilemur*, *Megaladapis*) in the adult. This may be associated with a 'browsing' habit analogous to that of various ungulates, as has been suggested by Avis (1961). The upper lip is used as a flat plucking pad operating against the inclined lower anterior teeth.

Alternatively, the upper incisors can become enlarged and protuberant, as has been noted for *Phaner* and *Allocebus* by Petter *et al.* (1971). This development may well be associated with further specialization on sap-eating, with the protuberant upper teeth acting in concert with the tooth-scraper to prise exudates from tree-trunks and lianes. This kind of development may indeed have been involved in the evolution of the Aye-aye. An early precursor of *Daubentonia* might well have specialized on a mixed diet of sap and insects living in crevices on tree-trunks, using procumbent upper and lower anterior teeth to obtain both food items. Competition between successive populations of proto-*Daubentonia* species, combined with the evolution of

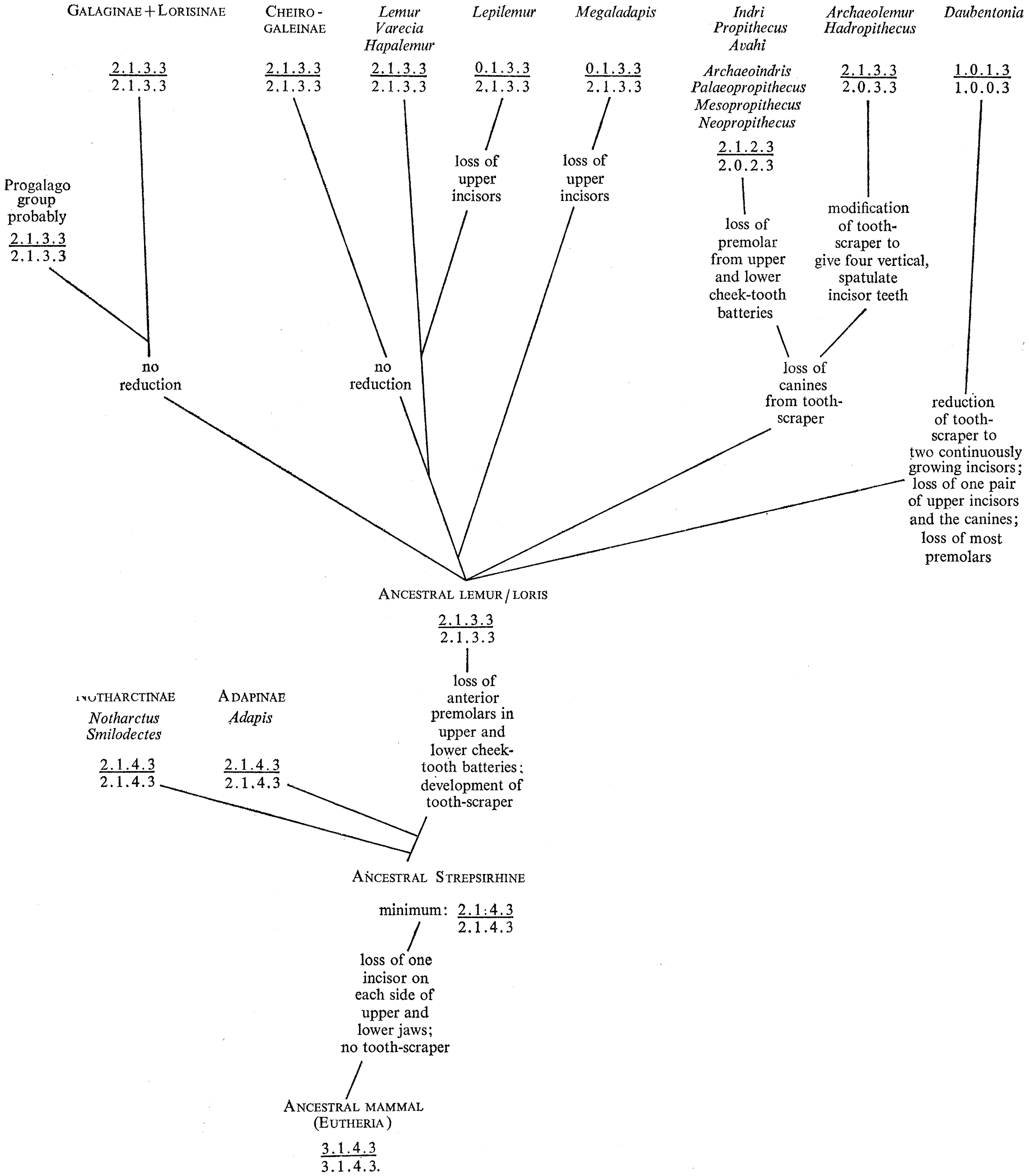

Figure 11. Chart showing characteristic dental formulae of the main groups of Strepsirhini, indicating the simplest hypothesis for evolution through loss of teeth and specialization of the remaining teeth. (Uncertainty about the dental formula of modern Indriidae has been resolved by Spreng (1938).) Derivation of the Aye-aye (*Daubentonia*) from a stock in which the tooth-scraper was already present is supported by the fact that all living Strepsirhini exhibit similar modifications of the sublingua as a reinforced structure for cleaning the lower anterior teeth (see Bluntschli 1938).

anti-predation mechanisms in the insect prey (accentuation of wood-burrowing), could have brought about the extreme specialization of the Aye-aye. It is noteworthy that a similar complex of characters for feeding on wood-boring insects has been developed quite independently in two nocturnal marsupials (*Dactylonax*, *Dactylopsila*). In both cases, the anterior dentition has been reduced, with a pair of strong, continuously growing incisors in the upper and lower jaws and one finger of each hand has become filiform. Certainly, it is quite possible that the dental formula of *Daubentonia* $\left(\frac{1.0.1.3}{1.0.0.3}\right)$ has been derived from the basic lemur/loris formula $\left(\frac{2.1.3.3}{2.1.3.3}\right)$ since it is only necessary to postulate *reduction* in the number of teeth (figure 11). In this process of reduction, *Daubentonia* has even lost the upper canine – something which is otherwise unique among the Strepsirhini.

The dental formulae of the various known Strepsirhine genera are indicated in figure 11, showing how it is possible to derive the various formulae from ancestral patterns exclusively on the basis of *reduction* from a basic Strepsirhine pattern $\left(\frac{2.1.4.3}{2.1.4.3}\right)$. The Afro-Asian Lorisiformes and the Malagasy Lemuriformes can all be derived from a hypothetical lemur/loris ancestral stock with a dental formula of $\frac{2.1.3.3}{2.1.3.3}$ which is retained in all known Lorisiformes and in the Cheirogaleinae and Lemurinae (except *Lepilemur*). *Lepilemur* and *Megaladapis* differ from this pattern only in the loss of the upper incisors (a trend also seen in *Hapalemur*, which has extremely small upper incisors). The remaining lemurs are characterized by reduction and modification of the tooth-scraper and loss of premolar teeth from the cheek-tooth battery. In living Indriidae, *Archaeoindris* and *Palaeopropithecus*, the canine teeth have been lost from the 'tooth-scraper', and the remaining incisors have tended to become more spatulate and more vertical. These forms have all lost one pair of premolars from the upper and lower jaws. *Archaeolemur* and *Hadropithecus* exhibit similar reduction and modification of the tooth-scraper; but they show no reduction in the cheek-tooth battery. Finally, *Daubentonia* has undergone the extreme reduction already discussed above.

Naturally, since all of these dental modifications are based on a process of *reduction*, it cannot be excluded that various lines have undergone loss of teeth quite independently. Figure 11 simply illustrates the picture obtained when parallel reduction is assumed to be minimal. In the absence of fossil evidence to the contrary, there is no real justification in suggesting a more complex arrangement.

4. *Locomotion*

The dominant feature of locomotion in the Malagasy lemurs is that of adaptation for *arboreal progression* – a feature which is similarly fundamental to the loris/bush-baby group and to the Haplorhini (tarsiers, monkeys, apes and man). Although a small number of living Primate species are not typically arboreal in habits, the inherent characters of an arboreal ancestry can be clearly recognized throughout the Order. An integral feature of the basic arboreal adaptation of the Primates is the grasping function of the hand (manus) and foot (pes). Whereas most other arboreal mammals progress by means of grappling actions of claws present on all digits, the majority of Primates are able to grasp relatively narrow supports by operating the first digit of the hand and the foot (pollex and hallux respectively) in a pincer action against the other digits. The grasping action is typically most evident in the foot, and it is somewhat less consistent in its range of occurrence in the Primate hand. Apart from the human foot, in which the grasping hallux has been radically modified as a result of relatively recent adaptation for bipedal progression, every single extant Primate species exhibits a well-developed hallux and a marked pincer-action in the foot. This feature also seems to have been present in those fossil Strepsirhine species for which adequate information is available (Notharctinae; some subfossil lemur species).

The grasping function of the Primate hand is far more variable, and is heavily dependent upon the particular mode of locomotion adopted by each species. In those Primate groups in which claws have been developed on 18 of the 20 digits (aye-ayes – Daubentoniidae; tamarins and marmosets – Callithricidae), the hand exhibits little grasping activity, although the hallux has a clear-cut grasping function and differs from the other digits in the possession of a nail instead of a claw. Alternatively, those Primates which use the hands extensively for arm-swinging locomotion exhibit a tendency to reduce the thumb, since suspension can be ensured by a hooking action of digits II to V. With these exceptions, manual grasping ability is generally characteristic of Primates, to the extent that objects can be picked up and held in one hand. Napier (1961) restricts the concept of 'true opposability' in the Primate hand to cases where there is a definite morphological basis for rotation (rather than a simple hinge-movement) at the carpo-metacarpal joint of the pollex. Accordingly, many Primate species (i.e. those other than the Old World monkeys, apes and man) are not regarded as possessing 'opposability' of the thumb, although the hand is utilized as a grasping pincer (e.g. in many lemurs). Napier's definition of 'opposition' was largely intended to highlight the special development of the human hand, and when this definition is used in general discussions of grasping ability in Primate hands, it is difficult to avoid confusion. This is well illustrated by the following quotation (Napier 1971, p. 182): 'The prosimian thumb operates on a hinge mechanism but, being set at an angle to the hand, it opposes the fingers as the jaws of a pair of pliers "oppose" each other. As we have seen the true opposability of the human thumb involves a large element of rotation which is totally absent in prosimians. The "opposition" of the prosimian thumb is called "pseudo-opposition".'

Concentration on human hand-use has also tended to obscure the fact that the grasping action of the *foot* has been far more important in Primate evolution. The utility of Napier's definition of 'opposability' is further limited by the fact that no parallel study has yet been made of the (typically far better developed) morphological basis for grasping in the Primate foot.† However, since the term 'opposition' has been so defined, it is preferable for the time being to refer simply to 'grasping hands and feet' in discussing lemur evolution. All of the Malagasy lemurs for which evidence is available exhibit a pronounced grasping adaptation of the foot, although the grasping ability of the hand is more variable, as already noted in the case of the Aye-aye.

In association with locomotion through grasping rather than claw-grappling, most Primates bear *nails* rather than claws on the terminal phalanges of the digits. The two main exceptions are the Daubentoniidae and the Callithricidae (hallux excluded). Apart from this, the only departure from the essential Primate pattern of nail-bearing digits is found in the Strepsirhini and the Tarsiers. In these, certain pedal digits bear elongated, curved nails which project away from the dorsal surface of the terminal phalanges. The Strepsirhini bear such a nail on digit II of the foot, whilst the Tarsiers bear one on digits II and III. It seems that these pedal claws are mainly used for cleaning the pelage, and they are usually referred to as 'grooming claws'

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† D. J. Morton's classic paper (1924) still provides the most useful source of general information about Primate foot structure.

although they are structurally far more similar to nails. It is significant that digit II is typically adapted for this grooming function, since this digit is not essential for the grasping function of the foot; adequate grasping power can be supplied by a pincer action between digit I (hallux) and digits III to V.

The special importance of these features in the Malagasy lemurs – and in Primates in general – has been critically re-evaluated by Walker (1967*a*) and Napier & Walker (1967). The characteristic pincer action of the hands and feet, the predominance of the grasping action of the foot over that of the hand, and the powerful development of the hallux are interpreted as adaptations essential for *hind-limb dominated arboreal locomotion.* In its most extreme form, this category of locomotion can be described as 'vertical-clinging-and-leaping' (Napier & Walker 1967). In this, the animal leaps primarily between vertical supports, thrusting off with the powerful back legs and swinging around in mid-air to take the first landing impact with the hind legs. The ability to cling and land with a pincer action of the feet is an integral part of such locomotion. Extreme vertical-clinging-and-leaping is found only in a minority of extant Primate species; but all living prosimians (and all of the well-known fossil forms accepted in this review as belonging to the Order Primates) exhibit some signs of hind-limb domination. Indeed, all of the well-known Eocene Primate groups (Adapinae, Notharctinae, early Tarsiidae, Omomyidae) exhibit such extreme hind-limb domination (Napier & Walker 1967) that it seems highly likely that they were adapted – at least to some extent – for vertical-clinging-and-leaping. In view of this, Napier & Walker suggest that vertical-clinging-and-leaping was the prevalent mode of Primate locomotion in the Eocene. The only obvious difficulty with this view stems from inclusion of the Plesiadapidae in the Primates, since there is no evidence whatsoever that *Plesiadapis* (or its relatives) exhibited any tendency towards hind-limb dominated locomotion or even grasping climbing. This fact is all the more incongruous in view of Napier's (1967) concept of a 'locomotor trend' in Primates from vertical-clinging-and-leaping (prosimian grade) through quadrupedalism (monkey grade) to brachiation and bipedalism (ape/man grade). It has yet to be explained why the 'earliest Primates' (viz. Plesiadapidae and other Palaeocene Primates), which were apparently clawed, quadrupedal runners, should have given rise to vertical-clinging-and-leaping prosimians as part of this 'locomotor trend'. This difficulty is, of course, overcome if the Plesiadapidae are recognized as quite unrelated to Primates.

The morphological correlates of hind-limb dominated locomotion extensively discussed by Walker (1967*a*), are summarized by Napier & Walker (1967):

(1) body-size small to medium;
(2) hind-limbs very long relative to forelimbs;
(3) humerus shorter than radius;
(4) femoral head tends to be cylindrical rather than spherical;
(5) pelvis has long iliac segment and short ischial segment;
(6) the grasping pes is well developed, and the hallux is very pronounced; digits II and III of the foot are relatively short;
(7) the calcaneus and navicular tend to be elongated in small-bodied forms;
(8) foramen magnum tends to point downwards rather than backwards.

It is maintained that these features possibly represent 'the earliest locomotor specialization of Primates'. However, a detailed comparison of Primates with other mammal groups would be necessary to establish which of these criteria unequivocally characterize grasping, hind-limb dominated locomotion and whether it is unique to the Order Primates. Only on this broad basis can the locomotor adaptations of fossil forms be analysed confidently.

Two of the criteria in the above list have been rigorously studied in prosimians by Walker. The ratio of the length of the humerus + radius to the length of the femur + tibia (intermembral index) is characteristically low in specialized vertical-clinging-and-leaping prosimians. Conversely, the ratio of the length of the radius to the length of the humerus (brachial index) tends to be high in such species. However, the latter criterion is not entirely satisfactory. Individual slow-climbing lorises may have higher brachial indices than those found in some vertical-clinging-and-leaping bush-babies (data from Walker 1967*a*), and the value of this index for discriminating locomotor adaptations in fossil Primates is very limited. It can be argued that the Lorisinae are derived from ancestors of an unspecialized Galagine type, and thus retain residual features of hind-limb dominated locomotion; but this does not facilitate functional interpretation of fossil Primate limb components.

In living Primates, the intermembral index gives a far more reliable indication of locomotor adaptation. In prosimians, there is an absolute distinction (regardless of body-size) between slow-moving quadrupeds (Lorisinae) and specialized vertical-clingers-and-leapers (*Lepilemur*; Indriidae; Galaginae; Tarsiidae), and the generalized quadrupedal forms (Cheirogaleinae; most Lemurinae; *Daubentonia*) are intermediate. However, certain inconsistencies arise in making precise statements about the locomotor patterns of these 'generalized quadrupeds'. *Microcebus* in fact exhibits several indications of hind-limb dominated locomotion, despite the fact that its intermembral index is very similar to that of *Cheirogaleus* – which is a clear-cut quadrupedal form with no tendency to vertical-clinging-and-leaping (see Martin 1972). Like the specialized vertical-clingers-and-leapers, *Microcebus* tends to hop, rather than run, across the ground, though its hopping is not fully bipedal as in (for example) the Indriidae. Although *M. murinus* is essentially quadrupedal in arboreal locomotion, Petter *et al.* (1971) report that *M. coquereli* is commonly observed leaping between vertical trunks. (This difference parallels that between *Galago demidovii* and *G. alleni* in Gabon – see Charles-Dominique 1971.) Similarly, *Hapalemur griseus* is most frequently observed leaping between fairly broad vertical trunks and branches, though its intermembral index does not differ significantly from that of *Varecia variegata* (a closely related, characteristically quadrupedal form). It is thus apparent that species with intermediate intermembral indices can exhibit different locomotor adaptations, whilst those with extreme intermembral indices do not. It can therefore be said that behavioural restrictions of locomotor patterns seems to precede morphological restriction; the typical locomotor patterns of the 'generalized quadrupeds' are inherent in the behavioural repertoire of each species, rather than dictated by specialized morphology.

Napier & Walker emphasized the elongation of the proximal tarsal bones which is characteristic of small-bodied vertical-clingers-and-leapers. As has been shown by Walker (1967*a*), this elongation can be analysed in terms of the lever-action of the hind-foot, following the principles established by Hall-Craggs (1965). The longitudinal axis of the tarsus (figure 12) can be represented by the combination of the calcaneus (C) and the cuboid (CU). The astragalus (A) rests upon the dorsal surface of the calcaneus and articulates with the tibia and fibula. The mid-point of this articulation can therefore be taken as the fulcrum of a lever operated in the overall extension of the hind-leg in leaping. The lever arm (LE) is represented by the calcaneal segment projecting behind the mid-point of the tibio-talar articulation. The load arm is represented by the remaining segment of the calcaneus and the cuboid, with the metatarsals and phalanges acting as a contact area for take-off and landing. As has been stated by Morton (1924), any lengthening of a foot which operates by *grasping* will occur in the heel region, providing the morphological basis for 'tarsi-fulcrumation'. (It follows from this that any elongation of the early Primate foot would have occurred in the calcaneus, rather than in the meta-tarsal area where it occurs in terrestrial saltatory mammals.)

On this basis, Hall-Craggs has calculated a 'foot-lever index' for Galagidae and *Tarsius* by taking the ratio of the length of the lever arm of the calcaneus (LE) to the combined length of the load arm of the calcaneus (LO) and the cuboid (CU). This index decreases with increasing specialization on vertical-clinging-and-leaping. However, it is difficult to apply this index to fossil material because of the rarity of discovery of associated calcanei and cuboids. Walker has instead calculated a 'calcaneal index', which is simply the ratio of the lever arm (LE) to the load arm (LO) of the calcaneus. Although this ratio does not take into account the functional co-ordination of the calcaneus and the cuboid in the lever action of the foot, it does give a fairly good indication of adaptation for vertical-clinging-and-leaping. With increasing elongation of the calcaneus, the part played by the cuboid becomes correspondingly less important.

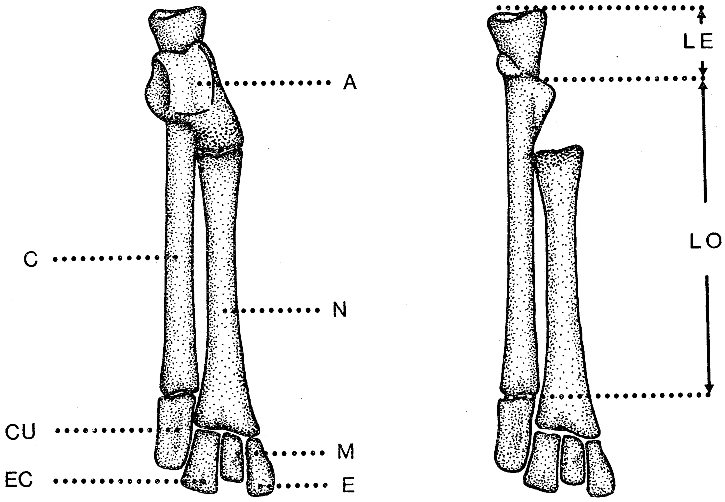

FIGURE 12. Diagram indicating the components of the Strepsirhine tarsus and the measurements taken on the calcaneus in order to calculate the ratio of 'lever arm' (LE) to 'load arm' (LO).

Key: A, Astragalus (Talus); C, Calcaneus; N, Naviculare; CU, Cuboid; EC, Ectocuneiform; M, Mesocuneiform; E, Entocuneiform.

Walker has plotted the 'calcaneal index' against the femur length on a logarithmic scale; but this method also has the draw-back that it is rare to find definitely associated fossil calcanei and femora. One solution to this problem is to plot the calcaneal index (CI) against the length of the lever arm (LE) of the calcaneus. Whereas the calcaneal index tends to decrease with increasing emphasis on the hind-limbs in locomotion, the length of the lever arm must increase with increasing body-size, irrespective of the relative length of the load arm of the calcaneus.† Although this method of plotting is not ideal, it does permit crude analysis of the adaptation of isolated fossil Primate calcanei, through direct comparison with the calcanei of living Primate species (figure 13).

† Measurements taken on single specimens from 24 representative prosimian species showed that the length of the lever arm is highly correlated ($r = 0.83$; $p < 0.001$) with maximum cranial length. Conversely, the length of the load arm was poorly correlated ($r = 0.12$; $p > 0.5$) with maximum cranial length.

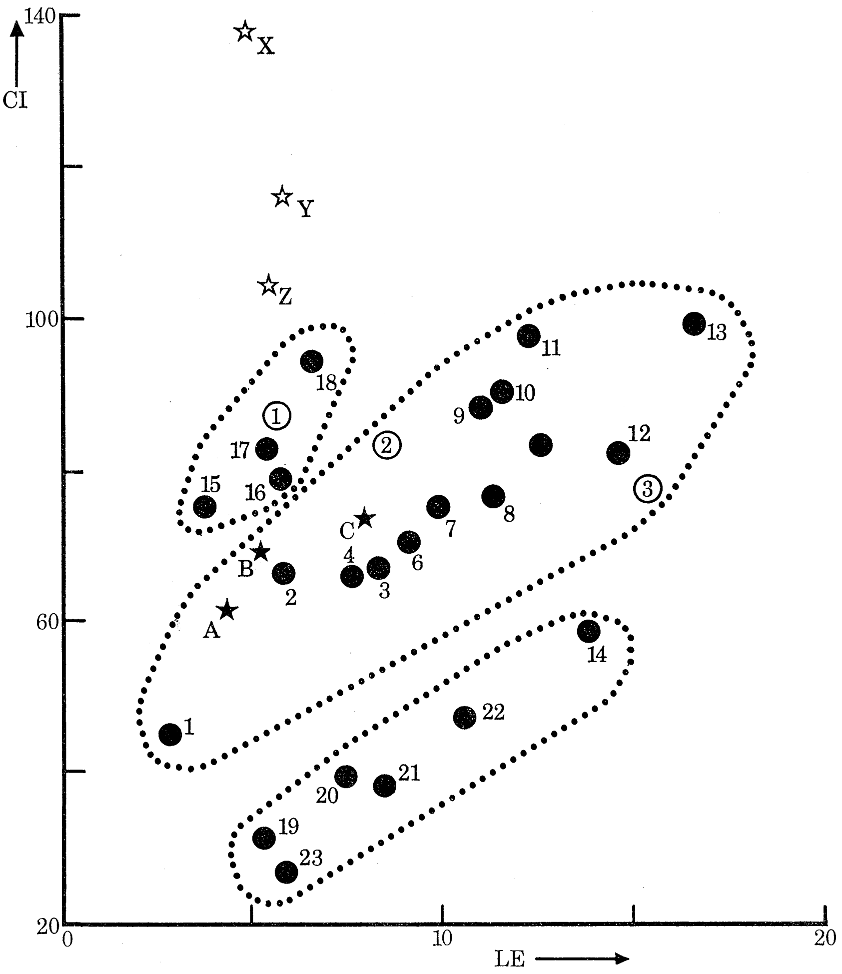

FIGURE 13. Graph showing the relationship between the calcaneal index (CI) and the length of the lever arm (LE) for the lemurs and various other mammals. *Key* (parentheses indicate number of specimens measured)

Numbered black circles:

Malagasy lemurs:

1. *Microcebus murinus* (2)
2. *Cheirogaleus major* (1)
3. *Lemur mongoz* (1)
4. *Hapalemur griseus* (2)
5. *Lepilemur mustelinus* (3)
6. *Avahi laniger* (1)
7. *Hapalemur simus* (1)
8. *Varecia variegata* (2)
9. *Daubentonia madagascariensis* (3)
10. *Lemur macaco* (2)
11. *L. catta* (2)
12. *Propithecus diadema* (1)
13. *Archaeolemur* sp. – subfossil (2)
14. *Indri indri* (1)

Living lorisoids:

15. *Arctocebus calabarensis* (2)
16. *Perodicticus potto* (3)
17. *Loris tardigradus* (3)
18. *Nycticebus cougang* (2)
19. *Galago demidovii* (4)
20. *G. alleni* (3)
21. *G. senegalensis* (7)
22. *G. crassicaudatus* (15)

(mainly based on data from Walker (1967*a*, 1970))

23. *Tarsius* sp.

Black stars:

Miocene lorisoids (after Walker 1970)

A. cf. *Komba minor* (1)
B. cf. *K. robustus* (1)
C. cf. *Progalago songhorensis* (1)

White circles:

New World Monkeys

1. *Callithrix* spp. (4)
2. *Aotus trivirgatus* (4)
3. *Ateles geoffroyi* (4)

White stars:

Tree-shrews

X. *Tupaia glis* (2)
Y. *Urogale everetti* (1)
Z. *Lyonogale tana* (3)

The (arbitrary) dotted lines in figure 13 indicate the three main categories of prosimian locomotion – specialized vertical-clinging-and-leaping (bottom section), 'generalized quadrupedalism' (central section), and specialized quadrupedalism (upper section). There is a clear-cut distinction between the slow-moving Lorisinae (15, 16, 17, 18) and the saltatory Galaginae (19, 20, 21, 22), which have a calcaneal index very close to that of *Tarsius* (23). Distinctions between the Malagasy lemurs on this basis are far less distinct (1 to 13), and only *Indri* (14) clearly falls into the specialized vertical-clinging-and-leaping range. This lack of distinction is partly due to the limitations of the technique of calcaneal measurement. The approximate location of the fulcrum can be taken either as the point where the lateral calcaneal facet for the astragalus meets the dorsal surface of the calcaneus (Hall-Craggs 1965), or as the point where the sustentaculum tali (on the right in figure 12) meets the lateral surface of the calcaneus (most of the data for figure 13). In either case, measurements taken with sliding calipers are not absolutely reliable, particularly when articulated specimens are involved. Nevertheless, it is clear that the lemurs do not generally exhibit the extremes of calcaneal development seen in extant members of the loris group (Lorisinae *vs.* Galaginae) and the living Tarsiidae. It is particularly interesting to note that the tail-less *Indri* (14) exhibits a markedly specialized calcaneus for vertical-clinging-and-leaping, whilst the closely related *Avahi* (6) and *Propithecus* (12) do not. The Cheirogaleinae and the Lemurinae, along with *Daubentonia*, *Avahi* and *Propithecus*, exhibit a generalized calcaneus. Among the Lemurinae, even those forms adapted for vertical-clinging-and-leaping (*Lepilemur*, *Hapalemur*) fail to show any specialization of the calcaneus.

This distribution indicates that the Strepsirhine ancestral stock was probably adapted for unspecialized hind-limb dominated locomotion of the kind now seen in *Microcebus*. The specialized locomotor patterns of the modern Lorisinae and Galaginae can be interpreted as a product of divergent evolution from this ancestral pattern. This interpretation is supported by the fact that the calcaneal indices of the Miocene lorisoids (calcanei assigned to *Komba* and *Progalago* by Walker 1970) fall within the general range of the Malagasy lemurs. If anything, the calcanei assigned to *Komba* and *Progalago* (black stars A to C in figure 13) indicate adaptation for quadrupedalism of a form intermediate between that exhibited by *Cheirogaleus* (2) and the extreme found in the Lorisinae (15, 16, 17, 18).

For the sake of general comparison, figure 13 includes data on three New World monkey species (circles: (1) *Callithrix* sp., (2) *Aotus trivirgatus*, (3) *Ateles geoffroyi*); and three tree-shrew species (white stars: (X) *Tupaia glis*, (Y) *Urogale everetti*, (Z) *Lyonogale tana*). It can be seen that the New World monkeys fall within the overall prosimian range, and that the calcaneal index of the clawed *Callithrix* is similar to that of the slow-moving Lorisinae. The tree-shrews, on the other hand, fall right outside the prosimian range, although they are not specialized slow-moving quadrupeds. The tree-shrews are also unusual in that the medium-sized, semi-arboreal *Tupaia glis* exhibits a *higher* calcaneal index than the larger terrestrial *Urogale everetti* and *Lyonogale tana*. In short, the Tupaiid foot lacks all of the features characteristic in the evolution of the Primate foot (grasping hallux; adaptation for hind-limb dominated locomotion).

While the data presented in figure 13 must be regarded as provisional, in view of difficulties inherent in measurement and in view of the small number of specimens measured, it is obvious that the structure of the calcaneus is a fairly reliable indicator of Strepsirhine locomotor adaptations. Extension of such measurements, with a large enough number of specimens to permit statistical treatment, should provide a sound basis for the interpretation of locomotor adaptations of fossil Primate species. The author has not yet been able to measure calcanei from Eocene

Primates; but a cast of a calcaneus from *Notharctus* (kindly provided by J. Fleagle of the Peabody Museum of Natural History, Yale) indicated that this Eocene Adapid had a calcaneus close to that of *Varecia variegata* in overall size and dimensions. This may indicate that *Notharctus* was less specialized for vertical-clinging-and-leaping than suggested by Napier (1967). Walker (1967*a*) gives the calcaneal index of *Notharctus* as 84.6 and that of *Adapis* as 89.5, and these figures generally indicate that the foot was not very specialized in these genera. However, *N. osborni* (Walker 1967*a*) apparently had an intermembral index of 64.6, which is almost identical to that of *Indri indri*, so it would seem that *Notharctus* had undergone specialization of the hind-leg (but not the foot) for vertical-clinging-and-leaping. This agrees with the hypothesis that the early Primates had already developed hind-limb dominated locomotion, but not specialization of the calcaneus.

The evolution of locomotion within the Malagasy lemurs can therefore be interpreted as follows: The ancestral form probably had a number of general developments of the foot (grasping hallux; extended load-arm of the calcaneus) underlying hind-limb domination. This general pattern has been retained in the Cheirogaleinae, Lemurinae, Indriidae (excluding *Indri*) and *Daubentonia*. Some Cheirogaleinae exhibit behavioural adaptations for quadrupedalism (*Cheirogaleus*, *Phaner*, *Allocebus*) whilst *Microcebus coquereli* exhibits a tendency to vertical-clinging-and-leaping. *Microcebus murinus* probably has the most generalized locomotor repertoire (Martin 1972). Among the Lemurinae, most species (*Lemur* spp.; *Varecia variegata*) tend to quadrupedalism, though most also exhibit some signs of hind-limb domination. *Hapalemur* exhibits a tendency towards vertical-clinging-and-leaping, whilst *Lepilemur* has become even more specialized for this kind of locomotion (decrease in intermembral index, but no specialization of the calcaneus). The Aye-aye is behaviourally specialized as a quadruped, though it shows little skeletal modification (intermediate intermembral index and calcaneal index). Finally, *Avahi*, *Propithecus* and *Indri* are behaviourally specialized for vertical-clinging-and-leaping and have low intermembral indices; but only *Indri* exhibits a calcaneus modified for this form of locomotion. All of these behavioural and morphological adaptations can be derived from an ancestral pattern rather like that found in the extant *Microcebus murinus*, and the same can be said of the loris group, if it is accepted that the Lorisinae and Galaginae have diverged from an intermediate common ancestor.

For a discussion of the probable locomotor adaptations of subfossil lemurs, the reader can only be referred to Walker's excellent study (1967*a*). Suffice it to say that some of the subfossil forms were apparently adapted for terrestrial life (e.g. *Lemur jullyi*, *L. insignis*, *Archaeolemur*, *Hadropithecus*), which may provide a simple explanation for their extinction at the time when the human invasion of Madagascar began in earnest. One genus (*Palaeopropithecus*) was evidently adapted for brachiation, as can be seen from the relatively long fore-limbs (high intermembral index) and the curved phalanges of the hands. *Megaladapis* remains an enigma. It has been suggested that this genus was arboreal, terrestrial or even aquatic; though a systematic search of the literature has failed to reveal any suggestion that *Megaladapis* was adapted for flying. Whatever the outcome, it is fairly obvious that the subfossil forms can be derived from a hind-limb-dominated ancestor of the kind suggested above. The calcanei of *Megaladapis* and *Archaeolemur* fit the general lemur pattern indicated in figure 13, but the dimensions are so large (particularly in *Megaladapis*) that a detailed comparison with living forms would require careful consideration of the allometric processes involved.

A final note should be added about the development of *claws* in Primates. It has been fashionable to assume that, because living reptiles and Insectivora have claws on all digits, the ancestral placental mammals must have had clawed extremities as well. It has aready been pointed out (Martin 1968*a*) that such *a priori* assumptions are not justifiable in the absence of adequate fossil evidence and a cohesive framework of interpretation. However, on the basis of this assumption it has been supposed that the tree-shrews, *Daubentonia* and the Callithricidae have 'retained' their claws from the ancestral Primate stock. In discussing *Plesiadapis*, Napier & Walker (1967) have tacitly accepted this interpretation. Such acceptance leads to serious inconsistencies in Napier's discussion of the evolution of vertical-clinging-and-leaping. Not one single living or fossil Primate genus which exhibits (or is assumed to have exhibited) even the least specialized level of vertical-clinging-and-leaping exhibits clawed extremities. Accordingly, one would not expect representatives of the prosimian grade in Napier's diagram of the evolution of Primate locomotion (1967) to have exhibited clawed extremities. Since the quadrupedal *Daubentonia* and the Callithricidae are presumed to have developed from this prosimian grade, these forms must have secondarily modified their nails to produce claws. Otherwise, there is no justification whatsoever for suggesting that the monkeys, apes and man are derived from ancestors with pronounced hind-limb domination; they would have to be separately derived from an early Primate stock which 'still' possessed claws on all extremities and exhibited quadrupedal branch-running. These inconsistencies are removed if it is accepted that *Plesiadapis* was not related to early Primates, and if it is proposed that the claws of the Aye-aye and marmosets and tamarins are secondarily modified nails.

Comparison of the extant lemurs provides support for secondary derivation of the claws of *Daubentonia*. A number of lemurs – particularly Cheirogaleinae – possess a central keel on each nail, terminating in a small point projecting beyond the distal margin of the nail. This point can be used as a tiny claw when extra attachment to a support is needed. When *Microcebus murinus* is held suspended below a broad support, the terminal phalange of the hallux is folded over so that the dorsal surface – and thus the point on the nail – is applied to the support. Petter *et al.* (1971) have reported that *Phaner furcifer* exhibits an extremely pronounced keel on each nail, and the author has observed this same character in *Allocebus trichotis*. Charles-Dominique (1971) discusses parallel developments in *Galago* (*Euoticus*) *elegantulus*. In all of these species, resins represent a major proportion of the diet (see p. 328), and the pointed keels on the nails can be interpreted as an adaptation for clinging to broad trunks whilst feeding on exudations of sap. Charles-Dominique (1971, p. 175) illustrates how folding of the terminal phalange is seen in all digits of *G. elegantulus* when the animal is supporting itself on a broad trunk surface. It is easy to imagine that, in the evolution of the Aye-aye, gradual concentration upon locomotion on broad trunk surfaces may have led to the total transformation of the nails (excluding that on the hallux) to laterally flattened claws. In the same way, the claws of the Callithricidae can be interpreted as a secondary adaptation for branch-running, rather than hind-limb dominated leaping (cf. figure 13).

It is a moot question whether the ancestral Eutherian mammals possessed claws or nails. If the early mammals were arboreal and progressed by grasping, the evolution of the Primates could be understood as a simple extension of leaping-and-grasping, and there would be no place for the tree-shrews or *Plesiadapis* in the picture of Primate evolution. If, on the other hand, the ancestral mammals were clawed, semi-terrestrial forms (as assumed by Napier 1971), the evolution of hind-limb-dominated locomotion must have occurred far more rapidly, through an early stage of grasping arboreal progression. Neither the Tupaiidae nor the Plesiadapidae exhibit any sign of such a development.

5. *Reproduction*

The extant Malagasy lemurs exhibit such striking similarities in their reproductive habits that one can reasonably infer a similar pattern of reproductive activity for the subfossil forms. All of the living forms exhibit a clearly demarcated *breeding season*, and the offspring are characterized by their *advanced state at birth*. The main features of maternal care and infant interaction are also essentially similar; but there is once again some degree of systematic variation.

Figure 14 provides an outline of the annual breeding cycles of the main species which have been studied. It is clear from this diagram that most of the species shown give birth some time before or during the rainy season (November to April). Since there is fairly wide variation in the length of the gestation period, according to body-size (2 to 5 months), there is wide variation between species in the times of mating. Gestating female lemurs of the various species can be found throughout the dry season and during the first half of the wet season.

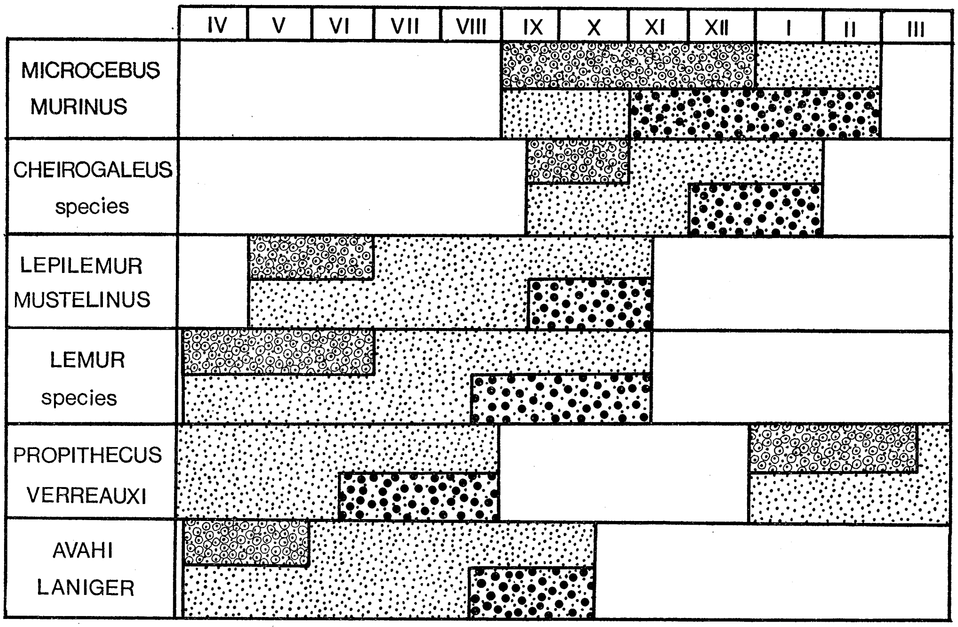

FIGURE 14. Chart showing the seasonal distribution of reproductive activity in lemurs. Roman numerals indicate the months of the year.

stippled area (inclusive)	period when gestating females occur
open circles over stippling	period when mating occurs
black spots over stippling	period when births occur

(Data from Petter-Rousseaux (1962), Kaudern (1914) and personal observations.)

In the smaller species (*Microcebus murinus*, *Cheirogaleus medius*, *C. major*), the first pregnant females are found as the dry season is drawing to a close (September/October), and the first babies are born more-or-less as the rains begin. In the lemurs of intermediate size (*Lepilemur mustelinus*, *Lemur* spp.; *Avahi laniger*), the first pregnant females are found near the beginning of the dry season, and the first babies are born about 2 months before the rains begin. Finally, with the largest lemurs (*Propithecus verreauxi*; probably *P. diadema* and *Indri indri*), gestation begins in the latter half of the rainy season, with the first births occurring up to 4 months prior to the next rainy season. Overall, this means either that gestation (and in some cases lactation) must often proceed on the basis of tissue reserves gathered during the previous rainy season, or that food gathered during the dry season suffices for these processes. In this context, the ability of various lemur species (particularly the smaller ones) to store fat at the end of the rainy season (p. 324) assumes a further degree of importance.

It is important to note that this strict seasonal pattern of breeding applies even to the east coast rain-forest domain, where more rain may fall in the dryest month of the year (e.g. in Maroantsetra) than falls in the wettest month of the year in the extreme south (e.g. Tsihombe). Thus, rainfall does not operate directly as a factor determining the time of breeding, though it may exert an indirect effect. Where closely related forms (e.g. *Cheirogaleus medius* and *C. major*) occur as geographical successors in the dry and wet areas of Madagascar, the timing of the breeding season is broadly the same throughout Madagascar. This may provide further evidence for the evolutionary model suggested on p. 313, in which there is a continuous process of expansion and replacement of species. However, it must be emphasized once again that the conditions under which the lemur species are now living need not be the same as the conditions operating when particular characters (e.g. timing of the breeding season) were determined by natural selection. At some time in the past, Madagascar may have been much drier overall.

Taking the present situation, one can look for selective pressures favouring maintenance of a strict breeding season in terms of lusher plant growth and greater availability of insect food in virtually all areas of Madagascar during the rainy season. It has already been shown that mating and gestation typically occur outside the wet season. Even births and lactation tend to occur prior to the rains in all but the smallest lemurs (*Microcebus*, *Cheirogaleus*.) However, a possible correlation with wet season food availability is seen if the *time of weaning* is examined. As a general rule, the time taken for maturation and subsequent accumulation of nutrient reserves in any offspring born increases with increasing adult body-size. The arrangement of the various seasonal breeding patterns in the different lemur species can thus be viewed as a pattern of adaptation for infant survival. The infants must mature some time before the end of the rainy season, so that they can accumulate adequate tissue reserves to survive the following dry season. With the smallest lemurs (*M. murinus*), the entire range of mating, gestation, birth and weaning can be accomplished during the wet season. In fact, there is some evidence that there is sufficient time during the last 2 months of the dry season (September/October) and the 6 months of the wet season (November to April) for some females to have two successive litters (Kaudern 1914; Martin 1972): gestation period I (2 months) + lactation period I (1½ months) + gestation period II (2 months) + lactation period II 1½ months) = 7 months, leaving one month (April) for the offspring of the second litter to accumulate food reserves for the coming dry season. With the largest lemurs (e.g. the Sifaka), on the other hand, the young are dependent upon the mother at least to some extent for at least the first 7 months of life, though the actual time of weaning has not yet been established. In both cases, the last infants born during the birth season have just enough time to become fully independent (and presumably equipped with nutrient reserves for the dry season) by the beginning of May.

On the basis of indirect evidence, Petter & Peyrieras (1970) report that *Hapalemur griseus* gives birth in December/January in Maroantsetra and Lac Alaotra (both areas in east coast rain-forest); yet in Perinet (also in east coast rain-forest), what appeared to be an adult *H. griseus* carrying a small baby on its back was spotted at night with a headlamp during the author's visit there in mid-October 1968. If the species identification (not entirely reliable at night) was correct, this may mean that *H. griseus* gives birth in the period October to December, with matings occurring in mid-May to mid-August, taking the gestation period as approximately 4½ months (see Petter & Peyrieras 1970). Even on this estimate, *H. griseus* must give birth later in the year than *Lemur*, *Varecia* or *Lepilemur* species, which implies that weaning should take place relatively rapidly in *Hapalemur*, if the criterion of juvenile maturation by the end of the wet season is to apply. From what is known of the maternal behaviour of *H. griseus* in captivity, early weaning appears to be characteristic.

An exception to the general rule is apparently provided by the Aye-aye (*Daubentonia*). Slight circumstantial evidence (possible post-partum swelling of the genital tract of a female trapped on 10 March) cited by Kaudern (1914), along with villagers' reports quoted by Petter (1962*c*) indicate that the Aye-aye gives birth in February/March. If this late date is typical, it is unlikely that the young Aye-aye would be completely independent by the close of the wet season (end of April), unless the lactation period is much shorter than in other lemurs of comparable size. This exceptional situation could be related to the specialized diet of the Aye-aye (p. 329; Petter & Petter-Rousseaux 1967). The availability of the wood-boring larvae and large-kernelled fruit consumed by the Aye-aye may show a peak just after the end of the wet season.

In summary, it is probably true to say that the seasonality of breeding seen in all extant lemur species represents an adaptation to seasonal food-availability, and that the main criterion for the timing of mating and births in each species is the requirement that the offspring should have sufficient time to develop and accumulate tissue reserves during the period of maximum food-availability, in order to survive the subsequent period of food scarcity.

In association with their relatively long gestation periods, the lemurs typically give birth to small numbers of infants at an advanced stage of development. The minimum gestation period is approximately 60 days (*Microcebus murinus*), and in all lemur infants the eyes and the ears are open a few days after birth (at the latest). The fur is already well developed at birth, and the infants are able to grasp supports and move around quite actively soon after birth. Portmann (1965) refers to mammals with this complex of characters as 'nidifugous' (Nestflüchter), in contrast to typical 'nidicolous' mammals (Nesthocker) which give birth to their infants in a nest and exhibit the following characteristics:

(1) eyes of infants closed at birth – open late during nest-phase;
(2) ears of infants closed at birth – open late during nest-phase;
(3) teeth not through at birth – erupt during nest-phase;
(4) pelage poorly developed at birth – hair emerges late;
(5) gestation period short (about 30 days for small-bodied forms);
(6) litter-size and number of mammae in female large.

None of these characters can be traced in fossil forms; so reconstruction of the evolution of reproductive features in mammals must be carried out by a process of inference. Unfortunately, some of Portmann's conclusions are based on the assumption that living Insectivora are primitive in every respect, and that the 'nidicolous' pattern must necessarily be ancestral to the 'nidifugous' pattern seen in Primates. However, there are some independent indications that the nidicolous pattern is indeed primitive in mammals. In the first place, small mammals tend to build nests and exhibit the nidicolous pattern, and it is well established that early mammals were probably very small in size. Secondly, Portmann has remarked that closure of the eyelids over the eyes – which apparently serves a protective function in young nest-living mammals – still occurs *in utero* in 'nidifugous' species in which the infants are born with the eyes open. With 'nidifugous' species, the early part of the nest phase (during which the eyes are closed in nidicolous species) is – so to speak – incorporated into the gestation period. Nevertheless, these facts give no indication as to the ancestral litter-size in mammals, and Portmann may be unjustified in assuming that the early mammals had large litters (10 or more) as in many living Insectivora.

As has been noted (p. 325), the Cheirogaleinae have relatively small bodies and inhabit nests of various kinds. The infants are born in such nests (leaf-nests or tree-hollows) and are not normally carried on the parent's fur. When an infant is carried, it is carried in the mother's mouth, either during retrieval or during transfer to a new nest. The Cheirogaleinae are also unusual among Primates in that there may be two or three infants in a litter as a regular occurrence (e.g. in *Microcebus murinus* and *Cheirogaleus* spp. – see Martin (1972)). Other lemurs, and most other Primates, typically have one infant at each birth, with twinning occurring as an occasional exception.† This correlates with the fact that the vast majority of Primate species (Cheirogaleinae and Galaginae excluded) exhibit carriage of the infant on the parent's fur. Among the lemurs, this pattern is typically observed in *Lemur* species, Indriidae and possibly *Daubentonia*. Within the Lemurinae, *Varecia*, *Hapalemur* and *Lepilemur* all deposit the infant in a nest at least for part of its development. *Varecia* seems to deposit its infant in a nest for the entire period of its development, and the infant is born in a relatively poorly developed state (Petter 1962*c*). Klopfer & Klopfer (1970) have recently compared the maternal behaviour of *Varecia* and *Lemur* in captivity, emphasizing the difference between these two genera. When transport is necessary, *Varecia* carries the infant in its mouth (see Petter-Rousseaux 1964). *Hapalemur* and *Lepilemur* are unusual in that the infant is initially carried in the mother's mouth, but later rides upon her fur. *H. griseus* females leave their infants in natural epiphyte 'nests' initially; but they later carry them on the pelage almost continuously (Petter 1962*c*; Petter & Peyrieras 1970). *Lepilemur mustelinus* females typically have one infant, which passes the day clinging to the mother's fur. At night, the infant can be left clinging to small branches (Petter-Rousseaux 1964). *Hapalemur* and *Lepilemur* thus provide a link between the Cheirogaleinae, on the one hand (via *Varecia*) and to the Indriidae on the other (via *Lemur* spp.). Unfortunately, there is no published account of infant-care in the Aye-aye; but in view of the fact that *Daubentonia* constructs a complex nest, it seems likely that the infant may (at least initially) be left alone in the nest. At a later stage, the mother may carry her infant on the fur, like *Hapalemur* and *Lepilemur*. When faced with this fairly complete series of maternal adaptations in the living lemurs, one is tempted to regard the Cheirogaleinae as primitive (nest-use; oral carriage) and the Indriidae as specialized (no nest; pelage carriage). However, carriage of the infant on the pelage is so characteristic among Primates that it seems highly likely that the ancestral Primate exhibited this pattern of behaviour to some degree. A possible model is provided by *Tarsius*, which does not seem to construct or use nests of any kind, and can carry the single infant either on the fur (normal progression) or in the mouth (rapid escape). *Tarsius* may even exhibit 'parking' of its infant on fine branches. Since *Galago* species and *Microcebus* species build extremely similar nests (p. 325), the ancestral lemur/loris stock was probably to some extent nest-living. However, there may have been only a single infant, which could have been carried on the mother's fur

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† The only prominent exception is provided by the Callithricidae, which typically have twins which exhibit placenta-sharing during development. Some *Galago* species also have multiple litters as a common occurrence.

after the first phase of development in the nest. The evolution of 'baby-parking' in some Galaginae and the availability of tree-hollows as nests for the Cheirogaleinae may have relieved the mothers from the task of carrying the infant on her fur. In all the larger Primates (except *Varecia*), the relatively small weight of the infant has probably favoured the development (or retention) of carriage on the fur. The grasping extremities of the infant are particularly important in this context. Oral transport of the infant was probably developed in many early nest-living mammals (see Martin 1968*b*, p. 518) – perhaps as a common ancestral feature. Accordingly, the presence of oral transport in Galaginae, Cheirogaleinae and some Lemurinae can be interpreted as retention of an early mammalian adaptation, which may be lost if the baby is carried from birth onwards on the mother's fur. Thus, the Cheirogaleinae again seem to be relatively primitive, though the complete lack of infant carriage on the fur may represent a secondary reduction. (Note, for example, the wide divergence of the hallux in the neonate *Microcebus*, figure 16*t*, plate 38.) On the other hand, *all* of the Strepsirhini (including the Cheirogaleinae and the Galaginae) seem to be relatively far removed from the ancestral mammalian pattern of reproduction suggested by Portmann (1965) – and generally retained in the Tupaiidae (Martin 1968*b*).

6. *Territoriality and social behaviour*

Patterns of territoriality and social interaction in the lemurs present the greatest difficulty in systematic analysis, since there is very little direct correlation between morphology and such behaviour. (The occurrence of skeletal sexual dimorphism could provide one exception to this rule.) It is therefore to be expected that territorial and social behaviour might be more labile (in evolutionary terms) than other behavioural categories. According to the hypothesis that there is little direct hereditary control of behaviour, one would expect the lemurs to exhibit far more variation in their social patterns than in any other kind of behaviour (which would usually be linked to, and limited by, morphology). However, the systematic groups of lemurs are almost as cohesive in their social/territorial behaviour as in other forms of behaviour. Crook & Gartlan (1966) (summarizing Petter 1962*c*), have briefly listed the tendencies of various lemur species to form social groups as follows: Cheirogaleinae, 'solitary'; Lemurinae, 'solitary' or form family groups and larger troops; Indriidae, family parties; Aye-aye, 'solitary'. Once again, the greatest variation is found in the Lemurinae; this sub-family includes representatives of all of the various kinds of social grouping found in the Malagasy lemurs.

Another difficulty encountered in the attempt to analyse the distribution of social behaviour patterns in the lemurs resides in the need to conduct long-term field studies. Even the simple statement of characteristic social group size requires long-term study, particularly because the sizes of groups may change according to locality and seasonal factors. If there is any hereditary basis for social/territorial behaviour, it probably exists in the form of a fixed range of possibilities, rather than as a rigid structural template. The *dynamic* aspect is all-important in considering the evolution of spacing and aggregation mechanisms.

More detailed study has shown that the simple classification of social groups given above is extremely superficial. Jolly's study (1966) of *Propithecus verreauxi verreauxi* has shown that this lemur may occur in groups of up to 10, and that there is a tendency to find more males than females in each group (at least in her study area). In Ampijoroa (figure 6*b*), the author found that two 'separate' groups of *P. verreauxi coquereli*, which fed separately during the daytime, regularly joined up to sleep in a particular area. It is therefore misleading to regard the Sifaka as having a social system based on 'family groups'. Further down the scale, it has now emerged that two 'solitary' lemurs (*Microcebus murinus*, Martin (1972); *Lepilemur mustelinus*, Charles-Dominique & Hladik (1971)) in fact exhibit a weakly developed form of social organization, with a spatial pattern of inter-individual relationships. It seems highly likely that other 'solitary' lemurs have a similar pattern, with the possible exception of the Aye-aye, which may indeed be truly solitary. These new data permit refined classification of the social groupings of lemurs as follows:

(1) Weak system of spatial social organization: Cheirogaleinae, *Lepilemur*, Aye-aye?
(2) Small groups of two to five members: *Indri*, *Avahi*, *Propithecus*, *Varecia*, *Lemur rubriventer*?
(3) Social groups of intermediate size (*ca.* 5 to 15 members): *Propithecus*, *Lemur macaco*, *L. mongoz*?, *Hapalemur griseus*.
(4) Large social groups (up to 30): *L. catta*

As can be seen, *Propithecus* bridges two categories and the genus *Lemur* includes categories 2 to 4, indicating some lability in group-size. On the other hand, the Cheirogaleinae are relatively consistent in their social behaviour patterns.

It is difficult to establish whether the various lemur species are strictly *territorial*, since it would be necessary to demonstrate defence of an area by an individual or group against a conspecific individual or group. Jolly (1966) provides evidence for inter-troop territorial disputes in *Propithecus verreauxi verreauxi*; but her observations indicated that troops of *Lemur catta* simply avoid one another and may even intermingle temporarily. Charles-Dominique & Hladik (1971) have demonstrated that *Lepilemur* males probably defend territories against intruders, and Petter & Petter-Rousseaux provide circumstantial evidence of territoriality in *Daubentonia*. Information on other species is lacking, but it is fairly clear that all Malagasy lemur species live in relatively well-defined home ranges, and it seems likely that there is some mechanism for spacing in every case, even though this may not involve actual fighting. It has often been observed that a single agonistic encounter is sufficient to establish priority in animals; so it may be exceedingly difficult to observe actual cases of territorial demarcation in some lemurs. Even though *L. catta* has not been observed to engage in territorial disputes, it is clear from Jolly's account that some system of troop spacing is operative. Overall, home-range attachment may be regarded as generally characteristic of the lemurs.

Because of the gradation of social organization in living lemurs, it is tempting to regard the various systems as evolutionary stages (e.g. passing through *Microcebus murinus* to *Hapalemur* and on through *Lemur macaco* to *L. catta*). It is, however, impermissible to construct evolutionary sequences with living forms, and the evolution of social organization in lemurs should be traced by reconstruction of ancestral stages. Crook & Gartlan (1966, p. 1200) state that 'anatomical investigations of fossil and living material reveal a progressive adaptive radiation from forest-dwelling insectivorous Primates to larger open-country animals, predominantly vegetarian', and they analyse the evolution of Primate social behaviour in five grades (all represented among living Primates) according to this view. But these authors tend to obscure the fact that adaptive radiation of Primates has given rise to a whole range of specializations in living Primates, and that progressive changes must be sought in actual ancestral sequences rather than by straightforward comparison of living forms. Forest-dwelling insectivorous Primates still exist, and there is no obvious reason why they should not have undergone specialization as well as the plains-living herbivorous species.

The crucial contribution made by Crook & Gartlan is the observation that Primate social structure is intimately correlated with ecological factors. Study of the relationship between past and present ecology and the evolution of social structure should eventually lead to a cohesive theory of the evolution of social behaviour, and the lemurs will provide a compact test-case for such a theory.

As a general approach, the following statements can be made about lemur social behaviour:

(1) Nocturnal species are less likely to exhibit social groups than diurnal species. (The 'family group' is the largest observed stable feeding group in nocturnal lemurs.)

(2) Insectivorous species are less likely to exhibit social groups than herbivorous (frugivorous/folivorous) species. (The partially insectivorous Cheirogaleinae and *Daubentonia* have all been described as 'solitary'.)

(3) Clear-cut territorial defence seems (according to available data) to decrease with social group size.

(4) Diurnal species which tend to move in open areas (especially *Lemur catta*) exhibit larger social groupings.

(5) Social organization cannot be primarily based upon mating patterns, since reproduction is seasonal, whereas social organization persists throughout the year.

In line with these statements, the ancestral lemurs probably lived in weakly developed social groups on an essentially territorial basis. It has already been suggested that the early lemurs were nocturnal, partly insectivorous and nest-living. If the living lemurs are all derived from an ancestor of this kind, the widespread characteristic of home-range attachment may be viewed as an ancestral retention. The degree to which a given species exhibits actual home-range defence (i.e. territoriality) is doubtless determined by factors such as the availability of food and the pattern of food-distribution.

Since the ancestral lemur pattern of social organization was probably fairly close to that of the extant 'solitary' nocturnal forms, it is important to examine the meaning of the term 'solitary'. Detailed study of *Microcebus murinus* and *Lepilemur mustelinus* has shown that, although individual animals are usually seen feeding alone at night, a definite spatial pattern of individual relationships exists. This pattern can broadly be defined in terms of peripheral adult males, central adult males and central females (figure 15) in population nuclei which are separated to a greater or lesser extent. The central males have fairly large home-ranges (probably territories) which overlap the home-ranges of one or more central females, whilst the peripheral males have smaller home-ranges on the fringes of each population nucleus. In the most primitive situation, the central females probably live apart, with their male and female offspring moving off at some stage to establish themselves elsewhere. In such a case, the only social link is between each central male and one or more females within his home range. This is virtually the situation in *L. mustelinus*, though the female infants may remain associated with their mothers for some time after attainment of maturity (Charles-Dominique & Hladik 1971). In *M. murinus*, the situation is more complex, in that the females are organized into groups which share nests (Martin 1972). So, in this respect, the Lesser Mouse Lemur is probably somewhat specialized, although the basic pattern of spatial social organization is similar to that of *Lepilemur*.

Charles-Dominique (1972) has recently demonstrated that the same spatial pattern of social organization is present in *Galago demidovii*, and it is possible that this is true of other Galaginae and of the Lorisinae as well. The Galaginae generally exhibit a greater tendency to form social aggregations than the Lorisinae, and it is likely that these aggregations are essentially female groups associated with a single adult male. Thus, the genera *Microcebus* and *Galago* probably exhibit specialization of the primitive Strepsirhine pattern of social organization, in the form of enhanced association between females.

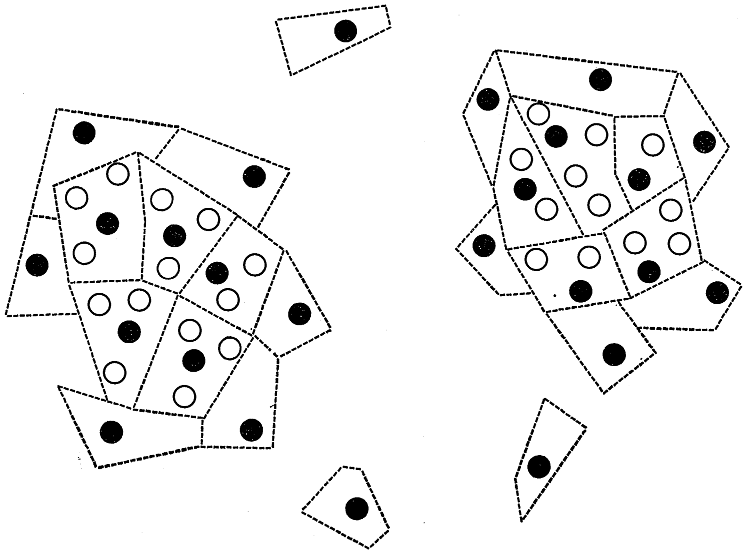

FIGURE 15. Diagram illustrating the system of spatial social organization found in *Microcebus* (Martin 1972) and *Lepilemur* (Charles-Dominique & Hladik 1971). There are two localized 'population nuclei', each containing a core of central males and associated females, and surrounded by a fringe of peripheral males. (Dotted lines indicate approximate male home-ranges.) Peripheral males can migrate between population nuclei, and can replace central males under certain conditions.

black spots	males
open circles	females

By extrapolation from bird studies, it has often been assumed that large social groups evolve through pair-formation and establishment of social groups. For example, Crook & Gartlan (1966) state that grade I in the evolution of Primate social organization is characterized by solitary species which 'occur in pairs where known'. Yet there is little evidence of classical pair-formation in 'solitary' Strepsirhine species. The idealized pattern of spatial relationships in figure 15 in fact provides a suitable model from which all Primate social patterns can be derived. (Indeed, all Eutherian mammal patterns of social behaviour could be derived from such a precursor.) The exclusion of peripheral males from direct breeding access to females provides for some degree of selective mating and ensures that there is a pool of available males to replace any central male which disappears from the system (e.g. through predation). Migration of peripheral males between population nuclei would further ensure genetic interchange between semi-isolated, localized groups.

By gradual stages, the system shown in figure 15 could have given rise to the following Primate social patterns:

(1) Restriction of central male links to one female per male, combined with home-range coincidence, could give rise to *pair-bonding*. Retention of the infants beyond weaning would give rise to small *family groups*.

(2) Augmentation of central male links with several females per male could give rise to *harem groups*. Grouping of peripheral males could produce *bachelor male groups*.

(3) Multi-male social groups could be produced in several ways. Gradually increasing toleration of maturing subadults in family groups would give rise to multi-male social groups, with some indications of dominance of older males over younger males. Alternatively, the dominant male in a harem group could become decreasingly aggressive to adjacent bachelor males and/or to maturing subadult males born to his own group of females. Although the products of these different processes may be numerically indistinguishable, there should be pronounced differences in social structure. In particular, evolution of multi-male social groups through a harem system should be identifiable by the far greater refinement of female–female bonding behaviour.

This pattern of evolutionary possibilities would explain why the harem system has developed so frequently in social Primates (and, incidentally, in other social mammals, e.g. some plains ungulates). It is significant that there is no documented instance of pair-bonding in lemurs, whereas the harem system seems to be quite common. The social structure of the 'solitary' nocturnal lemurs can be regarded as a spatial harem system (e.g. in *Microcebus murinus* and *Lepilemur mustelinus*), and there is some evidence that *Lemur rubriventer* (Petter 1962*c*) and *Hapalemur griseus* (Petter & Peyrieras 1970) form one-male groups containing two or more adult females. Jolly (1966, p. 155) has reported that in *L. catta* troops, all females are dominant over all males, and A. F. Richard (personal communication) has found that the same is true of *Propithecus verreauxi verreauxi* and *P. v. coquereli*. It is also apparent for both *L. catta* (Jolly) and *Propithecus* (Richard) that the males and females have separate dominance hierarchies. Among females, the dominance hierarchy was maintained with less overt fighting behaviour than among males – indicating that females are better adapted for group-living than males. With *P. verreauxi verreauxi*, the situation is far less clear, in that there is no established explanation for the frequent occurrence of groups containing a majority of males in *P. verreauxi* and certain *L. macaco* subspecies (Jolly 1966; Petter 1962*c*); but new data (A. F. Richard, personal communication) show that *P. verreauxi* adults have an overall 1:1 sex-ratio. In these lemurs, it seems that social behaviour has evolved without passing through a harem stage, probably developing through the evolution of mechanisms for reduction of aggressivity between individual central males and individual peripheral males. In *L. catta*, there is a pronounced tendency towards peripheralization of males, both in the formation of troops with a greater number of females than males, and in differential location when a troop is on the move (females, juveniles and dominant males lead; subordinate males move along behind). In *P. verreauxi* and *L. macaco*, such peripheralization seems to be poorly defined.

One unifying feature of lemur social systems – from the simplest to the most complex – is provided by social grooming. In Strepsirhini, self-grooming is heavily dependent upon the use

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DESCRIPTION OF PLATE 34

FIGURE 16*a–d*

a: Lesser Mouse Lemur (*Microcebus murinus*) emerging from tree-hollow at night. Note large, forward-facing eyes (life-size).

b: Nest of *M. murinus* in semi-arid bush; nest-diameter approx. 25 cm. (Nest material = *Rhus perrieri* leaves in *Euphorbia* tree.)

c: Fat-tailed Dwarf Lemur (*Cheirogaleus medius*) from littoral rain-forest (Mandena). This nocturnal species is essentially quadrupedal (½ life-size).

d: Nocturnal Sportive Lemur (*Lepilemur mustelinus leucopus*) in gallery forest near Berenty, S. Madagascar. Note grasping hands and feet and vertical squatting posture (⅓ natural size).

FIGURE 16 *a–d*. For legend see facing page

Figure 16 *e–h*. For legend see facing page

Description of plate 35

Figure 16*e–h*

e: Female Ringtail (*Lemur catta*) in gallery forest of Berenty, carrying two infants ventrally (note tails). The adult tail posture is characteristic in terrestrial locomotion. Note relative lengths of hind-limbs and flexure of fingers in walking ($\frac{1}{10}$ life-size).

f: Two *L. catta* play-fighting. Note the use of the grasping hands.

g: Coquerel's Sifaka (*Propithecus verreauxi coquereli*) in deciduous forest near Ampijoroa. Note the very long hind-limbs, and the characteristic shoulder and thigh flashes of this subspecies ($\frac{1}{10}$ life-size).

h: Verreaux's Sifaka (*P. verreauxi verreauxi*) in gallery forest near Berenty. Note powerful hallux and distinctive pelage coloration.

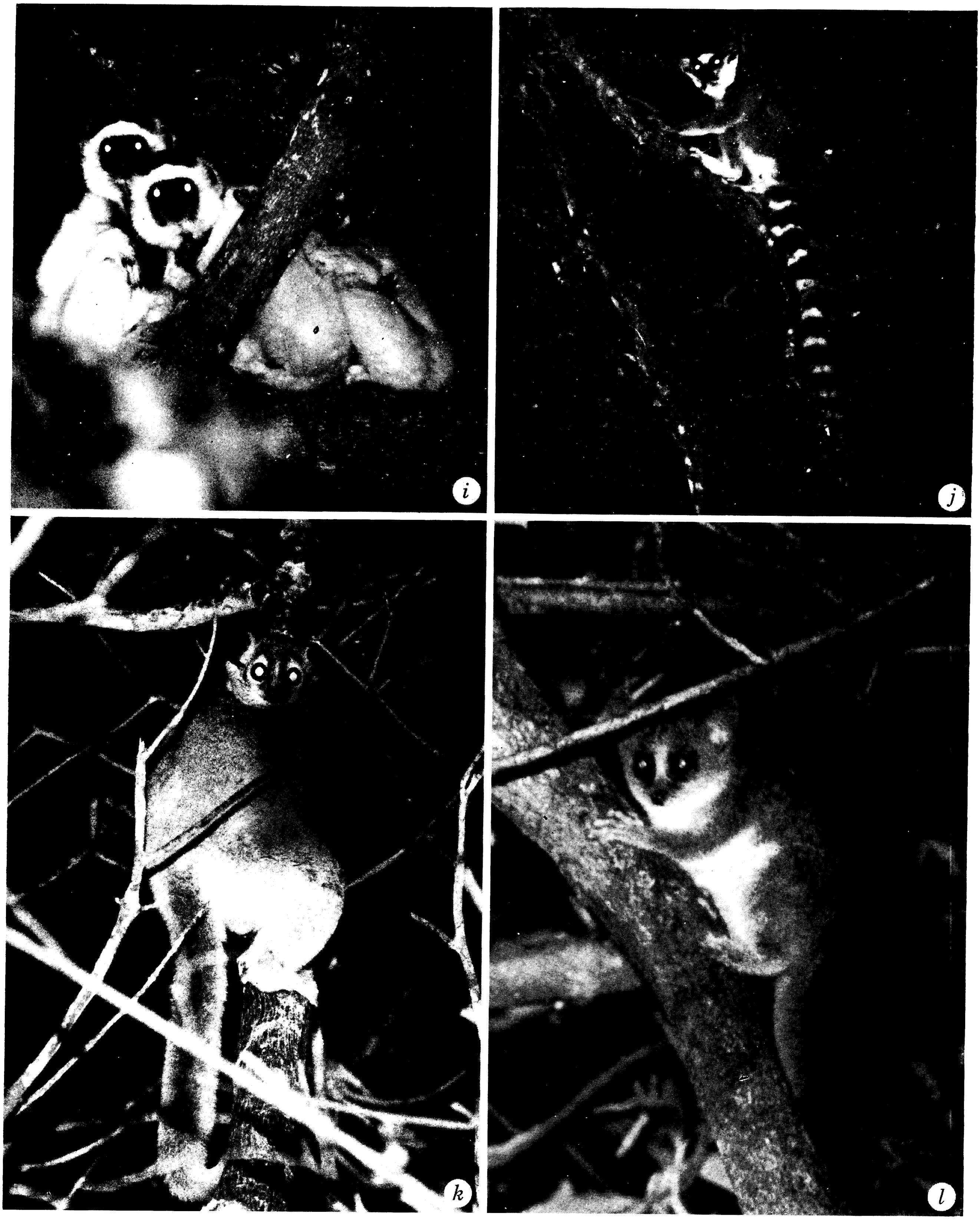

FIGURE 16 *i–l*

i: Three diurnal *Propithecus verreauxi verreauxi* photographed in Berenty gallery forest at night, whilst huddled in a sleeping group. Note reflexion of tapetum.

j: Diurnal *Lemur catta* photographed at night, whilst feeding briefly in Berenty gallery forest. Note reflexion of tapetum.

k: Sportive Lemur (*Lepilemur mustelinus leucopus*) photographed at night in semi-arid forest near Hazafotsy (S. Madagascar). Note powerful hind-limbs, well-developed pes and glowing tapetum.

l: *Microcebus murinus* photographed at night. Note the application of the hands and feet on the sides of the broad support. Reflexion from the tapetum can be seen.

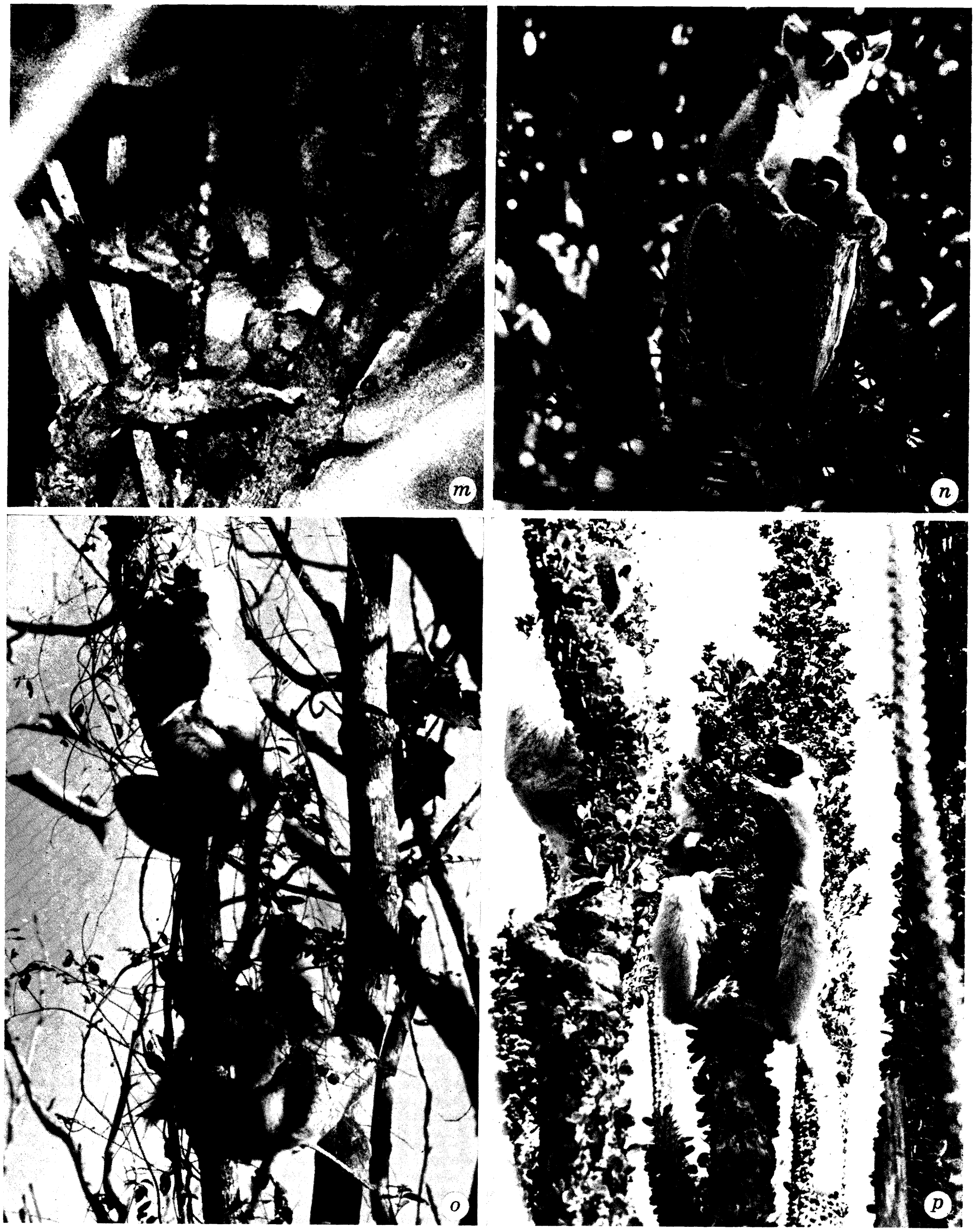

Figure 16 *m–p*

m: *Microcebus murinus* in the process of trapping and eating a large spider (Hazafotsy; S. Madagascar). Note use of hands and the protective closure of the eyelids.

n: Female *Lemur catta* with infant clasping her ventral fur. The leaves in the lower part of the picture are those of the kily tree (*Tamarindus indica*), which provides a staple food for the Ringtails, Sifakas and Sportive Lemurs in the Berenty gallery forest.

o: *Propithecus verreauxi coquereli* (Ampijoroa area) feeding on the fruits of an introduced teak tree. Note the use of the hand to pull food towards the mouth. The distinctive shoulder and thigh markings may act as a disruptive pattern when the animal is viewed against the sky.

p: *P. verreauxi verreauxi* feeding on the inflorescences of *Alluaudia ascendens* in semi-arid forest (Hazafotsy, S. Madagascar). Note how carriage of the baby on the parent's fur facilitates introduction to preferred foods of the adults. This plant also provides staple food (leaves and inflorescences) for the nocturnal Sportive Lemurs in semi-arid forest.

FIGURE 16 *q–t*. For legend see facing page of the tooth-scraper (Buettner-Janusch & Andrew 1962), and it is the tooth-scraper which is used in social grooming. Although the hair of the recipient animal is grasped in the groomer's hands, the actual grooming is conducted with the teeth. In its simplest form, such social grooming consists of brief bouts of scraping of inaccessible areas of the recipient's fur (top of the head, neck, upper back). This form of social grooming is found in *Microcebus*, *Cheirogaleus*, *Phaner* and possibly *Lepilemur*. In lemurs with more elaborate social organization, such grooming is more extensive and more frequent (*Lemur*, *Hapalemur*, *Propithecus*, *Indri*, *Avahi*?). It has been noted with hand-reared *M. murinus* that mutual grooming can elicit a 'purring' vocalization (Martin 1972), and Jolly (1966) reports that *L. catta* utter a similar vocalization when engaged in social grooming, though *Propithecus* lacks such a vocalization. Since rudimentary social grooming and a similar 'purring' vocalization have been reported for some Lorisiformes, it is possible that the ancestral pattern of Strepsirhine social relationships included social grooming and accompanying vocalization between associated animals with overlapping or adjacent home ranges. The more complex patterns of social behaviour in the diurnal lemurs can be interpreted as specializations from this basic system.

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Description of plate 38

Figure 16*q–t*

q: Avahi (*Avahi laniger*) mother carrying an infant on her back (littoral rain-forest; Mandena). Note the powerful hind-legs and well-developed pes of this nocturnal relative of the Sifaka ($\frac{1}{10}$ life-size).

r: Sifaka (*Propithecus verreauxi verreauxi*) mother with baby clinging ventrally. Note tight grasp of infant's hand in the mother's fur.

s: *Lemur catta* mother, carrying a relatively old infant on her back and grooming another member of her troop (Berenty; S. Madagascar). Note tight grasp of infant on mother's back.

t: Neonate Mouse Lemur (*Microcebus murinus*) from Mandena (2 × life-size). Note wide divergence of hallux and lesser divergence of pollex. There is already a well-developed covering of body-fur at birth.

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FIGURE 16 *a–d*. For legend see facing page

FIGURE 16 *e–h*. For legend see facing page

FIGURE 16 *i–l*

- *i*: Three diurnal *Propithecus verreauxi verreauxi* photographed in Berenty gallery forest at night, whilst huddled in a sleeping group. Note reflexion of tapetum.
- *j*: Diurnal *Lemur catta* photographed at night, whilst feeding briefly in Berenty gallery forest. Note reflexion of tapetum.
- *k*: Sportive Lemur (*Lepilemur mustelinus leucopus*) photographed at night in semi-arid forest near Hazafotsy (S. Madagascar). Note powerful hind-limbs, well-developed pes and glowing tapetum.
- *l*: *Microcebus murinus* photographed at night. Note the application of the hands and feet on the sides of the broad support. Reflexion from the tapetum can be seen.

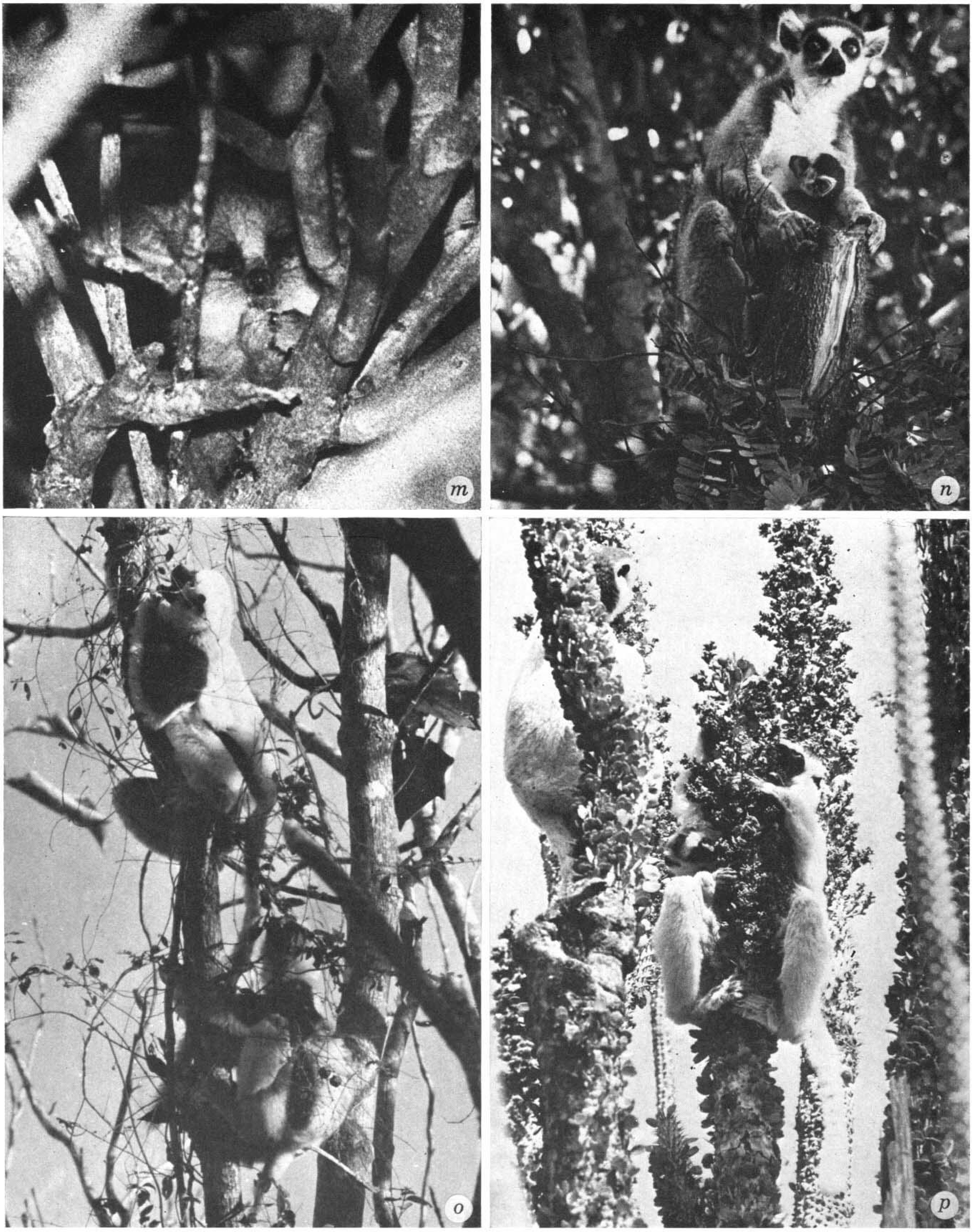

FIGURE 16 *m–p*

m: *Microcebus murinus* in the process of trapping and eating a large spider (Hazafotsy; S. Madagascar). Note use of hands and the protective closure of the eyelids.

n: Female *Lemur catta* with infant clasping her ventral fur. The leaves in the lower part of the picture are those of the kily tree (*Tamarindus indica*), which provides a staple food for the Ringtails, Sifakas and Sportive Lemurs in the Berenty gallery forest.

o: *Propithecus verreauxi coquereli* (Ampijoroa area) feeding on the fruits of an introduced teak tree. Note the use of the hand to pull food towards the mouth. The distinctive shoulder and thigh markings may act as a disruptive pattern when the animal is viewed against the sky.

p: *P. verreauxi verreauxi* feeding on the inflorescences of *Alluaudia ascendens* in semi-arid forest (Hazafotsy, S. Madagascar). Note how carriage of the baby on the parent's fur facilitates introduction to preferred foods of the adults. This plant also provides staple food (leaves and inflorescences) for the nocturnal Sportive Lemurs in semi-arid forest.

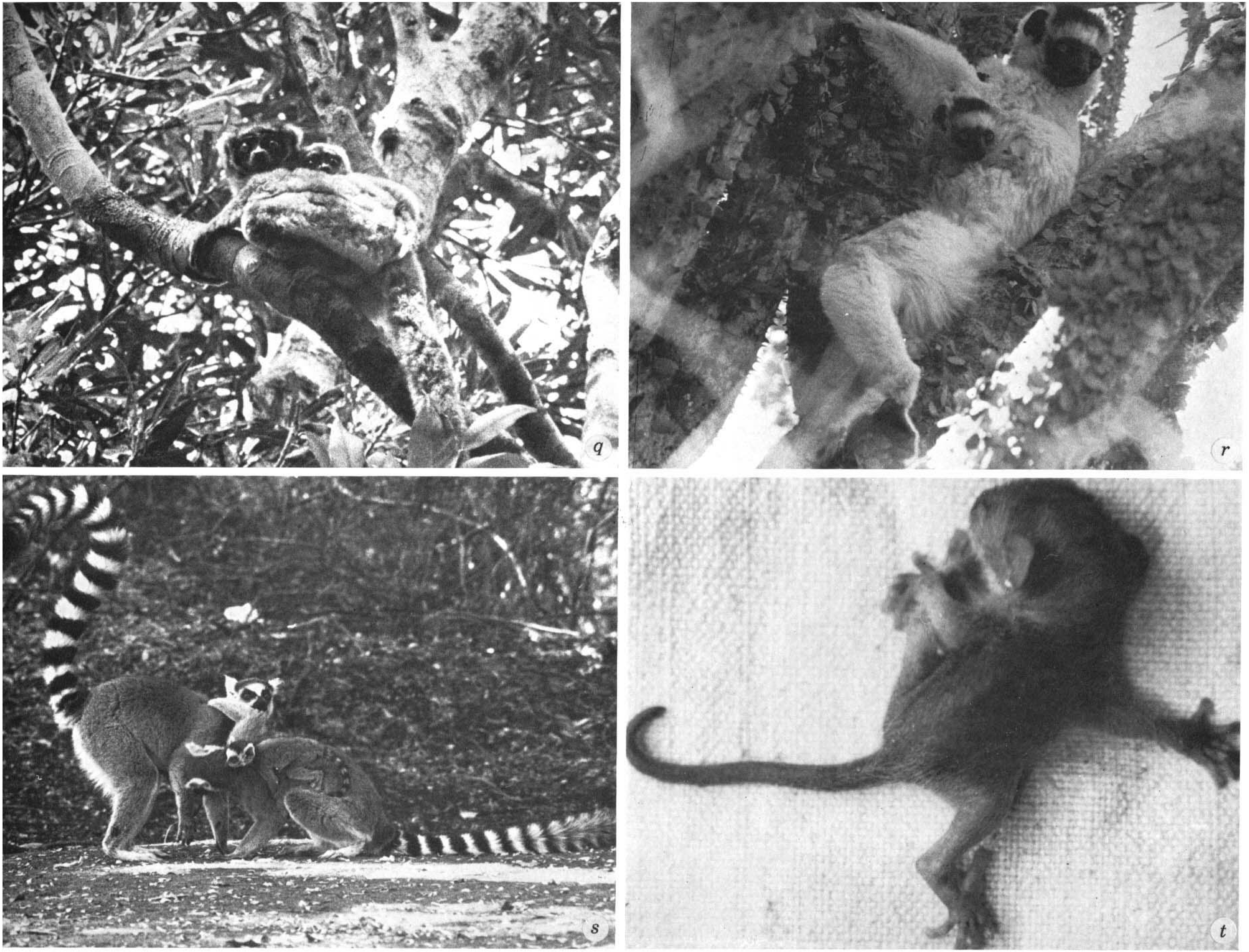

FIGURE 16 *q–t*. For legend see facing page