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PHYLOGENY AND
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STREPSIRHINE PRIMATES

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ABSTRACT

There has been considerable recent controversy over the nomenclature appropriate to the group of species generally classified in the Malagasy strepsirhine primate subfamily Lemurinae. This discussion has not, however, been based on an explicit set of phylogenetic hypotheses. We attempted to redress this situation by undertaking a quantitative parsimony analysis of some 37 craniodental characters that are consistent within the subspecies and monotypic species constituting the group, but which vary among them. Our analysis revealed a very high degree of homoplasy among these forms, with remarkable inconsistencies of distribution of character states. It was virtually

impossible to obtain a single most parsimonious cladogram even on the basis of subsets of our data set, and we regard the relationships specified in our cladogram as tentative at best. Among our more robust conclusions is that *Varecia*, *Lemur catta*, and the species of the “*fulvus*-complex” do indeed form a monophyletic group; but in view of the uncertainties that continue to surround relationships within this group we strongly doubt that nomenclatural innovation is justified at this point. The least misleading move under present circumstances would be to return to the earlier orthodoxy of including all these forms within the single speciose genus *Lemur*.

INTRODUCTION

Much controversy has recently been generated over the nomenclature appropriate to the close-knit group of subspecies, species, and/or genera that constitute the endemic Malagasy primate subfamily Lemurinae (e.g., Groves and Eaglen, 1988; Simons and Rumpler, 1988; Tattersall, 1988; Tattersall and Koopman, 1989). It is notable, however, that this nomenclatural debate has flourished in an almost total systematic vacuum: there is no agreement on relationships within this subfamily, which Tattersall (1982) limited to the two genera *Lemur* and *Varecia* (placing *Hapalemur* in its own subfamily within the family Lemuridae), although older classifications also include *Hapalemur* and even *Lepilemur* (e.g., Hill, 1953) within Lemurinae.

It is probably fair to say that at this point a consensus exists that *Lepilemur*, whatever its precise relationships (which recent studies indicate to be with Indridae, e.g., Schwartz and Tattersall, 1985; Groves and Eaglen, 1988), deserves separate familial recognition. The affinities of *Hapalemur*, on the other hand, continue to be hotly debated. Schwartz and Tattersall (1985) viewed this genus as the sister of a clade containing *Varecia* (one species, two subspecies) and *Lemur* (six species: four monotypic, one with two subspecies, one with six or seven). In contrast, Simons and Rumpler (1988) argued that *Hapalemur* and *Lemur catta* together form a monophyletic group distinct from a monophyletic *Eulemur*.

This latter genus contains the other species traditionally assigned to *Lemur*: *mongoz*, *macaco*, *fulvus*, *coronatus*, and *rubriventer*. Groves and Eaglen (1988) independently and almost simultaneously examined the evidence for the same proposition. They concluded that while the characters they examined failed to demonstrate a high probability that *Lemur catta* and *Hapalemur* together formed a monophyletic entity, the “*fulvus*-group” was sufficiently “distinctive” from *Lemur catta* to be raised to generic status. Hence they created the new genus *Petterus* for the five non-*catta* species of *Lemur*. These two nomenclatural innovations have produced a great deal of practical uncertainty over what to call the various members of a group of primates which is being studied with increasing intensity. The legalistic nomenclatural debate has the potential to drag on for years, with competing systems of nomenclature creating ever greater confusion in the literature. If the nontraditional views of the relationships within Lemurinae can be demonstrated to have substance, then a protracted period of nomenclatural uncertainty or outright confusion is almost guaranteed. However, if it can be shown that *Lemur catta* is more closely related to members of the “*fulvus*-group” than to any other lemur, or even that available evidence is insufficient to resolve satisfactorily the question of relationships within this group, then retention of the familiar and widely accepted traditional no-

TABLE 1
Taxa Studied (with sample sizes)

<i>Lepilemur edwardsi</i> (2)	<i>Lemur rubriventer</i> (4)
<i>Lepilemur leucopus</i> (2)	<i>Lemur coronatus</i> (6)
<i>Hapalemur griseus</i> (10)	<i>Lemur fulvus fulvus</i> (3)
<i>Varecia v. variegata</i> (7)	<i>Lemur fulvus albifrons</i>
<i>Varecia v. rubra</i> (3)	(13)
<i>Lemur catta</i> (9)	<i>Lemur fulvus rufus</i> (10)
<i>Lemur mongoz</i> (2)	<i>Lemur fulvus collaris</i> (8)
<i>Lemur macaco macaco</i> (2)	<i>Lemur fulvus albocollaris</i>
<i>Lemur macaco flavifrons</i>	(4)
(1)	<i>Lemur fulvus sanfordi</i> (5)

menclature will be justified, and a great deal of confusion, not to mention undignified squabbling in the literature, will be avoided. It is against this background that we have reexamined the craniodental evidence for relationships within Lemurinae.

MATERIALS AND METHODS

Using materials in the collections of the American Museum of Natural History, we have examined 77 skulls representing all of the species and subspecies of *Varecia* and *Lemur* (as traditionally constituted), with the aim of identifying characters which vary consistently among these groups. The Mayotte lemur is not represented in these collections, but in any case we regard it as an island pop-

ulation of *Lemur fulvus fulvus*. For outgroup comparison we examined specimens of *Lepilemur edwardsi*, *Lepilemur leucopus*, and *Hapalemur griseus*. To help determine morphocline polarities we also made comparisons with various lorids, galagids, cheirogaleids, indrids, and relevant Paleogene taxa, but these primates were not formally included in our quantitative analyses. Taxa and sample sizes are specified in table 1. Skulls were only included in our sample when accompanied by skins from which positive identification to species or subspecies could be made.

We were able to identify some 37 craniodental characters which were consistent within our samples at the subspecies or monotypic species level, and which varied at higher levels. Each feature was coded in order to permit computer entry, and the data were subjected to quantitative parsimony analysis using PAUP version 3.0A (Swofford, 1989) and MacClade test version 2.97.36 (Maddison and Maddison, 1989). PAUP was used to extract sets of maximally parsimonious trees, while MacClade enabled us to compute the lengths of alternative trees that we specified.

CHARACTERS USED IN THE ANALYSIS

Below we provide brief descriptions of the features used in our phylogenetic analysis, and we specify how variant states were nu-

TABLE 2
Distribution of Cranial Character States Among Taxa Examined

Char. no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Lepilemur</i>	0	9	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hapalemur</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>V. v. variegata</i>	0	0	0	1	1	2	0	0	1	1	1	0	0	0
<i>V. v. rubra</i>	1	0	0	1	1	2	0	0	1	1	1	0	0	0
<i>L. catta</i>	1	0	0	1	1	2	0	0	1	1	1	0	0	0
<i>L. mongoz</i>	1	1	1	1	2	2	1	0	3	1	1	0	4	2
<i>L. macaco</i>	2	1	1	1	2	2	1	1	2	1	1	0	3	1
<i>L. rubriventer</i>	2	1	1	1	3	2	0	1	3	1	1	1	2	3
<i>L. coronatus</i>	1	3	0	1	1	1	0	1	1	1	1	0	1	1
<i>L. f. fulvus</i>	1	0	1	1	1	1	0	1	1	1	1	0	1	1
<i>L. f. albifrons</i>	1	2	0	1	1	2	1	1	2	1	1	1	3	1
<i>L. f. rufus</i>	1	1	1	1	2	1	0	1	2	1	1	0	1	1
<i>L. f. collaris</i>	2	0	1	1	1	1	0	1	2	1	1	0	2	1
<i>L. f. albocollaris</i>	1	0	1	1	1	1	0	1	2	1	1	0	1	1
<i>L. f. sanfordi</i>	1	2	1	1	1	1	1	1	9	1	1	0	1	2

merically coded for quantitative review. Wherever possible, dichotomous characters were used. However, in many cases, up to five states of a single character were recognizable. Zero (0) was used to indicate hypothesized ancestral conditions, but the sequential numbering of states between 1 and 4 does not necessarily indicate the ordering of alternative states along a morphocline. Characters that were unrepresented in particular instances, or which were too variable within any given sample to characterize, were coded as missing (9). Certain multistate characters were ordered, i.e., the alternative states were specified to PAUP as falling along a morphocline. In the listing below, such characters are identified by the letters ORD. Tables 2 and 3 summarize the distribution of cranial and dental character states, respectively, among the various taxa we examined.

1. *Position of the nasopalatine foramen* (figs. 1, 3). The location of this foramen in the medial wall of the orbit is more variable within this group than previous analyses have tended to indicate. Its location on the palatine bone may be posteromedial (0), anteromedial (1), or posterocentral (2).
2. *Size of nasopalatine foramen* (figs. 1, 3). This feature is also highly variable. We have characterized it as small (0), moderate (1), large (2), or multiple (3).
3. *Contour of medial orbital wall* (fig. 1). This may be primitively concave (0), or swollen laterally (1). ORD.
4. *Contour of prenasopalatine portion of the palatine bone* (fig. 1). This element may be swollen laterally (1), or unswollen (0). ORD.
5. *Posterior expansion of the prenasopalatine* (fig. 3). This element may be unextended posteriorly, leaving the maxilla widely exposed in the posterior part of the orbital floor (0); or it may extend slightly posteriorly, partly obscuring the maxilla (1); moderately, to reach the edge of the temporal fossa (2); or greatly, intruding into the fossa (3). ORD.
6. *Paranasal sinus* (fig. 4). In some of the taxa considered here, an accessory sinus is walled off, to a greater or a lesser extent, lateral to the nasal fossa. It varies

TABLE 3
Distribution of Dental Character States Among Taxa Examined

Char. no.	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
<i>Lepilemur</i>	9	0	0	0	0	0	3	9	0	3	0	0	0	1	1	1	0	3	1	2	1	2	0
<i>Hapalemur</i>	0	0	0	1	0	0	3	9	0	3	1	0	2	1	0	0	0	1	1	2	0	0	0
<i>V. v. variegata</i>	0	0	2	2	2	0	3	3	0	3	2	0	0	0	2	1	9	0	0	1	1	2	1
<i>V. v. rubra</i>	0	0	2	2	2	0	3	3	0	3	2	0	0	0	2	1	9	0	0	1	1	2	1
<i>L. catta</i>	1	0	0	0	1	0	3	2	0	3	0	0	0	1	0	1	0	0	1	2	0	0	0
<i>L. mongoz</i>	1	0	1	0	3	1	3	4	2	3	0	0	1	1	1	1	9	2	1	2	0	2	0
<i>L. macaco</i>	0	0	2	0	3	3	1	4	1	1	0	0	1	1	2	9	0	1	0	1	9	1	0
<i>L. rubriventer</i>	0	0	1	3	3	2	3	4	3	3	2	0	1	0	2	9	0	1	0	1	9	1	0
<i>L. coronatus</i>	0	0	1	3	3	3	3	4	1	3	3	0	1	1	2	9	9	1	0	1	9	1	0
<i>L. f. fulvus</i>	1	1	1	0	3	2	3	4	1	3	2	0	1	0	2	9	1	1	0	1	9	1	0
<i>L. f. albifrons</i>	0	1	1	0	3	2	1	4	3	3	2	1	1	1	2	9	1	1	0	1	9	1	0
<i>L. f. rufus</i>	1	1	1	0	3	2	1	4	3	3	0	0	1	1	2	9	1	1	0	1	9	1	0
<i>L. f. collaris</i>	0	1	1	0	3	2	0	4	3	2	0	0	1	1	2	9	1	1	0	1	9	1	0
<i>L. f. albocollaris</i>	1	1	1	0	3	2	2	4	1	2	2	0	1	1	2	9	1	1	0	1	9	1	0
<i>L. f. sanfordi</i>	0	1	1	0	3	2	1	4	1	3	2	0	1	1	2	9	1	1	0	1	9	1	0

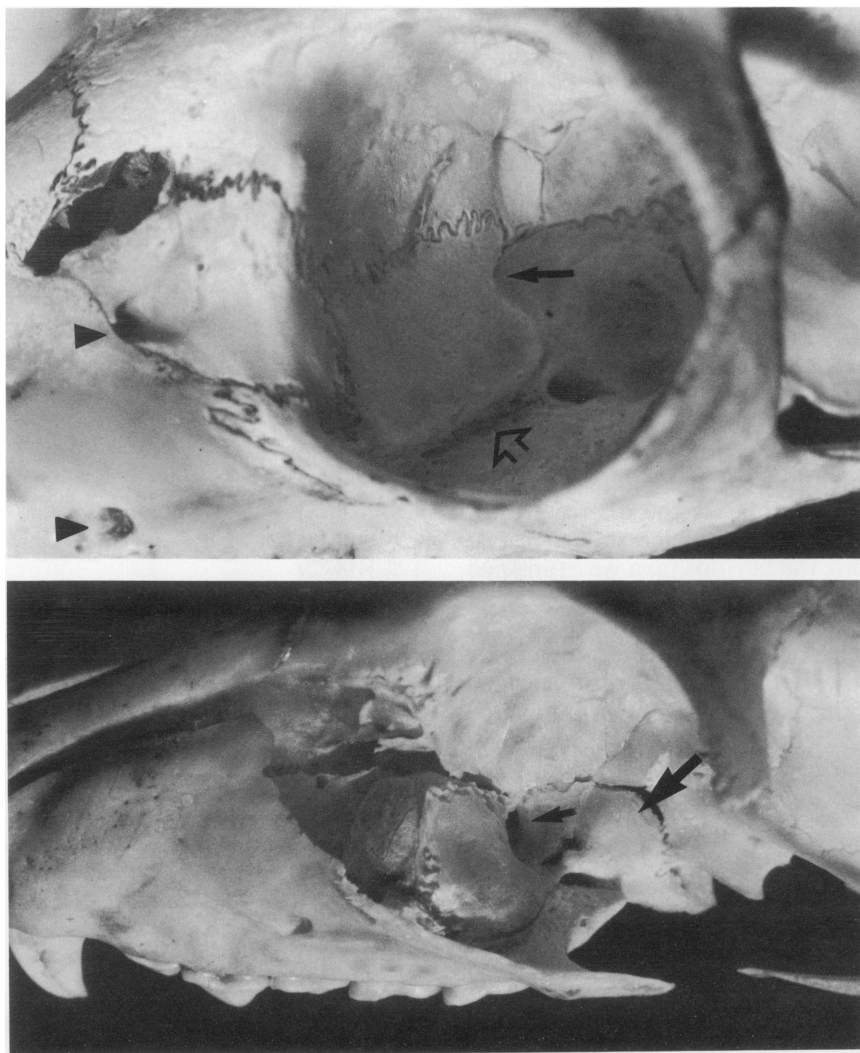


Fig. 1. Left orbital regions of *Lemur catta*, AMNH 100821 (above), and *Lemur fulvus albifrons*, AMNH 10590, with lacrimal and zygomatic removed (below). Small solid arrows show primitive size (small) and position (medial) of the nasopalatine foramen in *L. catta*, and derived (large) size in *L. f. albifrons*. Note the swelling of the prenasopalatine portion of the palatine in the area directly above the arrow in *L. catta*. The large solid arrow points toward the derived laterally swollen condition of the posterior portion of the palatine in *L. f. albifrons*. The open arrow is superimposed on the maxilla, which is primitively exposed in the orbital floor in *L. catta*, and points toward the derived lateral swelling in the medial orbital wall in this species. Triangles point toward the lacrimal foramen (above) and infra-orbital foramen (below); *L. catta* shows the derived condition whereby the latter lies anteriorly. Both taxa are typical for their group in excluding the maxilla from the medial wall of the orbit. Not to scale.

in its longitudinal development, being absent (0), present between P^3 and M^2 (1), or present along the entire length of the nasal fossa (2). ORD.

7. The posterior portion of the palatine (fig.

1). As exposed in the temporal fossa inferior to the orbitosphenoid, this element may be flat or slightly concave (0), or it may be swollen laterally (1). ORD.

8. The orbitosphenoid (fig. 3). This element

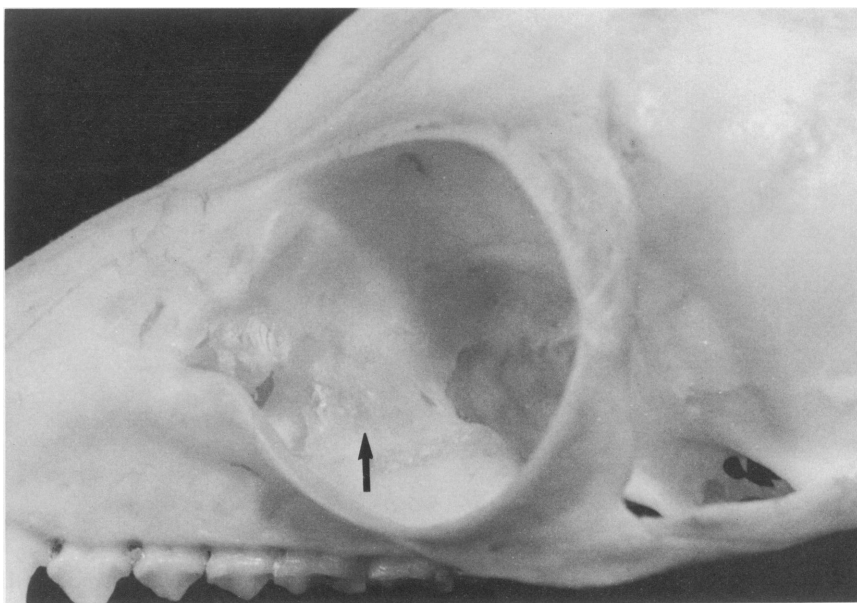


Fig. 2. Left orbital region of *Lepilemur leucopus*, AMNH 170578, showing primitive retention of maxilla (indicated by arrow) in the medial orbital wall.

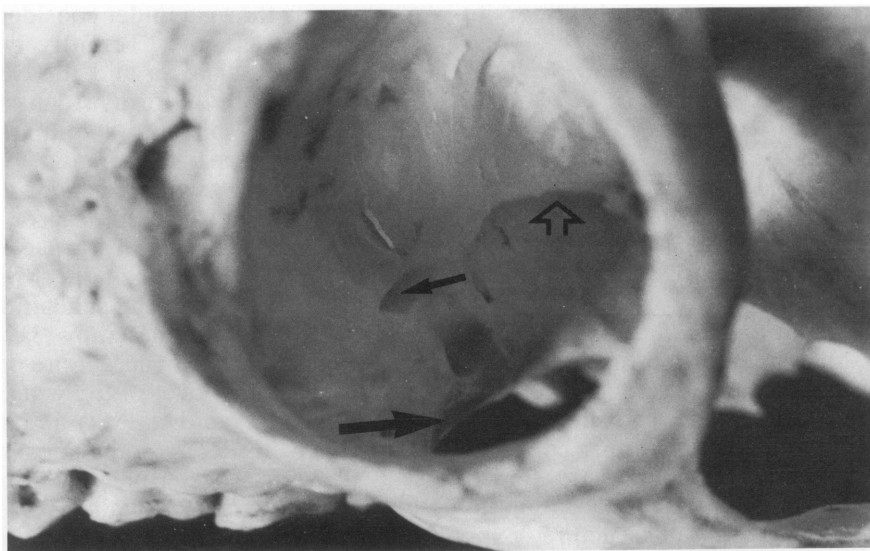


Fig. 3. Left orbital region of *Lemur macaco flavifrons*, AMNH 100606. The large arrow points to the derived posterior expansion of the posterior portion of the prenasopalatine that extends to the edge of the temporal fossa, excluding the maxilla from the orbital floor. The small arrow points toward the nasopalatine foramen, which is derived in size (moderate) and position (anteromedial). The open arrow indicates the swollen (derived) condition of the sphenoid in this region.

may be concave (0), or outwardly swollen (1). ORD.

9. Exposure of the maxilla laterally in the floor of the orbit (fig. 1). This element is

variably covered in superior view by the expansion of the postnasopalatine portion of the palatine bone. In some cases it is extensively exposed laterally (0), in

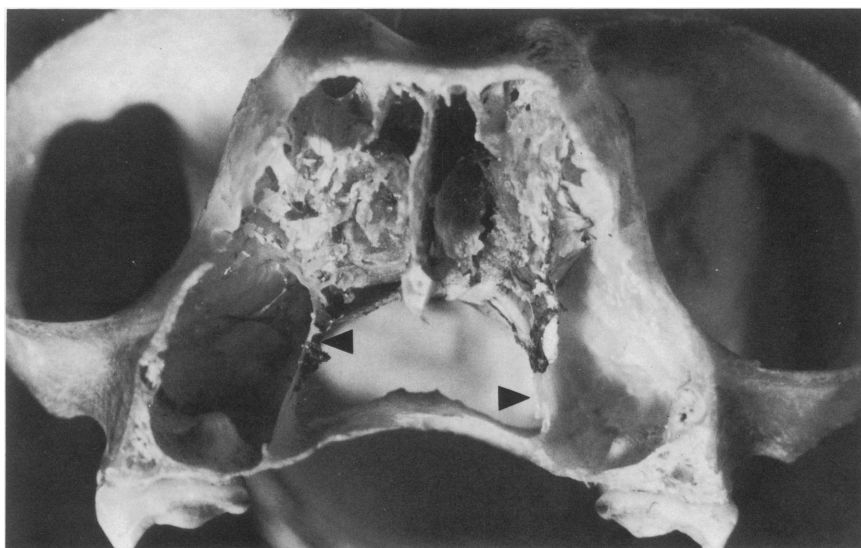


Fig. 4. Coronal section through the nasal region in *Varecia variegata variegata*, AMNH 18040. Triangles point to the laminae which wall off the paranasal sinuses laterally in derived forms such as this.

- others moderately (1), slightly (2), or not at all (3). ORD.
10. *Relation of the infraorbital foramen (IOF) to the lacrimal foramen (LF)* (fig. 1). In some cases the IOF lies in line with or posterior to the LF (0); in others it lies anterior to it (1).
 11. *Exposure of the maxilla in the medial orbital wall* (figs. 1, 2). In some cases this element is exposed (0); in others it is not (1). ORD.
 12. *Postnasopalatine "balloon"* (fig. 1). The postnasopalatine portion of the palatine bone is variably distended posteriorly into the orbital space. In some cases a distinct, encased, and approximately spherical bony "balloon" is developed within the posterior part of the paranasal fossa (1); in others, this structure is absent (0). ORD.
 13. *Inflation of the frontal sinus* (fig. 5). A well-developed frontal sinus is one of the most striking characteristics of some of the taxa under consideration here. This space may be absent (0), slight (1), slight to moderate (2), moderate (3), or extensively developed (4). ORD.
 14. *Cranial base behind the hard palate* (fig. 6). The morphology of this region varies among the taxa under consideration in a complex manner. Primitively, the roof of the nasal fossa and the cranial base posterior to it form a continuous flat plane, the sphenoid continuing into the posterior part of the nasal fossa at the same level as the sphenoccipital synchondrosis (0). In some taxa, however, the roof of the nasal fossa is raised anterior to the level of the M³s, a steep plane forming in the sphenoid medially and the palatine laterally (1); in others, this plane commences more posteriorly, at about the level of the wing of the internal pterygoid plate (2); and in *L. rubriventer* this depression is most marked of all, with a posterior excavation toward the occipital producing paired "post-choanal pits" (3). ORD.
 15. *Crest development on P⁴* (figs. 6, 8). This tooth may possess a protocone foldlike feature that runs down the distolingual portion of the tooth (0), or it may have a postprotocrista (1).
 16. *Lingual development of P⁴* (figs. 6, 8). In some taxa this tooth is unadorned lingually (0); in others it bears a protostyle (1).
 17. *Preprotocrista of P⁴* (figs. 6, 8). This crest

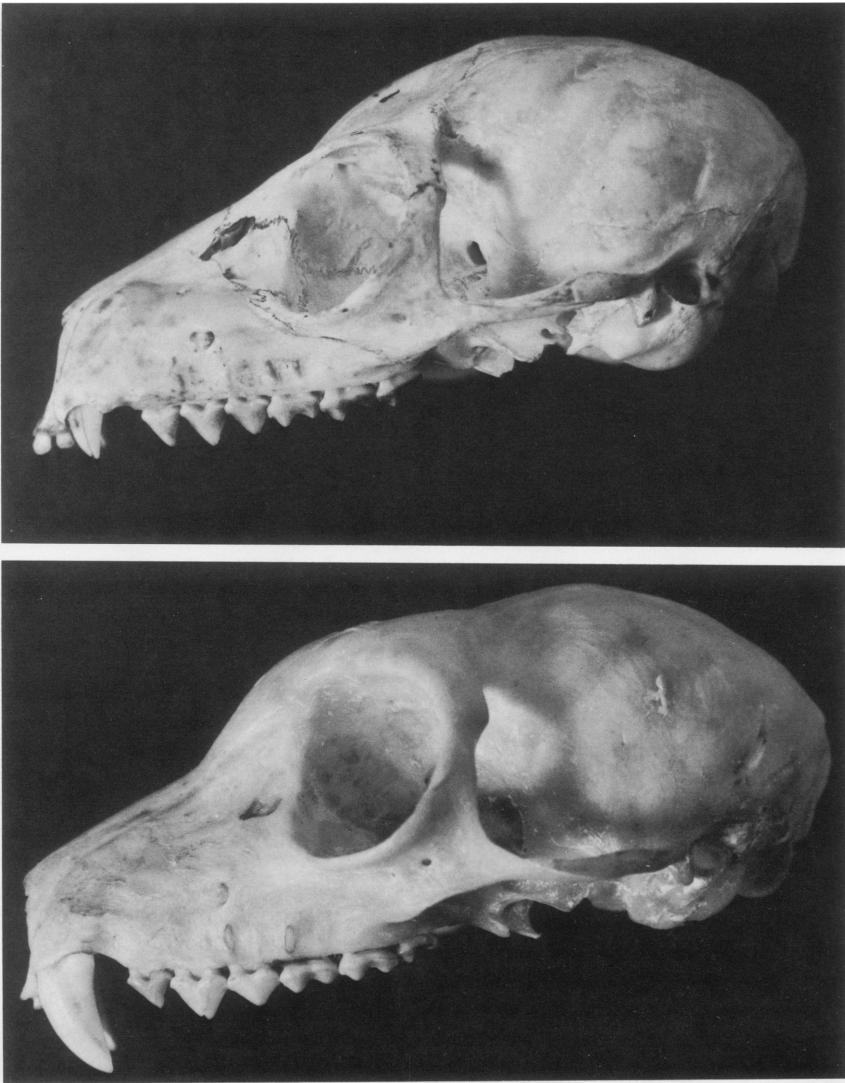


Fig. 5. Lateral views of *Lemur catta*, AMNH 100821 (above) and *Lemur fulvus albifrons*, AMNH 170699. The swollen frontal profile in the latter reflects the derived inflation of the frontal sinus. The canine tooth of the *L. catta* is not fully erupted, but the bony morphology is adult. Not to scale.

may run from the protocone to the parastylar region (0), slightly anterior to the paracone (1), or to the paracone (2).

18. *Crest development on M¹* (figs. 6, 8). This tooth may have a postprotocrista (0); have a protocone fold (2); have a protocone fold and a postprotocrista (3); or it may lack both altogether (1).
19. *Cingular development of M¹* (figs. 6, 8). On this tooth the lingual cingulum may

be absent (0); ledgelike (1); expanded anteriorly (2); or be elaborated into styles (3).

20. *Stylar development of M¹* (figs. 6, 8). This tooth may lack styles (0). If present, the protostyle and hypostyle may be confluent (1), separated by a crease (2), or broadly separated (3).
21. *Conules on M¹* (figs. 6, 8). This tooth may bear both a paraconule and a metaconule

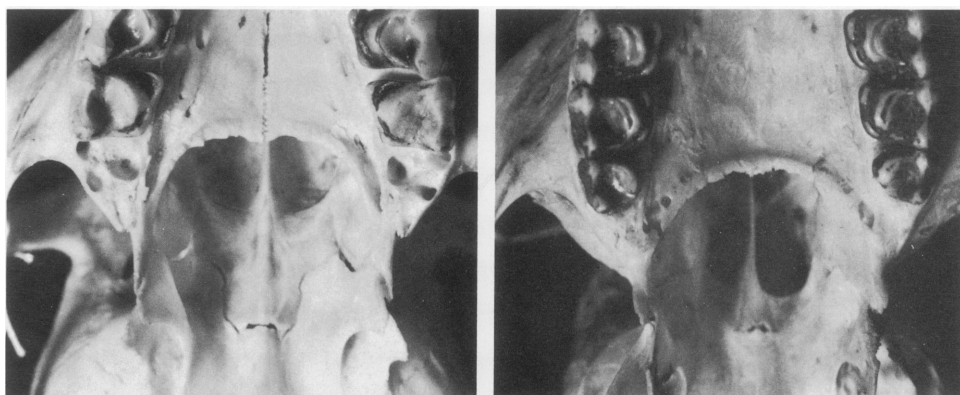


Fig. 6. View of *Lemur fulvus albifrons* AMNH 100590 (left) and *Lemur rubriventer* AMNH 100603, showing derived conditions of cranial base morphology. *L. f. albifrons* shows a posteriorly displaced excavation of the cranial base behind the hard palate, while *L. rubriventer* shows the development of full-blown "post-choanal pits." See fig. 8 for the primitive condition of this region.

- (0); a metaconule only (1); a paraconule only (2); or it may lack conules altogether (3).
- 22. *Cingular development of M^2* (figs. 6, 8). On this tooth the lingual cingulum may be absent (0); ledgelike (1); expanded anteriorly (2); or have style(s) (3).
- 23. *Stylar development of M^2* (figs. 6, 8). This tooth may lack styles (0); or it may have a protostyle (1); a confluent protostyle and hypostyle (2); or a protostyle and hypostyle that are broadly separated (3).
- 24. *Conules on M^2* (figs. 6, 8). On this tooth a paraconule and a metaconule may be present (0); or there may be a metaconule only (1); a paraconule only (2); or no conules (3).
- 25. *Crests on M^2* (figs. 6, 8). This tooth may bear a postprotocrista (0); no cristae (1); a protocone fold (2); or a postprotocrista and a protocone fold (3).
- 26. *P_3 metaconid* (figs. 6, 9). This structure may be absent (0), or present (1).
- 27. *P_4 metaconid* (figs. 6, 9). This cusp may be absent (0); present (1); or, in the case of *Hapalemur*, present but with a distinctive morphology (2).
- 28. *Metastylid on M_1* (figs. 6, 9). On this tooth a metastylid may be present (1), or absent (0).
- 29. *Lingual notch on M_1* (figs. 6, 9). A notch-like opening may be present on this tooth between the metaconid and the entocoid. This opening may be narrow or pinched (0), broad (1), or it may be absent (2), with a crest connecting the two cusps.
- 30. *Talonid opening on M_1* (figs. 6, 9). The lingual notch of this tooth, if present, may open centrolingually (0), or posterolingually (1).
- 31. *Position of entoconid of M_1* (figs. 6, 9). This cusp, if present, may be lingually placed (0), or centrally shifted (1).
- 32. *Paracristid of M_1* (figs. 6, 8). This crest may be confluent with the metaconid (0), disjunct from this cusp (1), truncated (2), or anteriorly directed (3).
- 33. *Metastylid on M_2* (figs. 6, 9). On this tooth a metastylid may be present (1), or absent (0).
- 34. *Lingual notch on M_2* (figs. 6, 9). A notch-like opening may be present on this tooth between the metaconid and the entocoid. This opening may be narrow or pinched (0), broad (1), or it may be absent (2), with a crest connecting the two cusps.
- 35. *Talonid opening on M_2* (figs. 6, 9). The lingual notch of this tooth, if present, may open centrolingually (0), or posterolingually (1).
- 36. *Shape of lower molar entoconids* (figs. 6, 9). These structures may be cusplike (0), crestlike (1), or absent (2).
- 37. *Talonid basins of the lower molars* (figs. 6, 9). These may be relatively short (0), or distally elongate (1). ORD.

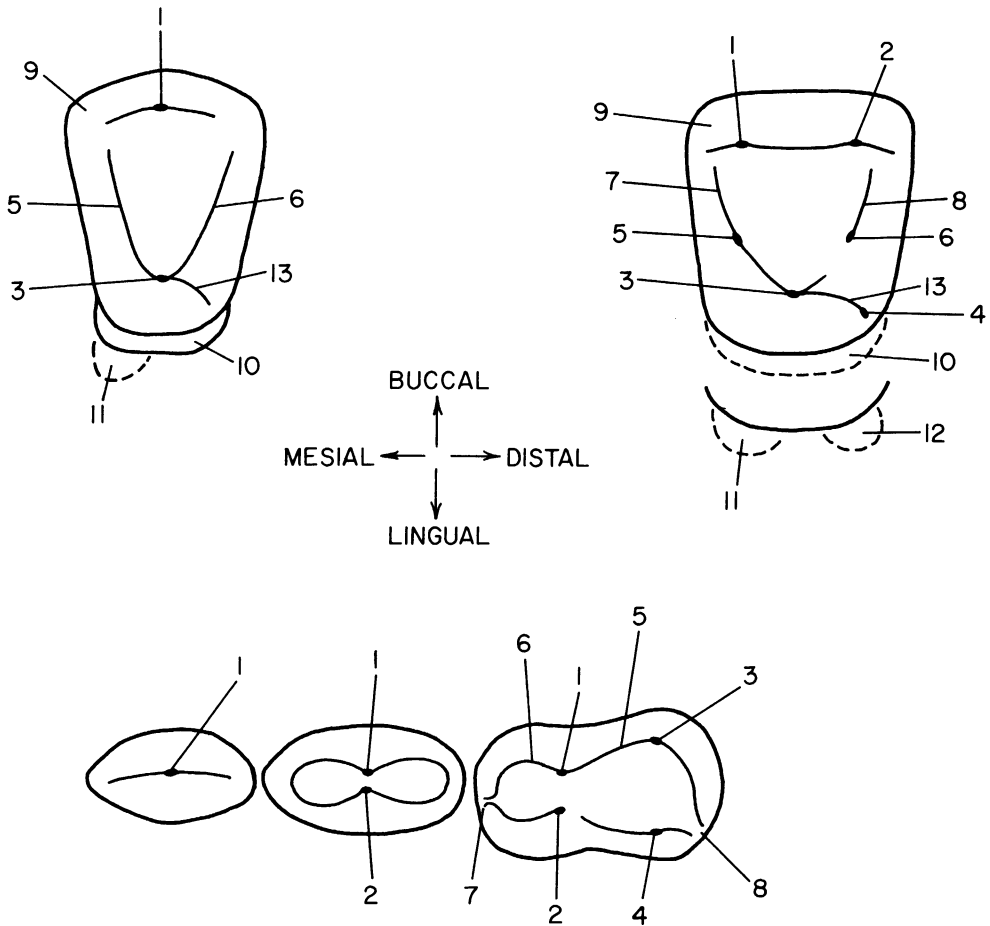


Fig. 7. Diagram to illustrate dental nomenclature employed here. Top left is a left P_4 ; top right is a left M_1 ; below, from left to right, are right P_3 , P_4 , and M_1 . Features of upper teeth: 1, paracone; 2, metacone; 3, protocone; 4, hypocone; 5, paraconule; 6, metaconule; 7, preprotocrista; 8, postprotocrista; 9, parastylar region; 10, cingulum; 11, protostyle; 12, hypostyle; 13, protocone fold. Features of lower teeth: 1, protoconid; 2, metaconid; 3, hypoconid; 4, entoconid; 5, cristid obliqua; 6, paracristid; 7, crease in paracristid; 8, lingual opening/notch.

The characters enumerated above do not concord with those used by Groves and Eaglen (1988) in their parsimony analysis of relationships within Lemurinae, partly because these authors dealt with a somewhat different spectrum of taxa than those considered here. It is noteworthy in this connection that Groves and Eaglen lumped together, in a "*L. fulvus*-complex," the taxa *L. mongoz*, *L. macaco*, *L. rubriventer*, *L. coronatus*, and the six subspecies of *L. fulvus*. As the data summarized in tables 2 and 3 attest, these taxa actually compose a diverse assemblage

whose homogeneity has, up to now, simply been assumed. Any phylogenetic analysis of the larger clade under scrutiny here quite clearly demands that each of these species or subspecies be considered in its own right.

Our character set also differs from that of Groves and Eaglen because many of the features they analyzed pose problems of recognition or interpretation. For example, the relative size of the upper incisors is a feature that is too greatly affected by wear to be applicable in the taxa we examined. In some cases these characters lack consistency. The



Fig. 8. Upper dentitions of (left) *Lemur catta*, AMNH 100825, and (right) *Lemur fulvus rufus*, AMNH 100569. *L. f. rufus* shows the derived condition of the postprotocrista on P^4 , preprotocrista on P^4 running slightly anterior to the paracone; postprotocrista on M^{1-2} ; M^{1-2} cingula divided into proto- and hypostyles that are broadly separated; no conules on M^{1-2} . *L. catta* shows P^4 with postprotocrista but lacking protostyle, and preprotocrista running to parastylar region; M^{1-2} have postprotocristae, ledgelike cingulae, no styles, no conules. Both taxa show the primitive condition of the cranial base. Not to scale.

size of P^2 relative to P^3 , for instance, appears to be excessively variable regardless of wear. Thus, in a randomly chosen sample of four *Lemur catta*, a species claimed by Groves and Eaglen to be distinguished from the “*fulvus*-complex” by a relatively unreduced P^2 , two individuals (AMNH 100596 and 170737) had substantially reduced P^2 relative to P^3 . Similarly, the condition of the paroccipital process showed too much intrataxon variation in the specimens we examined to permit its use in the formulation of phylogenetic hypotheses. Some of these characters are also primitive for the taxa under consideration and thus do not help to resolve relationships.

In certain cases the distribution of character states as listed by Groves and Eaglen

conflicts with our observations. For example, we did not encounter the variation described by these authors in the morphology of the posterior margin of the auditory bulla. Elevation of the orbital rims above the frontal bones is not characteristic of the *fulvus*-group, as claimed, but rather of the list of taxa characterized as lacking this feature. Similarly, with regard to the presence or absence of upper molar hypocones, *Hapalemur simus*, *Lemur catta*, and cheirogaleids as a group are listed by Groves and Eaglen as having a small hypocone, which by their definition should be “invariably seen on M^1 , and variably on M^2 ” (p. 520). Our observations show that *Lemur catta*, *Cheirogaleus major*, and *C. medius* lack anything that could reasonably

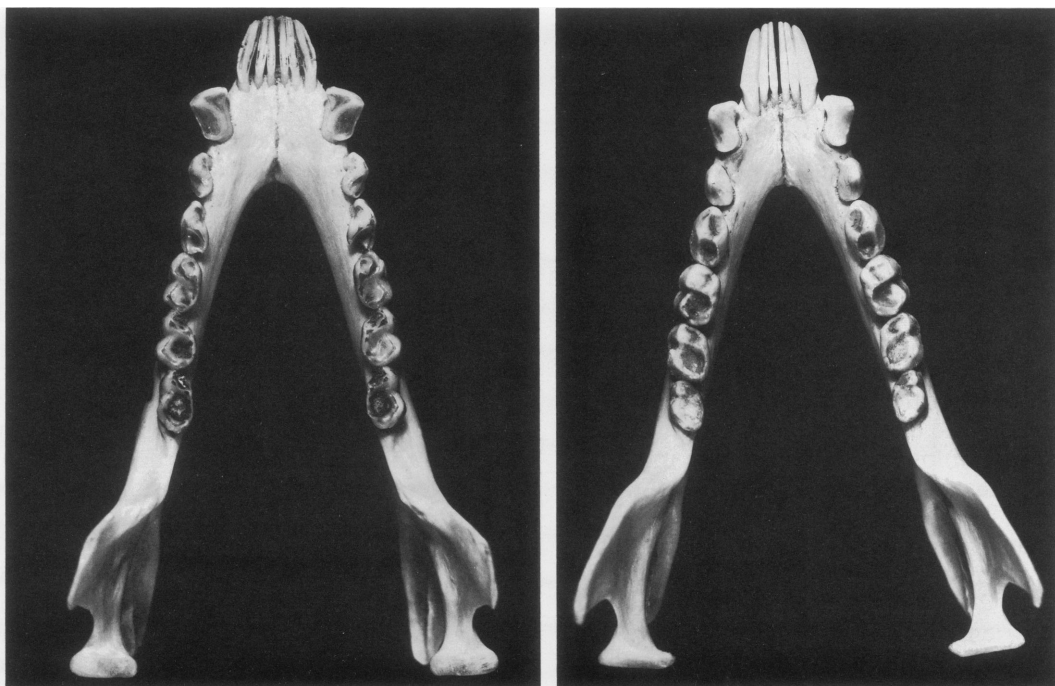


Fig. 9. Lower dentitions of (left) *Lemur catta* AMNH 100825, and (right) *Lemur fulvus rufus* AMNH 100569. *L. f. rufus* has: a P_3 without metaconid; a P_4 with metaconid; a M_1 with metastylid and without lingual notch; a centrally shifted entoconid and a disjunct paracristid. The M_2 lacks a metastylid and a lingual notch; all lower molars have crestlike entoconids and relatively short talonid basins. *Lemur catta* lacks metaconids on P_{3-4} ; has metastylids on M_{1-2} ; the posterolingual notch is pinched and posterolingual on M_1 , but broad and centrolingual on M_2 ; the M_1 entoconid is lingually placed and the paracristid is confluent with the metaconid; the lower molar entoconids are cusplike and the talonid basins relatively short.

be described as a hypocone on either of these molars (see, e.g., Schwartz and Tattersall, 1985, fig. 18). A more general problem with upper molar hypocones is one of definition: in species of the “*fulvus*-complex” the structure that Groves and Eaglen identify as a hypocone bears no resemblance to the cusp generally so identified in others of the taxa considered here. When present, this “hypocone” is a small, style-like accretion to the distolingual face of the protocone. It is morphologically identical to, and may be even smaller than, the structure on the same tooth generally identified as a protostyle. For this reason, and in recognition of its distinctiveness, we have chosen to identify this structure as a hypostyle rather than as a hypocone.

Groves and Eaglen gleaned from the literature a list of some 14 nonosteodental char-

acters which they incorporated into their analysis. In many cases these are known only from archaic or anecdotal descriptions, or are not known for a sufficiently large number of the taxa of interest here. Additionally, some of these characters are variable within the “*fulvus*-complex” (thus, in pigmentation of the ocular fundus, *L. mongoz* groups with *L. catta* and not with the other members of the “*fulvus*-complex”) and are therefore inappropriate for an analysis in which all members of this group are lumped together; in this case, states of this character in all taxa considered are not known. Nonetheless, among the soft tissue features enumerated by Groves and Eaglen, one, in particular, requires consideration in any systematic analysis of this group: the presence or absence of antebrachial glands. We have, however, limited our

quantitative analysis to the craniodental characters listed above.

RESULTS

As in our previous qualitative analyses of relationships among strepsirrhines (e.g., Schwartz and Tattersall, 1985), and as revealed by Groves and Eaglen's (1988) quantitative approach, the most striking result of our parsimony analysis is the demonstration of an astonishing degree of homoplasy, or parallelism, among the primates studied here. About half of the characters we used showed a remarkable degree of inconsistency of distribution among taxa even on the most parsimonious cladogram we obtained. Specifying an ancestor with state 0 for all 37 characters, but treating every character as unordered, a heuristic (nonexhaustive) search in PAUP yielded 80 trees each with the minimum length of 113. Ordering those characters specified in the list above still produced 14 trees of the minimum length of 115. Using ordered/unordered cranial characters only, we obtained 12 trees of length 40, with a low consistency index of 0.571 that, by itself, suggests extensive homoplasy. Running the ordered/unordered dental characters alone produced 11 trees of an identical minimum length of 64, but with a slightly more encouraging consistency index of 0.705. Only by excluding all characters with consistency indices of below 0.6 (i.e., numbers 1, 3, 6, 7, 8, 12, 13, 15, 23, 28, 33, 34, 35, and 36 in the list above) were we able to extract a single most parsimonious tree of length 62. Even this tree, however, was unable to recognize *Lemur fulvus* as a monophyletic assemblage. Interestingly, most of the characters with low consistency indices were cranial rather than dental, and they included some of the most striking morphological features observed.

In cases where homoplasy quite evidently contributes a great deal of "noise" to the system, as it clearly does here, it is legitimate to doubt whether the most parsimonious tree is in fact the correct one, even where a single such tree can be identified. Given a data set that produces a larger number of alternative trees of equal or near-equal probability, it seems more reasonable to ask whether particular relationships are consistently specified

in these sets of trees (a question also posed by Groves and Eaglen in their analysis). It is reassuring to note that among the taxa studied here, a high degree of such consistency is achieved in a number of cases. It is these consistencies that are reflected in the cladogram shown in figure 10, even though this arrangement of taxa does not yield the most parsimonious tree. With the hypothetical ancestor included in the analysis, tree length here is 120, in contrast to the 14 minimal-length ancestor-containing trees of length 115 found by PAUP. Omitting the ancestor from this same tree reduced its length to 114.

All 14 of the maximally parsimonious ordered/unordered trees constructed using all characters show *Hapalemur* as the sister taxon of all the other taxa studied, including *Lepilemur*. Both of these genera, however, retain the primitive condition in most of the characters examined, and are autapomorphic in almost all of the rest. It is noteworthy, and significant, that *Hapalemur* exhibits no characters of this craniodental set that would link it specifically with *L. catta*; but this analysis provides only a slender basis for making *Hapalemur* rather than *Lepilemur* the sister taxon of all other taxa analyzed. Indeed, switching these two genera in the cladogram shown in figure 10 resulted in no change in tree length; and in all of the 12 maximally parsimonious trees computed from cranial data alone, it is *Lepilemur* which emerges as the sister taxon of all the other taxa studied.

In contrast, the "*Lemur*-group" (*L. catta*, *Varecia*, and the "*fulvus*-complex") emerges as a monophyletic unit linked by a substantial group of synapomorphies, notably cranial ones. These include a laterally swollen prenasopalatine portion of the palatine bone and at least some posterior expansion of this element; possession of a paranasal sinus; some obscuring, at least, of the maxilla in the lateral part of the orbital floor; an infraorbital foramen lying anterior to the lacrimal foramen; maxilla unexposed in the medial orbital wall; and some cingular development on M¹⁻². Within this group, *Lemur catta* is shown in all 14 37-character trees to be the sister taxon of all the other taxa examined. Synapomorphies are few and far between, however; among characters in our data set, *Varecia* and the "*fulvus*-complex" are united only by lack-

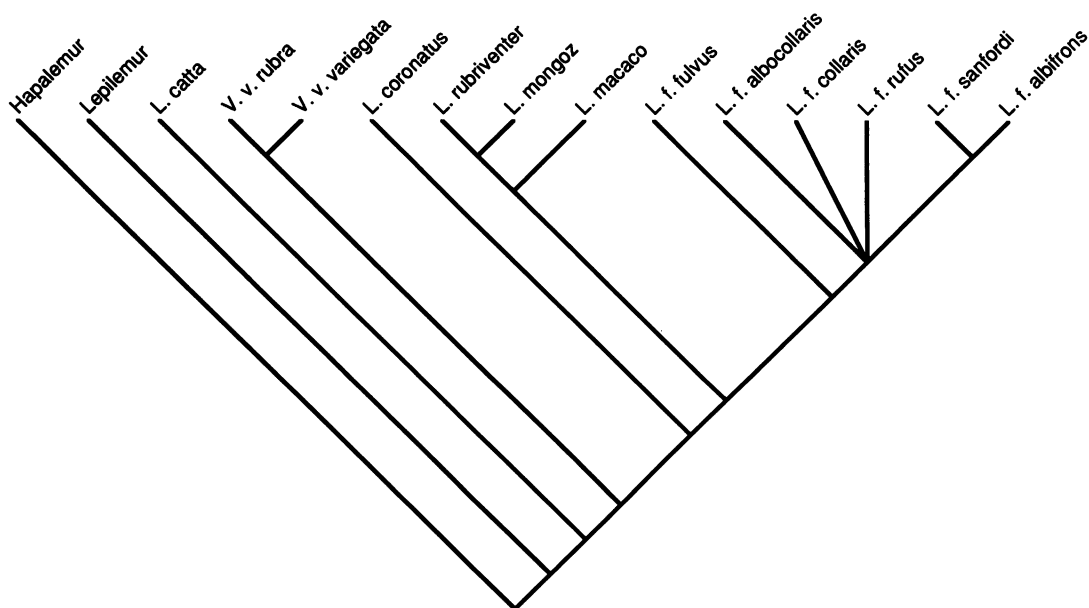


Fig. 10. Highly tentative cladogram to express some possible relationships among the taxa represented. However, few of these relationships are demonstrable with any degree of confidence on the basis of our craniodental data set. Treelength 114. Names are those in current general use; see text for discussion of relationships and nomenclatural proposals.

ing the lingual notch on M_{1-2} . We find it difficult to conclude that the relationship suggested by the set of maximally parsimonious trees is well established.

In contrast, the consistent relationship of *Lemur coronatus* as the sister taxon of all other members of the “*fulvus*-complex” (specified in all 14 maximally parsimonious 37-character trees), is supported by a substantial number of synapomorphies. These include an outwardly swollen orbitosphe-noid, some inflation of the frontal sinus, some excavation of the cranial base behind the hard palate, a P^4 preprotocrista running slightly anterior to the paracone, elaboration of styles on the cingulum of M^{1-2} , presence of a metaconid on P_4 , an M_1 paracristid disjunct from the metaconid, and crestlike lower molar entoconids.

Within the non-*coronatus* “*fulvus*-complex” there is considerable discordance among the 14 37-character trees. Nonetheless one consistent association occurs, that of *Lemur mongoz*, *L. rubriventer*, and *L. macaco*, the first two species forming a subclade. The whole group is united by a nasopalatine fo-

ramen of medium size, a moderately-to-greatly posteriorly expanded prenasopalatine, and a paranasal sinus present along the length of the nasal fossa. *Lemur mongoz* and *L. rubriventer* are linked by elimination of the maxilla from the lateral floor of the orbit, any by a moderate-to-extreme excavation of the cranial base posterior to the hard palate. We regard this as at best a moderately well-established monophyletic grouping. Interestingly, all 14 maximum parsimony trees place this grouping within a larger clade containing the various subspecies of *Lemur fulvus*, a fact which reflects in part the great morphological variety found within this latter species.

The clade containing the non-*coronatus* “*fulvus*-complex” is only rather weakly defined by the possession of a swollen medial orbital wall, and also by slight or nonexistent exposure of the maxilla in the lateral orbital floor, if *L. f. fulvus* is regarded as having secondarily enlarged this exposure. Given the distribution of character states in the group under consideration, assumptions of the latter kind must be made in many cases if one is to produce workable numbers of synapo-

morphies. Many derived characters in our set show considerable modification or even outright reversal within the groups they define, even under the most parsimonious hypothesis of relationship.

Lemur fulvus is, so far as we know (and we wish we knew more), a single species. Conventional criteria of allopatry, interfertility, and (at least in the case of the subspecies *fulvus*, *albifrons*, *rufus*, and *sanfordi*) karyology all attest to this. In terms of our craniodental character set this species is identified by a protostyle on P⁴, separation by a crease of the protostyle and hypostyle on M¹, and a centrally shifted entoconid on M₁. But despite this, none of our maximum parsimony trees, not even the single tree produced by eliminating those characters with consistency indices below 0.60, represents *L. fulvus* as a monophyletic assemblage. Perhaps this is because, as its geographic distribution suggests, *Lemur fulvus* represents a later radiation that closely mimics that of the genus *Lemur* itself. But the ability to explain (if indeed we can) the extraordinary degrees of homoplasy and autapomorphy that characterize the components of this species makes it no easier to decipher relationships within it. Given the inability of PAUP to recognize *Lemur fulvus* as a monophyletic unit, we analyzed its various subspecies separately from the other taxa in our sample and generated a large number of possible trees of maximum or near-maximum parsimony. The shortest trees we were able to find tended to be those in which *L. f. fulvus* was placed as the sister taxon of a clade formed by the other five subspecies, and within which *L. f. sanfordi* and the highly autapomorphic *L. f. albifrons* formed a subclade united by possession of a large nasopalatine foramen and a swollen posterior portion of the palatine. The cladogram in figure 10 incorporates the relationships suggested by these rather oblique observations. Its main feature, however, is a large unresolved polytomy, and it is clear that the craniodental evidence is inadequate for unambiguous or even plausible resolution of relationships among the subspecies of *Lemur fulvus*. These will evidently have to be decided on the basis of an alternative data set.

Our craniodental characters may have been somewhat disappointing in their ability to

resolve relationships between many of the taxa studied here, but they nonetheless emphasize a remarkable degree of autapomorphy among these taxa which permits us to define some of them for the first time on the basis of features of this kind. Our results demonstrate that many of these autapomorphies must have arisen many times within the group; below we list some of these characters that arise less frequently and that, individually or in combination with others, are of particular utility in recognizing the crania of the various species or subspecies of Lemurinae.

Varecia variegata: Elongate talonid basins of lower molars; absence of entoconids on lower molars; P⁴ preprotocrista runs to paracone; M¹ has protocone fold; talonid basin of M₂ opens posterolingually; lingual cingulum of M¹⁻² is expanded anteriorly. *Varecia v. variegata* has a posteromedially placed nasopalatine foramen, and is additionally distinguished from *V. v. rubra* by the much larger relative size of its cheek teeth.

Lemur catta: Ledgelike lingual cingulum on M¹⁻²; metastylid present on M₂.

Lemur mongoz: Orbitosphenoid unswollen laterally; extensive inflation of frontal sinus; steep plane excavates the cranial base posteriorly to level of wing of internal pterygoid plate; styles on M² confluent; broad lingual notch on M₁₋₂; M₁ paracristid truncated; metastylid present on M₂; entoconids absent on lower molars.

Lemur macaco: Preprotocrista of P⁴ runs to paracone; styles on M¹ broadly separated; M² bears a metaconule only.

Lemur rubriventer: Prenasopalatine greatly expanded posteriorly; prenasopalatine terminates posteriorly in "balloon"; postchoanal pits present in cranial base; M¹ bears protocone fold and preprotocrista.

Lemur coronatus: Nasopalatine foramina multiple; styles on M¹ broadly separated; M¹⁻² bear protocone fold and preprotocrista.

Lemur fulvus albifrons: Medial orbital wall unswollen laterally; paranasal sinus extends along length of nasal fossa; prenasopalatine terminates posteriorly in "balloon"; metaconid present on P₃.

Lemur fulvus albocollaris: M¹ bears paraconule only.

Lemur fulvus sanfordi: Steep plane exca-

vates cranial base posteriorly to level of wing of internal pterygoid plate.

DISCUSSION

It is rather disconcerting that, despite the existence of a substantial amount of craniodental variation among the taxa studied here, so little of that variation can be made pertinent to relationships within the group. Clearly we are dealing with a high degree of homoplasy. This might well be expected in a group of forms as closely related as these lemurs, for the more similar two organisms are structurally, the more likely identical character states are to arise in parallel. Nonetheless, the degree to which this has evidently happened here is unexpected, and it precludes the formulation of anything but the most provisional theory of relationships among the forms involved. Among the more robust conclusions that arise from this analysis is the monophyly of a subfamily Lemurinae containing *Varecia*, *Lemur catta*, and the "fulvus-complex"; the association of these taxa is supported by several synapomorphies. But whether *Hapalemur* is the sister of this subfamily remains equivocal to doubtful, and whether *L. catta* or *Varecia* is the outlier within the group is far from firmly demonstrable using our craniodental data.

What does emerge with reasonable certainty, however, is that these data lend no support to the sister relationship between *Hapalemur* and *L. catta* recently claimed by Simons and Rumpler (1988) and more weakly mooted by Groves and Eaglen (1988). Simons and Rumpler based their argument on the mutual possession by *Lemur catta* and *Hapalemur* species of antibrachial glands and associated behaviors, and on aspects of the karyotype. We have reservations about the procedure Rumpler and his associates used to reconstruct ancestral karyotypes, and thus relationships: a parsimony method based on character commonality is claimed, but the fact that this procedure allows even remote ancestral karyotypes to be specified in their entirety using banded chromosomes from members of the extant fauna (e.g., Rumpler and Dutrillaux, 1986) points to some degree of inconsistency in the methodology employed (although nowhere completely speci-

fied) by these authors. Further, while the antibrachial glands of both *Hapalemur* and *Lemur catta* certainly provide a striking aspect of similarity between the two taxa, marking glands are widely and inconsistently distributed among the lemurs and the strong possibility of parallelism cannot be discounted, especially since the antibrachial gland of *Hapalemur* is not associated with a spur as is that of *L. catta*. Given the unusually substantial suite of craniodental synapomorphies linking *L. catta* with *Varecia* and the "fulvus-complex" we prefer to recognize this as a monophyletic assemblage and to regard as parallel acquisitions the resemblances between *Hapalemur* and *L. catta* cited by Simons and Rumpler.

Within the "fulvus-complex" the position of *L. coronatus* as outlier seems well established by synapomorphies, but beyond this the pattern of relationships is unclear. If *L. fulvus* is accepted as a monophyletic unit, it seems reasonable to place the *L. macaco*-*L. rubriventer*-*L. mongoz* clade as a sister to it, but based on craniodental evidence, relationships at and especially below this level cannot be stated with any degree of certainty. Evidently, at degrees of relatedness as close as those within Lemurinae, the amount of morphological "noise" in the system tends to drown out the phylogenetic signal. This is particularly disappointing since the generation of reliable area cladograms, an aim clearly not achievable on present evidence, provides the only viable approach to reconstructing the history of diversification of Lemurinae on the island of Madagascar.

Of more immediate practical import is the effect of this systematic uncertainty on the nomenclature of this group of lemurs. As noted earlier, two new names (*Eulemur* Simons and Rumpler, 1988, based on *L. mongoz*; *Petterus* Groves and Eaglen, 1988, based on *L. fulvus*) have recently been proposed for members of the "fulvus-complex," and have created the potential for prolonged nomenclatural uncertainty. Our analysis shows that while a sister relationship between *L. catta* and *Hapalemur* appears unlikely, it is possible though not certain that the ringtailed lemur is more remotely related to the "fulvus-complex" than is the ruffed lemur, which, though earlier classified within genus *Lemur*,

is nowadays assigned by most authors to the separate genus *Varecia*. On current evidence any hypothesis of relationships among these forms is tentative at best, and uncertain phylogenies of this kind hardly warrant the wholesale confusion threatened by the recent nomenclatural innovations.

One possible solution to this problem would be to continue to use the current nomenclature, with *Varecia* recognized on phenetic grounds as distinct from a genus *Lemur* containing the species *catta*, *mongoz*, *macaco*, *fulvus*, *rubriventer*, and *coronatus*. A more robust resolution, and in our view a preferable one, would be to return to the systematics of a decade or two ago, synonymizing *Varecia* with a genus *Lemur* that thus contains the species *L. variegatus* in addition to those just listed. This would result in a genus *Lemur* that is not excessively speciose by primate, still less by general mammalian, standards; it would reflect the fact that this apparently monophyletic group is structurally so close-knit that it is extremely difficult to establish relationships within it; and, since the craniodental evidence suggests that a definitive demonstration of a *Lemur catta*–*Hapalemur* affinity is unlikely to be forthcoming, it would have the highly desirable result of establishing a stable nomenclature.

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