Toothcomb Origins: Support for the Grooming Hypothesis

ALFRED L. ROSENBERGER

University of Illinois at Chicago

and ELIZABETH STRASSER

City University of New York

ABSTRACT. Debate over the original adaptive significance of the lemuriform toothcomb, whether it was principally a grooming organ or a scraper-feeding tool, currently hinges upon the functional morphology of the lower incisors and canines of lemurs and lorises, and the fossil adapids thought to be their ancestors or structural prototypes. We suggest that the morphology of the upper incisors and the oronasal complex of the latter, given the context of a more general theory of incisor evolution within the primates, exhibits preadaptive conditions foreshadowing the emergence of the toothcomb and also evidence of strepsirhine monophyly. We find in all underived lemuriforms and in most fossil adapids where the elements are known, a striking continuity in upper incisor form, including such derived features as an interincisal diastema, strong central incisor prong, low-crowned morphology and reduced premaxillary size. The pattern suggests a basic strepsirhine reduction in the functional significance of the anterior dentition in feeding and harvesting roles. These features may be related to a novel connection of the rhinarium with the vomeronasal organ via a sulcate pair of labial folds, which serves as a component of a specialized behavioral-physiological complex dealing with olfactory communication. Rather than being the anatomical nucleus of this system, the toothcomb may have been added secondarily in the lemuriform descendants of the preadapted adapids, possibly as a device to stimulate glandular secretion of pheromones by direct pressure, and to simultaneously distribute odorants through the fur.

Key Words: Toothcomb; Lemuriforms; Adapids; Grooming; Phylogeny; Adaptation.

INTRODUCTION

Ideas concerning the evolution of the lemuriform toothcomb developed about two focal questions, disconnectedly: (1) From what phylogenetic and anatomic source did the toothcomb emerge? (2) What are the functional and adaptive explanations underlying its evolution? Until a truly comprehensive fossil record reveals the morphological changes involved in the transition from a non-toothcombed ancestor, to answer these questions we must rely upon reconstructions using morphological information from fossils and extant species in concert with behavioral observations.

In this paper we propose that the *upper* incisors of toothcombed primates offer clues regarding the preadaptive morphology which evolved into the toothcomb complex. Albeit vestigial in some living species, we find in the morphology of the $I^{1, 2}$ traces of a unique phylogenetic and adaptive heritage. Eocene adapids and most living strepsirhines combine the same set of derived features in $I^{1,2}$, although the fossils do not exhibit many indications of a toothcomb morphology in $I_{1,2}$, or C_1. We suggest that the highly modified condition of the lower incisors and canine may have been a secondary development contingent upon a preestablished

behavioral shift experienced by the earliest strepsirhines, whereby feeding roles of the snout became less important and were supplanted by olfactory and tactile roles relating to communicative processes.

MATERIALS AND METHODS

Our study is based upon morphological observations of nearly all modern strepsirhine genera, tupaiids, several modern Insectivora, pertinent primate fossils such as *Pelycodus*, *Notharctus*, *Adapis*, *Leptadapis* and casts of others. The critical fossil specimen forming the basis of our interpretation of notharctine morphology is YPM 12956, assigned to *Notharctus tenebrosus* and fully described elsewhere (ROSENBERGER, STRASSER & DELSON, 1985). It is the most complete anterior dentition known for notharctine adapids. Taxonomic nomenclature follows SZALAY and DELSON (1979), wherein lemurs and lorises are collectively referred to Lemuriformes. Other terms, and the conceptual-interpretive model of adaptation to which we ascribe, are developed in BOCK (1981).

ORIGINS OF THE TOOTHCOMB

GREGORY (1920) was perhaps the first to give detailed attention to the problem of the tooth-comb's origin. He concluded that *Protoadapis sciureus* showed resemblances to living lemuriforms which foreshadowed the toothcomb's morphology, particularly in its low-crowned, subcaniniform lower canine and narrow incisor alveoli. The idea was an outgrowth of GREGORY's conviction that adapids were broadly ancestral to extant lemuriforms. GINGERICH (1975) developed this hypothesis further but chose another formative ancestor, *Adapis parisiensis*. GREGORY had explicitly rejected that species because he thought it too "specialized" to represent a structural ancestor. GINGERICH, however, argued that "The lower canines of *Adapis parisiensis* are functionally incisors.... Once the lower teeth in this species came to function as a unit, it is not difficult to understand how all its teeth were modified similarly to form a dental scraper" (1975: 73).

LE GROS CLARK (1959), believing that tupaiids were primates, indicated that their comb-like lower incisors presaged the lemuriform pattern. In his scenario the adapid stage was presumably bypassed. LE GROS CLARK and THOMAS (1952) also regarded the Miocene fossil lorisoids of Africa as evidence that the toothcomb was not then established in its modern form, implying that lemurs and lorises independently evolved the complex. Further study of that material, however, demonstrated otherwise (WALKER, 1969) and supported the conclusion that the toothcomb had a monophyletic origin (e.g., MARTIN, 1972; SZALAY & KATZ, 1973). It has also since become clear that tree shrews are more distantly related to primates than LE GROS CLARK thought (LUCKETT, 1982), and that their morphology is inappropriate for modeling an early primate or an early lemuriform.

ADAPTIVE SIGNIFICANCE OF THE TOOTHCOMB

Two schools of thought have emerged with explanations of the causal factors leading to the evolution of the toothcomb. A full presentation of these opposing arguments can be found in MARTIN (1972) and SZALAY and SELIGSOHN (1977). In brief, advocates of the Tooth Scraper

Hypothesis (e.g., MARTIN, 1972; GINGERICH, 1975; GINGERICH & MARTIN, 1981) presume that the scoring and prising of bark, using the lower incisors and canines as a tool, is a primitive behavioral and morphological complex of lemurs and lorises and the selective foundation of the original toothcomb. MARTIN (1972) cited dietary "specialists" such as *Phaner*, which feeds on exudates and exhibits an hypertrophied toothcomb, and the recently extinct *Megaladapis*, which was probably highly folivorous and evolved a premaxillary palatal pad to substitute for the lost upper incisors, to demonstrate that the anterior dentition of modern strepsirhines is subject to selectional forces associated with feeding. This makes plausible the hypothesis that similar functions were operative among early strepsirhines when the anterior teeth supposedly served as a "tooth-scraper." In addition, it is reasoned (GINGERICH & MARTIN, 1981) that the anatomical "compression" of the lower incisors and canines into the unitary functional complex which we find in *Adapis parisiensis* is covergent to the "short-tusked" exudativorous adaptation of *Callithrix* (e.g., KINZEY, ROSENBERGER & RAMIREZ, 1975), thus substantiating their original function as a feeding mechanism.

The Grooming Hypothesis (e.g., BUETTNER-JANUSCH & ANDREW, 1962; SZALAY & SELIGSOHN, 1977) emphasizes another lemuriform universal, the combing of the fur with the anterior teeth. SZALAY and SELIGSOHN, in particular, justify this idea on theoretical and mechanical grounds. They maintain that the structure of the lower incisors and canines is ill-suited mechanically to withstand the stresses of gouging (except in such obviously derived cases as *Phaner*) but is designed to maintain even interdental spaces. They thus repudiate the Dietary Hypothesis and explain the morphotypic lemuriform condition as a mechanism to clean, align and stroke hairs.

Many of the theoretical weaknesses of the Tooth Scraper Hypothesis have been noted by SZALAY and SELIGSOHN (1977). Their major criticism is that the adaptive connection between comb-like anterior teeth and incisivation was made entirely via an arbitrary application of the analogy principle (e.g., MARTIN, 1972) without an accompanying mechanical analysis of form and function. A thread of inconsistency also appears to run through some of its justifications. MARTIN (1979) disavows the necessity to postulate gouging and scraping behaviors in the lemuriform ancestral stock, theorizing that as a preadaptation they could have symbiotically fed on natural gum licks produced by wood boring insects. GINGERICH and MARTIN (1981), however, ascribe mechanical incisivation specializations to their pre-toothcombed ancestor, *Adapis parisiensis*. In addition, the Tooth Scraper Hypothesis seems to presuppose a continuity of selective pressure from the Eocene onwards in concert with a dramatic morphological transformation. If the so called "short-tusked" scraper of *A. parisiensis* was already well adapted for gouging (and descendant from an anatomically different condition), why should a novel lemuriform pattern replace it if the latter's major biolotical role is still gouging and scraping?

Regarding the phylogenetic origins of the toothcomb complex, the GINGERICH-MARTIN hypothesis also becomes problematic by literally specifying *Adapis parisiensis* as a true ancestor where a morphotype pattern might be more defensible. A number of uniquely derived features are known in this species and its closest relative, *Leptadapis magnus*, which bar either from being directly ancestral to modern lemuriforms. These include the fusion of the mandibular symphysis and anatomy of the corpus (e.g., BEECHER, 1983), and a large number of postcranial traits that are convergences on lorisoid morphology (DAGOSTO, 1984). Whereas both GREGORY (1920) and GINGERICH (1975) theorized that a "simple" genetic event could alter the mandibular symphysis to conform with the modern syndesmosis, the transformation

to an open symphysis seems irreconcilable with the notion that selection to more efficiently endure the heavy stresses of gnawing was responsible for the change.

Thus the Grooming Hypothesis survives as perhaps the best working hypothesis of the functional-adaptive significance of the lemuriform toothcomb. However, its phylogenetic derivation from a more primitive strepsirhine ancestor is still a matter which requires resolution in order to make the transformational hypothesis maximally robust (SZALAY, 1981).

INCISOR FORM AND FUNCTION IN THE
EARLIEST PRIMATES

Hyopotheses concerning the phylogenetic derivation and early adaptations of the tooth-comb, or a non-toothcomb prototype, should be consistent with a general theory of incisor-canine evolution in other groups of primates for, as most believe, it is unlikely that a tooth-comb was present in the earliest members of the order. However, precisely what morphology characterized the first primates is a matter of dispute. The fossil record rather clearly demonstrates that Paleocene plesiadapiforms universally had relatively large, procumbent median incisors flanked by a smaller (or absent) lateral tooth. The majority of students have interpreted this pattern as aberrantly autapomorphic (e.g., SIMPSON, 1940; SIMONS, 1972), thus eliminating it from an ancestral pole in the transformation to other morphologies. GREGORY, for example, gave lengthy consideration to a reconstruction of ancestral primate incisor morphology and concluded that the "... lower incisors were of small size, not chisel shaped, not strongly procumbent" (1922:229). LE GROS CLARK gives a similar description for a primate and eutherian morphotype; "... incisors are small teeth, cylindrical with rounded tips or slightly spatulate" (1959:79).

ROSENBERGER and SZALAY (1980) have suggested an alternative view which has recently been elaborated in more detail (ROSENBERGER, STRASSER & DELSON, 1985). In considering the full range of variation in incisor proportions among the plesiadapiforms, two contrasting patterns emerge. One is represented by the peculiar—relative to euprimates—dentitions of the Families Plesiadapidae and Phenacolemuridae. The other comprises more primitive groups such as the Paromomyidae, which have less exaggerated I1:I2 proportions. We suggest that the primate morphotype was characterized by a moderately tall, stout, relatively upright, conical or cylindrical lower median incisor coupled with a smaller lateral tooth of roughly the same shape (Fig. 1), such as in *Palaechthon, Plesiolestes* and *Palenochtha* (SZALAY & DELSON, 1979). The morphology of I^1 would have been essentially similar but less pointed, and its lingual fossa would have been excavated to reciprocate the apical margin of I^1. Both upper and lower median incisors would have occluded exclusively with one another rather than exhibiting the tandem $I^1/I_{1,2}$ occlusion found in anthropoids and adapids (see ROSENBERGER, STRASSER & DELSON, 1985). I^2 would have been rotated out of the frontal plane, lying laterally behind the dominating I_1^1 unit. This reconstruction, and the hypothesis that it in fact reflects the ancestral primate pattern, economically explains several points: (1) The presence of a dominating anterior tooth in the very earliest known primates including *Purgatorius* (KIELAN-JAWOROSKA, BOWN & LILLEGRAVEN, 1979), which in all other dental features is considered to be highly primitive; (2) the incidence of a relatively large I1 in plesiadapiforms, omomyids, anthropoids and strepsirhines; (3) the offset spatial position of I^2 in plesiadapoids and primitive, notharctine adapids; and (4) the common presence of en-
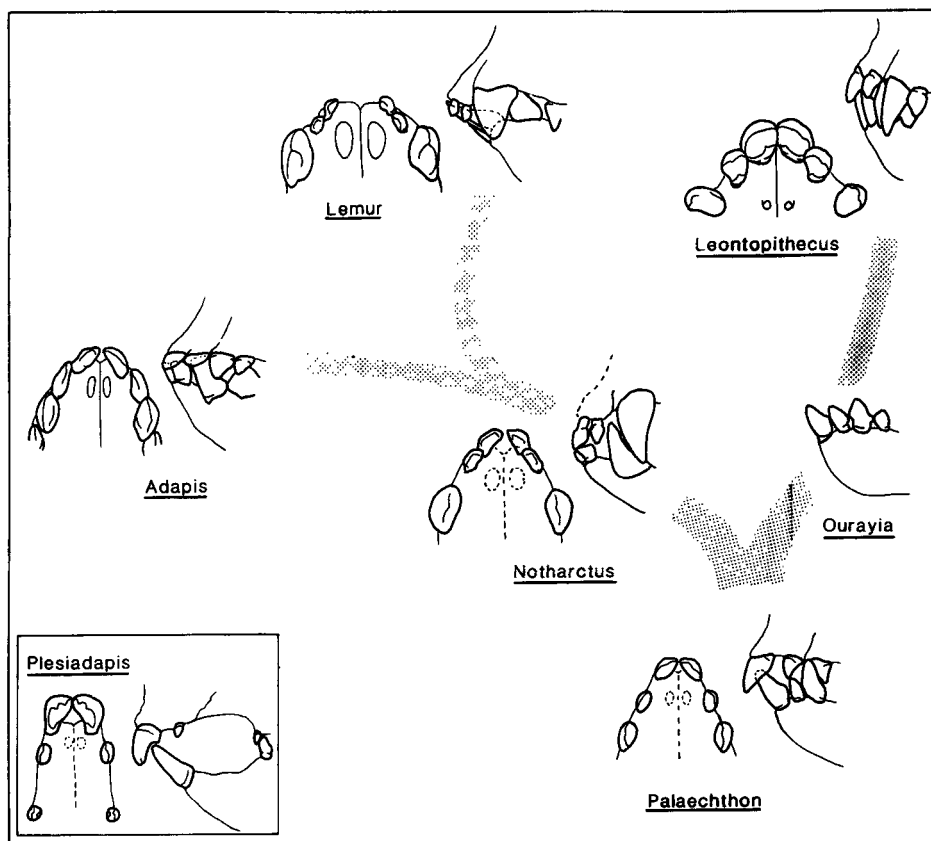
Fig. 1. A scenario of the evolution of the incisor-canine complex among the major groups of primates. Lateral views represent centric occlusion, others are oriented similarly on the palate. Examples of *Palaechthon, Adapis* and *Ourayia* are adapted from SZALAY and DELSON (1979) and/or STEHLIN (1916); others are based upon our observations. The largely hypothetical reconstruction of *Palaechthon* is presented as a morphotype model. Note the generally reduced upper incisors and premaxilla of strepsirhines. Also the somewhat larger, broader incisors of *Adapis*, contrasting the conditions in *Notharctus* and *Lemur*. *Ourayia* represents a hypothetical tarsiiform model of an anthropoid ancestor. The disproportionately larger upper median incisors and slightly staggered laterals of *Leontopithecus* are secondarily derived among platyrrhines. The uniquely derived *Plesiadapis* is offset to indicate that it cannot be ancestral to later euprimate patterns.

larged median incisors in eutherians that might be closely related to primates, such as the microsyopids and plageomenid dermopterans.

There is a range of functional hypotheses for the adaptive interpretation of an anterior dentition of this sort (see SZALAY & DELSON, 1979). Clearly, it was suitable for probing, prying and piercing, especially in its more specialized configurations (e.g., *Phenacolemur*). In the moderately large version which we postulate as morphotypic, similar roles would have prevailed but the anterior teeth would also probably have shown more flexibility. It is highly unlikely that large-calibered incisors were specifically selected for grooming behaviors, but the pervasive use of the anterior teeth for grooming among hairy mammals, in conjunction

with the recent evidence given by ROSE, WALKER and JACOBS (1981), suggests that such roles would have been part of their normal use.

Assuming our hypothetical anterior dentition as the starting point in primate evolution (see Fig. 1), two major derived conditions can be identified in two descendant lineages, in strepsirhines and in anthropoids. In this view we concur with GINGERICH (1976 et seq.) and SCHWARTZ, TATTERSALL & ELDREDGE (1978), who see the omomyids and plesiadapiforms as having homologously enlarged median incisors. Whereas we interpret this commonality as retained primitiveness, others (e.g., SZALAY, 1976; CARTMILL & KAY, 1978) regard it as parallelism. Our conclusions pertaining to adapid and anthropoid convergence in incisor form, which is implicit in this polarity hypothesis, are detailed elsewhere (ROSENBERGER, STRASSER & DELSON, 1985). We regard the "spatulate" incisors of adapids and anthropoids as nonhomologous, due to their underlying dissimilarity: low-crowned vs. moderate-to-high-crowned uppers; buccolingually thin vs. thick uppers; a dominating I^1 mesial process vs. a more symmetrically shaped tooth; minimal interstitial contact vs. intertooth compaction.

This transformational hypothesis also implies that the pattern shown by *Adapis parisiensis* and *Leptadapis magnus* is autapomorphic and probably not ancestral to the condition seen in the anterior teeth of lemuriforms (ROSENBERGER, STRASSER & DELSON, 1985). Unlike the notharctines (*Notharctus, Smilodectes*, and *Pelycodus*) in these adapinans I^2 is enlarged and not staggered behind I^1; the median interincisal diastema seems to be absent; $I_{1,2}$ are very low crowned, robust and possibly more vertical; C_1 is subcaniniform and bears a novel occlusal relationship with I^2. Others (e.g., KAY, 1980; MAIER, 1980a) have also noted that on phenetic grounds the lower anterior teeth of the *Adapis-Leptadapis* pattern bears little resemblance to the toothcomb. Apart from their relative narrowness and somewhat more proclivous orientation, however, those of *Notharctus* are not markedly similar to lemuriforms either. But the uppers of notharctines do resemble many lemurids and indriids strikingly: I^1 is low-crowned and presents a strong mesial process; interstitial contact is absent between median incisors; I^2 is staggered behind I^1 yet lies in the frontal plain; $I_{1,2}$ does not occlude with I^2. The notharctine pattern could easily become modified into that seen in adapinan adapines, according to the mechanisms implied by the "cropping" model of GREGORY (1920) and GINGERICH (1976). However, this also suggests that the notharctine condition is the more primitive one within the adapids.

PREADAPTATION AND THE ORIGINS OF
THE LEMURIFORM TOOTHCOMB

The relevant implications of the foregoing are threefold: (1) It emphasizes similarities of the anterior teeth shared by adapids and lemuriforms, despite the fact that their lower incisors and canines are quite different; (2) it supports GREGORY's (1920) view, based upon a striking number of phenetic similarities, that adapids are broadly ancestral to modern lemurs and lorises; and (3) it suggests that the primitive morphology of adapids may be preadaptive to the evolution of the toothcomb.

Although they have not been stressed by many later students, GREGORY (1920) discussed several similarities jointly found in the upper incisors of adapids and lemuriforms, including the development of an interincisal median diastema, a low-crowned I^1 bearing a mesial prong and a structurally gracile design. It follows from our previous discussion that this pattern is a likely synapomorphy of all strepsirhines, indicative of their monophyletic origin. This con-
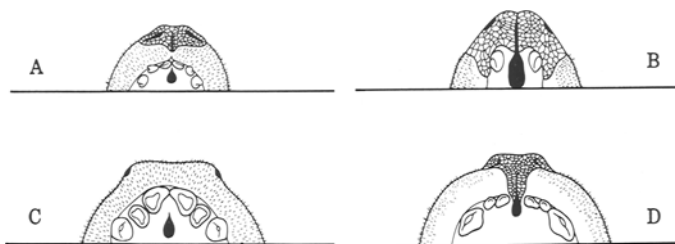
Fig. 2. Ventral views of (A) dog (MILLER, 1964), (B) tree shrew (WHORMANN-REPENNING, 1978), (C) titi monkey and (D) slow loris (MAIER, 1980a) showing how the philtrum connects directly with the palatine papilla (solid black) when a gap appears between median teeth (B, D), and when crowding of the incisors (A, C) prevents their attachment. Not to same scale.

clusion is in agreement with many workers (e.g., STEHLIN, 1916; GREGORY, 1920; LE GROS CLARK, 1959; SZALAY & DELSON, 1979) who sought to derive lemuriforms from one sort of adapid or another for a variety of reasons. However, it also implies that an equally derived functional-adaptive continuity links adapids and lemuriforms together, apart from whatever differences are present in their lower incisors.

The reduction in tooth robusticity and premaxillary size implies a transformational shift in the way foods were being treated with the incisors from the ancestral plesiadapiform manner of harvesting, where a set of pincer-like grips operated in unison or where I_1 was used as a high-pressure gouge. In adapids and lemuriforms, reduction and elimination of interstitial contact between the upper central incisors would increase the force per unit area incurred by each of the teeth individually because loads cannot be transferred between them. Furthermore, the exclusion of I^2 from occlusion with the paired lower incisors would concentrate forces on the median incisors as well. The comparatively gracile premaxilla also suggests that upper incisor roots and alveoli were not especially designed to endure heavy stress. Since mandibular harvesting behaviors were still surely retained in euprimates from a plesiadapoid ancestry, some other set of faculties must have directed the evolution of the new character complex which arose in the rostrum of adapids, with its seemingly diminished capacity to endure powerful loads.

What is the functional significance of this morphological pattern? Apart from being the seat of the feeding mechanism, the lemuriform snout serves as a platform for a complex of sensory organs dealing with communicative processes. The soft anatomy of this region has recently received detailed study in various lemuriforms and insectivorans (e.g., HOFER, 1977, 1982; WHORMANN-REPENNING, 1978), making it possible to reconstruct some gross anatomical features in related fossils of similar structure, like the adapids. HOFER (1977) has clearly shown that the interincisal diastema in lemuriforms is related to the development of a strong tethering of the upper lips with the palatine papilla (Fig. 2), which is situated in the incisive fossa at the base of the nasopalatine duct. The latter in turn communicates with the vomeronasal organ of Jacobson. The tethering philtrum passes between the median incisors and forms a sulcus which is continuous with the median nasal cleft of the rhinarium. The immediate mechanical effect of this arrangement is that it precludes lip eversion. On the other hand, it is thought that this configuration permits the channeling of liquid material from the moist rhinarium to the vomeronasal organ (HOFER, 1977, 1980). BAILEY's (1978) controlled study of olfactory behavior in *Lemur catta* demonstrated that the transfer of stimulating odorants from the environment to the mouth is usually accomplished by lapping scent with

the tongue and drawing it over the nose and into mouth, presumably to stimulate the vomer-onasal. This is accompanied by a *flehmen*-like grimace of the face, but without lip eversion. Thus the morphology and behaviors, which in *L. catta* males is elicited by genital secretion from a female and not by urine (BAILEY, 1978), may be confidently associated with the accessory olfactory apparatus. The latter is known to be related to reproduction in a wide variety of mammals (e.g., WYSOCKI, 1979) and the vomeronasal organ acts as a pheromone receptor for this system.

The behavioral constraint of a strongly tethered philtrum also suggests that the lemuriform vomeronasal complex employs liquid soluble odorants rather than airborne chemicals (BAILEY, 1978; HOFER, 1977). This contrasts with the behavioral pattern and significance of the classical *flehmen* face, which combines simultaneous inspiration to transport airborne odors into the mouth in forms like dogs, horses and bats (e.g., ESTES, 1972; COOPER & BHATNAGER, 1976), all of whom evert the upper lip during the gesture. This distinction may be of importance in explaining the origins of the toothcomb because the lemuriform pattern seemingly requires physical contact between stimulus and recipient, i.e., a lemur must physically collect scent with its rhinarium, lips or tongue. Touching with the nose, lapping and grooming are all parts of a preeminent behavioral suite in lemuriforms (e.g., JOLLY, 1968; SCHILLING, 1979) and these motor actions are often inseparable during grooming bouts. However, the accumulation of scent under experimental conditions has been shown to be a highly stereotyped, directed pattern (BAILEY, 1978). Clearly, the process of grooming with the toothcomb must often result in the stimulation of the vomeronasal organ (Fig. 3), and similar sequences would probably have been present among adapids having a similar organization of the tissues of the snout—even as they groomed without a toothcomb. By extension, the occurrence of a tethered sulcate philtrum in early strepsirhine adapids (e.g., MARTIN, 1973) would be a pre-adaptation to the evolution of accessory organs which enhance its selective value, perhaps by more efficiently collecting and distributing pheromones.

This explanation still leaves unanswered the question of "Why a comb?" We offer another hypothesis which can be tested by detailed behavioral study. The scent glands of lemuriforms appear not to be self-secretory but require frictional stimulation. Thus, lemurs and lorises have developed myriad ways to rub their anogenital region, forearms, throats, etc., against boughs, depositing odors on other objects and possibly spreading it on themselves. These surfaces are also the areas frequently presented by an individual at the start of a grooming bout (e.g., JOLLY, 1968). We propose that toothcomb grooming may also stimulate secretory output from the scent glands and, with the special assistance of this tined instrument, these scents can be distributed all over the body. Using the toothcomb and tongue for this purpose is not only advantageous because of its proximity to the pheromone receptor organ, but it may be the only way a lemur can monitor its efforts: it is an olfactory-gustatory process, not a visual one, and it may be specifically linked to Jacobson's organ. Other scents buried deep in the fur may also be exposed to the vomeronasal organ by parting and combing, and we would not venture our explanation as an exclusive causal one. However, the pervasive self-annointing behaviors of living lemuriforms, which even extends to include the hands and feet, lead us to suspect that a special tool would be most useful in trying to spread viscous stuff well through a coat of fur.

From a systematics point of view still another question presents itself: Is this soft anatomical configuration primitive or derived within the primates? As we have argued above, the osteological and dental aspects appear to be derived, suggesting that the immobile upper lip is
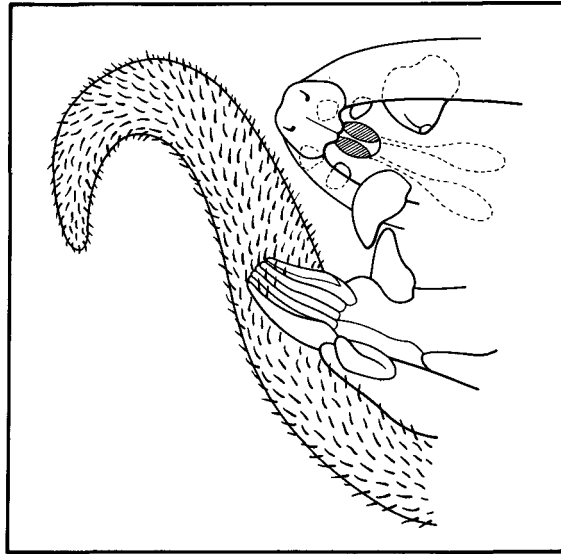
Fig. 3. A schematic view of toothcomb grooming, with the upper jaw rolled away to reveal the spatial relations of toothcomb, incisive foramen and palatine papilla (hatched), opening of vomeronasal organ (dotted), and cleft philtrum spaced between separated median incisors (dotted). Based on *Lemur.*

also apomorphic. This character state is not unique to primates, although HOFER (1977) believed that it is certainly distinctive. He noted that "... the upper lip of the strepsirhine primates is not cleft to the same extent that is found in insectivores, rodents, marsupials... (it) has developed towards the undivided condition..." (1977:851) seen in haplorhines. Other points imply that the strepsirhine tethering is derived as well. For example, in tenrecid insectivores that have infolded, tied upper lips there is a large gap between the upper incisors. The same holds true for *Tupaia* (Fig. 2), and MAIER (1979) has suggested that the derived loss of I^1 is what permits passage of their philtrum. The strepsirhine interincisal diastema seems to be an analogous case, where the derived wide spacing and low crown height permits the recurrent labial tethers access to the mouth across the shortest distance. On the other hand, in certain mammals having a relatively large I^1, or a full battery of closely spaced incisors, like haplorhine primates and dogs (Fig. 2), little or no tethering exists and the upper lip can evert. Although we do not know precisely how the upper median incisors of plesidapiforms were spaced, their large size implies a condition similar to haplorhines. This does not necessarily entail a hairy rhinarium, for various mammals have naked, cleft rhinaria in conjunction with a mobile upper lip (HOFER, 1980).

This extension of the grooming hypothesis gains importance in the context of other interpretations regarding the possibly derived nature of lemuriform olfaction and behavior. For example, in his study of the microanatomy of the nasal capsule, MAIER (1980b), like HOFER (1977), indicated that there were some underappreciated features of the Jacobson's organ which evinced phylogenetically advanced traits relative to the conditions seen in *Solenodon*, *Erinaceus* and *Setifer*. A similar point was made by STEPHAN and ANDY (1969) in their survey of the olfactory cortex and by CLARK (1978) in her study of *Lemur* communication, learning and social organization. More recently, STEPHAN, BARON and FRAHM (1982) have

shown that the lemuriform accessory olfactory bulb, which receives direct input from the vomeronasal organ, averages relatively larger in its size than in all insectivorans except erinaceids, *Elephantalus* and the tupaiids. Also, the laminar structure within the primate accessory bulb differs from all Scandentia and Insectivora, suggesting that enlargement is not homologously derived. What we suggest here is that the modern state of lemuriform olfactory behavior should not be assumed to represent a primitive eutherian pattern with primitive, widespread biological roles. If it is in fact derived, then the transition was already underway in adapids and is expressed in their characteristically strepsirhine rostral anatomy. The terminal stages of this shift could have been achieved by the evolution of tine-like lower anterior teeth in the lemuriform common ancestor.

SUMMARY AND CONCLUSION

The fossil adapids, including some of the more primitive notharctines, share many traits in common with living lemuriforms in the structure of their upper incisors. Although these teeth have not figured importantly in scenarios describing the origins and evolution of the toothcomb, we maintain that upper and lower teeth must be analyzed together in order to generate an adequate narrative explanation of the toothcomb as an adaptive complex. We suggest that the morphology of the lemuriform snout, with its blunt anterior rostrum, low-crowned upper incisors and elaborately tethered rhinarium communicating with Jacobson's organ are parts of an integrated physiological-behavioral system committed to interpersonal sensory and olfactory communication by pheromones. The snout of adapids already manifested a shift toward this pattern, forsaking the more primitive compromise state of feeding and nonfeeding faculties involving the incisors and rostrum. Thus the Tooth Scraper Hypothesis of toothcomb origins has less explanatory value than the Grooming Hypothesis even when the upper incisors of strepsirhines are anlayzed. Ancestral lemuriforms further elaborated the adaptive complex by adding the toothcomb as a grooming instrument, possibly to stimulate glandular secretion by physical contact and efficiently distribute odor through the fur.

Phylogenetically, this interpretation, if correct, clarifies two major points of dispute regarding the broad outlines of primate evolution (see SZALAY & DELSON, 1979), the origins of lemuriforms and anthropoids. As reviewed elsewhere (ROSENBERGER, STRASSER & DELSON, 1985), the evidence from the incisors denies rather than supports the hypothesis that anthropoids evolved from adapids, or that European adapines like *Adapis* are prototypes for the toothcomb morphology. Our perspective marks the strepsirhines as evolving an anterior snout to augment olfactory communication and microsmatic anthropoids as dominated by a snout responding to selection for harvesting and masticatory processes. Our anatomical interpretations see these as all but exclusive, perpendicular evolutionary dimensions.

REFERENCES

BAILEY, K., 1978. *Flehmen* in the ring-tailed lemur (*Lemur catta*). *Behaviour*, 65: 309–319.
BOCK, W. J., 1981. Functional-adaptive analysis in evolutionary classification. *Amer. Zool.*, 21: 5–20.
BEECHER, R. M., 1983. Evolution of the mandibular symphysis in Notharchinae (Adapidae, Primates). *Int. J. Primatol.*, 4: 99–112.
BUETTNER-JANUSCH, J. & R. M. ANDREW, 1962. Use of the incisors by primates in grooming. *Amer. J. Phys. Anthropol.*, 20: 127–129.
CARTMILL, M. & R. F. KAY, 1978. Craniodental morphology, tarsier affinities and primate sub-orders. In: *Recent Advances in Primatology, Vol. 3, Evolution*, D. J. CHIVERS & K. A. JOSEY (eds.), Academic Press, London, pp. 205–213.
CLARK, A. B., 1978. Olfactory communication. *Galago crassicaudatus* and the social life of prosimians. In: *Recent Advances in Primatology, Vol. 1, Behaviour*, D. J. CHIVERS & J. HERBERT (eds.), Academic Press, London, pp. 109–117.
COOPER, J. G. & K. P. BHATNAGAR, 1976. Comparative anatomy of the vomeronasal organ complex in bats. *J. Anat.*, 122: 571–601.
DAGOSTO, M., 1984. Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates). Adaptational and phylogenetic significance. *Folia Primatol.*, 41: 49–101.
ESTES, R. D., 1972. The role of the vomeronasal organ in mammalian reproduction. *Mammalia*, 36: 315–341.
GINGERICH, P. D., 1975. Dentition of *Adapis parisiensis* and the evolution of the lemuriform toothcomb. In: *Lemur Biology*, I. TATTERSALL & R. W. SUSSMAN (eds.), Plenum Press, New York, pp. 65–80.
————, 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Mus. Paleon., Univ. of Michigan, Pap. on Paleon.*, 15.
———— & R. D. MARTIN, 1981. Cranial morphology and adaptations in Eocene Adapidae. II. The Cambridge skull of *Adapis parisiensis*. *Amer. J. Phys. Anthropol.*, 56: 235–257.
GREGORY, W. K., 1920. On the structure and relations of *Notharctus*, an American Eocene primate. *Mem. Amer. Mus. Nat. Hist.*, 3: 51–243.
————, 1922. *The Origin and Evolution of the Human Dentition*. MacMillan, New York.
HOFER, H. O., 1977. The anatomical relations of the ductus vomeronasalis and the occurrence of taste buds in the papilla palatina of *Nycticebus coucang* (Primates, Prosimiae) with remarks on strepsirhinism. *Gegen. Morph. Jahrb.*, 123: 836–856.
————, 1980. The external anatomy of the oro-nasal region of primates. *Z. Morphol.*, 71: 233–249.
————, 1982. Anatomy of the oro-nasal region of some species of Tenrecidae and considerations of Tupaiids and Lemurids. *Gegen. Morphol. Jahrb.*, 4: 588–613.
JOLLY, A., 1963. *Lemur Behavior*. Univ. of Chicago Press, Chicago.
KAY, R. F., 1980. Platyrrhine origins: A reappraisal of the dental evidence. In: *Evolutionary Biology of the New World Monkeys and Continental Drift*, R. L. CIOCHON & A. BRUNETTO CHIARELLI (eds.), Plenum Press, New York, pp. 159–188.
KIELAN-JAWOROWSKA, Z., T. M. BOWN & J. A. LILLEGRAVEN, 1979. Eutheria. In: *Mesozoic Mammals*, J. A. LILLEGRAVEN, Z. KIELAN-JAWOROWSKA & W. A. CLEMENS (eds.), Univ. of California Press. Berkeley, pp. 221–258.
KINZEY, W. G., A. L. ROSENBERGER & M. RAMIREZ, 1975. Vertical clinging and leaping in a Neotropical anthropoid. *Nature*, 225: 327–328.
LE GROS CLARK, W. E., 1959. *The Antecedents of Man*. Univ. of Chicago Press, Chicago.
———— & D. P. THOMAS, 1952. The Miocene lemuroids of East Africa. *Fos. Mam. Afr.*, 5: 1–20.
LUCKETT, W. P., 1982. *Comparative Biology and Evolutionary Relationships of Tree Shrews*. Plenum Press, New York.
MAIER, W., 1979. A new dental formula for the Tupaiiformes. *J. Human Evol.*, 8: 319–321.
————, 1980a. Nasal structure in Old and New World primates. In: *Evolutionary Biology of New World Monkeys and Continental Drift*, R. L. CIOCHON & A. BRUNETTO CHIARELLI (eds.), Plenum Press, New York, pp. 219–241.
————, 1980b. Konstruktionsmorphologische Untersuchengen an Gebiss der rezenten Prosimiae (Primates). *Abh. Senckenb. Naturforsch. Ges.*, 538: 1–158.
MARTIN, R. D., 1972. Adaptive variation of behavior of Malagasy lemurs. *Phil. Trans. Roy. Soc. (B)*, 26: 295–352.

————, 1973. Comparative anatomy and primate systematics. *Symp. Zool. Soc. London*, 33: 301–337.

————, 1979. Phylogenetic aspects of prosimian behavior. In: *Studies of Prosimian Behavior*, G. A. DOYLE & R. D. MARTIN (eds.), Academic Press, New York, pp. 45–77.

MILLER, M. E., 1964. *Anatomy of the Dog*. W. B. Saunders, Philadelphia.

ROSE, K. D., A. WALKER & L. L. JACOBS, 1981. Function of the mandibular toothcomb in living and extinct mammals. *Nature*, 289: 583–585.

ROSENBERGER, A. L., M. E. STRASSER & E. DELSON, 1985. Anterior dentition of *Notharctus* and the adapid-anthropoid hypothesis. *Folia Primatol.*

———— & F. S. SZALAY, 1980. On the tarsiiform origin of Anthropoidea. In: *Evolutionary Biology of New World Monkeys and Continental Drift*, R. L. CIOCHON & A. BRUNETTO CHIARELLI (eds.), Plenum Press, New York, pp. 139–157.

SCHILLING, A., 1979. Olfactory communication in prosimians. In: *Studies of Prosimian Behavior*, G. A. DOYLE & R. D. MARTIN (eds.), Academic Press, New York, pp. 461–542.

SCHWARTZ, J. H., I. TATTERSALL & N. ELDREDGE, 1978. Phylogeny and classification of the primates revisited. *Yrbk. Phys. Anthropol.*, 21: 95–133.

SIMONS, E. L., 1972. *Primate Evolution: An Introduction to Man's Place in Nature*. Macmillan, New York.

SIMPSON, G. G., 1940. Studies on the earliest primates. *Bull. Amer. Mus. Nat. Hist.*, 77: 185–212.

STEHLIN, H. G., 1916. Die Saugetiere de schweizerischen Eozans. Critischer Catalog de Materialien, 7. Teil 2, Halfte. *Abhand. Schweiz. Palaeont. Ges.*, 51: 1299–1552.

STEPHAN VON, H. & O. J. ANDY, 1969. Quantitative comparative neuroanatomy of primates: an attempt at phylogenetic interpretation. *Ann. N.Y. Acad. Sci.*, 167: 370–387.

————, G. BARON & H. D. FRAHM, 1982. Comparison of brain structure volumes in Insectivora and Primates. II. Accessory Olfactory bulb (ABO). *J. Hirnforsch.*, 23: 575–591.

SZALAY, F. S., 1976. Systematics of the Omomyidae (Tarsiiformes, Primates): taxonomy, phylogeny and adaptations. *Bull. Amer. Mus. Nat. Hist.*, 156: 157–450.

————, 1981. Functional analysis and the practice of the phylogenetic method as reflected by some mammalian studies. *Amer. Zool.*, 21: 37–45.

———— & E. DELSON, 1979. *Evolutionary History of the Primates*. Academic Press, New York.

———— & C. KATZ, 1973. Phylogeny of lemurs, galagos and lorises. *Folia Primatol.*, 19: 88–103.

———— & D. SELIGSOHN, 1977. Why did the strepsirhine toothcomb evolve? *Folia Primatol.*, 27: 75–82.

WALKER, A., 1969. New evidence from Uganda regarding the dentition of Miocene Lorisidae. *Uganda J.*, 33: 90–91.

WOHRMANN-REPENNING, A., 1978. Geschmacksknospen an der Papillan palatina von *Tupaia glis* (DIARD, 1920), ihr Vorkommen und ihre Beziehung zum Jacobsonschen Organ. *Gegen. Morph. Jahrb.*, 124: 375–384.

WYSOCKI, C. J., 1979. Neurobehavioral evidence for the involvement of the vomeonasal system in Mammalian reproduction. *Neuros. Biobehav. Rev.*, 3: 301–341.

Authors' Names and Addresses: ALFRED L. ROSENBERGER, *Department of Anthropology, University of Illinois at Chicago, P. O. Box 4348, Chicago, Illinois 60680, U.S.A.*; ELIZABETH STRASSER, *Department of Anthropology, Graduate School and University Center, City University of New York, New York 10036, U.S.A.*