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Evolution of Feeding Niches in New World Monkeys

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ABSTRACT The adaptive radiation of modern New World monkeys unfolded as the major lineages diversified within different dietary-adaptive zones predicated upon a fundamentally frugivorous habit. The broad outlines of this pattern can be seen in the fossil record, beginning in the early Miocene. Cebids are obligate frugivorous predators. The smallest forms (*Cebuella, Callithrix*) are specialized exudativores, and the largest (cebines) are seasonally flexible omnivores, feeding particularly on insects (*Saimiri*) or "hard" foods, such as pith and palm nuts (*Cebus*), when resources are scarce. The smaller-bodied atelids (*Callicebus, Aotus*) may use insects or leaves opportunistically, but pitheciins (saki-uakaris) specialize on seeds as their major protein source. The larger atelines (*Alouatta, Brachyteles*) depend on leaves or on ripe fruit (*Ateles*). Locomotion, body size, and dietary adaptations are linked: claws and small body size opened the canopy-subcanopy niche to callitrichines; climbing and hanging, the fine-branch setting to the atelines; large size and strength, semiprehensile tails, and grasping thumbs, the extractive insectivory of *Cebus*; deliberate quadrupedalism, the energy-saving transport of folivorous *Alouatta*. Body size increases and decreases occurred often and in parallel within guilds and lineages. Conventional dietary categories, particularly frugivory, are inadequate for organizing the behavioral and anatomical evidence pertinent to evolutionary adaptation. Related models of morphological evolution based on feeding frequencies tend to obfuscate the selective importance of "critical functions," responses to the biomechanically challenging components of diet that may be determined by a numerically small, or seasonal, dietary fraction. For fossils, body size is an unreliable indicator of diet in the absence of detailed morphological information. More attention needs to be given to developing techniques for identifying and quantifying mechanically significant aspects of dental form, the physical properties of primate foods, their mode of access, and the cycles of availability and nutritional value.

Little effort has been given to *explaining* the adaptive radiation of New World monkeys. The major evolutionary studies have been strictly taxonomic in focus. Thus there are only a few synthetic hypotheses relating to evolution of feeding adaptations among platyrrhines. Hershkovitz (1977) proposed that the essence of the radiation was an inexorable evolution of body size, from small to large, with locomotor and dietary consequences. Rosenberger (1980) interpreted the radiation as differentiating arrays occupying two dietary-adaptive zones (Fig. 1), each making up a monophyletic guild, the cebid and atelid clades (Table 1). I proposed that different adaptive modalities evolved within these zones, canalized by heritage, as closely

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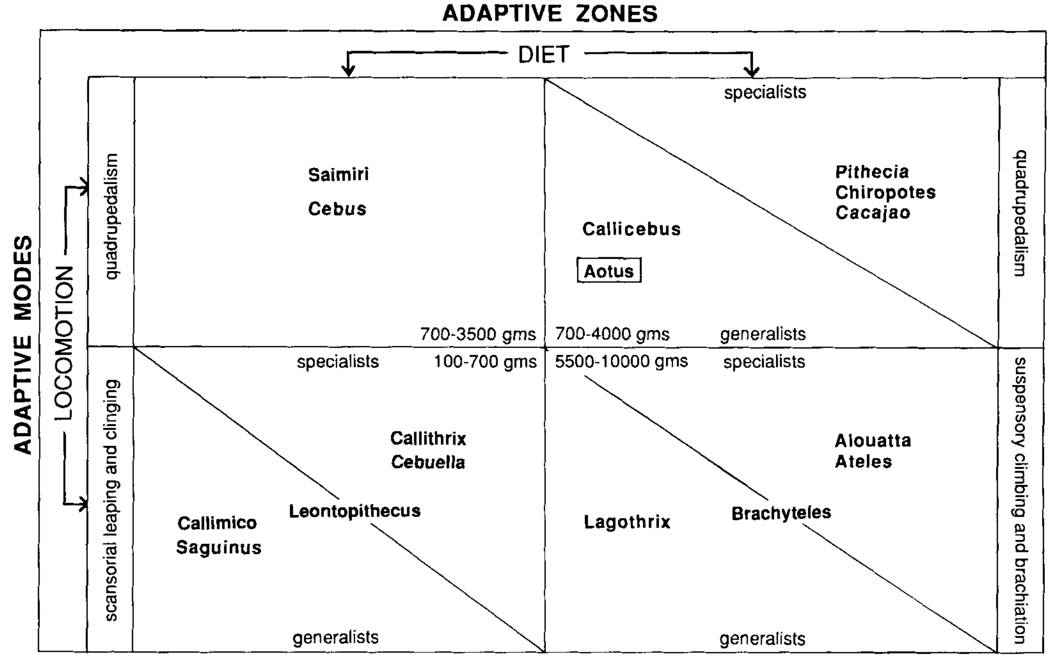

Fig. 1. Adaptive radiation and differentiation of feeding niches in New World monkeys (see text). A divergence in dietary strategies defines the major adaptive zones, represented by cebids and atelids, while differentiation within families involves locomotor/foraging specializations as well as body size separations. The uniqueness of the nocturnal/crepuscular *Aotus* is indicated by the rectangle; diagonals separate identifiable dietary specialists.

related taxa partitioned their broadly defined ancestral niches, evolved new ways of exploiting resources to reduce competition, and gravitated to become generalists or specialists within each sector. Kinzey (1986), Sussman and Kinzey (1984), Robinson and Janson (1987), Robinson et al. (1987), and Rosenberger and Strier (1989) also presented reviews of various platyrrhine groups emphasizing diet.

This paper attempts to outline the major features of platyrrhine evolution as an adaptive array of feeding strategies, building on a thesis presented previously in abstract form (Rosenberger, 1980, 1988). The discussion concentrates on the modern platyrrhines, their dental morphology, their body size diversity, and some elements of their foraging behavior. Geographical factors (see, e.g., Eisenberg, 1979; Emmons, 1984; Rosenberger, in press) influencing diet and social correlates (see, e.g., Rosenberger and Strier, 1989) are not addressed here. Feeding adaptations of fossil platyrrhines, and implications for the study of primate diets generally, are also considered briefly.

MATERIALS AND METHODS

Taxonomy and classification

During the past decade, several higher level platyrrhine classifications were proposed (see, e.g., Szalay and Delson, 1979; Rosenberger, 1981; Ford, 1986; Kinzey, 1986; Rosenberger et al., 1990) as alternatives to more conventional arrangements (see, e.g., Napier, 1976; Hershkovitz, 1977). The impetus for these changes stemmed from the recognition that a taxonomic division of platyrrhines into clawed and non-clawed families (e.g., Callitrichidae and Cebidae) probably does not conform to the criterion of monophyly (or holophly) and that the use of multiple subfamilies (e.g., Pitheciinae, Aotinae, Callicebinae, Alouattinae, Atelinae, of the Cebidae) has simply

TABLE 1. Taxonomic arrangement of New World monkeys, to the species level for the fossils (Dates are from MacFadden, 1990)

- Superfamily Ateloidea
  - Family Atelidae
    - Subfamily Atelinae
      - *Ateles Brachyteles Lagothrix Alouatta*
      - *Stirtonia tatacoensis*, La Venta, Colombia, middle Miocene (16-15 Ma)
      - *Stirtonia victoriae*, La Venta, Colombia, middle Miocene (16-15 Ma)
      - *Paralouatta varonai*, Cueva de Mono Fósil, Cuba, Quaternary
    - Subfamily Pitheciinae
      - Tribe Pitheciini
        - *Pithecia Chiropotes Cacajao*
        - *Soriacebus ameghinorum*, Pinturas, Argentina, early Miocene (18-15 Ma)
        - *Soriacebus adrianae*, Pinturas, Argentina, early Miocene (18-15 Ma)
        - *Cebupitheca sarmientoi*, La Venta, Colombia, middle Miocene (16-15 Ma)
      - Tribe Homunculini
        - *Aotus Callicebus*
        - *Tremacebus harringtoni*, Sacanana, Argentina, early Miocene (22-18 Ma)
        - *Homonculus patagonicus*, Rio Gallegos, Argentina, early Miocene (18-15 Ma)
        - *Aotus dindensis*, La Venta, Colombia, middle Miocene (16-15 Ma)
        - *Xenothrix mcgregori*, Long Mile Cave, Jamaica, subrecent (0.3 Ma-10,000 years ago)
      - Tribe indet.
        - *Carlocebus ameghinorum*, Pinturas, Argentina, early Miocene (18-15 Ma)
        - *Carlocebus intermedius*, Pinturas, Argentina, early Miocene (18-15 Ma)
  - Family Cebidae
    - Subfamily Cebinae
      - *Cebus Saimiri*
      - *Dolichocebus gaimanensis*, Gaiman, Argentina, early Miocene (19-18 Ma)
      - *Saimiri fieldsi*, La Venta, Colombia, middle Miocene (16-15 Ma)
      - "*S.*" *bernensis*, Cueva de Berna, Dominican Republic, subrecent (0.3 Ma-10,000 years ago)
      - *Laventiana annecteus*, La Venta, Colombia, middle Miocene (16-15 Ma)
    - Subfamily Callitrichinae
      - Tribe Callitrichini
        - *Callithrix Cebuella Leontopithecus Saguinus*
      - Tribe Callimiconini
        - *Callimico*
        - *Mohanamico hershkovitzi*, La Venta, Colombia, middle Miocene (16-15 Ma)
      - Tribe indet.
        - *Micodon kiotensis*, La Venta, Colombia, middle Miocene (16-15 Ma)
    - Subfamily Branisellinae
      - *Branisella boliviana*, Salla, Bolivia, late Oligocene (26 Ma)
      - *Szalatavus attricuspis*, Salla, Bolivia, late Oliogcene (26 Ma)

lost its heuristic value. The classification employed here (Table 1; Rosenberger et al., 1990; Rosenberger and Hartwig, in press) derives from earlier work (e.g., Rosenberger, 1981). It attempts to accommodate both the fossil and the living forms and their presumed phylogenetic relationships, and adaptations.

Data

The measurements of adult body weight and head and body length all come from museum records of wild-shot animals, with a few exceptions, maintained at the United States National Museum, Field Museum of Natural History, Museu Nacional do Rio de Janeiro, Museo Goeldii (Manaus, Brazil), and Centro de Primatologia do Rio de Janeiro. Other sources were field studies. The data are presented as sex-pooled samples, with all figures rounded to the nearest whole number.

Nearly all dental measurements were taken on specimens at the same institutions, except where indicated. Mesiodistal length and buccolingual breadth of the cheek teeth were measured to the nearest 1/10 mm at the crown surface, as the largest diameters along the two axes. Mesiodistal I_1 length was measured at the apical margin between the interstitial contacts. On I_2 (a highly asymmetrical crown), mesiodistal length was measured as a projection along the I_1/I_2 apical edge from the mesial corner of I_2 to a tangent intersecting the lateral-most point along the tooth's sloping distal margin. Buccolingual breadth for $I_{1,2}$ was taken below the apical margin at the plane of greatest diameter. Incisal crown height was measured only in teeth having no more than a 1 mm wide exposure of dentin, from the cementoenamel junction to the apical margin. The means of these measurements are from sex-pooled samples. Those derived from the literature represent the averages of male and female means.

The feeding data presented here (Table 2) summarize general patterns found among the platyrrhines and are not meant to be exhaustive. Most of the data was taken from recent reviews (Robinson et al., 1987) and other published sources. The data for each species were often collected in a number of ways and in different habitats, but the overall patterns are reliably represented. Additional detail for certain species may be found in Garber (1992), Kinzey (1992), Strier (1992), and Janson and Boinski (1992).

DIETARY CATEGORIES

Platyrrhines, while all largely frugivorous, are eclectic feeders (Table 2) that use a combination of foods to meet their nutritional needs. This has led to a number of practical and theoretical difficulties regarding the description of their feed and the classification of their dietary tendencies, preferences, and adaptations. For example, how does the ecologist decide to categorize food items? How does the behaviorist determine empirically which foods actually sustain a species' energetic needs? How does the morphologist relate the heterogeneity of foods, which normally represent scores of different plant and animal species and a great range of physical and chemical properties, to the structure of the dentition and masticatory apparatus? How does one generalize what a feeding adaptation actually is, especially when a monkey is known to shift its food choices markedly during the course of a year?

Hladik and Hladik (1969) introduced a practical, descriptive classification system in their pioneering comparative study of diets of monkeys on Barro Colorado Island, Panama. They divided the feeding spectrum into foliage, fruits, and prey, further separating these categories into: 1) bark, shoots, pith, young or old leaves, buds, flowers, sap; 2) unripe and ripe fruit, oily fruit, seeds, seed coats; and 3) eggs, cocoons, small and large insects, vertebrates. Minor adjustments to these categories have become commonplace. For example, some workers emphasize insects as a prey source (e.g., Kay, 1975, 1984; Fleagle, 1988) instead of the more general notion of predation, or "faunivory" (e.g., Chivers et al., 1984; Janson and Boinski, 1992). Compound terms, such as *frugivore-insectivore* and *frugivore-folivore*, have also gained favor because they involve less information loss than occurs with using the broader descriptive categories, while also conveying the idea that fruits are fundamental to nearly all primate diets.

As others have anticipated (e.g., Kay, 1975; Chivers et al., 1984), more field information now makes it desirable to refine the conceptual basis of this system, for the frugivore/folivore/insectivore trichotomy may obscure some fundamental aspects of dietary adaptation. A particular problem involves the concept of frugivory. Exudate feeding, especially as seen in *Cebuella pygmaea*, is a case in point. Although initially classified as a form of frugivory, it is now understood to involve a distinctive adaptive syndrome unlike the patterns of most other "frugivorous" platyrrhines (see, e.g., Kinzey et al., 1975; Sussman and Kinzey, 1984; Garber, 1992). In another respect, a hard and fast reliance on the tripartite division of primate diets tends to exclude the concept of omnivory as a real feeding strategy. *Cebus*, for example, a remarkably versatile feeder, is often described in this way (see, e.g., Terborgh, 1983; Robinson, 1986; Janson and Boinski, 1992). Is *Cebus*, morphologically and behaviorally, a "specialized omnivore," not nonselective but able to target strategically foods from several or all of the major categories?

Apart from these cases, the various components of fruits (e.g., woody shells, nuts, or skins; pulp or meat in various textures; soft or hard seeds), only some of which are edible, may present very different biomechanical demands on frugivores and thus multiple opportunities for morphological specialization. The adaptive solutions allowing access to the targeted nutritional part(s) may involve specializations for foraging, harvesting, mastication, or digestion in different species and to different degrees. Thus the notion of frugivory has different meaning for *Ateles* and *Chiropotes*. *Ateles* feeds mostly on ripe, fleshy fruits, taking them whole, swallowing the seeds, then defecating and dispersing the seeds (van Roosmalen, 1984; van Roosmalen et al., 1988; Kinzey and Norconk, 1990). *Chiropotes* frequently feeds on fruits that are protected by hard coverings, often taking them unripe, and chews and destroys the seeds (Ayres, 1989; Kinzey, 1992). The divergent frugivorous adaptations of these species probably include harvesting, masticatory, and perhaps digestive features. However, at the most general analytical/categorical level, unless one distinguishes between soft- and hard-fruit frugivory, it is likely that the causal selective forces driving the respective dental adaptations—the mechanical properties of food parts (see, e.g., Kay, 1975; Rosenberger and Kinzey, 1976)—will be overlooked. This point is not restricted to the morphologically "bizarre" pitheciins; even *Cebus* shifts its "frugivorous" diet considerably during the course of the year and, in doing so, encounters foods of radically different physical properties (Robinson, 1986; Teaford and Robinson, 1989).

The empirical data (Kinzey, 1992) mandate changes in our dietary lexicon, particularly with regard to frugivory. A good alternative is to recognize the specializations of hard-fruit and soft-fruit eaters, as with the distinction between *Ateles* and *Chiropotes*. As Kinzey and Norconk (1990) have shown, the amount and range of pressure required to puncture the pericarp (an action analogous biomechanically to incision with the anterior teeth or premolars) of fruit eaten by *Ateles paniscus* (0.03–1.4 kg/mm^2; N = 26 species) is much less than is required for the foods of *Chiropotes satanas* (0.03–37.8 kg/mm^2; N = 34 species). This shows that the biomechanics of harvesting *Ateles* fruits and *Chiropotes* fruits are markedly different and has important consequences for interpreting the different incisor, premolar, and mandibular (etc.) morphologies. To place these values in perspective, the maximum pressure for *Chiropotes* is roughly 20 times the amount of pressure required to puncture a raw Irish potato, summer squash, or beets with a hand-held device (Bourne, 1979) similiar to the Kinzey/Norconk tester.

Kinzey and Norconk (1990) also measured the crushing resistance of whole seeds ingested by these species (analogous to mastication). The crushing force needed to rupture seeds eaten by *Ateles* (1.36–148.18 kg; x = 17.09 kg; N = 13 species) was greater than that required by *Chiropotes* (0.23–22.27 kg; x = 7.16 kg; N = 19 species). What is most striking about this is that *Ateles* swallowed all seeds but *Chiropotes* chewed and ate theirs. This difference in preferences occurred in spite of the facts that six of the 13 species *Ateles* swallowed whole required less crushing force than the average *Chiropotes* seed and that ten of the 13 *Ateles* seeds were softer than the hardest species eaten by *Chiropotes*. It is likely that their contrasting selections partially reflect differences in the extractive abilities of the two species. However, it is even more likely that in *Ateles*, an animal of substantially larger body size, the jaws, muscles, and cheek teeth simply are not suited to processing items as hard as those eaten by *Chiropotes*. Conversely, the data also suggest the biomechanical limits that constrain *Chiropotes* seed selection.

There is additional quantitative information on the hardness of seeds eaten by other platyrrhines. It is indirect but may serve as a way of conceptualizing the animals' capabilities (Fig. 2). Kiltie (1982) gave measurements for dried *Astrocaryum* sp. palm nuts, such as those eaten by *Cebus apella* and *C. albifrons* (Terborgh, 1983; also, see below), and some of the seeds measured by Kinzey and Norconk (1990) are also eaten by *Pithecia*. The high loads required to break the *Astrocaryum* nuts eaten by *Cebus* and the typical pitheciin seeds are well within the limits of human ability, and the brittleness of the hard, dried nuts may be comparable to that of some hard chocolates.

An analogous spectrum of physical properties occurs among insect foods (see, e.g., Freeman, 1979). Even for leaves, perhaps the least complex type of primate food structurally, there is empirical evidence for *Alouatta seniculus* showing a twofold disparity in the ingestion (mastication) rates of leaf species that probably relates to the latter's

TABLE 2. Percentage of foraging time spent on fruits, leaves, insects, and other foods[1]

	Foraging (%)				
Species	Fruits	Leaves	Insects	Other	Sources
Ateles belzebuth	83	7	0	10	Klein and Klein, 1977
Ateles geoffroyi	80	20	0	0	Richard, 1970; Hladik and Hladik, 1969
Ateles paniscus	83	8	0	6	Van Roosmalen, 1980
Brachyteles arachnoides	39	57	0	4	Fonseca, 1983
	26	66	0	8	Young, 1983
	20	68	0	12	Milton, 1984
Lagothrix flavicauda	++	+		+	Leo Luna, 1981
Lagothrix lagothricha	91 (seeds 17)	6	0	3 (flowers)	Soini, 1986
Alouatta palliata	42	48		10 (flowers)	Milton, 1980
Alouatta fusca	16	71		9 (flowers)	Mendes, 1985
Alouatta seniculus	42	53		5 (flowers)	Gaulin and Gaulin, 1982
Pithecia albicans	69 (seeds 19)	30	0	2	Johns, 1986
Pithecia hirsuta	93 (seeds 38)	4	0	3 (flowers)	Soini, 1986
Pithecia monachus	71	16	0	13	Happel, 1982
	28-74 (seeds)	*	*	*	Sonini, 1987; Kinzey (this issue)
Pithecia pithecia	93 (seeds 47)	0	0	7	Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981; Kinzey (this issue)
Chiropotes albinasus	90 (seeds 36)	0	0	10 (flowers 3; other 7)	Ayres, 1989
	90	<10	0	0	Ayres, 1981
Chiropotes satanas	94	0	0	6 (flowers 5; other 1)	Ayres, 1989
	91 (seeds)	*	*	*	Kinzey and Norkonk, unpubl. data; Kinzey (this issue)
	72 (seeds 63)	0	0	27 (flowers 11; other 16)	Ayres, 1989
	93	1	0	6	Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981
	96 (seeds 66)	0	0	4 (flowers 3; other <1)	van Roosmalen, Mittermeier and Fleagle, 1988; Kinzey (this issue)
Cacajao calvus	85 (seeds 67)	0	5	9 (nectar 6; other 3)	Ayres, 1989; Kinzey (this issue); Ayres, 1986
Aotus trivirgatus	75	10	15	0	Wright, 1985
	16	40	11	33	Wright, 1985
Callicebus moloch	48	40	12	0	Terborgh, 1983
	54	28	17	1	Wright, 1985
	70	26	1	3	Kinzey, 1978
Callicebus personatus	81	18	0	1	Kinzey and Becker, 1983
Callicebus torquatus	67 (seeds 37)	13	14	6	Kinzey, 1977; Kinzey (this issue)
Cebus albifrons	80	0	20	0	Defler, 1979
Cebus capucinus	65	15	20	0	Freese and Oppenheimer, 1981
Cebus olivaceus	49	8	35	2	Robinson, in press
	47	8	37	1	Robinson, in press
Saimiri boliviensis	93 (seeds 2)	0	0	7 (nectar 6; flowers 1)	Soini, 1986

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[1] Individual sources culled mainly from Robinson, et al. (1987) and Robinson and Janson (1987). ++, Relies more extensively on this food source; +, relies less extensively on this food source; *, data unavailable.

TABLE 2. Percentage of foraging time spent on fruits, leaves, insects, and other foods[1] *(continued)*

Species	Foraging (%) Fruits	Leaves	Insects	Other	Sources
Callithrix kuhli	63-70	0	0	34-37 (exudates 31-34; flowers 3)	Rylands, 1989
Cebuella pygmaea	+		++	++ (exudates)	Soini, 1982
Leontopithecus chrysomelas	74-89	0	0	18-31 (flowers 15-20; exudates 3-11)	Rylands, 1989
Saguinus geoffroyi	38		39	15 (exudates; nectar 0.1)	Garber, 1980
Saguinus mystax	47		43	10 (nectar; exudates 1.5)	Garber, in press
Saguinus fuscicollis	37		49	14 (exudates; (nectar)	Garber, personal communication
Saguinus mystax	63	34		3 (exudates, nectar <.04)	Ramirez, 1989

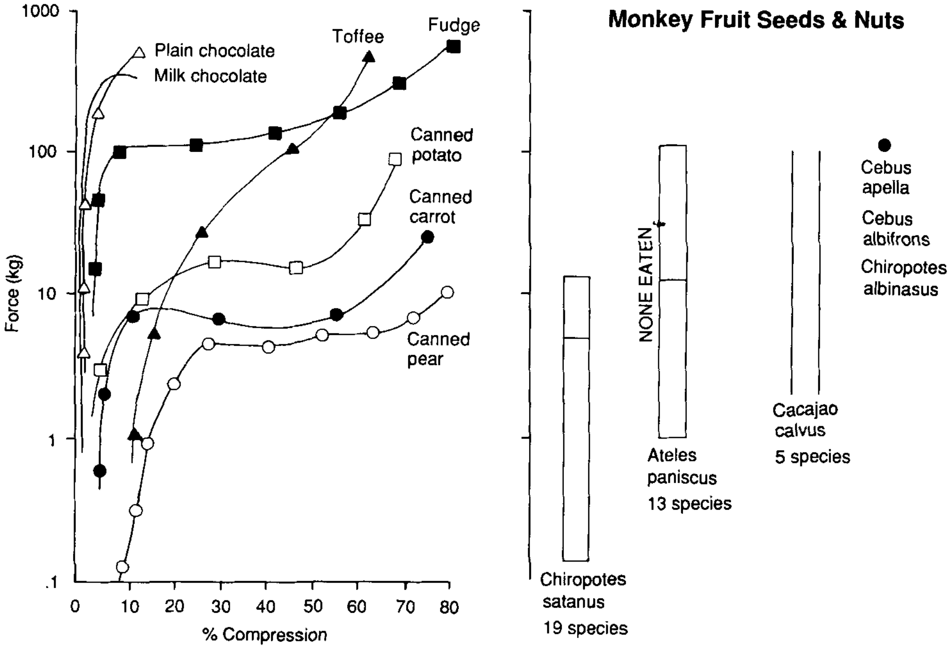


Fig. 2. Physical properties associated with crushing. Left panel (from Bourne, 1979, with permission of the publisher) shows amount of force and percentage of compression before rupture of familiar foods. Right panel shows crushing force required to break monkey fruits and seeds. Bars for *Chiropotes satanus, Ateles paniscus,* and *Cacajao calvus* (from Kinzey and Norconk, 1990, with permission of the publisher), show means, ranges, and numbers of species sampled. Note that no *Ateles* fruits and seeds were masticated; they were swallowed whole. Identification of *C. calvus* foods from Ayres (1989), crushing data from Kinzey and Norconk (1990). Single data point for *C. apella, C. albifrons* and *C. albinasus* represents the crushing resistance of the palm nut *Astrocaryum* sp. (Terborgh, 1983; Ayres, 1989) as measured by Kiltie (1982).

morphological differences (Oftedal, 1991). Thus, in general, these data indicate caution when drawing specific functional and adaptive interpretations from gross associations of animal morphology with food type. Rather than assuming that fruits, leaves, and insects or animals each pose uniform selective pressures on animal form, it may be more

TABLE 3. Model of the functional morphology and dietary adaptations of the feeding apparatus

Source/Object	Biological roles (materials)	Morphological solutions	Examples
Harvesting: incisors and canines			
1. Leaves	Cropping (stems)	I size reduction ("prehensile" lips?)	*Alouatta, Brachyteles*
Critical functions: Stabilize, tear and transport (with assistance from soft tissues) leaves, which are shorn or plucked by (relatively non-forceful) cutting or twisting actions			
Environmental factors minimal; stems generally yield under small amounts of tension and shear			
2. Insects/prey	Scraping, tearing (bark)	I and C tall, reinforced, durable enamel	*Cebus, Callithrix*
Critical functions: Concentrate applied force and minimize apical incisal/canine wear resulting from the fibrous, resistant woody substrate of trees where colonies of insects (ants, bees, and other social hymenoptera) and caterpillar burrows are harbored			
Environmental factors high-pressure, friction and bending; loads potentially eccentric relative to jaw's long axis			
3. Soft fruit	Cropping, husking (from stems, skins)	I broad	*Ateles, Saguinus, Cebus, Saimiri*
Critical functions: Varies with fruit size, similar to leaves for small fruits, and to "hard-fruit" (see 4b) husks for large fruits			
Environmental factors minimal, but over a large linear expanse (see 4 below).			
4. Hard fruit	Scraping, husking (from nuts, skins, pith)	I tall and narrow I tall and broad, durable enamel	*Callicebus (Jessinia* mesocarp) *Aotus*
Critical functions: Concentrate force (a) narrowly against resistant objects, or (b) broadly against tough but pliable husks on fruits of large size (making efficient removal of large bites)			
Environmental factors (a) High friction or (b) low-to-moderate torsion to produce the shearing action across a large section of a husk (see #3 above); scraping "nut meat" applies the apical edge of incisors against a dense, hard nut, causing them to wear heavily; tearing a tough husk produces less friction but requires more force and subjects teeth and jaws to more serious twisting loads			
5. Seeds	Cracking, piercing, shucking (sclerocarp, pods)	I tall and narrow, deeply rooted; C massive	Pithecia, Chiropotes, Cacajao
Critical functions: Concentrating force narrowly against resistant, noncompliant, fibrous objects, to puncture and/or pry open the woody casings that often protect seeds			
Environmental factors high pressure at incisal edge but also bending and friction below crown apex (in prying); loads eccentric relative to jaw			
6. Exudates	Scraping, gouging (bark)	I and C tall and narrow, durable enamel	*Callithrix, Cebuella*
Critical functions: Similar to 4a, 5.			
Environmental factors similar to 2, 5.			

(continued)

instructive to presume the opposite as a theoretical pillar for interpreting the stunning adaptive heterogenity of primate morphology, in concert with phylogeny, the source of morphologic homogeneity.

FUNCTIONAL MORPHOLOGY

Several general models relating diet to dental morphology (e.g., Andrews and Aiello, 1984; Kay and Covert, 1984; Lucas and Luke, 1984) share a common premise: The physical properties of foods must be the source of selective pressures driving adaptive change. In an interesting discussion derived from this work, Chivers et al. (1984; see also Teaford and Robinson, 1989) discussed the problems of relating form and function, given the diverse physical properties of the foods eaten and the vagaries of dietary categories, which do not reflect those properties with precision. They advocated a limited definition of *function* to refer to the inherent mechanical or chemical properties of structures (rather than their action or use, as in "eating" or "eating fruit"), following the form-function/biological role model of Bock and von Wahlert (1965). This is an alternative to "associative" or "analogy" approaches (see Andrews and Aiello, 1984; Kay and Covert, 1984) to functional morphology, which causally link the *frequency* (action) with which an animal partakes of a food category with anatomical design. The Bock and von Wahlert approach has been applied previously in studies of primate dentitions (see Rosenberger and

TABLE 3. Model of the functional morphology and dietary adaptations of the feeding apparatus (continued)

Source/Object	Biological roles (materials)	Morphological solutions	Examples
Mastication: postcanines			
1. Leaves	Shearing (leaves)	Perimeter crests carried by tall cusps, small shallow-walled basins, thin enamel	*Alouatta, Brachyteles*
Critical functions: Maximize the continuous length of intersecting linear edges to apply shearing over a large expanse of a highly pliant object; minimize food compaction and resistance to shearing stroke; maintain edge sharpness and occlusal precision			
Environmental factors minimal food resistance and abrasion, enabling a reduction in enamel thickness (and cusp cross-section) thus rapid wear at enamel-dentine interface, which promotes sharp leading edges			
2. Chitinous insect/prey	Shearing, piercing (chitin)	Cuspate crowns with long crests, steep basins	*Saimiri, Aotus*
Critical functions: Stabilize and apply high instantaneous pressure against a moderately deformable yet tough or brittle object at multiple loci, to force its yield by imposing complex shearing strains across the surface; to maintain occlusal precision			
Environmental factors high pressure without much abrasion; eccentric loads minimized by occlusal precision and point loading			
3. Soft fruit/ exudates	Crushing (mucilage, aril, gums, etc.)	Moderate relief, open construction	*Ateles, Cebuella*
Critical functions: Efficient mass pulping and transport of pliant, relatively non-structured materials			
Environmental factors minimal			
4. Hard fruit	Cracking, crushing (nuts, palm fronds)	Low relief, non-crested, durable enamel	*Cebus*, esp. *C. apella*
Critical functions: To apply continuous pressure and rupture relatively large objects that are fibrous and/or relatively undeformable; minimize enamel and cusp tip cracking, and enamel-dentine edge exposures			
Environmental factors high pressure over relatively large surface areas, probably for long periods, producing high friction and large eccentric loads, thus requiring thick enamel to minimize wear damage			
5. Seeds	Crushing	No relief, non-crested, crenulate enamel	*Pithecia, Chiropotes, Cacajao*
Critical functions: To stabilize and compress relatively small or medium-sized objects until they yield and maximize secondary particle breakdown			
Environmental factors moderately high orthal forces of long duration; minimal friction			

Kinzey, 1976; Kinzey, 1978; Seligsohn, 1977; Seligsohn and Szalay, 1978) and is followed here.

Table 3 is a first-order attempt to formalize some of the relationships linking diet, biological role (how the morphology is actually used in nature, e.g., to bite into an apple or to chew a leaf, two different biological roles), form, function, and adaptation of the feeding apparatus (see also Seligsohn, 1977). Table 3 is divided into two parts, one for the anterior teeth, including incisors and canines, and the other for the postcanines, to separate the selective factors involving food procurement from those pertaining to food processing. Various platyrrhines are listed as examples of these concepts and interpretations. As with other models, many necessary details are omitted, in part because the empirical work, such as the morphological description and quantification of structures in terms that accurately represent their mechanical potential or design, has yet to be done. An important contrast relative to some other models involves the "critical function" and "environmental factors" statements. These two notions are related. Under environmental factors, I propose which physical features of the environment contribute most to selection for dental morphology in a broad sense, and I note some of the immediate biomechanical consequences resulting from interaction with them. These environmental factors range from the physical structure of the location where food items are encountered, such as the bark crevices sheltering insects to the fibrous construction of a palm nut. A comprehensive list of the environmental factors relating to dietary adaptation would also include aspects of biological roles not performed by the dentition, such as those dealing with the locomotor and visual systems, which facilitate foraging (see below).

Critical functions are those mechanical (or chemical) potentials and processes that make specific harvesting and masticatory biological roles possible (and relatively efficient) given the crucial environmental factors encountered by the organism. Rosenberger and Kinzey (1976) first used the term *critical function* in reference to the overriding mechanical processes (shearing, crushing, puncturing, etc.) presumed to be most useful or necessary to a species in order to reduce specific food constituents from the full range of physical properties met with during feeding. We argued that these critical functions and, as defined here, the environmental factors are better indicators of the selective forces behind dietary adaptation than the quantity of food items taken from any trophic level and that, by corollary, there are "noncritical" functions, e.g., crushing of soft fruits in a soft-hard continuum, where the material properties do not select for morphology directly. Such biological roles are filled without specific adaptations.

For example, given a mixed diet of leaves and fruits in *Alouatta*, selection for shearing functions rather than crushing would be preeminent and conspicuously reflected in molar design, in spite of the fact that the time spent eating fruits and leaves may be equal (Strier, 1992). In other words, although two different biological roles, shearing leaves and crushing fruit, take up approximately equal amounts of feeding time annually, the morphology to shear fibrous leaves has been a stronger selective factor in the evolution of molar form than the potential or need to crush or pulp fruit. The postcanine equipment for the latter is presumably built into an *Alouatta* dentition by a combination of heritage factors and morphological/developmental compromise. Table 3 presents these critical functions along with a notation on the materials presenting the "critical" physical properties. Strategic benefits that exemplar species earn by selecting from such food sources are also proposed. The "morphological solutions" identify an adaptive feature or pattern that makes these critical functions possible.

Harvesting: Incisors and canines

The term *harvesting* is used to refer to the initial access stage of feeding with the teeth (not plucking leaves manually or locomoting to a foraging position). Harvesting may involve biting through the rinds of fleshy fruits with the incisors, cracking open the woody layers of fruits with the canines and/or adjacent premolar(s), scraping bark to produce a flow of exudate, or cracking a dead twig by clenching it in the mouth, perhaps to obtain burrowing insects or larvae. Harvesting challenges are common to primates feeding from all possible resources, which explains why their incisor morphology is probably more diverse than in any other mammalian order. Obviously, one would also expect foraging and locomotory specializations to evolve as behavioral correlates to harvesting given the various substrates and habitat conditions involved in this stage of the process.

The incisors of platyrrhines exhibit greater variety in design than either the extant catarrhines or the strepsirhines, which are canalized by the toothcomb apparatus. Little work has been done on their comparative functional morphologies. One notable exception is Eaglen's (1984) study of incisal scaling. He indicated that platyrrhines have relatively small incisors (measured as the sum of mesiodistal crown length for the four teeth) and concluded from his comparative study with catarrhines that the data ". . . confound all efforts to contrive a dietary hypothesis for explaining variations in *anthropoid* incisor size" (p. 272). This conclusion is not surprising in view of the *structural* (shape) diversity of platyrrhine incisor crowns, the various ways in which the incisors are planted in the jaws, and the simplicity of the biometric and biomechanical models Eaglen employed, which presume that "small" incisors are correlated with folivory and that "large" incisors indicate frugivory (Hylander, 1975; Kay and Hylander, 1978).

The impression that New World monkeys have exceptionally small incisors on the whole, which is at the root of Eaglen's (1984) conclusion, appears to be an artifact of sampling and lack of taxonomic control. The strong platyrrhine-wide negative allometry of upper bi-incisal width relative to body weight (with slope of 0.163 for a least-squares fit; Eaglen, 1984) is heavily influenced by the size of Eaglen's ateline sample (10 of the 26 platyrrhine species), including five species that are nearly obligate folivores (four *Alouatta*, one *Brachyteles*). This group differs from other platyrrhine lineages in demonstrating a strongly inverse relationship between bi-incisal width and body size (−1.063; $r^2 = 0.970$; least squares slope calculated from Eaglen's data, here and below). As with other leaf eaters, the mechanical benefit of small incisors is unclear. How much this may contribute to enhance prehensility of the lips, which may be advantageous in collecting forage, is unknown.

There is also a bias in measuring "size" as breadth, especially among the pitheciines. Here bi-incisal width does increase in relation to body size but with a low slope (0.134; $r^2 = 0.551$). Unlike the situation for folivores, in which limited use has been invoked as an explanation for size reduction (see, e.g., Kay and Hylander, 1978), the reason for the low slope among pitheciines is that they are designed to be very narrow and tall (Fig. 3) for special biomechanical reasons. The incisors are not reduced in size; they are transformed in shape. A third subsample of the Eaglen data set, the cebids, presents a higher slope (0.283; $r^2 = 0.882$), much closer to the least-square values he reported for female catarrhines (0.309; from Smith, 1981) and a pooled sample of platyrrhines and catarrhines (0.301; from Cachel, 1983). This similarity makes sense because most cebids resemble catarrhines more closely in overall incisor morphology than either pitheciines or atelines, such as *Alouatta* and *Brachyteles*. Thus the discrepancy in relative size between platyrrhines and catarrhines of comparable morphology is not very large and perhaps is not meaningful adaptively.

Another way of looking at incisor "size" is to examine the distribution of size-related quantities among body size classes and phyletic groups. Figure 3 ranks various platyrrhines according to the crude cross-sectional area (computed from perpendicular diameters taken apically and basally) of I_1. The distribution of I_2 is essentially similar (Table 4). Several interesting points emerge. 1) *Cebus apella* incisors are among the largest (see also Eaglen, 1984). They are twice the cross section of the nearest nonfolivorous species, *Aotus trivirgatus*, and are nearly as large as the frugivorous *Lagothrix*, a genus about three times heavier in body weight. 2) *Aotus* incisors are twice as large as the incisors of *Saimiri* and *Callicebus*, each with different shapes, although the three are similar in weight. 3) Incisors of *Pithecia* and *Chiropotes* are only slightly larger in crude area than those of much smaller callitrichines. For *Cebus* and *Aotus*, both with relatively large dimensions, "size" does not actually quantify a precise biomechanical quality, for the *Cebus* crowns are relatively taller, while the *Aotus* crowns are relatively broader. It thus appears likely that these enlargements of crude cross-sectional area entail different functions and parallel derived conditions within their respective subfamilies (see below).

As with the proportions, the morphology of pitheciin incisors differs radically from that of other platyrrhines (see Rosenberger et al., 1990). The lowers are closely appressed and are shaped like a wedge angling forward from the jaw. Each tooth tapers upward from a broad base to a narrow incisal edge. The root appear to be deep and thick buccolingually, more so than in most other platyrrhines, and the base of the crown does not enlarge or expand in diameter (i.e., to form a cingulum) at the cementoenamel junction. Uppers also have a distinctive shape and orientation but without clear functional import. The large buccolingual diameter at the base of the lowers (Fig. 3) indicates resistance to bending in this plane, while the narrow mesiodistal measurements at the incisal edge makes for the tapered wedge-like design. The most striking metric feature, however, is the extreme height of the incisor crowns in relation to the shape of their cross section. Pitheciins have the tallest incisors of all the platyrrhines, both absolutely and in relation to body mass (Fig. 3).

Callicebus lower incisors bear a strong resemblance to those of pitheciins in being rel-

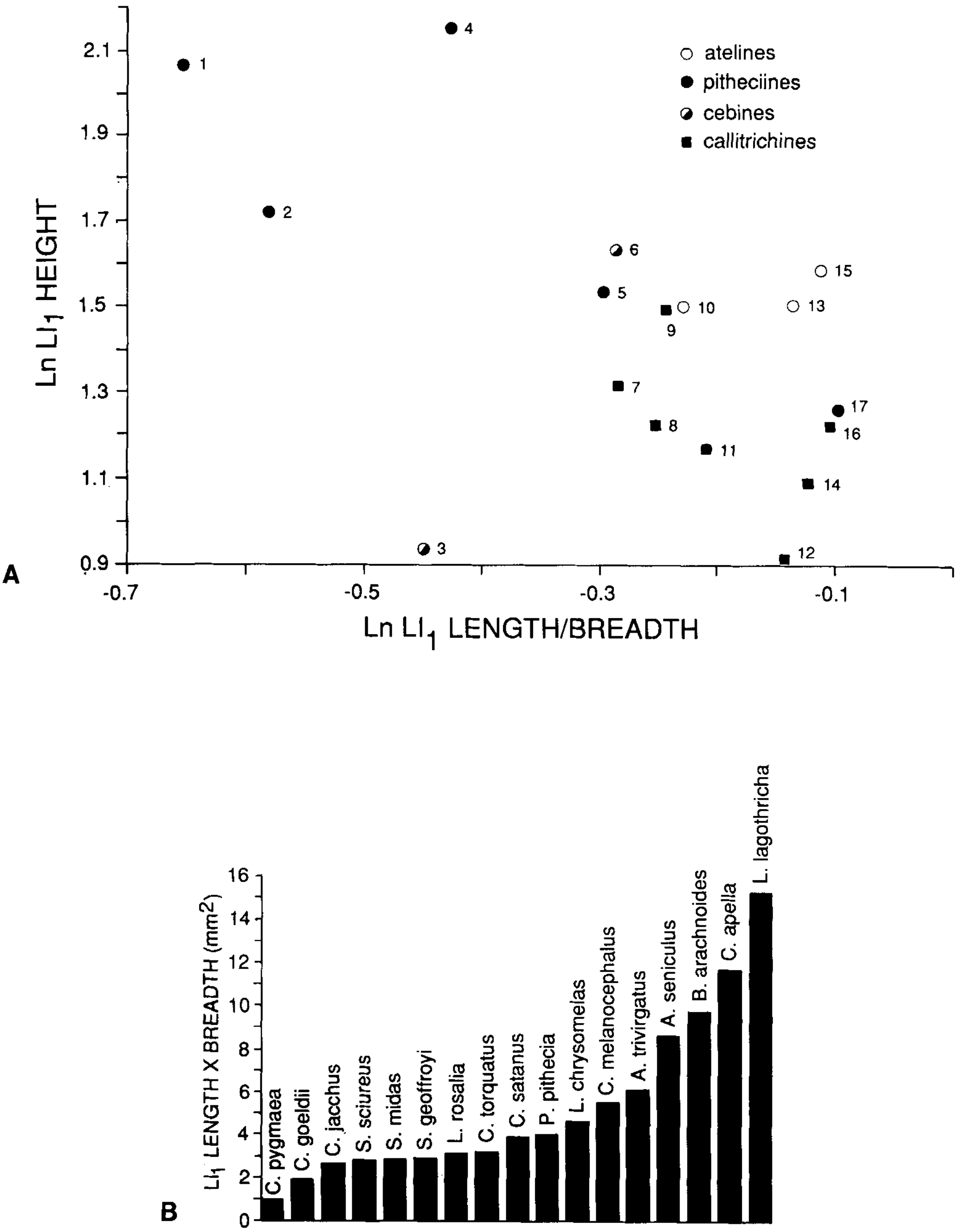


Fig. 3. A: Mean lower first incisor length/breadth ratio plotted against height. B: Histogram showing mean lower incisor area (see Table 4). 1, *C. satanus*; 2, *P. pithecia*; 3, *S. sciureus*; 4, *C. melanocephalus*; 5, *C. torquatus*; 6, *C. apella*; 7, *L. chrysomelas*; 8, *L. rosalia*; 9, *C. jacchus*; 10, *B. arachnoides*; 11, *C. pygmaea*; 12, *C. goeldii*; 13, *L. lagothricha*; 14, *S. midas*; 15, *A. seniculus*; 16, *S. geoffroyi*; 17, *A. trivirgatus*.

TABLE 4. Mean lower incisor dimensions (mm) of platyrrhine primates (range of sample sizes given in parentheses)

Species	N (range)	LI1L	LI1B	LI1H	LI2L	LI2B	LI2H
Brachyteles arachnoides	(1, 11)	2.8	3.5	4.5	3.4	4.3	4.8
Lagothrix lagothricha	(7)	3.7	4.2	4.5	3.9	4.6	4.7
Alouatta seniculus	(2, 8)	2.8	3.1	4.9	3.4	3.9	6.1
Pithecia pithecia	(4)	1.5	2.7	5.6	2.2	2.9	6.1
Chiropotes satanas	(3, 4)	1.4	2.8	7.9	2.0	3.2	8.0
Cacajao melanocephalus	(7)	1.9	2.9	8.6	2.5	3.5	8.6
Aotus trivirgatus	(5)	2.4	2.6	3.5	2.5	2.6	3.7
Callicebus torquatus	(6, 9)	1.6	2.1	4.7	1.9	2.5	4.7
Cebus apella	(5)	3.0	2.9	5.1	3.3	4.2	5.7
Saimiri sciureus	(4, 7)	1.3	2.1	2.6	1.8	2.4	2.6
Callithrix jacchus	(7, 14)	1.5	1.9	4.5	1.4	2.3	4.7
Cebuella pygmaea	(5, 7)	0.9	1.1	3.2	0.9	1.6	3.6
Leontopithecus chrysomelas	(6, 13)	1.8	2.3	3.7	2.5	2.8	4.1
Leontopithecus rosalia	(11, 22)	1.5	1.9	3.4	2.1	2.2	3.6
Saguinus geoffroyi	(6, 12)	1.6	1.8	3.4	1.8	1.8	3.3
Saguinus midas	(6, 10)	1.6	1.8	3.0	1.7	1.9	3.2
Callimico goeldii	(2, 7)	1.3	1.5	2.5	1.4	1.7	2.8

atively tall and slender and lacking transversely expanded apical margins or basal crown enlargements. They differ from incisors of saki-uakaris mostly in their vertical orientation and in having a more flaring I_2 crown. Although the buccolingual diameters are less expanded than in the highly derived pitheciins, incisor height has clearly increased in *Callicebus* (Fig. 3; Table 4), especially by comparison with other genera in the same size class, such as *Saimiri* and *Aotus*. This raises questions about *Aotus*. Owl monkeys are distinctive in having an expanded apical margin on both lowers, producing a large lingual fovea and a broad, scoop-like battery of all four lowers combined. Correspondingly, *Aotus* presents a heteromorphically enlarged I^1, with a large, flattened lingual fovea. Since many elements of the *Aotus* incisal complex are uniquely modified, it is possible that the moderately tall lowers are secondarily derived from a taller, ancestral pitheciine pattern, as owl monkeys evolved a broader feeding niche in the less competitive nocturnal/crepuscular environment.

As has been argued elsewhere, the pitheciin incisal system is functionally adapted to exert high pressure loads, perhaps to wedge apart or scale the strong protective coverings of certain fruits (see, e.g., Rosenberger et al., 1990; Kinzey, 1992; Rosenberger, 1979). This biological role has been called *sclerocarpic harvesting* (Kinzey and Norconk, 1990) to emphasize its importance in splitting the hard pericarp of certain fruits. The procumbent orientation of the incisors may confer several advantages. It may enhance gape at the front end of the jaw, permitting an efficient, precise placement of a fruit (hand-held) for prizing, and it may realign the apicobasal axis of the incisors so that the reaction forces of incision pass close to the temporal mandibular joint, which minimizes dorsoventral bending in the mandible and maximizes the mechanical advantage of the adductor muscles.

In *Callicebus*, the recessed, vertical arrangement of the incisors is associated with reduced canines and an abbreviated premaxillae, unlike the massive canines and jutting incisors of pitheciins. Thus the moderately tall lower crowns of *Callicebus* may be a useful morphological and behavioral model for the biological roles associated with the ancestral version of the sclerocarpic syndrome (Kinzey, 1992). *Callicebus* may not employ its lower incisors in cracking open pericarp in pitheciin fashion, but, as Kinzey (1977) showed, *Callicebus* uses $I_{1,2}$ and the lower canine to peel or open moderately tough husks (e.g., *Brosimum, Clarissia*) and to scrape off the thin edible tissue from very hard palm nuts (*Jessinia*), activities that produce a characteristic style of dental abrasion (Kinzey, 1974). The fact that *Callicebus* *torquatus* also spends a large proportion of its feeding time (17%; Kinzey, 1992) taking seeds increases their utility as an ancestral pitheciin analogue.

Another important element of the sclerocarpic harvesting pattern relates to the involvement of the lower canines (see, e.g., van Roosmalen et al., 1988; Ayres, 1989), highly specialized in pitheciins (see, e.g., Kinzey, 1992) and often used to pierce and wedge open hard, woody endocarp. Furthermore, the space behind the canine provides another morphological locus where an item can be lodged securely and split as the sharp P_2 (reinforced buccally by a thickening of enamel) is closed against the broad upper premolar platform. Thus the sclerocarpic harvesting adaptation of the pitheciin dentition potentially extends beyond the anterior teeth.

At the other end of the taxonomic spectrum are the convergently evolved front teeth shared jointly by *Cebuella* and *Callithrix* (see, e.g., Hershkovitz, 1977; Rosenberger, 1976, 1977, 1978; Kinzey et al., 1977). Their lower incisors are relatively tall, as in pitheciins, but are pointed when unworn, covered with thick buccal enamel and aligned en echelon along with an incisiform canine. The role of the canine has been virtually co-opted functionally by the harvesting incisors. This complex is well suited as a reinforced (viz thick enamel) scraping tool for gouging and removing bark to stimulate exudate flow (Sussman and Kinzey, 1984; Garber, 1992) or to uncover concealed insects (e.g., *Callithrix aurita*: Muskin, 1984). Although the literature strongly emphasizes the exudate-harvesting potential of the pattern, the more primitive lineages of *Callithrix* (i.e., the "*humeralifer* group," see Hershkovitz, 1977) appear, on morphological grounds, to be much less committed to this strategy than the smaller species that are more closely related to *C. jacchus* and to *Cebuella* (see Sussman and Kinzey, 1984). Thus the initial selective motivation for bark-gouging adaptations may reflect either insect or exudate harvesting, or it may simply have benefitted both types of diets.

Few other platyrrhines present such novel incisor/canine patterns as those emphasized above. *Ateles* and *Lagothrix* have large, spatulate incisors, whereas *Alouatta* and *Brachyteles* have reduced incisors with crowns shaped almost like teardrops in lingual view. The latter two taxa may have evolved leaf-eating features convergently, for ancestral atelines were probably not as committed to a leafy diet, and the derived, folivorous masticatory adaptations of their postcanines are not homologous (Rosenberger and Strier, 1989). In cebines and most callitrichines, the lowers are also broad and spatulate, but *Saimiri* has low-crowned, relatively slender incisors, unlike *Cebus*, in which the incisors are quite tall with a large cross section (Fig. 3). The *Cebus* pattern implies a relatively dispersed rather than concentrated (cf. pitheciins) loading pattern, possibly against heavily textured or abrasive material. This is consistent with their tendency to harvest from dead branches and other concealments where insect colonies are sequestered (see Janson and Boinski, 1992).

The stunning variety of incisor patterns exhibited by platyrrhines can be attributed to different factors, for, although they are relatively simple teeth structurally, incisal shape has important functional consequences. The relative "size" of platyrrhine incisors has not been shown to be a particularly sensitive functional feature; however, incisors are consistently small among folivores. Clearly there has been strong selection for specific biological roles, which in some cases are grossly similar even though the species involved feed on basically different resources (e.g., *Callithrix* and *Pithecia*). Thus there are woody seam-splitters (pitheciins), fiber-shredders (*Callithrix*), crunchers (*Cebus*), scrapers (*Callicebus*), and peelers (*Aotus*). Diversity in form may also be related to the fact that the mechanical objectives of the incisors are less constrained than those of the molars, where the purpose is to produce an effectively small particle size. Anatomically, the incisors may be coupled with canines (*Callithrix*, *Cebuella*), and in some cases the premolar region (pitheciins), to complete the harvesting apparatus. At the front of the oral cavity there probably are more available morphological options than deep within the mouth or within a complex articulating machine such as the molar dentition. Consequently, there may also be fewer canalizing constraints.

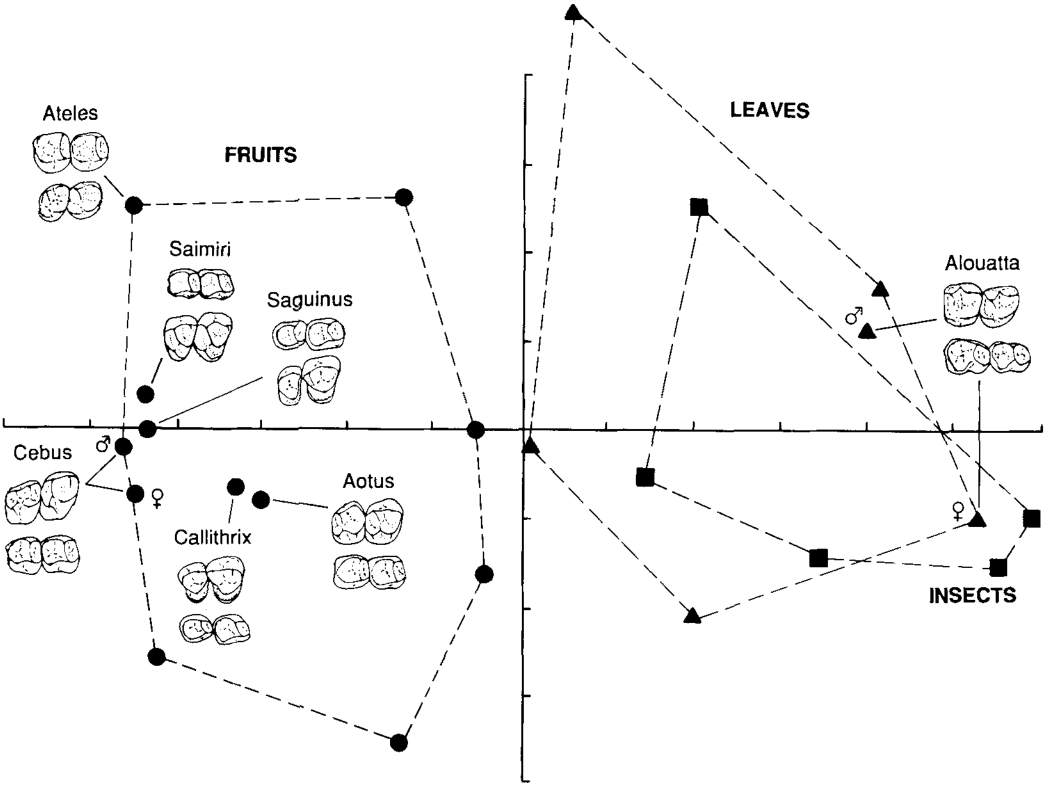


Fig. 4. Dispersion of noncercopithecoid primates in multivariate (principle component) space based on molar measurements (adapted from Kay, 1975 or with permission of the publisher). Polygons enclose boundaries of conventional dietary groups. The upper and lower first and second molars of platyrrhines are shown.

Mastication: Molar and premolar patterns

The functional morphology of molar teeth in certain platyrrhines has been considered by Kay (1975) and Rosenberger and Kinzey (1976; see also Maier, 1984). Kay (1975) employed bivariate allometry and multivariate analysis in a primate-wide survey (justifiably excluding the biolphodont cercopithecoids). He found that the seven platyrrhine genera of his sample separated along the order's frugivory-folivory/insectivory axis but recognized that his platyrrhine "frugivores," *Ateles*, *Aotus*, *Cebus*, *Saimiri*, *Saguinus*, and *Callithrix*, exhibit "... undoubtedly great variation in the amounts of insects eaten" (p. 209). Some of the gross morphological differences in the molars of these forms are shown in Figure 4, which was modified from Kay (1975, Fig. 4) to display their position within the first two principle component axes of multivariate space (see also Fig. 5). Rosenberger and Kinzey (1976) discussed the molar morphology of *Callithrix*, *Cebus*, *Pithecia*, and *Alouatta* in qualitative terms and how their occlusomechanical properties emphasized high or low occlusal pressure functions, linear shearing features, crushing, grinding, or puncture-crushing potential. We concluded that these genera were functionally adapted to insectivory, omnivory, soft-fruit frugivory, and folivory, respectively.

The diversity of molar patterns found among the 16 modern platyrrhine genera is displayed as centric occlusion overlays in Figure 5. The dendrogrammatic arrangement of images also reflects phylogeny (Table 1). *Saimiri* occupies a central position as a modern analogue for the ancestral platyrrhine molar pattern (see, e.g., Rosenberger,

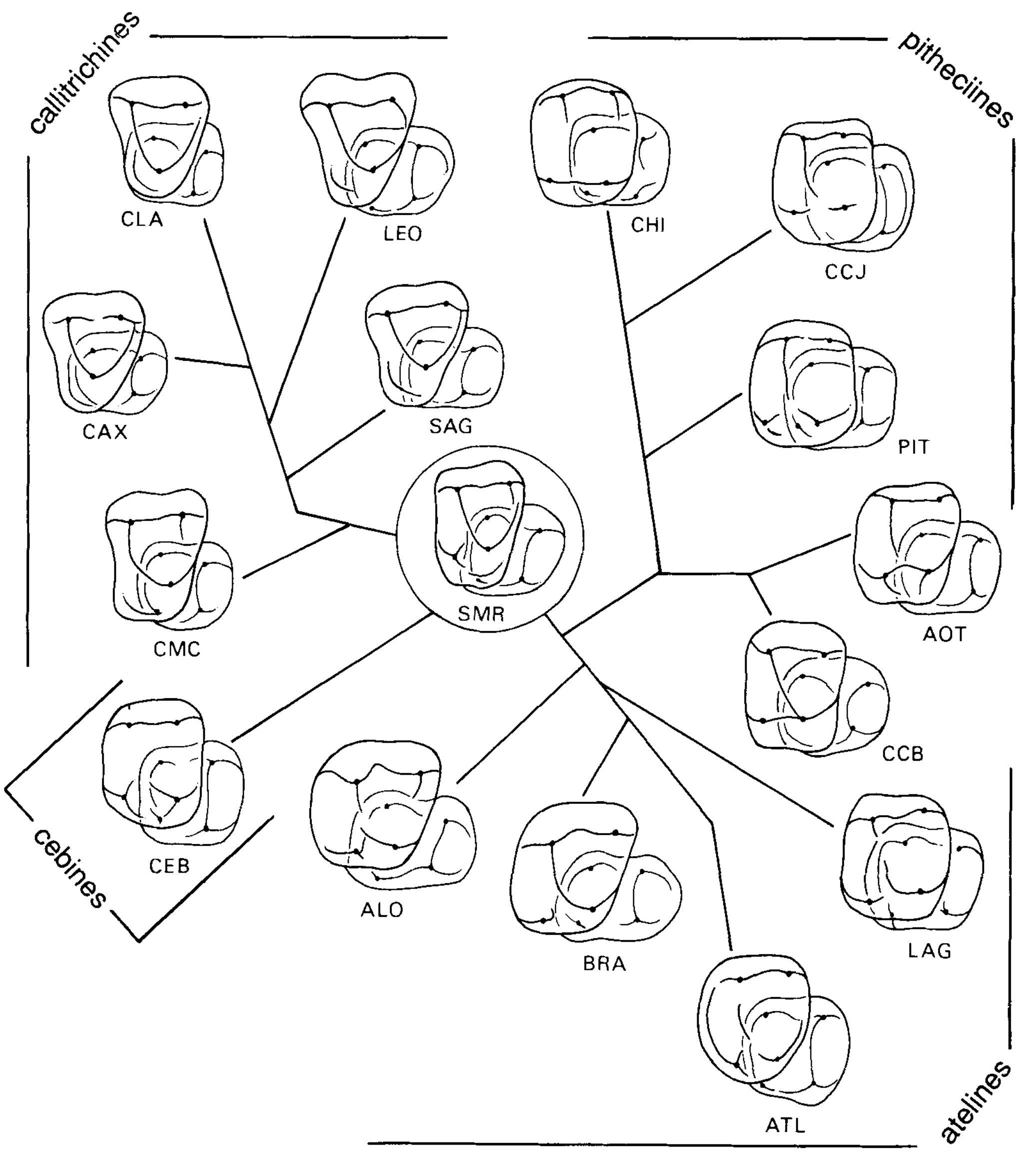


Fig. 5. Overlays of left molars in centric occlusion of all modern platyrrhine genera arranged cladistically (drawn by Dr. Nobuhiko Hagura). Buccal to top of page, mesial to the right. *Saimiri* is a possible model of the ancestral platyrrhine molar pattern (but see text). Abbreviations: ALO, *Alouatta*; AOT, *Aotus*; ATL, *Ateles*; BRA, *Brachyteles*; CAX, *Callithrix*; CCB, *Callicebus*; CCJ, *Cacajao*; CEB, *Cebus*; CHI, *Chiropotes*; CLA, *Cebuella*; LAG, *Lagothrix*; LEO, *Leontopithecus*; PIT, *Pithecia*; SAG, *Saguinus*; SMR, *Saimiri*.

1977; Gingerich, 1980; Kay, 1980; Maier, 1984), although it should not be taken literally as such without recognizing several significant caveats, among them the contrasting morphology of the oldest known platyrrhines, the branisellines from Salla, Bolivia (see Rosenberger et al., 1990).

A uniform molar pattern occurs within two groups only, callitrichines and pitheciins. The molars of callitrichines are characterized by moderate to high relief, a tricuspid pattern (rather four cusped in *Callimico* M^1, however), a raised trigonid, and, due to the triangular outline of the uppers, large interproximal embrasures between P^4 through M^2. Various authors have commented on the reduced lingual or "grinding" features in callitrichines (this is evident in Figure 5 by the small size of the trigon basin and the lack of a hypocone or enlarged upper lingual cingulum) and on their reduced capacity for buccal shear (e.g., Rosenberger and Kinzey, 1976; Maier, 1984). However, the large embrasures provide alternative shearing and puncture-crushing surfaces.

A striking feature of the callitrichine postcanine dentition is the reduction of the molar teeth from behind (Table 5), beginning with the relatively small M3 of *Callimico*, which is about 22% the size of summed molar area (Rosenberger et al., 1991), and culminating with the loss of M3 and the marked reduction of M2 in many species. A survey of 11 species representing all genera of the two-molared callitrichins indicated that, in most species, crude M^2 area (length × width) was approximately 50–60% the area of M^1 (Kanazawa and Rosenberger, 1988). In addition, by comparison with all other anthropoids except hominoids (Kanazawa and Rosenberger, 1989), callitrichines also appear to have smaller molars relative to body weight (see also Pirie, 1978), with a least-squares slope of 0.516 ($r^2 = 0.762$) as compared with 0.730 ($r^2 = 0.863$) for atelids, 0.881 ($r^2 = 0.942$) for cercopithecoids, and 0.484 ($r^2 = 0.876$) for pongids.

Taken together, the shape, relatively small size, posterior reduction, and overall proportions of callitrichine molars suggest that the entire postcanine row is best treated as the unit of study in a functional analysis, for the morphology basically indicates that the major mechanical emphasis is on premolar, or premolar-like, processing (Rosenberger, 1977). The premolars of callitrichines vary morphologically from being transversely expanded to being nearly unicuspid but are frequently tall or built with high relief. The overall pattern of the cheek teeth therefore implies that puncture-crushing plays a predominant role in mastication. This is consistent with an insectivorous adaptation. Small molar "surface area" (=size) per se may be beneficial because occlusal pressure for piercing chitin, for example, can be increased by decreasing the unit area over which force is applied and/or by enlarging tooth embrasures to expose perimeter shearing blades and puncturing surfaces. Smaller molars also reduce posterior resistance while closing the jaws against foods, enhancing the force applied forward in the premolar region. Thus a reasonable adaptive explanation for the organization of callitrichine postcanines relates to the critical functions (of an insectivorous diet, in which puncturing and shearing would be at a premium.

Pitheciin molars, in contrast, display a radically modified pattern of exceptionally low topographic relief. The crowns are shaped like simple rectangular blocks, with only traces of ridges or crests and widely spaced, low cusps. The upper buccal ectoloph, typically a crucial locus of relief relating to buccal phase engagement and shearing, is a thin, low ridge. This effectively increases the size of the occlusal basins. Enamel crenulation is common in unworn crowns, although it is not known how long the wrinkling remains patent ontogenetically. Viewed in centric occlusion (Fig. 5), it is clear that these features produce a relatively large, planar reciprocal surface area as the teeth engage.

The functional morphology of the pitheciin pattern has been discussed by Rosenberger and Kinzey (1976) and Kinzey (1992). Based on *Pithecia*, Rosenberger and Kinzey interpreted these features as soft-fruit adaptations, suitable for pulping water-laden fruits but not for puncturing or shearing more durable or resilient materials. However, a soft-fruit adaptation is an oversimplification. It would not be entirely consistent with field evidence, and it may be an inadequate explanation of the radical morphology in the context of the critical-function paradigm. This view relegates pitheciins to the frugivore category on negative evidence: They lack the biomechanical potentiality of insectivorous or folivorous designs.

TABLE 5. Mean lower postcanine dimensions of platyrrhine primates (range of sample sizes given in parentheses)[1]

Species	N (range)	LM1L	LM1B	LM2L	LM2B	LM3L	LM3B	LMA	N (range)	LP2L	LP2B	LP3L	LP3B	LP4L	LP4B	LPA	PCA
Ateles belzebuth	(16, 19)	5.3	5.1	5.2	5.3	4.9	4.8	78.1	(19)	4.4	4.9	4.0	4.6	4.1	4.6	58.4	136.4
Ateles geoffroyi	(23, 27)	5.3	5.0	5.2	5.2	5.0	4.7	76.7	(26)	4.0	4.4	3.5	4.3	3.7	4.6	49.3	125.9
Brachyteles arachnoides	(11, 15)	7.6	5.8	7.4	5.9	6.8	5.4	123.8	(9, 14)	4.7	5.6	4.9	5.2	5.4	5.4	80.1	203.9
Lagothrix lagothricha	(9, 10)	5.5	5.1	5.7	5.3	5.6	5.1	87.4	(9)	4.7	5.2	4.0	4.6	4.0	4.7	61.6	149.0
Alouatta belzebul	(18, 20)	7.2	5.6	7.9	6.1	8.4	5.6	135.2	(20)	5.4	5.8	5.2	5.1	5.5	5.1	86.2	221.4
Alouatta seniculus	(7, 9)	7.2	5.6	7.8	6.2	8.3	5.8	136.0	(8, 9)	5.3	6.3	4.9	5.4	5.2	5.4	88.1	224.1
Pithecia monachus	(16)	4.0	3.8	4.0	3.9	4.0	3.7	45.7	(16)	3.7	3.6	3.0	3.4	3.2	3.5	34.8	80.5
Cacajao calvus	(9)	4.5	4.2	4.2	4.3	3.9	3.9	51.5	(9)	4.0	4.4	3.6	4.3	3.5	4.4	48.5	100.0
Aotus trivirgatus	(19, 22)	3.3	3.0	3.3	2.9	3.1	2.6	27.3	(20, 21)	2.3	2.2	2.1	2.3	2.4	2.6	16.8	44.1
Callicebus moloch	(11)	3.4	3.2	3.5	3.2	3.2	2.9	31.5	(11)	2.0	2.4	2.1	2.6	2.2	2.8	16.4	47.9
Callicebus torquatus	(8, 9)	3.6	3.5	3.6	3.2	3.3	2.8	32.9	(8, 9)	2.2	2.8	2.1	2.7	2.2	3.0	18.3	51.1
Cebus apella	(39, 53)	5.3	5.0	4.7	4.9	3.9	4.1	65.0	(45, 47)	5.1	4.6	4.0	4.7	3.9	5.1	62.6	127.6
Saimiri oerstedii	(14, 22)	3.0	2.6	2.6	2.5	2.2	1.9	18.6	(19)	2.9	2.8	2.3	2.5	2.2	2.6	19.5	38.1
Saimiri sciureus	(5, 7)	2.7	2.5	2.5	2.4	2.1	1.9	16.8	(5, 7	3.3	2.7	2.1	2.5	1.9	2.7	19.0	35.8
Callithrix jacchus	(14, 15)	2.3	2.0	1.9	1.7	NA	NA	7.8	(13, 14)	2.3	2.1	1.8	2.0	1.8	2.0	11.9	19.7
Cebuella pygmaea	(10, 13)	1.7	1.5	1.5	1.3	NA	NA	4.3	(10)	1.4	1.0	1.4	1.2	1.3	1.3	4.8	9.1
Leontopithecus chrysomelas	(11, 12)	2.9	2.8	2.6	2.2	NA	NA	13.5	(9, 12)	3.1	2.8	2.5	2.8	2.5	2.9	22.9	36.4
Leontopithecus chrysopygus	(4, 6)	3.2	2.8	2.7	2.4	NA	NA	15.4	(4, 6)	3.2	2.6	2.6	2.8	2.5	3.1	23.1	38.5
Leontopithecus rosalia	(20, 23)	3.1	2.8	2.6	2.3	NA	NA	14.4	(2, 21)	3.2	2.6	2.3	2.7	2.3	3.0	21.4	35.8
Saguinus geoffroyi	(10)	2.7	2.1	2.2	1.8	NA	NA	9.7	(9, 10)	2.5	2.2	2.1	2.3	2.2	2.4	15.7	25.3
Saguinus midas	(10)	2.6	2.1	2.3	1.6	NA	NA	9.2	(9. 10)	2.5	2.3	2.1	2.2	2.1	2.2	14.9	24.1
Callimico goeldii	(6)	3.1	2.8	3.0	2.5	2.2	2.0	20.4	(2, 4)	2.5	2.5	1.9	2.3	2.0	2.5	15.7	36.1

[1] Abbreviations: LMA, lower molar area; PCA, postcanine area. Sources include: Hershkovitz, 1977; Orlosky, 1973; Rosenberger, 1979; Rosenberger, unpublished data; Rosenberger and Coimbra-Filho, 1984.

An alternative interpretation (see Kinzey, 1992) that is more concordant with new field data and a preliminary study of molar microwear (Kay, 1987), is that the critical biological roles of the postcanines are to process compliant, resistant food items, seeds. Comparisons with soft-fruit eating platyrrhines illustrate a contrasting set of mechanical and selective consequences of such a diet. The seeds that *Chiropotes* eat require less crushing force than those ingested by *Ateles paniscus*, but spider monkeys apparently cannot, or at least do not, masticate even the softest varieties (Kinzey and Norconk, 1990). Observers have noted that *Chiropotes* may indeed prefer younger, softer seeds when available, but they regularly take seeds requiring considerable amounts of force to reduce (Fig. 2) (Ayres, 1989; Kinzey and Norconk, 1990).

For pitheciins eating moderately hard or resilient seeds, a reduction in cusp relief may protect the crown surface from incurring high levels of local stress that might otherwise cause or propagate enamel cracking. Given the large fraction of tough, woody materials pitheciins encounter while harvesting with the anterior teeth and premolars, one also cannot rule out the possibility of a pleitropic influence on molar form. The corrugated pattern of surface enamel may act to stabilize a hard item that requires considerable force and deformation per unit time before its yield point is reached. In other words, crenulations, in the absence of anything else, may contain and retard displacement of resistant items as they are squeezed until the yield point is reached. Crenulations can also be important in facilitating the secondary breakdown (Lucas and Luke, 1984) of food particles. After a seed is initially ruptured into a mass of irregular fragments, the derivative pieces can be trapped and stabilized for a second round of processing during the same stroke. Soft fruits presumably do not require such extensive, detailed treatment. Simple crushing actions should suffice to disrupt their intercellular matrix and mash them into a size small enough for bolus formation and swallowing. Additionally, Maas (1986) has suggested that the strongly interlaced enamel prism pattern of *Chiropotes* (and *Cebus*) may be related to resistance to fracture.

Other platyrrhine genera show various postcanine modifications related to diet, but these do not sort out at high taxonomic levels (Fig. 5). The contrast between certain close relatives is noteworthy, however. For example, *Cebus* and *Saimiri* differ from one another in molar form but the molars have similar proportions, both sharing a strongly reduced M3 and broad, dominant premolars. As with callitrichines, this broadly implies an insectivorous heritage, mediated by puncture-crushing mastication. However, the molars of *Saimiri* are relatively small and strongly crested whereas those of *Cebus* are large (Fig. 6), bunodont, and thickly enameled (Kinzey, 1974; Rosenberger and Kinzey, 1976; Kay, 1980). This indicates that squirrel monkey molars emphasize shearing and puncturing, whereas those of capuchins are designed more for crushing—and enhanced wear resistance—possibly with particularly heavy muscular force (Rosenberger and Kinzey, 1976).

The pitheciines *Aotus* and *Callicebus* differ from one another and from the saki-uakaris in molar form (Fig. 5). Although *Callicebus* bears some similarities to pitheciins in having moderately reduced crown relief and a molarized P_4, *Aotus* is quite different, resembling the crested pattern of *Saimiri*, for example. One way of interpreting these patterns is that they serve as a generalized compromise that permits frugivorous folivory and/or insectivory but without selection for an undue emphasis on either source (see, e.g., Kinzey, 1978). Thus, as is argued below, *Aotus* and *Callicebus* primitively rely more on insects and leaves than the closely related pitheciins, in which seeds have become a basic nutritive source (see Kinzey, 1992).

The morphology of ateline cheek teeth has recently been considered by Rosenberger and Strier (1989). They concluded that the low relief, shallow basins, and small size of *Ateles* molars represented a low-force crushing paradigm related to their preference for soft, ripe fruits. The somewhat greater relief and slightly bunodont pattern of *Lagothrix* might be indicative of a preference for harder fruits, to which they are attracted in

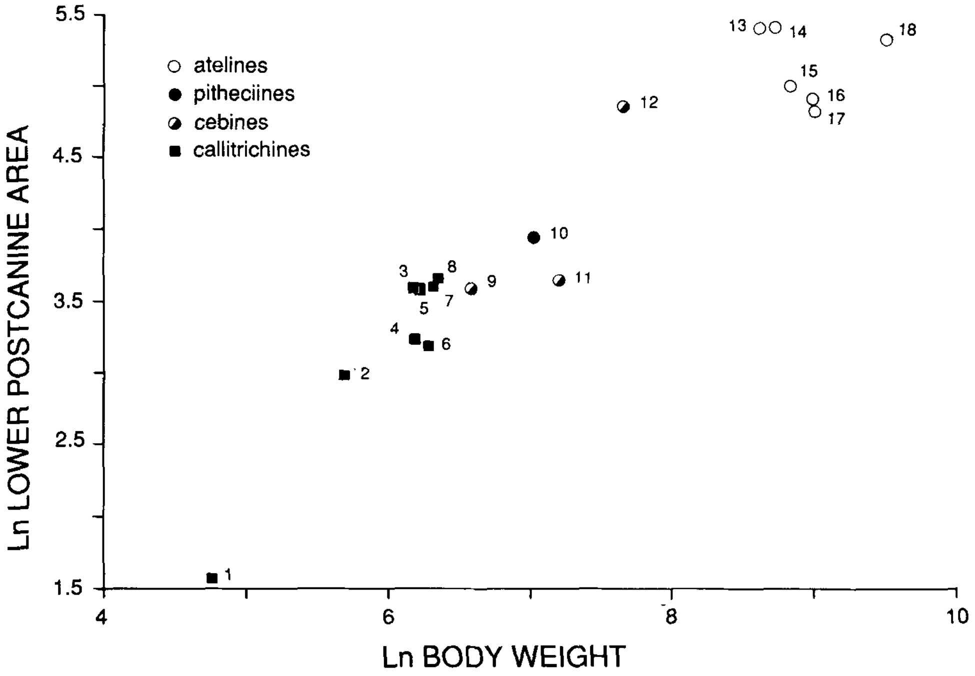


Fig. 6. Bivariate plot of mean body weight against lower postcanine area. 1, *C. pygmaea*; 2, *C. jacchus*; 3, *C. goeldii*; 4, *S. geoffroyi*; 5, *L. rosalia*; 6, *S. midas*; 7, *L. chrysomelas*; 8, *L. chrysopygas*; 9, *S. sciureus*; 10, *C. torquatus*; 11, *S. oerstedii*; 12, *C. apella*; 13, *A. belzebul*; 14, *A. seniculus*; 15, *L. lagothricha*; 16, *A. belzebuth*; 17, *A. geoffroyi*; 18, *B. arachnoides*.

captivity (Milton, 1984). *Alouatta*, as is well known, presents a host of buccal shearing features (see, e.g., Rosenberger and Kinzey, 1976) and relatively very large molars (Kay, 1977; Fig. 6), as with many other folivores. However, the details of occlusal structure in *Brachyteles*, the largest platyrrhine, emphasize lingual shear, and its cheek teeth are absolutely and relatively smaller than in *Alouatta* (Table 5; Rosenberger and Strier, 1989; see also Kay et al., 1987). Thus in *Alouatta* the buccal side of the crown is dominated by a W-shaped ectoloph carrying long crests, and the lower has a long, buccally crested talonid to reciprocate it (Fig. 5). *Brachyteles* has a simple, transversely narrow buccal ectoloph on the uppers, without crest elongation, and the talonid is also not elongate. Together with other evidence from the skull and postcranium, these contrasting patterns indicate a convergence in the folivorous masticatory adaptations of howlers and muriquis (Rosenberger and Strier, 1989).

Body size

Hershkovitz (1977) proposed that body size increase was a major feature of platyrrhine evolution (Table 6; Fig. 7), with the smallest being the most primitive forms and the largest the most derived. It is now generally agreed that this interpretation is incorrect. Various workers have argued that the callitrichines are secondarily reduced in size (see reviews in Ford, 1980; Sussman and Kinzey, 1984) and have offered some ecological explanations supporting this idea (see, e.g., Rosenberger, 1980; Garber, 1992). Ford and Davis (1992) have also written extensively on their views regarding size increase and decrease in various platyrrhine clades.

Field studies demonstrate that the differentiation of body size is a significant factor in the partitioning of platyrrhine diets and foraging strategies (see, e.g., Janson and Boinski, 1992; Garber, 1992; Rosenberger and Strier, 1989; Strier, 1992). However, it is not easy to determine the direction or ex-

TABLE 6. Mean body weight and head and body lengths for sex-pooled, wild-shot platyrrhines[1]

Species	Body wt (g)	N	H & B length (mm)	N	Source
Ateles belzebuth	8,076	17	495	17	USNM
Ateles geoffroyi	8,168	8	426	8	USNM
Brachyteles arachnoides	13,500		587	6	RO-ST/BO
Lagothrix lagothricha	6,875	8	475	17	FOO
Alouatta belzebul	6,319	18	513	18	USNM
	5,372	62	501	62	MPEG
Mean	5,585	80	504	80	
Alouatta caraya	4,712	8	525	6	MNRJ
	5,771	7	593	7	USNM
Mean	5,206	15	562	13	
Alouatta fusca	4,725	8	496	8	USNM
	4,273	17	465	7	MNRJ
Mena	4,418	25	482	15	
Alouatta palliata	6,015	19	472	20	USNM
Alouatta seniculus	6,111	20	534	20	USNM
	7,400	2	589	8	MNRJ
Mean	6,228	22	550	28	
Pithecia pithecia	1,843	9	349	9	OLI
Pithecia monachus	2,406	12			HE87
Chiropotes albinasus	2,847	10	399	10	AY81
Chiropotes satanus	2,482	17	387	17	USNM
	2,754	33	354	33	AY81
Mean	2,662	50	365	50	
Cacajao calvus	3,967	3	396	3	AY87
Cacajao melanocephalus	2,975	8	415	10	USNM
Aotus trivirgatus	860	16	298	20	USNM
Callicebus moloch	973	9	309	9	MPEG
Callicebus torquatus	1,121	14	334	17	USNM
Cebus albifrons	2,428	15	427	16	USNM
Cebus apella	2,242	20	363	20	USNM
	1,964	18	347	18	MPEG
Mean	2,110	38	355	38	
Cebus capucinus	3,128		388	50	FO-DA/ROS
Saimiri oerstedii	1,350	>21	299	6	BO/NAP
Saimiri peruviensis	940	2	291	14	AY85
Saimiri sciureus	722	36	277	36	MPEG
Saimiri vanzolinii	841	11	266	11	AY85
Callithrix aurita	429	2	223	11	MNRJ
Callithrix flaviceps	406	4	221	5	MNRJ
Callithrix geoffroyi	359	46	222	46	MNRJ
Callithrix jacchus	248	11	191	20	USNM
	307	40	206	40	MNRJ
Mean	294	51	201	60	
Callithrix penicillata	340	12	211	12	USNM
Cebuella pygmaea	116	71	138	71	SO88
Leontopithecus chrysomelas	556	8	240	8	RO-CO
Leontopithecus chrysopygus	575	4	269	7	RO-CO
Leontopithecus rosalia	495	20	246	27	RO-CO
Saguinus fuscicollis	413	33			GA-TE
	354	39			SO-CO
	367	3	200	3	MNRJ
Mean	380	75	200	3	
Saguinus geoffroyi	486	53	238	20	DAW
Saguinus labiatus	491	17			YON
Saguinus midas	533	16	253	21	MNRJ
Saguinus mystax	564	16			GA-TE
	505	161			SO82
	460	5	228	5	MNRJ
Mean	509	182	228	5	
Saguinus oedipus	432	25	238	20	HE77/USNM
Callimico goeldii	482	11	225	12	LO-HE/HE77

Grand means are listed for species with more than one source. Acronyms following slash indicate source of head/body lengths, when different from weight. Abbreviations: AY81, Ayres, 1981; AY85, Ayres, 1985; AY87, Ayres 1987; BM, British Museum (Natural History); BO, Boinski, 1989; CPRJ, Centro de Primatologia do Rio de Janeiro; DAW, Dawson, 1976; FO-DA, Ford and Davis, 1992; FOO, Fooden, 1963; GA-TE, Garver and Teaford, 1986; HE77, Hershkovitz, 1977; HE87, Hershkovitz, 1987; LO-HE, Lorenz and Heinemann, 1967; MNRJ, Museo Nacional de Rio de Janeiro; MPEG, Museu Paraense Emilio Goeldi; NAP, Napier, 1976; OLI, Oliveira et al., 1985; ROS, Rosenberger; RO-CO, Rosenberger and Coimbra-Filho, 1984 (MNRJ, CPRJ); RO-ST, Rosenberger and Strier, 1989 (USNM, FOO); SO82, Soini, 1982; SO88, Soini, 1988; SO-CO, Soini and Coppula, 1981; USNM, United States National Museum; YON, Yoneda, 1981.

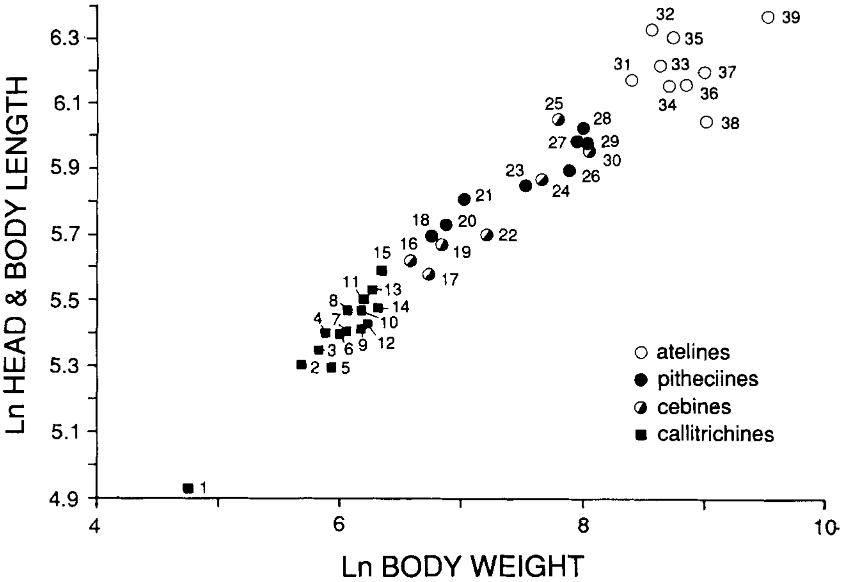


Fig. 7. Bivariate plot of mean body weight against head and body length. Date from Table 6. 1, *C. pygmaea*; 2, *C. jacchus*; 3, *C. penicillata*; 4, *C. geoffroyi*; 5, *S. fuscicollis*; 6, *C. flaviceps*; 7, *C. aurita*; 8, *S. oedipus*; 9, *C. goeldii*; 10, *S. geoffroyi*; 11, *L. rosalia*; 12, *S. mystax*; 13, *S. midas*; 14, *L. chrysomelas*; 15, *L. chrysopygus*; 16, *S. sciureus*; 17, *S. vanzolinii*; 18, *A. trivirgatus*; 19, *S. peruviensis*; 20, *C. moloch*; 21, *C. torquatus*; 22, *S. oerstedii*; 23, *P. pithecia*; 24, *C. apella*; 25, *C. albifrons*; 26, *C. satanas*; 27, *C. albinasus*; 28, *C. melanocephalus*; 29, *C. calvus*; 30, *C. capucinus*; 31, *A. fusca*; 32, *A. caraya*; 33, *A. belzebul*; 34, *A. palliata*; 35, *A. seniculus*; 36, *L. lagothricha*; 37, *A. belzebuth*; 38, *A. geoffroyi*; 39, *B. arachnoides*.

tent of size shifts in any given taxon using neontologic data. It is even more difficult to reconstruct the ecological conditions or selective advantages present at the time of differentiation. In this section, I briefly discuss several of the better examples of size shifts that relate to the diversification of feeding adaptations. It is to the point to recall that the dental measurements of the earliest known fossil platyrrhines (~ 26 Ma), *Branisella boliviana* and *Szalatavus attricuspis*, from the same Bolivian locality (Rosenberger et al., 1991), are similar to those of *Saimiri*, and the teeth of the smallest fossil platyrrhine, *Micodon kiotensis* (~ 15 Ma), are about the size of the teeth of a moderate-sized *Callithrix*.

The miniature *Cebuella pygmaea*, nearly 50% smaller than the closely related *Callithrix jacchus* (Fig. 7), is the best example of phyletic size decrease among platyrrhines (contra Hershkovitz, 1977). Their small size is probably linked directly to their specialized feeding on exudates, perhaps enabling them to reduce search and locomotor costs. The home ranges for *Cebuella* groups are extremely small (<1 ha) and appear to be concentrated around productive exudate-producing trees (Ramirez et al., 1977). Once the local food supply is exhausted, the troop moves. In occupying small territories and spending considerable amounts of time excavating and feeding below the canopy, *Cebuella* may also be prone to predation. Small size and cryptic, agouti coloration are benefits here.

Several derived features have often been invoked to support the idea that callitrichines are "dwarves," including reduced cheek tooth size and molar morphology (Rosenberger, 1977; Ford, 1980), large fetal size, twinning, a "monogamous" social system (Leuttenegger, 1980), and relatively large eyeballs in relation to the bony orbit (Martin, 1990). However, some of these features are not causally linked with dwarfism or are not universally found among callitrichines. For example, molars without hypocones occur in the *Cebus*-sized *"Saimiri" bernensis* from Haiti, but hypocones are also present on the M^1 of *Callimico*, a bona fide callitrichine; third molars are lost in the *Callicebus*-sized *Xenothrix mcgregori* from Jamaica; large neonates occur in *Saimiri*; twinning does not occur in *Callimico*.

In spite of these difficulties, dwarfism remains a viable evolutionary explanation. Callitrichines exploit a canopy-subcanopy feeding niche that is made accessible by the evolution of digital claws (see, e.g., Cartmill, 1974; Rosenberger, 1977, 1980; Garber, 1992). Since the claws of callitrichines, an independently derived feature, may be associated with a reduction or loss of hallucial grasping, which appears to be unarguably derived among euprimates, the locomotor pattern also connotes a derived shift in foraging strategies.

Although I have previously cautioned (Rosenberger, 1983) that the body size gap (Fig. 7) between callitrichines and other platyrrhines was exaggerated in the literature—the sizes of *Saimiri*, *Saguinus*, and *Leontopithecus* virtually overlap—the taxonomic distribution of this trait does lend support to the notion that a significant size threshold was passed as callitrichines differentiated. The reason for this is that two of the lineages that narrow the gap between callitrichines and cebines show indications of their own heterochronic size shifts (see Shea, 1989, for a review of heterochrony and its indicators). I refer to a likely increase in body size in *Leontopithecus* and a reduction in *Saimiri*. *Saimiri* presents a number of features at odds with its moderate to small body size as well as several possible correlates of dwarfism, including a relatively very large brain size, short face, centrally located foramen magnum, lightly built skull, absence of intracranial pneumatisation, and relatively heavy neonates. *Leontopithecus*, as is more fully argued elsewhere (Du Brul, 1965; Rosenberger, in press), may be a "mega-marmoset," much larger than their closest relatives, the *Callithrix*/*Cebuella* clade (Rosenberger and Coimbra-Filho, 1984) (Fig. 7). One feature possibly associated with a secondary size increase is unusually large interorbital sinuses.

Regarding possible body size increases, *Cebus*, two to four times the weight of *Saimiri* and as much as six times larger that the largest callitrichines, may also be a "phyletic giant." Much of the biology of *Cebus* appears to involve specializations that enable the genus to maintain (Fig. 8) a form of the ancestral frugivorous-insectivorous feeding habit of cebids, which is generally predicated upon small body size, by using other tactics. Hence the large, bunodont, thick-enamelled premolars and molars are used to crunch the dead ends of branches to obtain hidden insects, the "pseudo-opposable" thumbs to extract prey, and the semiprehensile tail to anchor the body during such activities. Janson and Boinski (1992; Fedigan, 1990) also argue persuasively that the large, muscular physique of *Cebus* is useful in tearing apart branches to expose insects and in securing vertebrate prey, such as bird nestlings and mammals of large size, weighing up to 1 kg.

At the other end of the spectrum, atelines also underwent size increase, at the subfamily level as well as within the *Ateles*/*Brachyteles* lineage. Rosenberger and Strier (1989) argue that the initial size shift, which may have involved a twofold increase relative to the last common ancestor atelines shared with the pitheciine stock, could have enabled ancestral atelines to exploit more immature and mature leaves as a constant resource by increasing the capacity of the gut. A second likely shift occurred in connection with the brachiating body plan in the common ancestor of *Ateles* and *Brachyteles*, for more obscure reasons.

In summary, the differentiation of body size as an adaptive character has probably been a principal feature of platyrhine evolution within and between the chief lineages, but not in the orthogenetically stable manner proposed by Hershkovitz (1977). Among cebids, there is a 20-fold difference in the approximate average weights of the largest and smallest species, *Cebus* and *Cebuella* (Ford and Davis, 1992), one possibly being a "giant" and the other the most likely example of a "dwarf." Dwarfism and gigantism may thus have evolved in parallel several times among cebids alone, which suggests an abundant ecological potential for body size evolution in their phylogenetic-adaptive zone.

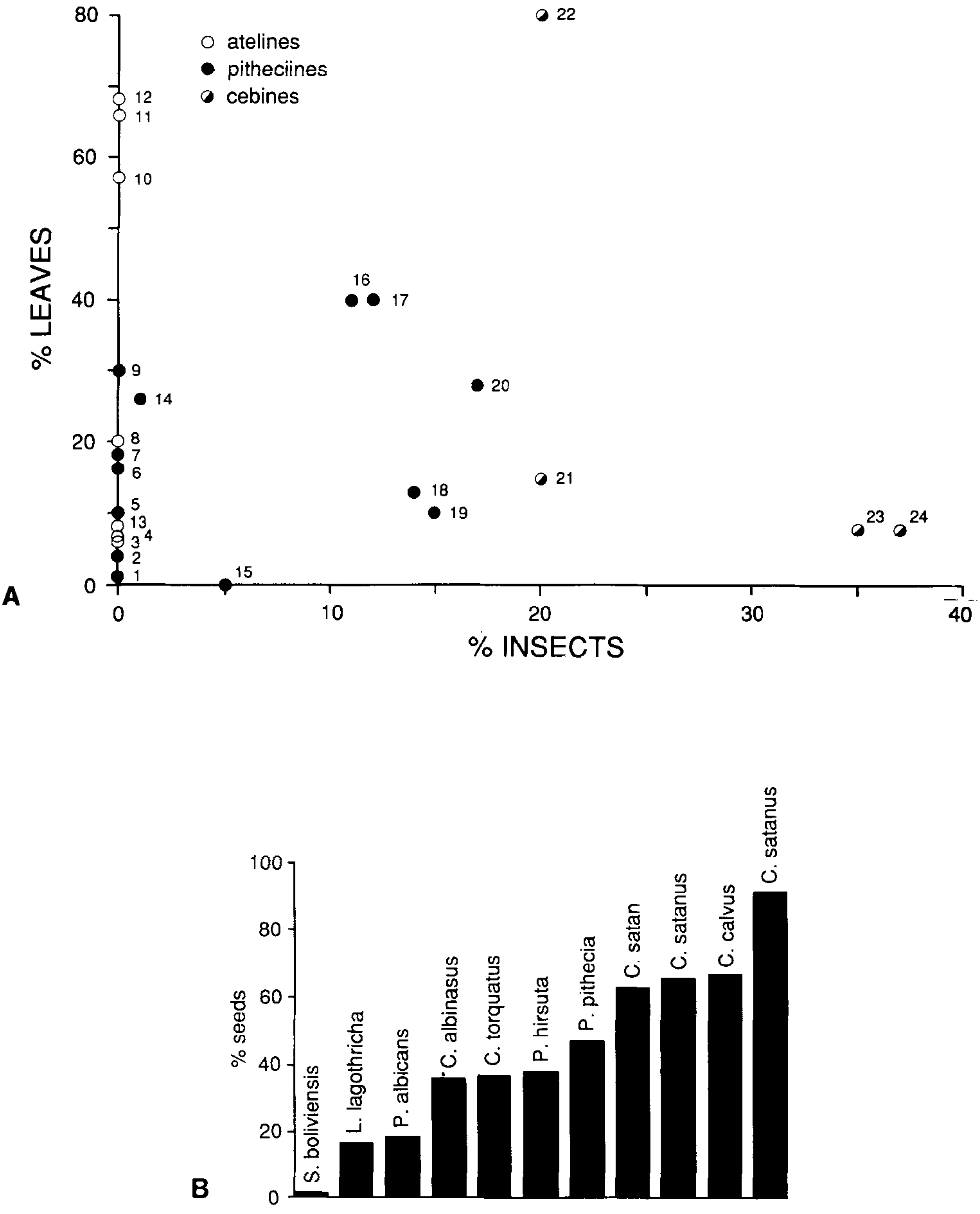


Fig. 8. A: Bivariate plot showing percentages of insects eaten compared with leaves for three subfamilies of New World monkeys (callitrichines are not known to eat leaves). B: Percentage of seeds eaten as part of overall diet. 1, *C. satanas*; 2, *P. hirsuta*; 3, *L. lagothricha*; 4, *A. belzebuth*; 5, *C. albinasus*; 6, *P. monachus*; 7, *C. personatus*; 8, *A. geoffroyi*; 9, *P. albicans*; 10, 11, 12, *B. arachnoides*; 13, *A. paniscus*; 14, *C. moloch*; 15, *C. calvus*; 16, *A. trivirgatus*; 17, *C. moloch*; 18, *C. torquatus*; 19, *A. trivirgatus*; 20, *C. moloch*; 21, *C. capucinus*; 22, *C. albifrons*; 23, 24, *C. olivaceus*. Data from Table 2.

Foraging

Fleagle and Mittermeier (1980), drawing from observations of seven sympatric species in Surinam, concluded that the evolutionary rules governing the interaction between feeding and locomotion were loose and unpredictable. There were quadrupedal frugivores, folivores, insectivores, and omnivores at their site; some frugivores leapt more than others, whereas some were more suspensory; some insectivores tended to leap, whereas others walked quadrupedally. Rosenberger (1980) suggested that the linkage between diet and positional behavior among platyrrhines was through phylogeny (Fig. 1). I have proposed that within the two main phylogenetic-adaptive zones of the platyrrhine radiation, different ecological modalities developed as descendant taxa evolved alternative positional, locomotory, and foraging adaptations to partition further the food-resource spectrum within every sector. Each modality was again sorted by lower level taxonomic differentiation (tribes, genera, etc.) along the generalist-specialist continuum. Although the original model (Rosenberger, 1980) of a basic dichotomy into frugivore-insectivore and fruigvore-folivore zones has its weaknesses (Kinzey, 1986, 1992), the major point of this idea was to showcase the structured (but not deterministic) interplay between phylogeny, feeding, and foraging in the radiation of neotropical primates. Various monophyletic groups have emerged to exploit their ancestral adaptive zones in their own ways, by evolving unique foraging adaptations of the locomotor system. A similar point was also made by Fleagle (1984) in a broader taxonomic context. He noted that ". . . there is increasing evidence of underlying heritage features in the patterns of food procurement of most primates" (p. 112), despite much variation and flexibility in the manner of travelling locomotion, ranging patterns, and percentages of fruit and leaves eaten.

Among platyrhines, some of the phyetic links between food, foraging, and phylogeny occur at high taxonomic levels, whereas others are specializations at the generic or species level. A generalized form of leaping quadrupedalism (see Szalay and Dagosto, 1988; Gebo, 1989; Ford, 1990) was probably the ancestral platyrrhine pattern and is, therefore, the most widely distributed. It is retained as a *bauplan* among the frugivorous-faunivorous cebines, but is modified in callitrichines, as the latter shifted to a vertically ranging use of habitat and a foraging pattern that exploited insects and exudates within and below the canopy. Critical here is the evolution of claws and small body size as postural, foraging adaptations (Kinzey et al., 1975; Garber, 1980, 1992). *Cebus*, with its larger body size and sheer muscular force, abetted by the stabilizing role of a semiprehensile tail, enlarged its predaceous search image to include vertebrate prey, but also still feeds on ants and insects by using an extractive method, taking them in large numbers from concealed quarters in dead tree branches and dead-leaf masses (Janson and Boinski, 1992). The manifest parallelism to the ateline prehensile tail (Rosenberger, 1983) resulted in no dietary convergences whatsoever.

The ancestral locomotor adaptation of atelines represents another marked shift from a primitive quadrupedalism (Rosenberger and Strier, 1989). In addition to the prehensile tail, atelines share a variety of derived pedal adaptations related to climbing (Gebo, 1989). Along with their relatively large body size, climbing and tail-hanging behaviors may be related to locomotion in the canopy generally rather than benefitting any specific type of foraging pattern. This would be similar to the callitrichine cause, where claw-based scansorial locomotion facilitated foraging in a broad sense among a diversity of substrates. Grand (1972), however, showed that hanging postures increased the feeding/foraging sphere for a large-sized primate, and Kinzey (personal communication) suggested that new leaves are more easily distinguished from old leaves by scanning from above, as *Alouatta* does while tail hanging. It is thus possible that ateline locomotion is more closely connected with an ancestral leaf-eating tendency, as their quantum shift in size may imply (Rosenberger and Strier, 1989). The unusual, cautious, deliberate quadrupedalism of *Alouatta* has also been interpreted as an energy-saving tactic, whereas the energetically expensive brachiation of *Ateles* and *Brachyteles* has been related to an ancestral diet of rich, ripe fruit (Rosenberger and Strier, 1989). *Brachyteles* later became more folivorous in the isolated, drier forests of eastern Brazil.

Although the relationship between diet and locomotion among the unevenly studied pitheciines remains obscure, there appears to be coherence, and in ways a conservatism, in the organization of positional behavior and foraging strategies among the other major groups (Fig. 1). Conservatism is evident among cebids, for example, in which the evolution of a semiprehensile tail in *Cebus* has not deflected capuchins from its ancestral feeding strategy and towards a more *Alouatta-* or *Ateles*-like pattern, as one might suppose. Rather, tail prehension has augmented the capuchin's predaceous heritage. More directly, the radiation of callitrichines appears to be fundamentally predicated on the strong connection between a positional/locomotor-foraging method and access to food. In focussing on leaves as a form of protein, the climbing atelines may have become more efficient in coping with the general difficulties of a large primate negotiating the canopy.

Seasonality

Seasonality can influence dietary choices in a number of ways, and it is a well-established dictum among ecologists that feeding preferences are a seasonal phenomenon even in tropical rain forests (for cebids, Terborgh, 1983; Janson and Boinski, 1992; for atelines, Strier, 1992; for *Aotus* and *Callicebus*, Wright, 1989; see also Hladik, 1988). A central question is whether niche segregation has emerged in some species or monophyletic groups through morphological adaptations specific to seasonal shifts in diet, changes that ensure reduced competition for alternative resources when cheap foods are less abundant or accessible. Several examples are given.

Terborgh (1983) described how two congeneric omnivores, *Cebus apella* and *C. albifrons*, sympatric at Manu, southern Peru, showed an exaggerated partitioning of foods during the drier seasons when ripe fruits are more scarce. After nearly seven consecutive months when palm products are little used (1–4% of total feeding time), *C. apella* began to concentrate on *Astrocaryum* palms, taking immature inflorescences and mature nuts as well as the pith from its hard palm fronds. When dried, some species of *Astrocaryum* nuts are very hard, requiring 110–170 kg force to break (Kiltie, 1982). Nevertheless, *C. apella* foraged for them explicitly and ". . . routinely crushed intact nuts with a single bite" (Terborgh, 1983:83–84). *C. albifrons*, on the other hand, continued to collect other fruits while adding *Astrocaryum* nuts to its menu, albeit with a different approach. It foraged on the ground for the fallen nuts, which were weakened structurally by the larvae of bruchid beetles, which had already partially eaten them out. *C. albifrons* then cracked open the nuts by biting or by bashing them manually. Among nonsympatric capuchins, a similar, marked seasonal flux in the intake of ripe fruit (70% in wet season, 10% in dry season: Robinson, 1986) occurs in *C. nigrivittatus* (or, *olivaceus*).

This interspecific and intraspecific contrast in behavior is consistent with Kinzey's (1974) study of tooth size and cranial morphology, which led to his prediction that *C. apella* would be found to feed on harder materials than members of the non-*apella* group, such as *C. albifrons*. Since it is believed that *C. apella* is craniodentally more derived that *C. albifrons*, it seems likely that selection for the capacity to harvest and reduce hard palm products—the critical functions—is seasonally occurring rather than ever-present. However, this notion does not exclude the possibility that similar selective forces concerning other food items, such as the process of extracting burrowing insects, are not prevalent at other times of the year, or annually constant. The dietary flux in *Cebus* resembles the seasonally shifting focus on vertebrate prey among *Saimiri* (Janson and Boinski, 1992). Squirrel monkeys, exercising the critical-function potential of their shearing/puncture-crushing postcanines, shift from a soft-fruit fig diet to an exclusively insect diet during parts of the dry season at Manu (Terborgh, 1983). Both cases are consistent with the view that cebines are opportunistic, but canalized (Rosenberger, 1980), faunivores.

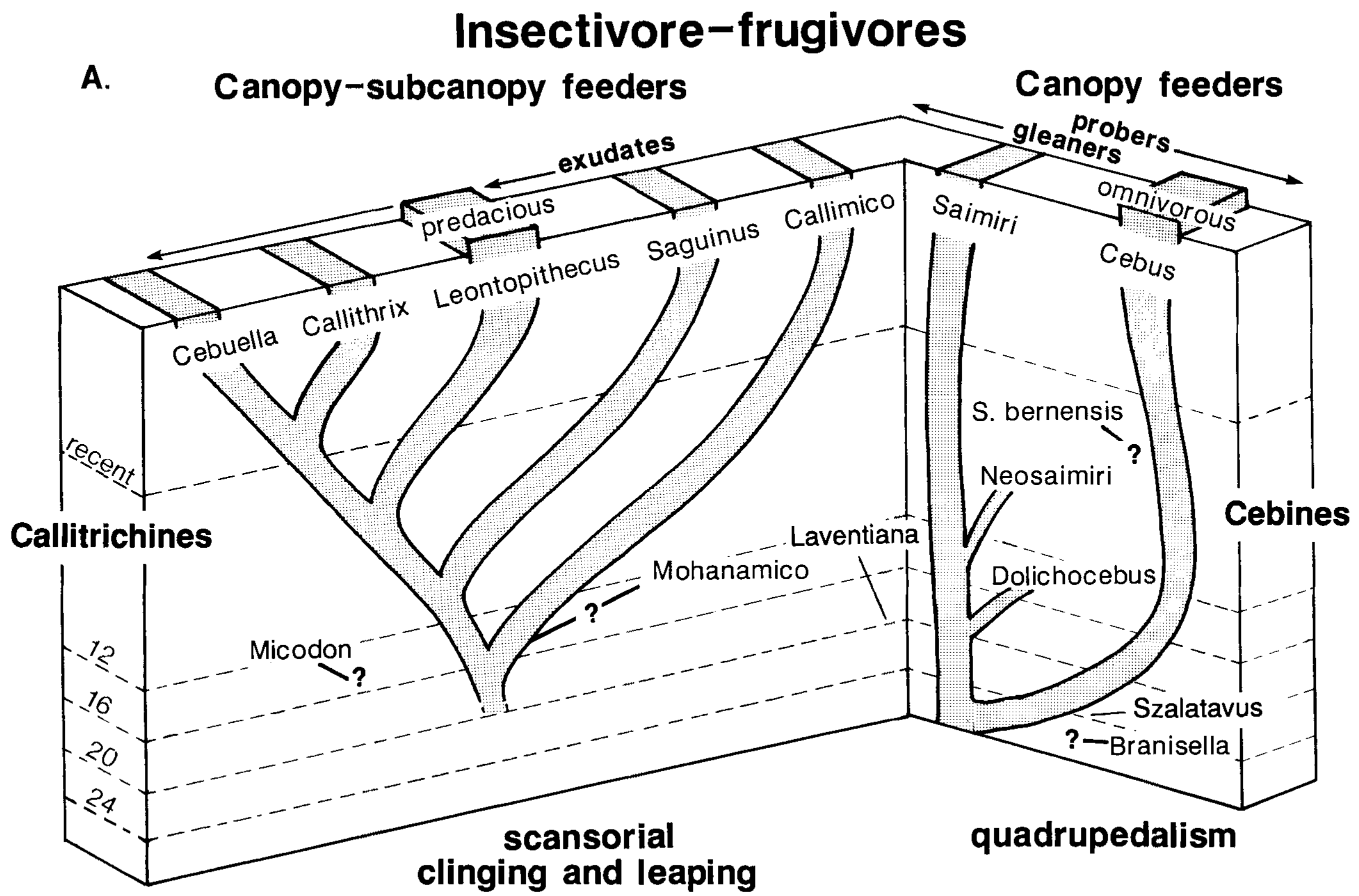
Another intriguing way in which seasonal changes in fruit phenology or supply are exploited to segregated niches was described for two sympatric frugivores in Surinam, the soft-fruit feeder *Ateles paniscus* and the sclerocarpic harvester and seed-eating *Chiropotes satanas* (Kinzey and Norconk, 1990). Although they fed on the same species, *Chiropotes* consistently chose fruits when they were less ripe and tougher, while *Ateles* waited until ripening had softened them. As was discussed above, the essence of the morphological adaptations to feeding among pitheciins relates to hard-fruit frugivory and especially sclerocarpic harvesting. Thus it is quite possible that the successful shift among saki-uakaris from a more conventional type of frugivory began as a temporal advantage in competition for the same classes of fruits exploited by other monkeys.

Fossils

There has been an explosion of information regarding the fossil record of platyrrhines, including the description of many new forms (Fleagle and Rosenberger, 1990; see Rosenberger and Hartwig, in press, for a complete review of platyrrhine fossils). Many taxa are still known from fragmentary dentitions, and only a few skulls are available, but several collections provide reliable or even diagnostic information pertaining to diet. These will be reviewed briefly in this section, mainly to demonstrate that the historical evidence also shows a close correspondance between phylogeny and adaptation: Closely related taxa at several levels of the hierarchy present similar combinations of adaptations. Figure 9 places the platyrrhine fossils into a phylogenetic and adaptive context, but it should be emphasized that the morphological basis for dietary inference is scant for many taxa.

The early Miocene forms from Argentina, *Dolichocebus* and *Tremacebus*, provide basically cranial evidence. *Tremacebus*, a relative of *Aotus*, is known only from an edentulous skull (see, e.g., Fleagle and Rosenberger, 1983). However, its orbits are enlarged, suggesting that an adaptive shift to nocturnal and/or crepuscular activity (see Wright, 1989) was already underway. *Dolichocebus* is also best known from a toothless skull (see, e.g., Rosenberger, 1979), but a series of isolated cheek teeth have recently been discovered (Fleagle and Kay, 1989). They lack both the bunodonty of *Cebus* and the extreme cristodonty and occlusal pattern of *Saimiri* and are thus of a basic frugivorous-insectivorous design. However, the rounded braincase of *Dolichocebus* recalls that of *Saimiri*, with an expansive occipital region and large frontal and lightly built superstructures (tori, crests). Cebines generally have a relatively large brain (see, e.g., Martin, 1990) in comparison with other platyrrhines, with particularly well-developed visual structures (Frahm et al., 1984; Stephan et al., 1984). They also contrast with callitrichines, which, according to Stephan and colleagues (1984), have a relatively unspecialized visual system. Thus the cebine pattern may relate to their highly visual foraging technique, which may involve an extractive search image and good manipulative skills, shown by *Saimiri* and especially *Cebus*. Perhaps it also relates to the morphological plasticity that Janson and Boinski (1992) attribute to both genera. While still little known, the braincase of *Dolichocebus* is thus also suggestive of a cebine-like foraging strategy.

Collections of *Homunculus*, *Soriacebus*, and *Carlocebus* from the early Miocene of Argentina are growing rapidly (see Fleagle, 1990), but the material of *Homunculus* and *Carlocebus* is either too fragmentary or too new to be included here. The dental and mandibular morphology of *Soriacebus*, which resembles that of pitheciins in many ways, has been discussed in detail (Fleagle et al., 1986; Kay, 1990; Rosenberger et al., 1990). In brief, Rosenberger et al. (1990) argued that the detailed similarities of the incisors, the massive size of the canine base, the complimentary configuration of P_2, and the greatly enlarged mandible connote a sclerocarpic harvesting adaptation like that of saki-uakaris. The absence of pitheciin-like molars and posterior premolars, however, suggests that *Soriacebus* may not have been a committed seed predator, although it did harvest hard-shelled fruits. By the middle Miocene, all of the elements of the pitheciin dental pattern are evident in *Cebupith-*


Insectivore–frugivores
A.
Canopy–subcanopy feeders
Canopy feeders
exudates
predacious
probers
gleaners
omnivorous
Cebuella
Callithrix
Leontopithecus
Saguinus
Callimico
Saimiri
Cebus
S. bernensis
?
Neosaimiri
Dolichocebus
Laventiana
Mohanamico
?
Micodon
?
Szalatavus
?
Branisella
recent
12
16
20
24
Callitrichines
Cebines
scansorial
clinging and leaping
quadrupedalism

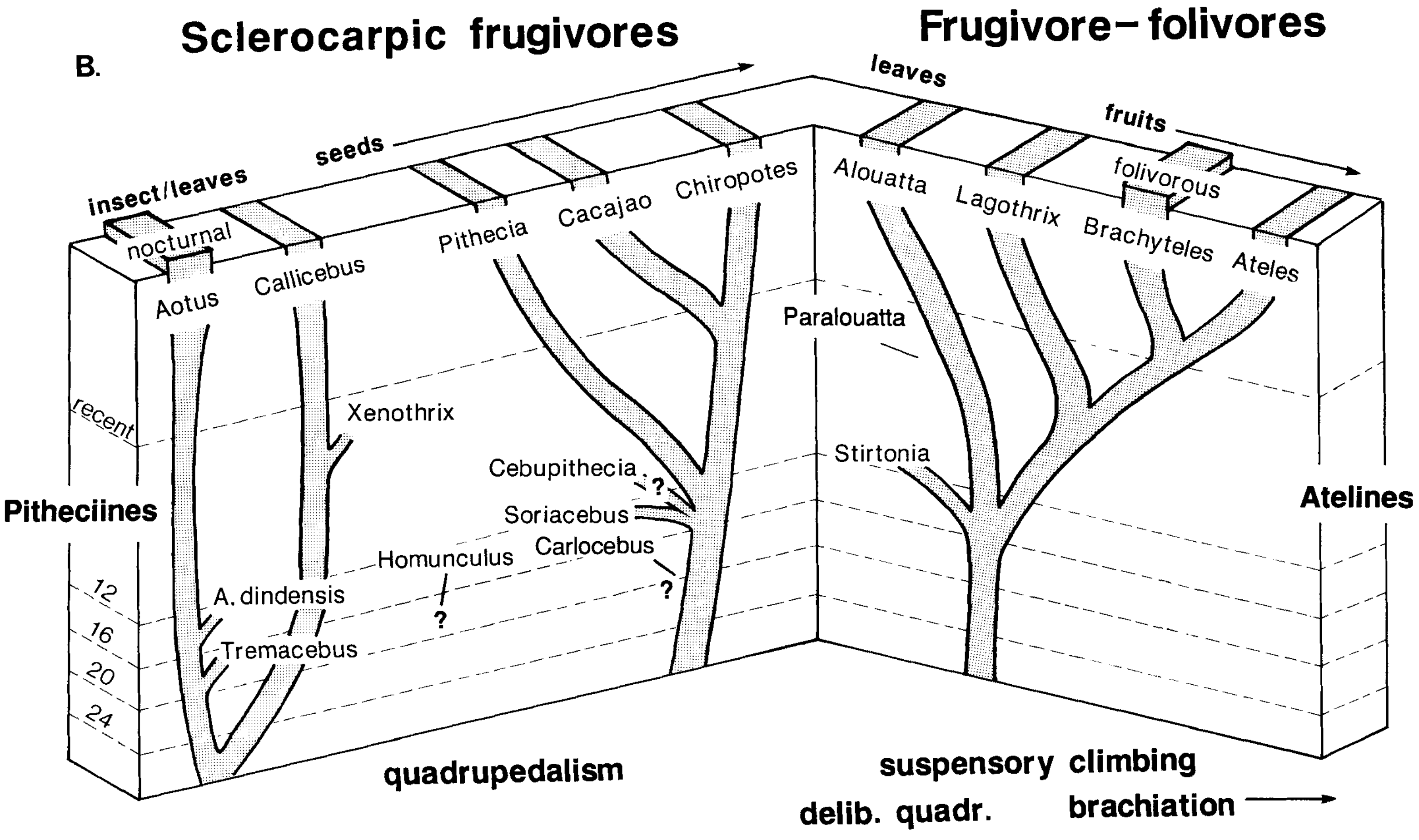


Fig. 9. A. Adaptive radiation of living and fossil cebids. B. Adaptive radiation of living and fossil atelids. Time scale: Numbers at left refer to millions of years.

ecia, which is well represented by dental and postcranial remains at La Venta, Colombia.

Three other species from La Venta, all known by diagnostic dental parts and/or relatively complete mandibular dentitions, also provide good dietary evidence. They are extraordinarily similar to modern taxa in morphology, and two have been classified as species of extant genera. *Aotus dindensis* (Setoguchi and Rosenberger, 1987; see Kay, 1990, for a different view), represented by a nearly complete lower dentition and mandible and a facial fragment preserving part of the orbital floor and the inferior aspect of the postorbital plate, had enlarged orbits, but quantitative comparisons with *Tremacebus* and living *Aotus* are not yet possible. Its incisors display the characteristic, transversely expanded apical blade and crown shape of *Aotus*; cheek teeth and canines are also quite similar, although perhaps less crested. Thus the diet and activity pattern of *A. dindensis* were very much like that of modern owl monkeys. Similarly, *Saimiri* (=*Neosaimiri*) *fieldsi*, which was recently synonymized with modern squirrel monkeys (Rosenberger et al., 1991a), is hardly distinguishable from the living species in its well-preserved mandibular dentition, implying a similar faunivorous diet. A third taxon, *Stirtonia*, is considered barely distinct generically from, and matches the basic dental pattern of, *Alouatta* (see, e.g., Szalay and Delson, 1979; Delson and Rosenberger, 1984; Setoguchi, 1986; Kay et al., 1987). This form is the ecological equivalent of howling monkeys in the La Venta fauna.

Other primates from La Venta, *Mohanamico*, *Laventiana*, and *Micodon*, offer less definite dietary information. The latter is poorly represented. The first resembles *Callimico* in occlusal structure and tooth proportions (Rosenberger et al., 1900; see also Kay, 1990) but differs in mandibular morphology. Generally, its relatively well-crested cheek teeth suggest a commitment to insectivory, especially in having incipiently elevated premolar crowns, which would be beneificial to puncture-processing. The I_2 is relatively tall and narrow but is gracile, unlike the low-crowned mandibular incisors of *Callimico* (Fig. 3). Also, little can be said about the early branisellines, *Branisella* and *Szalatavus*, or about *Paralouatta*, a recently discovered howler-like form from Cuba known only from a skull containing well-worn teeth (Rivero and Arrendondo, 1991). However, the *Paralouatta* skull is more primitive than *Alouatta* in ways suggestive of lifestyle, possibly reflecting a less specialized vocal mechanism and a lesser development of howler-like folivory and its associated positional behavior syndrome.

DISCUSSION

The initial, operational classification of primate diets into three broad categories—frugivory, folivory and insectivory—has become an inadequate guide to the behavioral and morphological adaptations of the platyrrhines. The problem is not unique to the primates. In surveying the feeding habits of mammals generally, Eisenberg (1981) noted the difficulty of categorizing a species' diet according to the quantity or proportions that it consumes over the course of a year. The crucial issue here, however, is the perspective that such classifications cast regarding functional morphology and natural selection.

The logic of a modal diet was applied influentially by Kay (1975), who proposed that an allocation to any of the three major categories was justifiable if a species consumed at least 45% of one item. His rationale was that "large amounts of food must be habitually ingested before its *physical* properties have a selective influence on molar design (p. 203)." However, dietary bulk, or the higher "feeding frequencies" associated with certain foods, may select merely for contingent adaptations rather than for major design features. For example, the useful life of incisors working against wood may be increased by a taller crown in *Callithrix* and *Cebuella*, but the crown's shape is conditioned by mechanical consequences related to bark prizing. Food bulk may also select for special (chemical) digestive capacities in *Alouatta*, but it has still to be shown that the large molars of folivores correlate with mass processing rather than some other phenomenon, either intrinsic or extrinsic to the animal. The durability of crown structure may be enhanced by thick enamel in *Cebus*, but the highly abrasive woody nuts and bark that they might search for and crack are but a small portion of their feed intake. An alternative to the frequency-dependent view is that selection will favor a morphology that enhances the critical functions required to harvest or masticate foods even when they are, in fact, a smaller fraction of a species' annual diet (Rosenberger and Kinzey, 1976), such as items that are nutritionally crucial during seasonal shortages.

Assuming that insects or leaves are the principal protein sources for primates, Kay (1973, 1975) also argued that there is a natural size threshold, ~700 gm, dividing insectivores from folivores, for it would be too costly for larger species to forage and capture a sufficiently large number of insects to fulfill their requirements. This notion has been applied broadly to the fossil record (see, e.g., Fleagle, 1988). However, data on platyrrhine feeding habits, particularly the long-term studies of pitheciins and *Cebus* (Fig. 8), indicate that mid-sized atelids and large cebids do not cross over to a folivorous habit. Instead, some elaborate their predaceous feeding pattern, and others may use seeds, potentially richer and more accessible chemically than leaves (Waterman and McKey, 1989), as a major source of protein, at least occasionally. For example, *Cebus*, weighing three to five times more than the threshold level, eats few leaves but may take in pith as protein (Janson and Boinski, 1992). Capuchins rely heavily on insects and other prey, and *C. apella* can narrow its feeding regime drastically to feed on hard palm nuts when more succulent fruits are unavailable (see, e.g., Terborgh, 1983; Janson and Boinski, 1992; see also below), presumably to obtain protein. Critical functions and morphological adaptations suitable to seed eating in pitheciins, and in *Cebus* for predacious foraging, insect and pith extraction, and hard-fruit mastication, are evident. This makes them excellent analogues for interpreting fossil primates of this body-size class. These points reveal that, without a detailed functional analysis of the harvesting and masticatory features together, body size may be a misleading indicator of diet among extinct species. And such examples are not confined to platyrrhines. One need only recall the larvivorous behaviors (MacPhee and Raholimavo, 1988) of *Daubentonia:* Neither incisors, nor cheek teeth, nor body size would make any sense if analyzed in isolation.

Morphological studies of platyrrhines also reveal that the functional morphology of primate dentitions is still poorly understood. Mechanically important features still must be defined and measured, and a method for comparing taxa of dissimilar morphologies must be developed further. Premolars have been studied hardly at all. Kay's (1975) pioneering application of a novel system of molar measurements appears to have had only limited sensitivity to the marked dietary differences of the predaceous *Saimiri* and the soft-fruit-eating *Ateles*, among others (Fig. 4). The basic premise of such work—that homologous structures have homologous functions—is tenuous. Teaford (1985) showed that the microwear signature on homologous facets differed among three species of *Cebus*, indicating that the mechanical effects of their occlusion differed. Additionally, Rosenberger and Kinzey (1976) showed that there were fundamentally different shapes of the ectoloph in various platyrrhines, which changed ontogenetically in some species but not in others, implying different functional consequences. Certainly the sharply crested ectoloph of a howler cannot function identically to the dull buccal ridge of a saki. For the structurally simpler incisors, linear measures purporting to represent size (Eaglen, 1984), even when appropriately scaled against body mass, have dubious functional value for many taxa.

Seasonality is perhaps the most underrated variable in determining the selective influence of food items on dietary adaptation. Recent field studies have shown marked fluctuations in feeding patterns (e.g., Janson and Boinski, 1992), which may also involve shifts in the basic physical and chemical properties, and nutritional qualities, of the foods eaten. At Manu, Peru, *Saguinus fuscicollis* spends three times as much time feeding on nectar during the two dry season months, when their preferred fruits are depleted (Terborgh and Stern, 1987). During those months, only 10% of the full quantity of fruits produced in the forest are ripe. The potentially severe physiological consequences of the dry season are shown by the fact that some *Saguinus* lose as much as 15% of their body weight when they consume nectar. It would indeed be remarkable if there were not an extensive array of morphological/behavioral adaptations among these tamarins and the forest's other primate frugivores that mitigated this flux—hence the alternative diets adopted during periods of fruit scarcity by forms like *Saimiri*, *Cebus albifrons*, and *C. apella* (Terborgh, 1983).

Folivory, as in *Alouatta* and to a lesser extent *Brachyteles*, also conforms to the seasonal rhythms of plant phenology. Folivores prefer the younger, more tender, and often more nutritious flush than older leaves. The periodic scarcity of high-quality items (young leaves, fruit, flowers) has important demographic consequences in *Alouatta* and may contribute significantly to mortality (Milton, 1982). However, leaves present essentially the same *relative* makeup of physical properties throughout the year. Therefore, behavioral and morphological compromises are less likely to occur among obligate folivores once they have solved such crucial problems as mastication and detoxification. This makes possible the relatively comprehensive biological commitment to energy conservation in forms such as *Alouatta*. In effect, the yearround reliance on leaves becomes another way of solving the global problem of seasonal resource fluctuation.

The fossil record has revealed clues that tactical differences in food selections may reflect evolutionary adaptations on a larger taxonomic scale, suggesting a hypothesis for the evolution of the pitheciin adaptive radiation based on seasonality. The living pitheciins are adapted as sclerocarpic foragers (Kinzey and Norconk, 1990; Kinzey, 1992). *Soriacebus* resembled modern pitheciins in having tall, narrow, and strongly rooted lower incisors but lacked the everted canines and radically modified cheek teeth of extant saki-uakaris. This mosaic suggests that the initiation of the pitheciin feeding adaptation involved a hard-fruit-harvesting syndrome but not an obligatory seed-eating diet. In the early stages of their differentiation, pitheciins may have gained a competitive edge over other platyrrhine frugivores simply by being able to get at the same foods earlier in the phenology cycle. The (nearly?) fullblown seed-eating pattern, already present in the middle Miocene *Cebupithecia* from Colombia, may have evolved locally in Amazonia, in regions where more typical frugivores (and their fruits) are rare and modern pitheciins are now confined (see Ayres, 1989).

If one reduces the feeding spectrum to a range of food types characterized by a limited number of classes of physical properties (Table 3), it becomes evident that optimum morphological design is not the sole driving force behind platyrrhine dental diversity. Rather, it is the seemingly chaotic interplay of phylogeny, function, and adaptive compromise in different lineages that promote the *different* ways that platyrrhines manage to feed in the same forests. At the same time, closely related forms continue to maintain an adaptive continuity despite ecological opportunities that would permit cross over to another adaptive zone.

Parallelisms within dietary categories provide important evidence pertaining to phylogeny and can reveal diet-specific adaptations. Some of this challenges certain prevailing concepts. For example, the two most folivorous platyrrhines, *Alouatta* and *Brachyteles* (Strier, 1992), share striking convergent similarities (no distinction is made here between parallelism and convergence) in their incisor teeth, but the resemblance in their cheek teeth is less marked (see Rosenberger and Strier, 1989, for details). *Alouatta* is the earliest independent branch of the monophyletic atelines, and *Brachyteles* is most closely related to *Ateles*. (*Lagothrix* is the sister taxon of the *Ateles*-*Brachyteles* clade.) If the incisors of *Alouatta* and *Brachyteles* are indeed convergently reduced, they provide a powerful demonstration that these teeth are highly sensitive to selective forces associated with folivory, more sensitive perhaps than the molars. What these forces may be, however, is difficult to determine, since harvesting leaves seems to present few environmental factors selecting for critical functions. A tactile function is a possibility.

Convergences in the shapes of the cheek teeth involve emphasis on shearing crests. In *Alouatta*, the crests are concentrated on the buccal side of the crown in a classic W-shaped ectoloph, as with many other folivores. In *Brachyteles*, the ectoloph is reduced (as with *Ateles*), and the crests are arranged diagonally across the crown, along the crests of the metaconid, the trigonid's distal wall, and the entoconid and entocristid. *Brachyteles* postcanines are also absolutely and relatively smaller than those of *Alouatta* (Fig. 6), an animal of smaller body mass. These patterns are consistent with the idea that their postcanine shearing capacity evolved in parallel (Rosenberger and Strier, 1989). It also suggests a functional decoupling of size and shape. Therefore, do some primate folivores have relatively very large teeth because they must process mass quantities to extract sufficient nutriment (see, e.g., Kay, 1975) or are their molars large for geometric or mechanical reasons, in order to maximize the linear length and arrangement of occluding crests given the design contraints of the chewing cycle and the ancestral platyrrhine crown pattern? Real measures of leaf intake per body weight, which would be useful for test these hypotheses by comparison, and accurate "true" measurements of molar surface area—as opposed to crude estimates (mesiodistal length × buccolingual breadth = area)—are obtainable but are not yet available. It thus remains possible that molar tooth size in folivores is determined not by food mass but by geometric requirements.

Cebus and the pitheciins present a profound morphological contrast in hard-fruit-eating or seed-eating patterns, both in harvesting and in masticatory anatomy. As was discussed above, there are few specific resemblances in their dentitions, although both seem to access and/or reduce some of the toughest items eaten by neotropical primates. With tooth proportions much like those of *Saimiri*, with reduced posterior molars and broad premolars, and also with wider and taller incisors, the functional strategy evolved by *Cebus* seems to be centered on protecting the shape and longevity of the crowns with thick enamel. The jaws are also buttressed by thickening. In pitheciins, there is no evidence of postcanine enamel thickening, but the cheek teeth are crenulate, the premolars are rectangular and tend to be molariform, the incisors are extremely narrow and tall, and the jaws are deep but are not thickened transversely. Thus different anatomical routes and environmental factors are implicated as a basis for similar mechanical potentials and biological roles. A frugivorous-insectivorous heritage conditioned the morphology of *Cebus*, whereas the sclerocarpic adaptations of the incisor teeth probably channeled mandibular evolution and the shift to seed eating in pitheciines.

The platyrrhines offer a powerful affirmation that phylogeny and adaptation go together (Fig. 9). Despite (silent) claims that parallelism is rampant among platyrrhines, it is evident that *functional-adaptive systems* do not evolve in parallel, only isolated traits within those systems, and these are indeed discernible in most cases. Even the many body-size shifts of platyrrhines can be traced genealogically once their morphological correlates are researched and placed into an ecological context. The meager fossil record of New World monkeys suggests that some of the major adaptive outlines of the modern fauna have been in place since the early Miocene. As the rate of fossil discovery increases along with our knowledge of functional morphology, it will be interesting to see how tightly constrained the platyrrhine radiation is by the adaptive heritage of its lineages.

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