

Nuciruptor rubricae, a New Pitheciin Seed Predator From the Miocene of Colombia

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ABSTRACT A new genus and species of platyrrhine primate, *Nuciruptor rubricae*, are added to the increasingly diverse primate fauna from the middle Miocene of La Venta, Colombia. This species displays a number of dental and gnathic features indicating that it is related to living and extinct Pitheciinae (extant *Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*, and the Colombian middle Miocene *Cebupithecia sarmientoi*). *Nuciruptor* is markedly more derived than *Callicebus* but possesses a less derived mandibular form and incisor-canine complex than extant and extinct pitheciins (*Cebupithecia*, *Pithecia*, *Chiropotes*, and *Cacajao*), suggesting that it is a primitive member of the tribe Pitheciini within the larger monophyletic Pitheciinae. *Nuciruptor* has procumbent and moderately elongate lower incisors and low-crowned molars, suggesting that it was a seed predator, as are living pitheciins. Its estimated body size of approximately 2.0 kg places it within the size range of extant pitheciins. The dental and gnathic morphology of *Nuciruptor* clarifies several aspects of dental character evolution in Pitheciinae and makes it less likely that the enigmatic *Mohanamico hershkovitzi* (m. Miocene, Colombia) is a pitheciin. *Am. J. Phys. Anthropol.* 102:407-427, 1997. © 1997 Wiley-Liss, Inc.

The monophyly of the modern Pitheciinae, *Pithecia* (the saki), *Chiropotes* (the bearded saki), and *Cacajao* (the uakari), as proposed by Mivart and many times since, seems well established (reviewed in Kay, 1990). Rosenberger suggested a special relationship of *Callicebus* (the titi) and *Aotus* (the owl monkey) to the pitheciines and has advocated their inclusion in the Pitheciinae (Rosenberger, 1979, 1981). Rosenberger's allocation of *Callicebus* to the Pitheciinae is strongly supported by recent analyses of DNA nucleotide sequences (Meldrum, 1995; Schneider et al., 1993, 1995), but molecular studies indicate that *Aotus* is not related to pitheciines, but rather is placed with the callitrichine clade. The classification of Schneider et al. (1993) reflects these cladogenetic events and is followed here. The sub-

family Pitheciinae represents a clade including the monophyletic tribe Pitheciini with the extant genera *Pithecia*, *Chiropotes* and *Cacajao* and the tribe Callicebini Pocock, 1925, *Callicebus* alone. (Should *Homunculus* [early Miocene, Argentina] prove to be the sister taxon to *Callicebus*, as Rosenberger et al. [1990] contends, the correct

Abbreviations: IGM, Instituto Nacional de Investigaciones Geológicas Mineras; UCMP, University of California Museum of Paleontology.

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name for the Callicebini would be Homunculini Ameghino, 1894.)

To avoid confusion, we call attention here to the use of formal and informal taxonomic terms in the text. The taxon Pitheciinae as we use it refers to a "closed descent community" or stem-based clade (Fig. 1; Ax, 1985; Williams and Kay, 1995). Pitheciinae is the clade of all species, living or extinct, that are more closely related to living pitheciines than to the next most closely related taxon (the clade consisting of *Alouatta*, *Ateles*, *Lagothrix* and *Brachyteles*; Rosenberger, 1979, 1981; Schneider, et al., 1993). The informal term "pitheciine" is used for members of the subfamily Pitheciinae, including the extant *Callicebus*, *Pithecia*, *Cacajao*, and *Chiropotes*. The informal terms "callicebini" and "pitheciini" are used for the tribes of the subfamily Pitheciinae. They should include *Callicebus* in the first case, and *Pithecia*, *Cacajao* and *Chiropotes* (as well as several extinct taxa discussed below) in the second case.

In this paper, we describe a new species of fossil pitheciin from the Miocene of Colombia, review its adaptations, and place it into the context of pitheciine phylogeny and character evolution. Special attention is paid to several extinct taxa that are often considered pitheciines. Like the new taxon described here, *Cebupithecia sarmientoi* is a species that comes from middle Miocene rocks of the Honda Group cropping out in the Tatacoa Desert north of the village of Villavieja, in the Magdalena valley of central Colombia (Kay et al., 1996). This region is also called La Venta and its mammalian fauna forms the basis for the Laventan Stage/Age (Madden et al., 1996). The holotype (UCMP 38762) was found in the Monkey Beds at the base of the Villavieja Formation (Guerrero, 1996; Stirton, 1951; Stirton and Savage, 1951). Other specimens provisionally referred to *Cebupithecia* have been recovered from the Monkey Beds nearby in the El Dinde area (Setoguchi et al., 1987) and elsewhere in the Tatacoa Desert from older deposits lying below the Chunchullo Sandstone, in the La Victoria Formation of the Honda Group (Meldrum et al., 1990; Meldrum and Kay, 1996).

Another middle Miocene species possibly relevant for understanding pitheciine evolu-

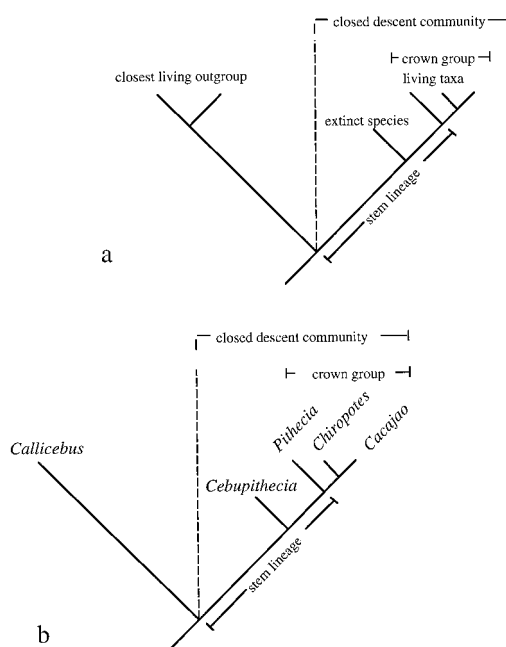


Fig. 1. Phylogeny of Pitheciinae. **a:** Phylogenetic tree illustrating the terms crown group, closed descent community (= stem-based clade) and stem lineage (after Williams and Kay, 1995). The crown group contains only living taxa and their last common ancestor. A stem-based definition (used here) includes all species, living or extinct that are more closely related to the living members of that group than to any other living taxon. **b:** Cladogram of Pitheciinae recognizing two stem-based tribes Callicebini and Pitheciini. The stem-based tribe Pitheciini includes *Cebupithecia*.

tion is *Mohanamico hershkovitzi*. This species also comes from the Tatacoa Desert. The type mandible (IGM 181500) comes from the Monkey Beds near El Dinde (Luchterhand et al., 1986). A second specimen of a primate (IGM-KU 8601) of similar size and morphology to *Mohanamico* and from the same stratigraphic level was allocated to a new species of *Aotus*, *A. dindensis* (Setoguchi and Rosenberger, 1987). Kay argues that IGM KU-8601 should be allocated to *Mohanamico*, whereas Rosenberger and colleagues recognize the distinctness of the two specimens as separate genera and even assign the two specimens to two different families (Kay, 1990; Rosenberger et al., 1990).

A third taxon, *Soriacebus*, with two species, *S. ameghinorum* and *S. adrianae*, comes from a suite of Patagonian localities collectively referred to as the Pinturas fauna

(Fleagle, 1990). The material is of early Miocene age, older than the Colombian material just described, and thought to pertain to the Santacrucian Land Mammal Age (McFadden, 1990). Considerable material of *Soriacebus* is known including mandibles, maxillae, and some postcranial bones.

We discuss the merits of allocation of *Cebupithecia*, *Mohamamico* and *Soriacebus* to the Pitheciinae. We demonstrate that *Cebupithecia* (middle Miocene, Colombia) is certainly a pitheciin, but that *Mohanamico* (middle Miocene, Colombia) and *Soriacebus* (early Miocene, Argentina) are less likely pitheciin candidates.

SYSTEMATICS

Order Primates

Subfamily Pitheciinae Mivart, 1865

Tribe Pitheciini Gray, 1849

Nuciruptor, gen. nov.

Type species. *Nuciruptor rubricae*, sp. nov.

Included species. The type species only.

Distribution. As for the type and only species.

Diagnosis. As for the type and only species.

Etymology. Derived from the Latin *nuci*, combining form denoting "nut" and *ruptor* denoting "break," suggesting the apparent adaptation for seed predation or nut-breaking.

Nuciruptor rubricae, species nov. (Figs. 2–8)

Type specimen. IGM 251074 (Duke University field no. 90-23), a mandible, preserving the fused symphysis, right corpus and portions of the ascending ramus, left I₁, and right C₁–M₂. Dental and gnathic dimensions are provided in Table 1.

Horizon and locality. The type is from Duke locality 32, in the El Cardón Red Beds, Cerro Colorado Member, Villavieja Formation, Honda Group, Colombia (following geological terms of Guerrero, 1996). The fossiliferous horizon lies immediately below the

TABLE 1. Selected dental metrics of the type specimen of *Nuciruptor rubricae*, gen. et sp. nov. (IGM 251074)

Crown	Length (md)	Width (bl)	Height ¹
I ₁	1.85	3.19	5.92
C ₁	3.18	4.60	6.46
P ₂	2.66	3.48	3.82
P ₃	2.93	3.49	3.04
P ₄	3.10	3.43	2.78
M ₁	3.94	3.93	2.60
M ₂	4.09	3.80	2.50

¹ Measured from the buccal cervical margin. md + mesiodistal; bl, buccolingual. All measurements in mm.

San Francisco Sandstone, dated to 12.8 (± 0.2) Mya by the Argon⁴⁰/Argon³⁹ method (Flynn et al., 1996; Guerrero, 1996). The type specimen of *Nuciruptor* is therefore approximately 0.5 myr younger than the holotype of *Cebupithecia*, which comes from the Monkey Beds of the Villavieja Formation. Locality 32 also has produced a mandible and associated talus, many dental specimens, and an isolated tibia of *Neosaimiri fieldsi* (= *Laventiana annectens*) as well as an isolated talus referred to *Aotus dindensis* (Gebo et al., 1990; Meldrum and Kay, 1996; Rosenberger et al., 1991; Takai, 1994).

Diagnosis. A *Pithecia*-sized platyrrhine sharing with the living Pitheciini styliform, moderately high-crowned mandibular incisors; molars having trigonids and talonids of similar height, shallow hypoflexids and reduced posterior trigonid walls. Distinct from, and more primitive than, living Pitheciini in lacking an enlarged P₂; lacking molarization of P₃₋₄; in having weak hypoconids on P₃₋₄ (versus strong, large hypoconids), and in lacking premolar and molar enamel crenulation. In these features, *Nuciruptor* compares favorably with *Callicebus*. Distinct from living pitheciins and *Cebupithecia* in having no incisor-canine diastema, in possessing a canine with a rounded lingual crest and a well-developed heel, and in having molars lacking buccal cingulum, and mandible with a more acute symphyseal angle and rudimentary genial fossa. *Nuciruptor* is also distinguished from *Cebupithecia* by having a much larger alveolus for M₃, implying reduction of the third mandibular molar in *Cebupithecia*, but not in *Nuciruptor*.

Nuciruptor differs from *Callicebus* by having higher-crowned incisors, a more project-

ing canine, and less trenchant premolar and molar cresting. *Nuciruptor* differs from *Mohanamico* in having a posteriorly deepening mandible, more compressed and higher-crowned incisors, and more bunodont molars. *Nuciruptor* is distinguished from *Soriacebus* in having a proportionately much smaller I₁, canine, and P₂, compared with molar size.

Etymology. From the Latin *rubrica*, meaning "red earth," with reference to the red sediments of the El Cardón Red Beds.

DESCRIPTION

Comparisons and contrasts are emphasized between *Nuciruptor* and the roughly contemporary *Cebupithecia*, establishing the distinctness of the two, and are generally restricted to the extant pitheciins in this section. Further comparisons with *Callicebus* and additional selected taxa (*Soriacebus*, *Mohanamico*) are relegated to subsequent sections.

Mandible

(Figs. 2–4)

The specimen preserves the symphysis, right mandibular corpus and a portion of the ascending ramus. The corpus is less robust than that of *Cebupithecia*. It is both longer, measuring 23% longer from I₁ to M₃, and shallower, approximately 13.0 mm at the level of P₂ compared to 16.6 mm in *Cebupithecia*. The 13.0 mm value for the *Nuciruptor* reconstruction should be taken as a minimum. Distally, the corpus deepens moderately, and the inferior border has a slight sinusoidal curve. The symphysis is preserved, as well as most of the alveolus for the left central incisor. The external profile of the symphysis is more inclined than in *Cebupithecia*, forming an angle with the estimated basal mandibular plane of approximately 35° compared with an estimated value of 50° for *Cebupithecia*. Both of these estimated values fall within the extreme upper and lower limits for a large sample of *Pithecia* species (range 30°–57°, n = 205, Hershkovitz, 1987). The genial fossa and digastric grooves are rudimentary, in contrast to *Cebupithecia* where they are well developed. The ascending ramus arises distal to the alveolus for M₃ in contrast to *Cebupithecia* where the M₃ alveolus is nearly

TABLE 2. Contrasts in mandibular form distinguishing *Nuciruptor rubricae* and *Cebupithecia sarmientoi*

Trait	<i>Nuciruptor rubricae</i>	<i>Cebupithecia sarmientoi</i>
Corpus robusticity	slight	moderate
Depth at P ₂	13.0 mm	16.6 mm
Toothrow length	28.6 mm	26.3 mm
Symphyseal angle	35°	50°
Genial fossa	rudimentary	well-developed
Incisor row	more transverse	I ₂ more set back from I ₁
Incisor canine diastema	none	weak
Ascending ramus	distal to M ₃	lateral to M ₃

hidden by the ascending ramus. Table 2 summarizes the traits discussed above.

Incisors

(Figs. 2, 4, 5)

A pattern of derived features of the anterior dentition distinguish the living pitheciins from other extant platyrrhines. The lower incisors are procumbent, styliform and high crowned (elongate), with indistinct lingual cingula and a reduced or absent lingual heel. The lower incisor roots and crowns are compressed mesiodistally. In *Cacajao* and *Chiropotes*, the central incisors are much smaller than the lateral incisors, whereas in *Pithecia*, the disparity in the size of the central and lateral incisors is less. In *Callicebus*, the incisors are nearly subequal.

In *Nuciruptor*, the crown of the left central incisor is very styliform, and of a height comparable to *Pithecia*, and less elongated than those of *Chiropotes* or *Cacajao*. There is no lingual cingulum and only slight development of the lingual heel, comparable to *Callicebus*. The alveoli of the central and lateral incisors are nearly equal in size, another similarity to *Pithecia* and *Callicebus*, as distinct from *Chiropotes* and *Cacajao*. Only the roots of the incisors are preserved in *Cebupithecia*: the alveoli of the central incisors are considerably smaller than those of the lateral incisors.

Canine

(Figs. 2–4, 6)

In living pitheciins, a diastema separates the mandibular canine from the procumbent incisor battery. Additionally, in *Cacajao* and *Chiropotes*, the maxillary and the mandibu-

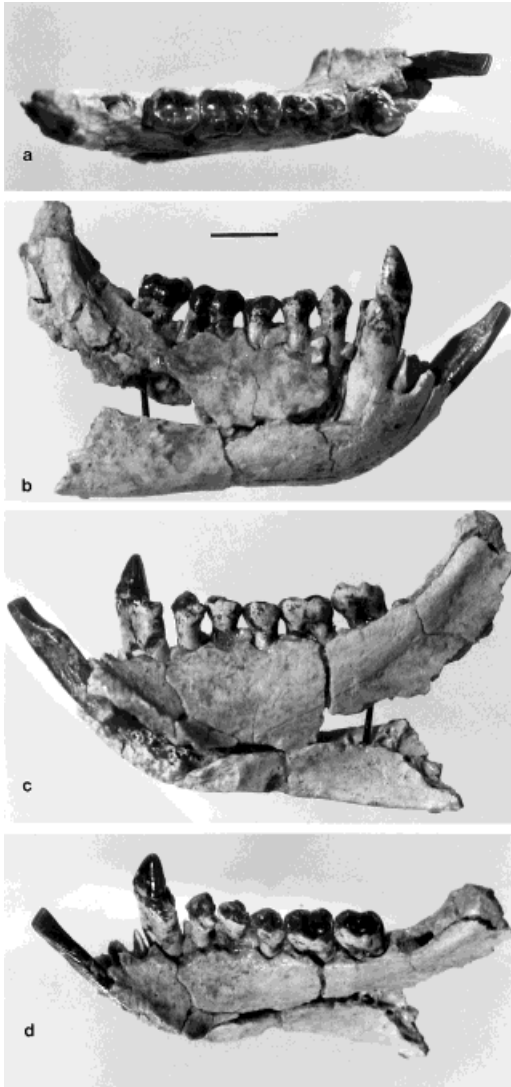


Fig. 2. Reconstructed mandible and dentition of *Nuciraptor rubricae* (IGM 251074) as seen in (a) occlusal, (b) buccal, (c) lingual, and (d) occlusolingual views. Scale bar equals 5.0 mm.

lar canines are exceptionally large, splayed and chisel-like in both sexes. Sexual dimorphism in the linear occlusal dimensions of the mandibular canines, however, ranges up to 22% in *Cacajao* to a low of 5% to 6% in *Chiropotes*. The lingual crest (entocristid) is very prominent and sharp, producing a triangular cross-sectional shape to the canine crown. *Pithecia*, and specifically the *Pithecia pithecia* species group (*P. p. pithecia* and *P.*

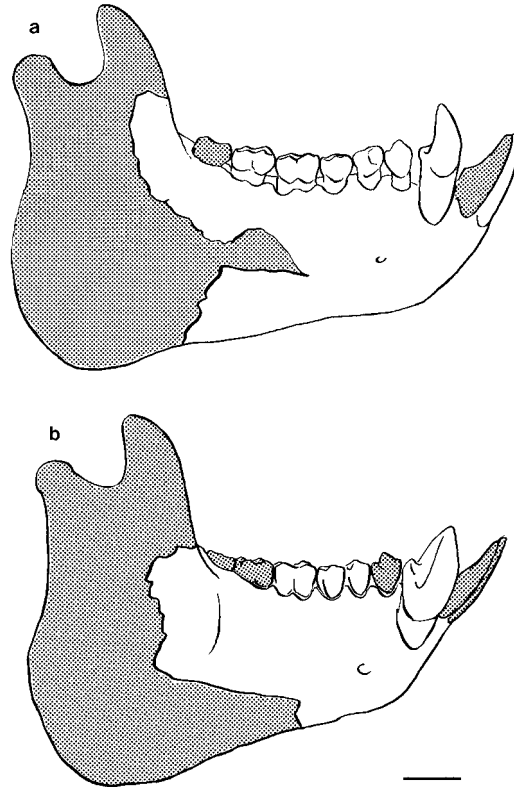


Fig. 3. Reconstructed mandibular profiles of (a) *Nuciraptor* and (b) *Cebupithecia*, based on the type specimens IGM 251074 and UCMP 38762, respectively. Reconstructed portions are indicated by stippling. Scale bar equals 5.0 mm.

p. chrysocephala, after Hershkovitz, 1987), presents the most primitive morphology in that the entocristid tends to be concave in profile and end at a noticeable distostylid, supported on a small lingual heel of the canine crown. In the *P. monachus* species group (*P. monachus*, *P. irrorata*, *P. aequatorialis*, and *P. albicans*, after Hershkovitz, 1987) as also in *Chiropotes*, and *Cacajao*, the entocristid is sharper, convex in profile and passes mesial to a small distal cusp. There is no crown heel due to expanded convex entocristid.

In *Nuciraptor*, there appears to have been only a very small (or no) incisor-canine diastema as occurs in *Cebupithecia* and modern pitheciins. The mandibular canine is vertically projecting, not splayed as in *Cebupithecia* and the modern pitheciins. It is smaller and much less chisel-like than *Ce-*

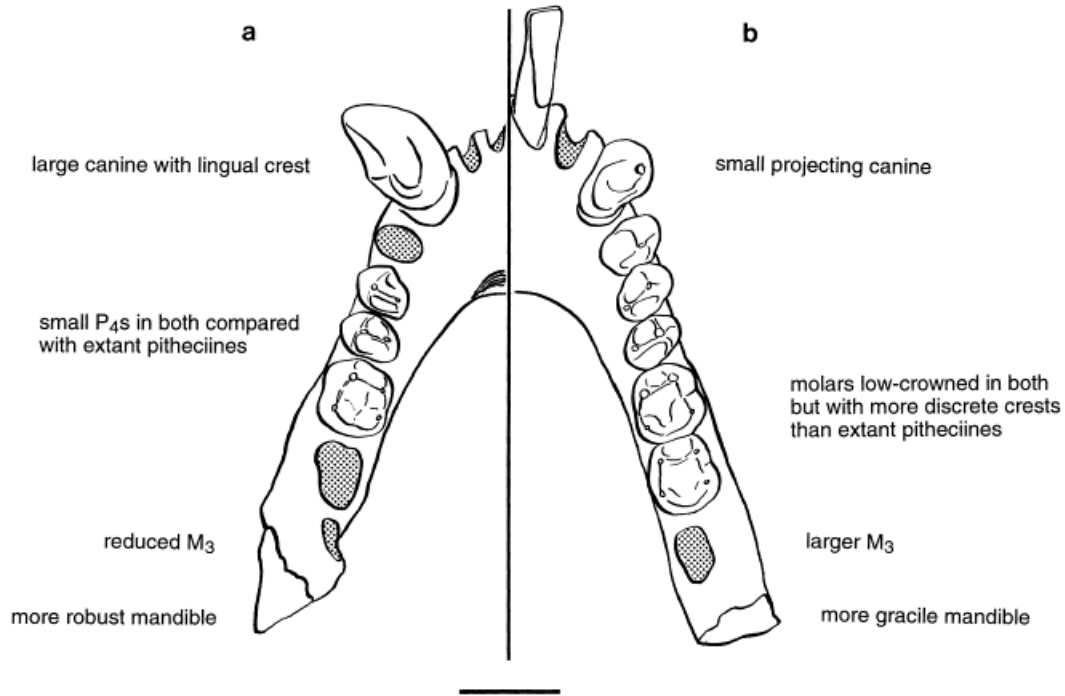


Fig. 4. Comparison of the occlusal views of the mandibular dentitions of (a) *Cebupithecia* and (b) *Nuciruptor*. Scale bar equals 5.0 mm.

bupithecia, or most living pitheciins, excepting some *Pithecia* and *Callicebus*, having a rounded concave entocristid ending in a distostylid on the lingual heel. The lingual cingulum is complete. A well-marked honing facet for the upper canine is present. This tooth most approaches the condition seen in some *Pithecia pithecia*, as described above, whereas *Cebupithecia* resembles the condition seen in *P. monachus*, *Chiropotes*, and *Cacajao*.

Given the lack of any apparent sexual dimorphism in shape (though not in size) in the highly specialized mandibular canines of extant pitheciins, the marked distinctions in canine morphology between *Nuciruptor* and *Cebupithecia*, together with the numerous distinctions in mandibular morphology, it seems reasonable to rule out the possibility that these represent male and female specimens of a single pitheciin taxon.

Premolars

(Figs. 3, 7–9)

The combined features of the premolar row of *Nuciruptor* is distinct from the living

pitheciin clade. The P_2 s are massive in both sexes and project above the level of the other premolars. The paracristid is elongated and may be inflated to form a modified honing platform for the large splayed triangular upper canine. The P_2 has a sharply raised protocristid that usually supports a small but distinct metaconid. The P_{3-4} are molari-form in that the talonid is longer than the trigonid and is bounded buccally by a large hypoconid. The premolar enamel often is crenulated.

Nuciruptor does not conform to this pattern in that the P_2 protoconid is not massive, nor does it project appreciably above the level of the other premolars. The preprotoconid is not elongate, nor is that part of the tooth inflated as in living pitheciins. There is very little evidence of honing wear by the upper canine, suggesting an only moderately projecting, or splayed upper canine. In the P_2 of *Nuciruptor*, the protocristid is weak and a metaconid is absent. The trigonid is steep and open lingually as in *Pithecia monachus* and *Chiropotes satanas*; in *Cacajao*

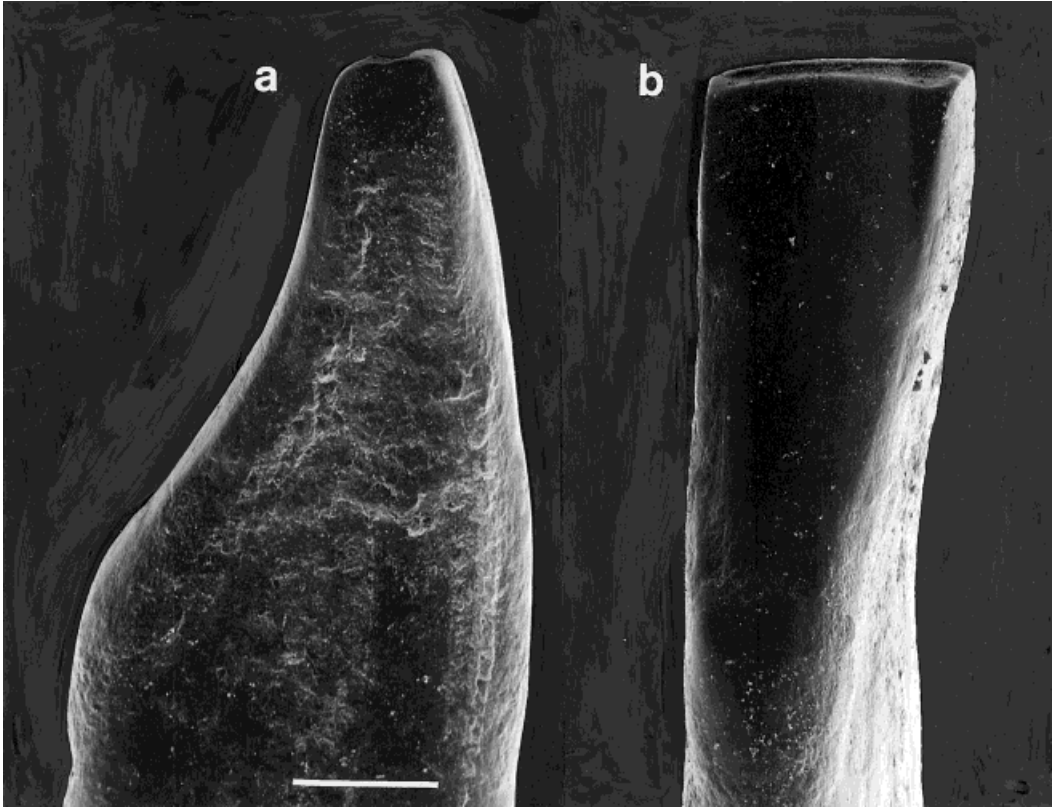


Fig. 5. Scanning electron micrographs (SEM) of the left central mandibular incisor of *Nuciraptor rubricae* (IGM 251074) seen in (a) mesiodistal and (b) buccolingual view. Scale bar equals 1.0 mm.

there is a strong lingual cingulum on the trigonid. A discrete entoconid is present. The P_2 of *Cebupithecia* is not preserved and therefore no direct comparisons can be made with *Nuciraptor*. However, the small alveolus for P_2 in *Cebupithecia* resembles that of *Nuciraptor*, as distinct from the large P_2 s of extant pitheciins.

The P_3 metaconid of *Nuciraptor* is smaller and not as widely spaced from the protoconid compared with living pitheciins and more closely resembles the condition in *Cebupithecia*. The trigonid basin is steeply sloped lingually, but enclosed lingually by a slight marginal crest. The talonid is short mesiodistally, and buccolingually compressed. The hypoconid is small. The entoconid is present, but does not stand out on the lingual talonid marginal crest. The P_3 of *Nuciraptor* differs markedly from that of *Cebupithecia* in that the posterior trigonid

wall of the former is deeply notched. *Nuciraptor* also displays slightly more buccal flare.

The P_4 metaconid of *Nuciraptor* is larger and more widely spaced than on the P_3 , but still not to the extent seen in living pitheciins. In *Cebupithecia*, the cusps are more closely approximated. The trigonid is more horizontal and enclosed by a more prominent marginal crest, as in living pitheciines. The posterior trigonid wall is deeply notched (Figs. 7–9). The talonid is wider mesiodistally than the trigonid and bounded by a discrete entoconid, small hypoconid and a weak hypocristid. This is a resemblance to *Cebupithecia*, but contrasts with the condition in living pitheciins in which the talonid is very expanded, leaving a molarized tooth. While buccal inflation of the crown is evident on all premolars, no cingulum is present. Although the P_4 talonid is slightly enlarged, the occlusal area of the premolar

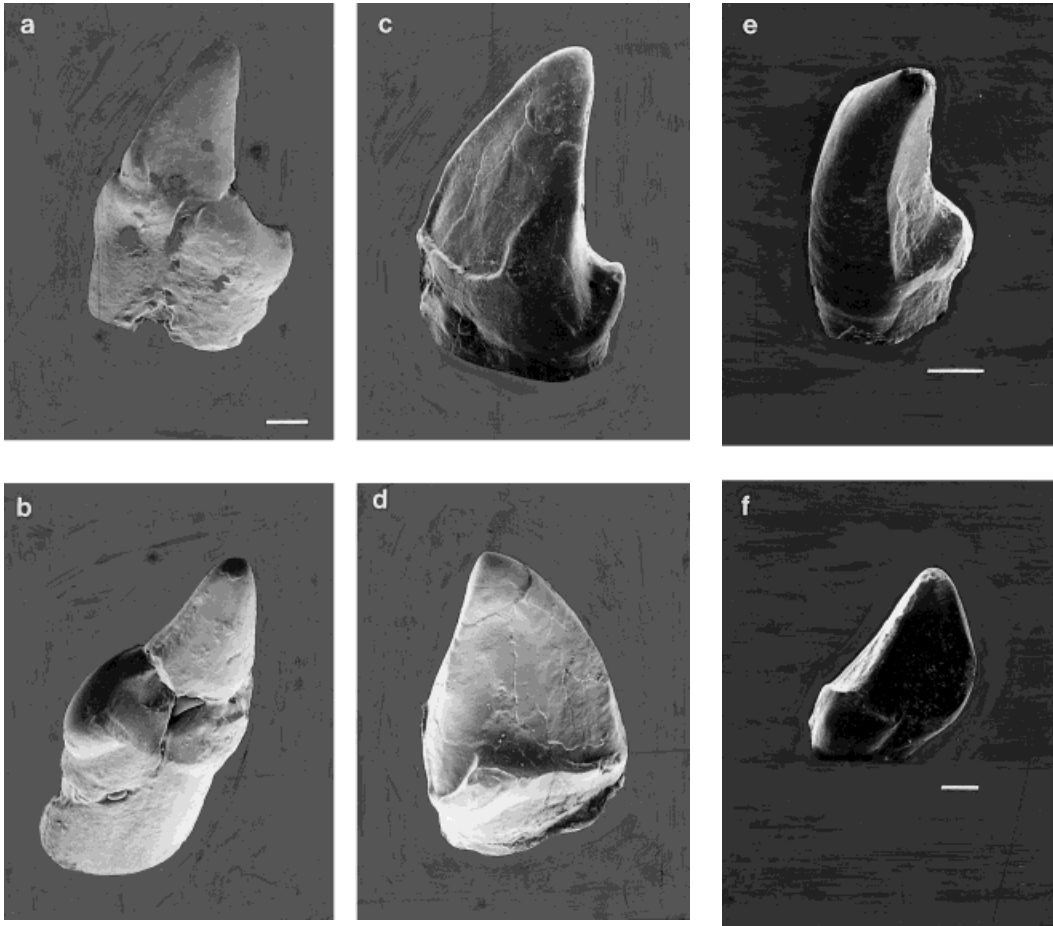


Fig. 6. SEM of the right mandibular canine of (a, b) *Nuciruptor*; (c, d) *Cebupithecia* and (e, f) *Mohanamico*. Top row (a, c, e) depict buccal views and bottom row (b, d, f) depict lingual views. Scale equals 1.0 mm.

row of *Nuciruptor*, as also *Cebupithecia*, remains quite small relative to the molar occlusal area, and displays little molarization so characteristic of the extant pitheciins.

Molars

(Figs. 3, 7–9)

The molars of living pitheciins are characterized by virtually no disparity of height between the trigonid and talonid, with the intervening protocristid represented by a low, often indistinct, ridge. The trigonid is very short mesiodistally, but just as broad buccolingually as the talonid. The principal molar cusps (except the paraconid and hypoconulid, which are absent) are marginalized and blended with the margins of the crown

leaving the crown generally flat and steep sided. The buccal crests are aligned mesiodistally so that the hypoflexid is very shallow. The crown surface of the enamel is often crenulated. M_{3s} show little or no reduction in occlusal area relative to M_{1-2} (Fig. 4 in Kay, 1994).

In *Nuciruptor*, only M_{1-2} are preserved. The molar crown relief is low, but not as flat as in living pitheciins, while more so than in *Callicebus*. The enamel lacks any crenulation. As in living pitheciines, paraconids are lacking, but the trigonids are very narrow mesiodistally (vs. broad). The metaconids stand taller than the protoconids and are only slightly distal to the protoconid. Protoconids are more bulbous than in living

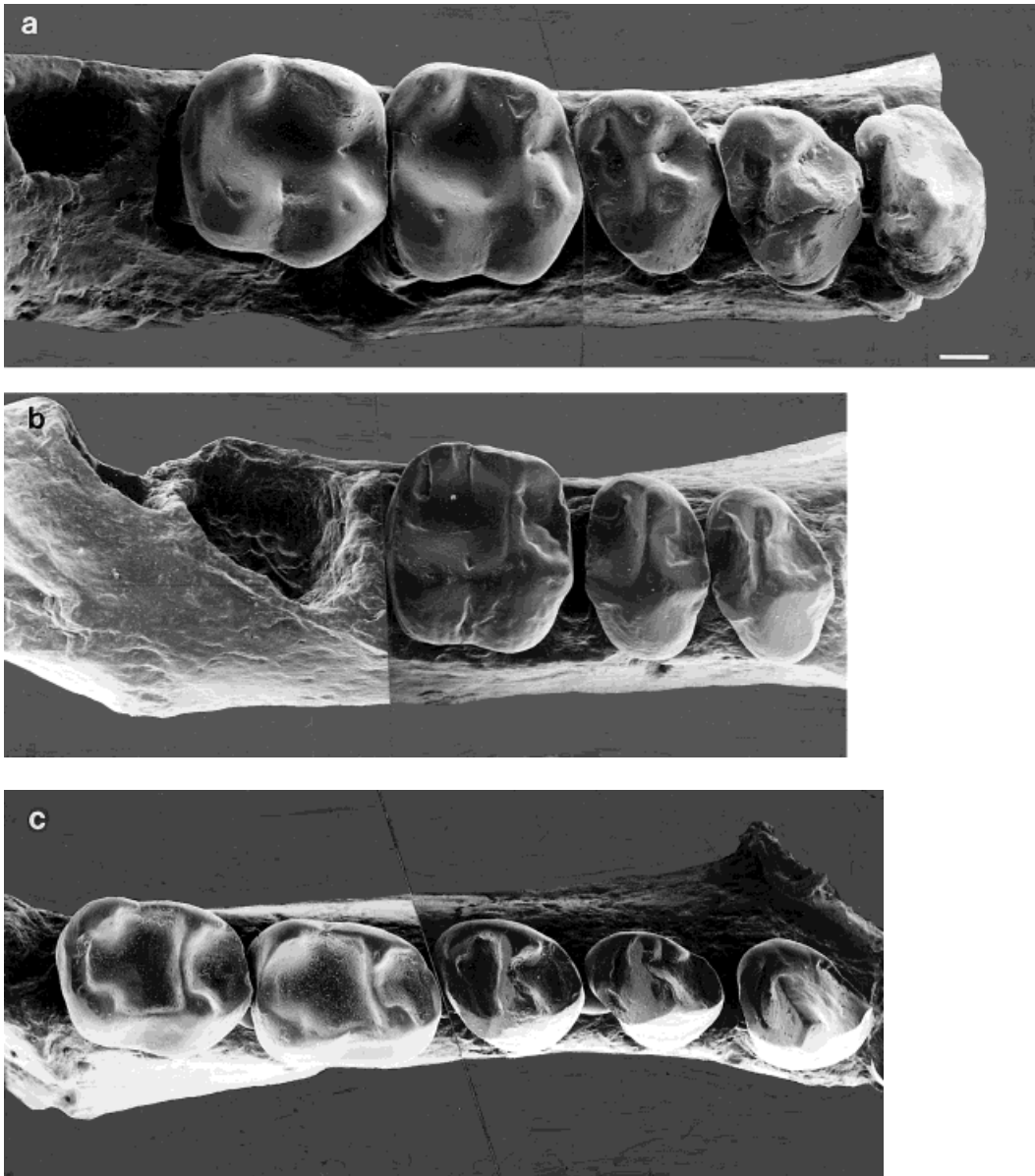


Fig. 7. SEM of the postcanine dentition seen in lingual view of (a) *Nuciraptor*; (b) *Cebupithecia*, and (c) *Mohanamico*. Scale equals 1.0 mm.

pitheciin. The posterior trigonid walls and protocristids are very low, but intermediate to the condition seen in living pitheciins and *Callicebus*, and are deeply notched by a distinct protoconid/metaconid sulcus. The talonids are raised and shallow. The entocoinids are large and more discrete than in living pitheciins and *Cebupithecia*, but less

so than in *Callicebus*. As in living pitheciins, the cristid obliqua are straight and rounded and reach the trigonid walls distal to the protoconids, but are more oblique than in living pitheciins. The hypoflexid is shallower than in *Callicebus*, but not to the extent seen in living pitheciins. No buccal cingulum is present.

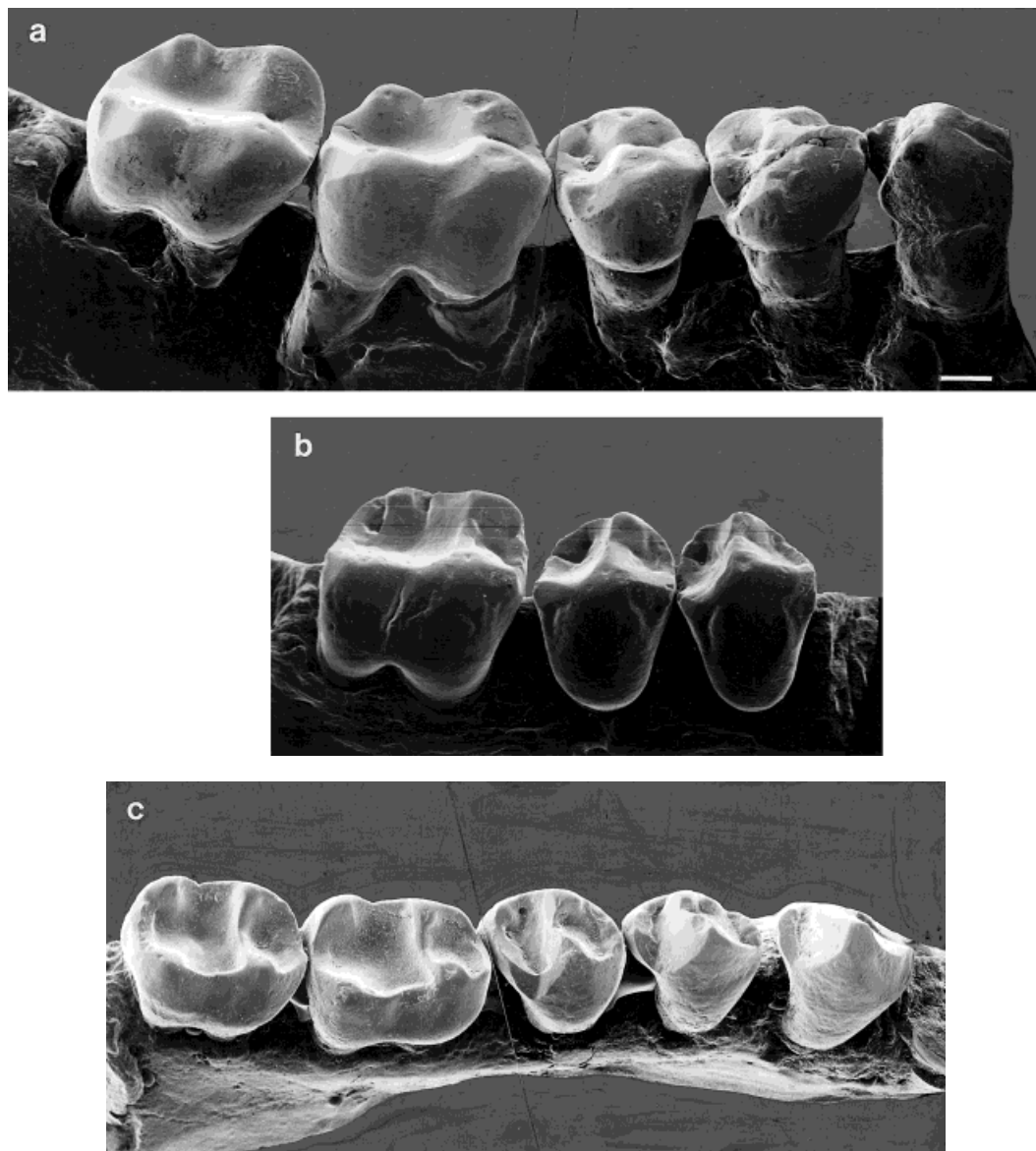


Fig. 8. SEM of the postcanine dentition seen in occlusal view, of (a) *Nuciruptor*; (b) *Cebupithecia* (reversed), and (c) *Mohanamico*. Scale equals 1.0 mm.

Compared with *Nuciruptor*, the M_1 of *Cebupithecia* (the only molar preserved in that taxon) more closely resembles extant pitheciin M_1 s in that the trigonid is quite broad, the protocristid is low and the buccal crests are aligned mesiodistally so that the hypoflexid is extremely shallow. On the other

hand, *Cebupithecia* resembles *Nuciruptor*, but not living pitheciins, in having some disparity in height between the trigonid and talonid, a mesiodistally slightly longer trigonid (compared with the talonid), the principal molar cusps not so marginalized nor blended with the margins of the crown leaving the

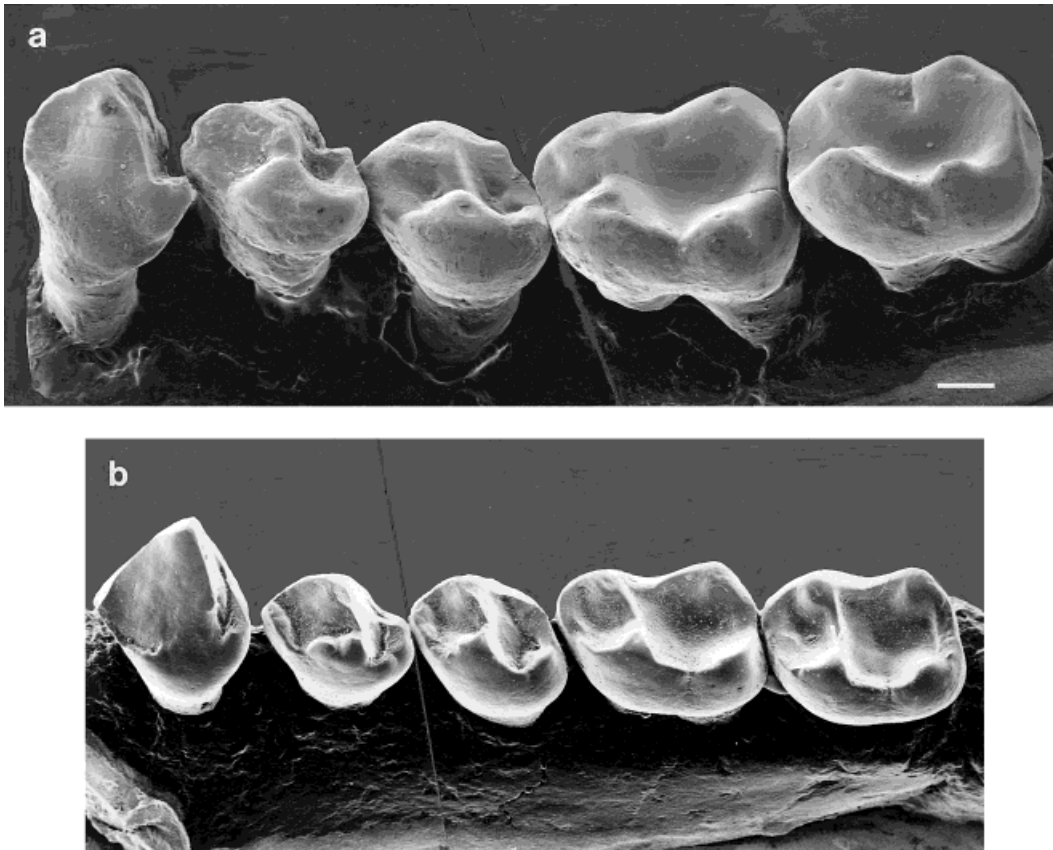


Fig. 9. SEM of the postcanine dentition seen in lingual view, of (a) *Nuciruptor* and (b) *Mohanamico*. Scale equals 1.0 mm.

crown margins more sloping. Further, the crown surface of the enamel is not crenulated.

The M_3 of *Nuciruptor* is missing, but its single-rooted alveolus is preserved for comparison with that of M_2 . *Cebupithecia* also had a single-rooted M_3 . Hershkovitz (1987) reports that the third molar of *Pithecia* can be either single- or double-rooted, as is also the case in *Callicebus*. In *Nuciruptor*, the ratio of M_3 to M_2 alveolar area (greatest m-d length times greatest b-l length) is 0.67, compared with 0.31 for *Cebupithecia*. The M_3 alveolus in *Nuciruptor* is approximately 95% of the m-d length of the M_2 alveolus. It lies nearly in line with the tooth row, with only a slight lingual inclination. This contrasts with the condition in *Cebupithecia*, where the M_3 alveolus has a strong lingual angulation (Fig. 4).

Table 3 summarizes the principal distinctions in dental morphology and serves to emphasize the contrasts between *Nuciruptor* and *Cebupithecia*.

Anomalies

(Figs. 1, 8)

A localized enamel hypoplasia is seen as a pitted line, or crease, across the buccal surface of the canine and premolars. This probably occurred as the result of a systemic disturbance during the time of crown formation. The position of the crease on the crown surfaces indicates the relative state of development of the crowns when the disturbance occurred: P_4 was the most developed, followed by P_3 , P_2 and finally C_1 . However, without the lateral incisor and third molar

TABLE 3. Summary of dental contrasts distinguishing *Nuciraptor rubricae* from *Cebupithecia sarmientoi*, with comparisons to other selected pitheciines

Trait	<i>Callicebus torquatus</i>	<i>Nuciraptor rubricae</i>	<i>Cebupithecia sarmientoi</i>	<i>Pithecia pithecia</i>
Relative size of I ₁₋₂	I ₁ < I ₂	I ₁ = ≤I ₂	I ₁ << I ₂	I ₁ < I ₂
Canine shape	gracile; rounded crest; lingual heel	gracile; rounded crest; lingual heel	robust; triangular; chisel-like	robust; triangular; chisel-like
P ₃ metaconid	small	small	moderate	large
P ₃₋₄ posterior trigonid wall	notched	deeply notched	not notched	not notched
P ₃ hypoconid	absent	absent	present/doesn't stand out	large
P ₄ entoconid	small discrete cusp	small discrete cusp	present/doesn't stand out	large
M ₁ posterior trigonid wall	notched	notched	not notched	not notched
M ₁ postentoconid sulcus	absent	absent	present	present
M ₁ buccal cingulum	absent	absent	present/faint	absent
Ratio M _{3/2} alveolar area	moderate	0.67	0.31	high
M ₃ alveolus orientation	in line with toothrow	in line with toothrow	strong lingual angulation	slight angulation

little can be deduced about the relative eruption sequence.

cf. **NUCIRUPTOR**
IGM-KU 8602

This is a maxilla with right C¹ and P² recovered from the El Dinde area of the Monkey Unit (Setoguchi et al., 1987) and referred to *Cebupithecia sarmientoi* on the basis of similarities in size and morphology between its canine and that of the holotype specimen of *Cebupithecia* (UCMP 38762, Fig. 10) but the presence of another pitheciin of similar size leaves open the possibility that IGM KU-8602 could belong to *Nuciraptor*. Setoguchi et al. (1987) acknowledge subtle differences between IGM-KU 8602 and UCMP 38762 that leave open the possibility that these specimens represent two taxa. Such a possibility remains conjectural, however, without an associated upper and lower dentition of *Nuciraptor*.

IGM 184074

This is an isolated left talus recovered from Duke locality 43, El Cardón Red Beds, Cerro Colorado Member, Villavieja Formation (Ford et al., 1991). This locality is immediately adjacent to, and penecontemporaneous with, Duke locality 32, where the type of *Nuciraptor* was recovered. The talus is well preserved with superficial erosion of the head, posterior tubercles and calcaneal

facets. It measures approximately 14.0 mm in length. An analysis of the correlation of talar length with M₁ mesiodistal length for a large sample of platyrrhines (Meldrum, 1990) indicates that this talus is of an appropriate size to belong to *Nuciraptor*. In general form, it is very similar to the talus of the type specimen of *Cebupithecia*, differing by having a slightly narrower head and neck and a slightly more rounded lateral trochlear crest. These differences could well be accommodated within intragroup variation. Therefore, on the basis of provenience, appropriate size, and comparable morphology, it is tempting to associate this talus with the closely related pitheciin, *Nuciraptor*. However, allocation of this specimen and inferences about its functional morphology must await complete analysis (Ford et al., in prep.).

IGM 184667

This is a partial pelvis and pelvic limbs recovered from Duke locality 79, in the Perico Member, below the Chunchullo Sandstone, La Victoria Formation (Meldrum et al., 1990; Meldrum and Kay, 1996). IGM 184667 has been referred to *Cebupithecia* on the basis of similarities to the holotype UCMP 38762. However, owing to the lack of associated dental material, and the presence of a second pitheciine in the La Ventan

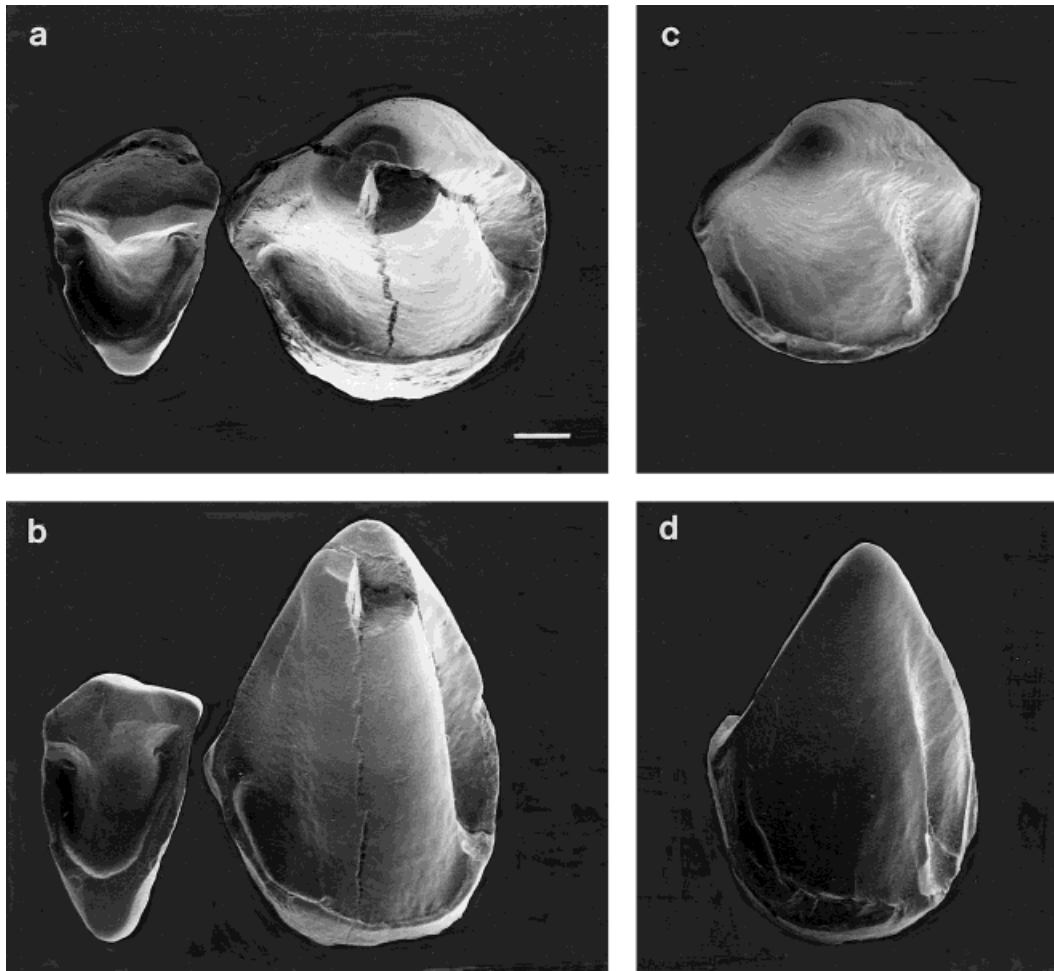


Fig. 10. SEM of the maxillary canine and P² attributed to *Cebupithecia* (IGM KU 8602) seen in (a) occlusal and (b) lingual views. Maxillary canine of type of *Cebupithecia* (UCMP 38762) seen in (c) occlusal and (d) lingual views.

primate fauna, the possibility exists that this specimen represents *Nuciraptor*.

CHARACTER EVOLUTION IN PITHECIINAE

In the following discussion of character evolution in Pitheciinae, we first describe the dentition in the living taxa. Next we take up the phyletic position of *Nuciraptor*, and *Cebupithecia*. Several nodes and lineage segments are numbered in reference to cladogenesis of Pitheciinae (Fig. 11). Cladogenesis and character evolution of living pitheciines are described elsewhere (Kay, 1990).

Node 1

The hypothetical last common ancestor of Pitheciinae and its closest living outgroup (*Alouatta*, *Ateles*, *Lagothrix*, and *Brachyteles*) had vertically implanted, low-crowned, and broadly spatulate incisors with prominent lingual heels. I₁ was smaller than I₂. There was no diastema separating the lower incisors from the moderately large, vertically projecting lower canine. The latter tooth had a well-developed paracristid and a rounded, indistinct protocristid.

The cheek teeth were set in a moderately deep jaw that did not deepen appreciably

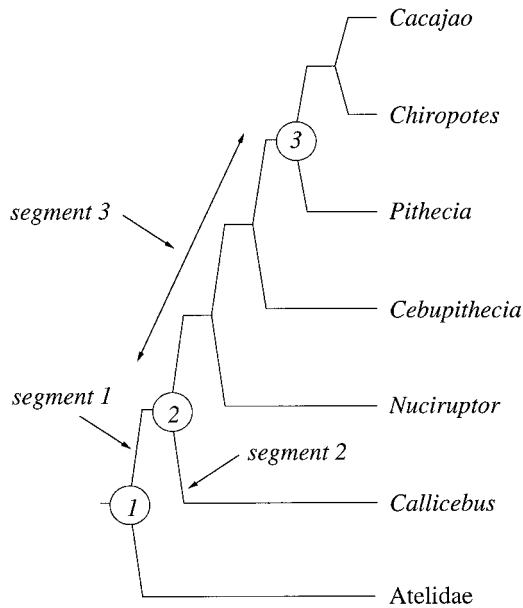


Fig. 11. Cladogenesis within Pitheciinae in which *Nuciraptor* figures as the sister taxon to the clade comprising *Cebupithecia* and the living pitheciine genera. Nodes 1–3 represent branch points on a cladogram for the last common ancestors of (1) Pitheciidae and Atelidae; (2) Pitheciidae; and (3) Pithecini. Features defining nodes and lineage segments are described in the text.

posteriorly. P_2 was a simple tooth that lacked a prominent protocristid and had no metaconid; it was a nonprojecting tooth that blended smoothly in size relative to the other premolars. P_3 and P_4 had metaconids of increasing size distally. The trigonids dominated these teeth, whereas the talonids were small. None of the premolars bulge buccally towards their cemento-enamel junctions.

The molars had low crowns with trigonids slightly higher than talonids. Molar enamel was smooth rather than crenulated. Molar trigonids were narrow buccolingually and short mesiodistally compared with the talonids. Trigonids are separated from talonids by a distinct raised protocristid. Molar cusps were inset from the buccal and lingual margins of the teeth and shearing features were moderately developed with moderately deep hypoflexids. Molar entoconids were well developed and stood out on the distolingual crown margin. The posterior marginal crest of the molar crowns was not disrupted by a

postentoconid sulcus. A hypoconulid, if present, was small.

The upper incisors were vertically implanted. The first upper incisor was slightly larger than the second. The second upper incisor flared from cervix to crown apex. Canines were not laterally splayed. Upper incisors, canines, and premolars had moderate lingual cingula. A moderately large hypocone was present on the low distolingual cingulum of P^4 .

Lineage segment 1

This is the lineage segment leading to node 2, the last common ancestor of living Pitheciinae, i.e., of *Callicebus* and the pitheciins. In this lineage segment the lower incisors became more high crowned and more narrowly spatulate. Jaw depth increased markedly posteriorly under the molars. A basal tubercle evolved on the cingulum of the upper central incisors. (This tubercle is also developed in *Lagothrix*, *Brachyteles* and *Ateles*, so it may have characterized a more inclusive clade of platyrrhines.)

Lineage segment 2

This is the stem lineage leading to *Callicebus* the posterior marginal crest of the lower molar crowns was disrupted by a strong postentoconid sulcus and the M_{1-2} hypoconulids, are expanded in size. I_{1-2} , canine, and premolar lingual cingulum became much stronger.

Lineage segment 3

In this lineage segment leading to the last common ancestor of living pitheciins, the lower incisors became very high-crowned, procumbently implanted, and mesiodistally compressed, and lost their lingual heels. A diastema separated the lower incisors from the larger vertically projecting lower canine. The canine protocristid developed into a strong sharp lingually oriented crest.

P_2 developed a small metaconid; it became a massive tooth that projects above the other premolars. P_3 and P_4 talonids became much larger, with well-developed hypoconids and entoconids. The premolar slopes bulge buccally towards their cemento-enamel junctions.

The molar trigonids were reduced in height to become the same height as the talonids. Molar enamel developed crenulation. Molar trigonids were broadened. Trigonid-talonid separation became less distinct and the protocristid was weakened. Molar cusps became marginalized and shearing features became indistinct, with hypoflexids very shallow. Molar entoconids were reduced in size and blended with the distolingual crown margin. Hypoconulids were lost.

The upper incisors became more procumbent. I^1 is much larger than I^2 . The lateral margins of I^2 became straight-sided; that is, the crown was not much wider than the root at the cervix. The canines developed a lateral splaying. P^4 hypocones were lost.

Phyletic position of *Nuciruptor*

The mandibular and lower dental characters of *Nuciruptor* give a clear indication that this taxon fits along lineage segment 3 in the above scenario (Fig. 11); that is, that it possesses a combination of features indicating a closer relationship with living pitheciins than to *Callicebus*. For example, *Nuciruptor* resembles living pitheciins in having elongate, procumbent, and styliform lower incisors with very weak lingual heels. Moreover, as in living pitheciins, the incisors are set in a procumbently oriented mandibular symphysis, and its mandibular corpus deepens appreciably under the molars.

At the same time, *Nuciruptor* does not possess several of the distinctive synapomorphies of extant pitheciins. *Nuciruptor* remains more primitive than living pitheciins in that no diastema separates its lower incisors from the canine. Its lower canines retain the primitive structure in not having a sharply defined protocristid. P_2 is not a robust or high-crowned tooth and does not have a metaconid. Nor are the other premolars molarized by the addition of large talonids. The molars of *Nuciruptor* retain the structures evolved in lineage segment 1 but lack the progressive modifications that must have evolved along lineage segment 3: *Nuciruptor* has smooth rather than crenulate enamel, its trigonids are set off from the talonids by the protocristids, the trigonids are relatively narrower and the molar cusps are situated in from the margins of the

crowns. *Nuciruptor* does show some progressive molar features resembling living pitheciins such as some diminution of molar shearing (see below) and shallowing of the molar hypoflexids.

Phyletic position of *Cebupithecia*

As already widely reported in the literature, *Cebupithecia sarmientoi* displays a mosaic of derived features of extant pitheciins and derived features of the pitheciines (including *Callicebus*), indicating that this taxon fits along lineage segment 3 in the above scenario (Fig. 11). The extraordinarily complete postcranial remains bear further phenetic resemblances to *Pithecia*, but lack many of the derived characters of the limbs that characterize extant pitheciins (Davis, 1987, 1988; Fleagle and Meldrum, 1988; Ford, 1986, 1990; Meldrum, 1993; Meldrum and Fleagle, 1988; Meldrum and Kay, 1996; Meldrum and Lemelin, 1991). The preserved portions of the dentition clearly display pitheciin synapomorphies in the incisor-canine complex, and mandibular morphology, but to a lesser degree in the postcanine teeth (Kay, 1990; Orlosky, 1973; Rosenberger, 1979).

In several ways, *Cebupithecia* is more derived than *Nuciruptor* in the direction of living pitheciins. The lower canines are more enlarged and splay laterally. They possess the distinctive sharp, raised protocristid of extant pitheciins, lacking in *Nuciruptor*; making the tooth chisel-like and triangular in cross-section. The molars are further specialized in the direction of living pitheciins having reduced trigonid heights and even more shallow hypocristids. Taken together, this dental evidence suggests that *Nuciruptor* is the sister taxon to the clade of *Cebupithecia* and the extant pitheciins (Fig. 11).

Several instances are noted where some characters do not agree completely with this interpretation. For example, I_1 is much smaller than I_2 in *Cebupithecia* (as judged from the size of the root cross-section), *Cacajao*, and *Chiropotes*, but not in *Pithecia*. This suggests either that I_2 has reenlarged in *Pithecia* or been reduced in size independently in *Cebupithecia* and the common ancestor of *Cacajao* and *Chiropotes*. Similarly, *Cebupithecia* apparently had more re-

duced M_3 s than either *Nuciraptor* or extant pitheciines. We interpret these resemblances as parallel "crossing-specializations" indicating that *Cebupithecia* is not a suitable direct ancestor for the living pitheciines.

Status of *Soriacebus* and *Mohanamico*

Two genera of primates, *Soriacebus* and *Mohanamico*, are considered by some writers to belong in the pitheciin clade. In each case, allocation to this clade is far more doubtful than for either *Nuciraptor* or *Cebupithecia*. In the case of *Soriacebus*, while the anterior dentition greatly resembles that of living pitheciines, the cheek teeth show an odd combination of autapomorphies and primitive platyrrhine or callitrichine traits. The proposed pitheciin resemblances of *Mohanamico* are far less striking, and it also shows other apparent primitive platyrrhine and callitrichine traits. While not ruling out the possibility that either or both taxa ultimately may be assignable to Pitheciini, a broader reassessment of fossil recent platyrrhines will be needed to make such a phylogenetic allocations more convincing.

***Soriacebus ameghinorum*.** The phylogenetic position of the Patagonian fossil primate, *Soriacebus ameghinorum* (early Miocene, Pinturas, Santacrucian Land Mammal Age) is widely debated. Fleagle et al. (1987) draw attention to similarities in the mandible and dentition of *Soriacebus* to several platyrrhines and consider several possible interpretations of these similarities: (1) that *Soriacebus* is an oddly specialized callitrichine; (2) that it is a pitheciin; or (3) that it is an early offshoot of all living platyrrhines. Fleagle (1990) and Fleagle et al. (1987) withhold an opinion as to the relative merits of these alternatives; Rosenberger et al. (1990) and Theodor (1995) hold the view that *Soriacebus* is a pitheciin, whereas Kay (1990) has argued that *Soriacebus* is a primitive platyrrhine with pitheciine convergences. Each of these points of view has merit and each entails substantial homoplasy.

In *Soriacebus*, a suite of mandibular and dental features bear considerable similarity to callitrichines (Fleagle, 1990; Fleagle et al., 1987). The mandible is V-shaped; the premolars have reduced metaconids, large

trigonids, and relatively small talonids. The molars have mesiodistally elongate trigonids and very small cingulum-based hypocones.

Soriacebus resembles pitheciines especially in the anterior dentition and the lateral profile of the mandible (Fleagle, 1990; Fleagle et al., 1987; Kay, 1990; Rosenberger et al., 1990). Pitheciine resemblances include the possession of a deep mandibular corpus that deepens posteriorly, having mesiodistally compressed lower incisor roots, and procumbently arranged in a robust mandibular symphysis. A specimen of *Soriacebus adrianae* shows the incisors to have been styliform and lacking a heel, as in living pitheciines (Fleagle, 1990). Also, as in living pitheciines, P_2 is a robust tooth of only slightly smaller caliber than the canine, having bulging buccal enamel, and a protoconid that projects well above the other cheek teeth. In the molars, the entoconid is reduced, approaching the condition in pitheciines (but also as in callitrichines). *Soriacebus* is more primitive than living pitheciines (as is *Nuciraptor*) in lacking a diastema between the lower incisors and canine and in having a more vertically implanted, not splayed, canine root.

A third set of structural details of the premolars and molars of *Soriacebus* appears to be primitive for platyrrhines (Fleagle, 1990; Kay, 1990), or at least atelids (sensu Rosenberger, 1981). In *Soriacebus*, the P_2 lacks a metaconid and the P_3 metaconid is small and close to the protoconid; P_4 metaconid is larger but still compressed against the protoconid. The M_1 metaconid is placed distolingually relative to the protoconid. Also, *Soriacebus* molars have hypoconulids and distinct postentoconid sulci running lingually to the entoconids. P^{2-4} have hypocones and strong upper premolar lingual cingula. As noted by Fleagle et al. (1987), the upper premolars of *Soriacebus* are three-rooted.

Obviously, *Soriacebus* cannot at once be a primitive platyrrhine, a pitheciin, and a callitrichine. With *Callicebus* securely allocated to Pitheciinae (Meldrum, 1995; Schneider et al., 1993, 1995) several apparently primitive features of the molars of *Soriacebus* might now be regarded as hav-

ing been present in primitive pitheciines and thus could strengthen the case for its pitheciine placement. However, pending a broader phylogenetic analysis including the relevant fossils, it is unclear whether the apparent synapomorphies *Soriacebus* shares with *Callicebus* actually are synapomorphies of a more inclusive clade with *Alouatta* and atelins. Pending such analysis, we will continue to interpret *Soriacebus* as an early offshoot of platyrrhines.

***Mohanamico hershkovitzii*.** Represented by a mandible (Luchterhand et al., 1986), the type specimen (IGM 181500; Figs. 6–9) comes from the Monkey Beds near El Dinde. It was assigned with hesitance to the Pitheciinae, while recognizing that it was not as specialized as *Cebupithecia* or the extant pitheciines. In addition, some similarities to callitrichines and particularly *Callicebus* were noted. A second specimen of a primate (IGM-KU 8601) of similar size and morphology to *Mohanamico* and from the same stratigraphic level and locality was described by Setoguchi and Rosenberger (1987) and allocated to a new species of *Aotus*, *A. dindensis*. Rosenberger et al. (1990) argue that the phyletic affinities of IGM KU-8601 are (as with other *Aotus*) within the Pitheciinae, whereas IGM 186500 should be allied with the callitrichines. Kay (1990) argue that IGM KU-8601 should be allocated to *Mohanamico* and emphasized the pitheciin affinities of both. We still maintain that the two specimens belong to the same species.

Reconsidered in light of the character evolution described above, a number of features cited by Kay (1990) to support an affinity of *Mohanamico* to the pitheciines seem less likely. In the referred specimen of *Mohanamico* (i.e., the type of "*A. dindensis*") the ventral surface of the orbit closely approximates the maxillary alveolar bone such that only a very shallow maxillary sinus extends posterior to the zygomatic arch. Living pitheciines and *Callicebus* have well-developed maxillary sinuses (Hershkovitz, 1977) and personal examination of the type of *Cebupithecia* shows it to have had a large maxillary sinus as well. Both the type and referred specimen of *Mohanamico* have jaws that do not increase in depth posteriorly as

in *Callicebus*, *Nuciruptor*, *Cebupithecia*, and living pitheciines. While the canine of the type of *Mohanamico* is worn in such a way as to suggest the presence of a sharp transverse lower canine crest, as in living pitheciines, the less-worn referred specimen has a more rounded crest. While the lower incisors of the type of *Mohanamico* are fairly elongate, although not as mesiodistally compressed as in *Callicebus*, the referred specimen has a slightly more low-crowned incisors. While *Mohanamico* possesses a projecting P₂, this tooth is not massive and more closely approximates the condition seen in tamarins than in pitheciines.

In summary of the above, the addition of IGM KU-8601 to the hypodigm of *Mohanamico* adds information about the orbital structure and intraspecific variability in the structure of the incisors and canines. Each bit of this new data, considered in light of what we know about character evolution in Pitheciinae, especially with the inclusion of *Callicebus* and the newly described *Nuciruptor*, diminishes the likelihood that *Mohanamico* belongs with the Pitheciinae. Other possibilities, including allocation to Callitrichinae, should be reconsidered.

ADAPTATIONS OF NUCIRUPTOR

Body size

Determination of body weight for *Nuciruptor* is based on its molar occlusal area. From body weights of 15 species of female platyrrhines and molar areas of the same species measured by Plavcan and Kay (unpublished data), the following least-squares regression was derived, with an r² of 0.935:

In female body weight =

$$\ln M_1 \text{ area } (1.565) + 3.272.$$

Based on this equation, the estimated weight of IGM 251074 was 2,044 grams. This is somewhat larger than the estimated weight for *Cebupithecia* of 1,792 grams, but both fall within the reported size ranges of male and female *Pithecia pithecia* and female *P. monachus* (Hershkovitz, 1987).

Dietary patterns

The functional design of the primate dentition is selectively modified to best deal

TABLE 4. The relative development of shearing crests on M_1 in platyrrhines¹

Taxon	N	M_1 length	Sum, M_1 shear	Expected shear	Shear quotient	Major dietary feature
<i>Callimico goeldii</i>	3	2.60	5.48	4.72	16.14	Insects
<i>Brachyteles arachnoides</i>	9	7.22	15.19	3.10	15.93	Leaves
<i>Alouatta palliata</i>	10	6.92	13.91	12.56	10.76	Leaves
<i>Alouatta caraya</i>	6	6.72	13.09	12.20	7.33	Leaves
<i>Alouatta fusca</i>	6	6.70	12.94	12.16	6.42	Leaves
<i>Aotus trivirgatus</i>	10	3.06	6.16	5.55	10.92	Fruit/Leaves
<i>Saimiri sciureus</i>	5	2.87	5.54	5.21	6.36	Insect/Fruit
<i>Lagothrix lagotricha</i>	8	5.47	10.12	9.93	1.94	Fruit/Leaves
<i>Leontopithecus rosalia</i>	5	3.09	5.62	5.61	0.22	Fruit/Insects
<i>Ateles geoffroyi</i>	10	5.26	9.31	9.55	-2.47	Fruit
<i>Callicebus moloch</i>	10	3.18	5.50	5.77	-4.70	Fruit
<i>Saguinus mystax</i>	5	2.52	4.03	4.57	-11.88	Fruit/Insects
<i>Callithrix argentata</i>	4	2.22	4.08	4.03	1.27	Fruit/Gum
<i>Cebuella pygmaea</i>	4	1.78	3.26	3.23	0.92	Gum/Fruit
<i>Pithecia monachus</i>	4	4.00	6.78	7.26	-6.60	Fruit/Seeds
<i>Cebus apella</i>	5	4.79	7.71	8.69	-11.31	Fruit/Seeds
<i>Chiropotes satanas</i>	5	3.64	5.50	6.61	-15.53	Seeds/Fruit
<i>Cacajao melanocephalus</i>	2	3.97	5.90	7.20	-17.70	Seeds/Fruit
<i>Soriacebus ameghinorum</i>	1	3.60	5.87	6.53	-10.15	Fruit/Seeds
<i>Soriacebus adriane</i>	1	3.23	4.67	5.86	-20.33	Seeds/Fruit
" <i>Aotus dindensis</i> "	1	3.23	6.14	5.86	4.74	Insects/Fruit
<i>Mohanamico hershkovitzii</i>	1	3.20	4.96	5.81	-14.59	Fruit/Seeds
<i>Cebupithecia sarmientoi</i>	1	3.52	5.15	6.39	-19.38	Seeds/Fruit
<i>Nuciraptor rubricae</i>	1	4.00	5.47	7.26	-24.65	Seeds/Fruit

¹ The estimate of shearing development is based on measurements of six lower molar crests (see Kay, 1975 for further details). A line was assigned to a bivariate cluster of the natural log of M_1 length (lnML) versus the natural log of the sum of the measured shearing crests (lnSH). The line was assigned a slope of 1.0 (slope of isometry) and passed through the mean lnML and mean lnSH for extant taxa. The equation expressing this line is:

$$\ln SH = 1.0(\ln ML) + 0.596$$

For each taxon, the expected lnSH was calculated from this equation. The observed (measured) lnSH for each species was compared with the expected and expressed as a residual (Shear Quotient, or SQ):

$$SQ = 100 * (\text{observed-expected})/(\text{expected})$$

Extant and extinct taxa are listed separately according to dietary categories (Fleagle et al., 1996). Diet is inferred for extinct taxa by comparison to a modern analog with a similar SQ. All measurements are in millimeters.

with the physical properties of the foods the species eats (Anthony and Kay, 1993; Fleagle et al., 1996; Kay, 1975; Kay and Anthony, 1991; Kay and Covert, 1984; Strait, 1991). One method of quantifying dietary adaptation is to measure the relative development of the shearing crests on molars, after molar size has been taken into account. Table 4 illustrates the development of molar shearing in selected living platyrrhines as a "shearing quotient." (Anthony and Kay, 1993; Fleagle et al., 1996). In Figure 12, the shearing quotients for living platyrrhine species are broken down by dietary preference. Species that eat considerable amounts of fibrous foods such as leaves high in cellulose (*Alouatta*) or chitinous insects (*Callimico*), have well-developed shearing edges on their molars (large SQs). In contrast, species that feed on less fibrous, soft fruits (*Ateles*) and tree gum (*Callithrix*) tend to have relatively flatter teeth, with shorter more rounded

shearing crests. The teeth of species that specialize in eating hard seeds or in splitting open tough, hard fruits (*Cebus* and the pitheciins *Pithecia*, *Cacajao* and *Chiropotes*) tend to have even less shearing than the soft-fruit eaters.

Nuciraptor and *Cebupithecia* both have a suite of dental traits suggesting that they were specializing in seed predation (Fig. 12). It must be considered, however, that the interpretation of the dietary adaptations of these extinct taxa is each based on single specimens and further material is required to assess the intragroup variability of this trait. Both *Nuciraptor* and *Cebupithecia* have very poorly developed shearing on their molars, with lower shearing quotients than any of the living pitheciines. This strongly suggests that they were masticating hard seeds. However, they lack other of the extreme morphological specializations of the postcanine dentition seen in the living

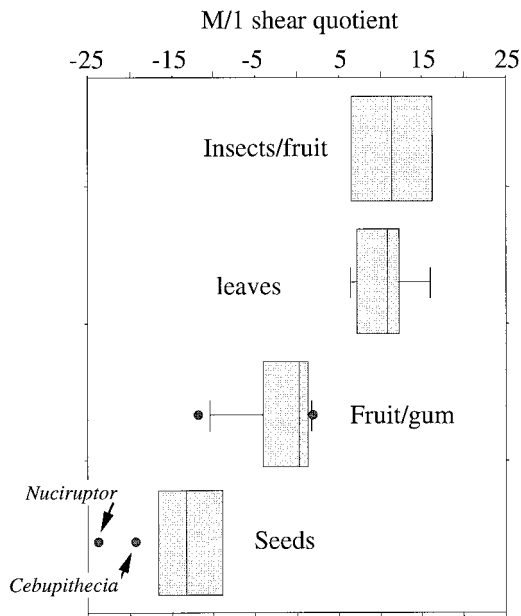


Fig. 12. Estimated shearing-crest development on the lower first molars of species of eighteen species of living platyrrhines. A shearing quotient is calculated from measurements of six lower molar crests (crests 1–6; for anatomical details see Kay, 1975, 1977). A line was assigned to a bivariate cluster of the natural log of M_1 length (lnML) versus the natural log of the sum of the measured shearing crests (lnSH). The line is assigned a slope of 1.0 (slope of isometry) and passed through the mean lnML and mean lnSH for extant taxa. The equation expressing this line is:

$$\ln SH - 1.0 (\ln ML) + 0.596.$$

For each taxon, the expected lnSH is calculated from this equation. The observed (measured) lnSH for each species is compared with the expected and expressed as a residual (Shear Quotient, or SQ):

$$SQ = 100 * (\text{observed-expected})/(\text{expected}).$$

Extant taxa used are: *Callimico goeldii*, *Brachyteles arachnoides*, *Alouatta palliata*, *Alouatta caraya*, *Alouatta fusca*, *Aotus trivirgatus*, *Saimiri sciureus*, *Lagothrix lagotricha*, *Leontopithecus rosalia*, *Ateles geoffroyi*, *Callicebus moloch*, *Saguinas mystax*, *Callithrix argentata*, *Cebuella pygmaea*, *Pithecia monachus*, *Cebus apella*, *Chiropotes satanas*, *Cacajao melanocephalus*. Data are abstracted from Fleagle et al. (1996).

pitheciins, e.g., crenulated enamel and molarization of the premolar row.

The differences in dietary patterns also are reflected in the structure of the anterior dentition. In the case of living pitheciins, these teeth are highly modified for opening the hard or tough pericarp preceding mastication of the pliable seed (Kay, 1990; Kinzey,

1987; Kinzey and Norconk, 1990). The incisors are elongated and mesiodistally compressed to form a gouge, while the canines are enlarged, splayed and chisel-shaped. The extinct pitheciins *Cebupithecia* and *Nuciruptor* show more similarities to the living pitheciins in these features of the anterior dentition than in the less-specialized morphology of their molars. Although the incisors of *Cebupithecia* are not preserved, it is clear from the alveoli that they were compressed mesiodistally and the central were narrower and set slightly forward relative to the lateral incisors. Furthermore, it can be reasonably deduced from the orientation of the preserved portions of the upper central incisor that the mandibular incisors had high crowns. While the mandibular canine of *Cebupithecia* closely resembles the strongly crested chisel-like form of the living pitheciins, the preserved maxillary canine lacks the distinctive triangular cross-section found in the upper canines of living pitheciins.

Nuciruptor also shows the pitheciine incisal structure of laterally compressed styli-form incisors, although the crowns are not as elongate and the alveoli of the central and lateral mandibular incisors appear to have been approximately subequal. The canines of *Nuciruptor* are not as specialized, i.e., chisel-like, as are those of *Cebupithecia* or living pitheciins. Instead the entocristid is weaker and rounded, leaving a well developed lingual heel.

From this combination of dental traits a number of inferences can be made about the evolution of pitheciin dental adaptations. First, dental specializations of extant pitheciins may have evolved in a mosaic fashion. As in *Cebupithecia*, the anterior dentition of *Nuciruptor* shows specializations for opening tough seed husks but not the characteristic pitheciine features of the postcanine dentition associated with seed crushing. As Kinzey (1992; p. 505) has suggested, "the more developed shared features in the Pitheciinae are found in the anterior dentition; it is the anterior dentition that is expected to evolve sclerocarpic foraging features first." Second, the dental morphology of *Nuciruptor* further supports the scenario set forth by Kinzey (1992) that the compres-

sion and raised crown height of the incisor battery together with increased canine robusticity preceded specialization of the chisel-like canine morphology. Third, the combination of a more blade-like maxillary canine with a more triangular chisel-like mandibular canine in *Cebupithecia*, and possibly to a lesser extent *Nuciraptor*; indicates that the highly derived features of the pitheciin canines first evolved in the mandibular dentition.

We concur with Kinzey (1992) that *Callicebus-Pithecia-Chiropotes-Cacajao* represent a morphocline of increasingly specialized dental features for sclerocarpic foraging. In fact, the mosaic of features displayed by *Nuciraptor* would seem to bear out Kinzey's prediction that specializations of the anterior dentition would precede those of the postcanine dentition in the evolution of sclerocarpy.

CONCLUSIONS

The array of taxa comprising the living Pitheciinae, *Callicebus-Pithecia-Chiropotes-Cacajao*, represents a morphocline of increasingly specialized dental adaptations for sclerocarpy.

Nuciraptor rubricae represents a new genus and species of pitheciin, being the sister taxon to the clade consisting of *Cebupithecia* and the extant pitheciin genera, *Pithecia*, *Chiropotes* and *Cacajao*.

The unique combinations of dental traits displayed by *Nuciraptor* and *Cebupithecia* indicate that the dental specializations for seed predation, as seen in the extant pitheciins, evolved in a mosaic fashion.

The morphology of *Nuciraptor* and recognition of the pitheciine status of *Callicebus* diminishes support to the hypothesis that *Mohanamico* is a primitive pitheciin. We withhold an opinion about the phylogenetic status of *Soriacebus* pending a full analysis of Miocene platyrrhines.

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