

The upper dentition of *Stirtonia* (Ceboidea, Primates) from the Miocene of Colombia, South America and the origin of the Postero-internal cusp of upper molars of howler monkeys (*Alouatta*).

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INTRODUCTION

In 1979 field season, the upper premolars and the molars of *Stirtonia tatacoensis* were found in the Upper Miocene La Venta badland of Colombia. These are described below. The geological work has not yet been completed so that the report on geology of the area will be published later. The discovery was done in the same general area as the University of California field parties directed by Dr. R. A. STIRTON worked during the 1940's (STIRTON, 1951).

The purpose of the present paper is two fold: First to described the upper dentition of *Stirtonia* that has not been previously described, and second to present criteria that can be used to trace the phylogenetic history of the postero-internal cusp of upper molars of extant howler monkeys (*Alouatta*). Based on the general similarity seen in the upper molar configuration between North American Eocene *Notharctus* and South American extant *Alouatta*, GREGORY (1920) wrote that the postero-internal cusp of upper molars of *Alouatta* is apparently a pseudohypocone as in *Notharctus*, because in *Alouatta* the postero-internal cusp is connected with the protocone by a ridge. *Stirtonia* is a direct ancestor to *Alouatta* as discussed below. In *Stirtonia* no connection between the postero-internal cusp and the protocone is observable. Instead, the postprotocrista runs postero-buccally from the protocone towards the posterior side of the metacone and the entoflexus separating the postero-internal cusp from the protocone is deep and long transversely. The *Nannopithec*-fold is not present on *Stirtonia*. The postero-internal cusp connects with the posterior cingulum posteriorly. Thus, the postero-internal cusp of *Stirtonia* is a hypocone or euhypocone (REMANE, 1960), not a pseudohypocone or pseudypocone (STEHLIN, 1916).

The following abbreviations have been used: IGM, Instituto Nacional de Investigaciones Geologico-Mineras, and, KU, Kyoto University Primate Research Institute.

ARE THE UPPER TEETH IDENTIFIED AS *STIRTONIA TATACOENSIS*?

No upper dentition of *Stirtonia* has been described. Isolated right P², P³, P⁴, M¹ and M², left M₁, and edentulous ramus of right maxillary fragment of a ceboid monkey were discovered in the La Venta badland. These specimens were collected on eroded surface of clay of the Honda Formation within a single spot (50 cm²).

The edentulous right maxillary ramus has three alveoli for premolars and broken roots of the premolars are enclosed in all the alveoli. The breaks of the roots are flesh. The roots of the isolated P², P³ and P⁴ discovered are broken but the breaks are also flesh. These premolars and maxillary fragment were carefully reconstructed and all these broken pieces beautifully

fit together. This means that the isolated P², P³ and P⁴, and the maxillary fragment belong to a single individual.

The M₁ is exactly identical morphologically to the corresponding tooth of the holotype of *Stirtonia tatacoensis*. The size of the M¹ and M² is almost the same as that of the M₁, and the width of the P⁴ is also the same as that of the M¹. All the teeth discovered are almost unworn and this fact means that they show the same degree of wear of teeth. Because of these evidences together with the fact that all the specimens at hand were found in a single spot, it is safely concluded that all the specimens belong to a single individual so that the upper teeth collected are identified as *Stirtonia tatacoensis*.

SYSTEMATIC ACCOUNT

Class Mammalia
Order Primates
Superfamily Ceboidea
Family Cebidae Bonaparte, 1831
Genus *Stirtonia* Hershkovitz, 1970
Stirtonia tatacoensis (STIRTON, 1951)
(Figs. 2. 3. 4 & 5)

Material: P², P³, P⁴, M¹, M² and M₁—IGM-KU-III-1

Locality: Near River Tatacoa, North-east of Villa Vieja, Huila Department, Colombia.

Age: Late Miocene

DESCRIPTION: P² is somewhat wider transversely. As in P³ and P⁴, in P² the paracone is the only prominent cusp. The metacone is not formed. The paracone is conical but a little compressed transversely. The paracone is situated a little anteriorly to the longitudinal mid-point of the tooth. Two acute ridges run from the tip of the paracone: one runs anteriorly but a little buccally, and the other posteriorly but a little lingually. The buccal wall of the paracone is very steep, but protrudes buccally. The buccal base of the paracone is truncated posteriorly so that the anterior corner of the buccal base protrudes more buccally. One broad ridge descends antero-lingually from the tip of the paracone. The lingual wall of the paracone posterior to the broad ridge is a little concaved. The lingual cingulum is very broad and occupies the lingual two-thirds of the tooth. The edge of the lingual cingulum forms a contiguous acute ridge. Any small cusps are not formed on the lingual cingulum at all. The anterior half of the ridge of the lingual cingulum runs almost horizontally surrounding the antero-lingual base of the paracone. The posterior half of the ridge descends postero-buccally from the lingual corner of the cingulum. The ridge continues to run horizontally and comes up again to join with the acute posterior ridge from the tip of the paracone. The point where these two ridges just mentioned above join is a little higher than the lingual corner of the lingual cingulum. Between the posterior half of the lingual cingulum and the paracone, a narrow and obliquely elongated shallow valley is formed. But the valley is confined posterior to the lingual corner of the lingual cingulum.

The morphology of P³ is almost identical to that of P². P³ is wider transversely and more stoutly built than P². The base of the paracone on P³ is broader than that on P². The paracone on P³ is situated a little more anteriorly than on P². The anterior ridge from the paracone descends antero-buccally and terminates buccal to the posterior end of the posterior ridge

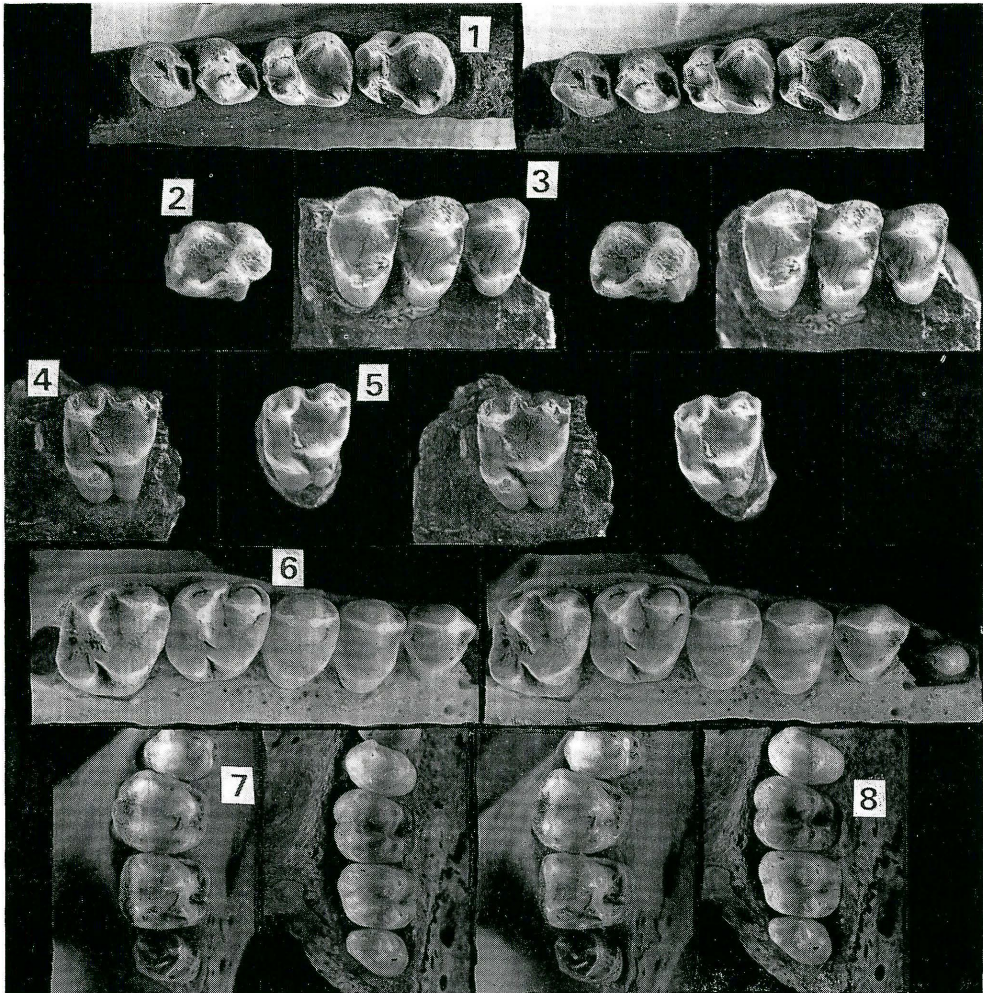


Fig. 1. Cast of the holotype of *Stirtonia tatacoensis*. UCMP No. 38989. Right P_{3-4} , M_{1-4} . $\times 2$.
 Figs. 2-5. *Stirtonia tatacoensis* found in the Honda Formation in Colombia. Fig. 2: Left M_1 , Fig. 3: Right p^{2-4} , Fig. 4: Right M^2 , Fig. 5: Right M^1 . $\times 2$. IGM-KU-III-1.
 Fig. 6. *Alouatta seniculus*. Right P^{2-4} , M^{1-2} . $\times 2$.
 Fig. 7. *Callicebus moloch*. Right P^4 , M^{1-3} . $\times 2$.
 Fig. 8. *Aotus trivirgatus*. Right P^4 , M^{1-3} . $\times 2$.

from the paracone of P^2 . The posterior ridge from the paracone runs almost posteriorly. The buccal wall of the paracone is also steep but more gentle than in P^2 . The truncation of the posterior half of the buccal base of the paracone is not so prominent than in P^2 . Instead, the buccal base is more round buccally. The antero-lingual ridge of the paracone is more stout than in P^2 , and the postero-lingual wall of the paracone forms a steep wall and is not concaved as in P^2 . The lingual cingulum occupies the lingual two-thirds of the tooth as in P^2 . The ridge forming edge of the cingulum is more stout than in P^2 . At the lingual corner of the cingulum, a small and low cusp is formed. Based on the analogy to the molar structure, this small cusp may be an incipient protocone. A somewhat broad ridge runs anteriorly from the

Table 1. Dimensions of teeth of *Stirtonia tatacoensis* (in mm)

	P ²	P ³	P ⁴	M ¹	M ²	M ₁
Length	4.1	4.5	4.5	6.3	6.6	6.9
Width	6.0	6.8	7.2	7.2	8.4	4.0 (trigonid) 4.9 (talonid)

protocone and the ridge connects with the lingual base of a conspicuous conule. The conule is situated just anterior to the paracone and elongated bucco-lingually on the lingual cingulum. The analogy of the conule to any structure of molars is uncertain. The posterior base of the conule is broad bucco-lingually. The tip of the conule is clearly higher than the protocone and very lower than the paracone. Buccal to the conule the lingual cingulum runs almost horizontally. Posterior to the protocone, the lingual cingulum a little descends postero-buccally forming a postero-lingual edge of the lingual cingulum. This part of the lingual cingulum is not so low in position as in P². The valley between this part of the cingulum and the postero-lingual wall of the paracone is a little shallower and broader than in P², and continues to run anteriorly to the protocone and lingually to the posterior base of the conule mentioned above. The valley near the protocone is very shallow, especially buccal and anterior to the protocone. The deepest portion of the valley is seen lingually to the posterior ridge from the paracone.

P⁴ is wider and more slender transversely than in P³. The paracone is conical and situated on just longitudinal midpoint of the tooth. The anterior ridge from the paracone runs nearly anteriorly and terminates buccal to the posterior end of the posterior ridge from the paracone of P³. The buccal wall of the paracone is a little steeper than in P³. The buccal base of the paracone is round symmetrically. The antero-lingual ridge from the paracone is not prominent, whereas in P² and P³ this broad ridge is conspicuous making the lingual configuration of the paracone asymmetrical. Because apparently the tooth is transversely elongated lingually, the lingual cingulum occupies the lingual almost three-fourths of the tooth. Just posterior to the lingual corner of the lingual cingulum, small but conspicuous protocone is formed. The protocone on P⁴ is larger than that on P³. Anterior to the protocone, the tooth structure is almost identical to that of P³, although the conule of P⁴ at hand is broken off. Posterior to the protocone, the lingual cingulum runs lingually and a little posteriorly. The ridge descends only slightly making this part of the tooth higher crowned than in P² and P³. The valley between the postero-lingual part of the lingual cingulum and the paracone is more elevated than in P³ so that the depth of the valley is essentially the same along the course of the whole valley. This valley is blocked lingually by the lingual cingulum as a somewhat tall wall and the protocone is well defined than in P³.

M¹ is squared. The paracone is larger and taller than the metacone. The paracone is situated very close to the anterior border of the tooth so that the parastyle is not well defined. The paracone is elongated antero-posteriorly and the lingual wall of the paracone forms a nearly flat plane. The buccal wall of the paracone protrudes buccally. One acute ridge descends from the tip of the paracone posteriorly but slightly buccally and continues to run postero-buccally. This ridge connects with the antero-lingual corner of the mesostyle which is somewhat compressed antero-posteriorly. The mesostyle is situated posterior to the longitudinal midpoint of the tooth. The styler shelf between the paracone and the mesostyle is concaved buccally. The metacone is V-shaped with the apex towards lingually. The antero-lingual and the postero-lingual walls of the metacone stand almost vertically. Two acute ridges run from the apex of the metacone: One descends antero-buccally and runs horizontally towards buccally

connecting with the postero-lingual corner of the mesostyle. Thus, the mesostyle connects with both the paracone and the metacone. The mesostyle is clearly lower than these two cusps. The other ridge descends postero-buccally and connects with the postero-lingual corner of the obliquely elongated metastyle. The metastyle forms the postero-buccal corner of the tooth. The metastyle is elongated towards antero-buccally so that the concaved stylar shelf between the metastyle and mesostyle becomes narrower buccally. The protocone is situated lingual to the midpoint between the paracone and the mesostyle. The protocone is somewhat elongated antero-posteriorly with the apex pointing upward. The protocone is as high as the metacone. The preprotocrista gradually descends antero-buccally from the apex of the protocone and this crista gradually ascends almost buccally to connect with the anterior extremity of the paracone. The buccal wall of the protocone forms a nearly flat plane. Posterior to the protocone, the only one ridge descends postero-buccally. This ridge runs straightly towards the crown surface and disappears just between the metacone and the postero-internal cusp. The ridge is completely separated from the latter cusp by the deep and long entoflexus. Thus, no direct connection between the protocone and the postero-internal cusp is seen. The *Nannopithec*-fold is not present on the specimen at hand. The ridge just mentioned above must be identified as the postprotocrista. Antero-buccal to the point where the postprotocrista disappears, a remnant of a small ridge runs transversely and its buccal extremity connects with the lingual base of the metacone. But the lingual extremity of this ridge is separated from postprotocrista by a small valley. The small ridge is situated really low in compared with the metacone. The homology of this structure is not certain; At the present stage, it is not possible to decide whether this structure might be identified as the metaconule or as the remnant of the buccal half of the postprotocrista. The postero-internal cusp is situated posteriorly and slightly lingual to the protocone. The former cusp is clearly lower than the latter. Between these two cusps, the V-shaped entoflexus runs obliquely towards postero-buccally. From the apex of the postero-internal cusp, one broad ridge descends towards the postero-lingual corner of the metastyle. This broad ridge forms the posterior cingulum. Because of the fact that the posterior cingulum and the postero-internal cusp are a contiguous single structure, together with the fact that the *Nannopithec*-fold is not present, the postero-internal cusp must be identified as the hypocone, and not as a pseudohypocone which is developed on the *Nannopithec*-fold or formed by the splitting off from the protocone.

The morphology of M^2 almost agrees with that of M^1 . M^2 is a little more elongated transversely than in M^1 . The buccal side of the paracone and the buccal half of the mesostyle are more well developed than in M^1 . The small ridge between the postprotocrista and the metacone is more well developed and well defined than in M^1 . On the middle of this ridge, a small cusp is developed. The entoflexus is narrower than in M^1 , and forms an acute V-shaped valley. The crown base lingual to the protocone and the hypocone extends lingually forming W-shaped ledge. This structure is more developed in M^2 than in M^1 .

The morphology of M_1 at hand is almost identical to that of the corresponding tooth of the holotype of *Stirtonia tatacoensis*. The only obvious difference between them is seen in the morphology of the postero-lingual corner of the tooth. On M_1 at hand, the entoconid is clearly separated from the hypoconulid by a small but distinct notch, whereas in the holotype, these two cusps are united by a low ridge. The other morphology is identical to each other.

THE DEGREES OF TOOTH WEAR: P^2 , P^3 and P^1 are almost unworn. The apex of the paracone of P^4 is just started to wear. On M^1 , the four main cusps are just started to wear: the species of these cusps are only slightly worn. M^2 is unworn. On M_1 , the trigonid

is worn; on the unworn holotype of *Stirtonia tatacoensis*, the protoconid is clearly high above the floor of the trigonid basin, whereas on M_1 at hand, the worn protoconid approaches to the level of the trigonid basin floor. The metaconid remains unworn. On the talonid of M_1 , the cristid obliqua and the entocristid are slightly worn, but the distinct hypoconid and entocristid are almost unworn.

As far as the occlusal pattern is concerned, the anterior half of M^1 occludes with the posterior half of M_1 . Specifically, the protocone occludes with the entocristid and the paracone does with the cristid obliqua. On the specimens at hand, the degree of wear of the protocone and the paracone of M^1 is almost identical to the degree of wear of the entocristid and the cristid obliqua of M_1 . The fact just mentioned is not antagonistic to the conclusion that all the specimens at hand belong to the same individual.

In adult individuals, the protoconid of M_1 occludes with the paracone and especially with the posterior ridge from the paracone of P^1 . But a discrepancy between the degrees of wear of M_1 and P^1 at hand is conspicuous: The protoconid of M_1 is well worn whereas the posterior ridge of the paracone of P^1 is almost unworn. Don't these two teeth belong to the same individual? It is deduced that the eruption of M_1 precedes the P^1 eruption so that M_1 occluded with the deciduous P^1 to begin with and started to wear, and a little before the death of animal P^1 erupted to occlude with the protoconid of M_1 . Because of the difference in time of eruptions of M_1 and P^1 , the difference in the degrees of wear of these teeth becomes clear. The difference in the degree of wear is not antagonistic to the conclusion that these two teeth must belong to the same individual.

The postero-lingual portion of P^1 is greatly depressed. The metaconid of M_1 comes in this depressed portion on P^1 when occlusion so that the metaconid does not occlude with any structure on P^1 . Because of this sort of structure-occlusion relationship, the metaconid of M_1 remains unworn.

DISCUSSION: The molars of *Stirtonia tatacoensis* are characterized by the following features; (1) M^1 and M^2 are squared, (2) the each main cusp of the upper is distinct, (3) a conspicuous mesostyle is present between the paracone and the metacone and the latter two cusps are widely separated from each other, (4) the hypocone is distinct but clearly lower than the protocone, (5) the *Nannopithecus*-fold is not present and the postprotocrista does not connect with the hypocone, and (6) the trigonid higher than the talonid, but not so higher than in, for example, *Saimiri*.

The South American monkeys (Ceboidea) are usually divided into two families: Callithricidae and Cebidae (including *Callimico*). In Callithricidae together with *Callimico*, the hypocone is greatly reduced or absent. *Stirtonia* is not a member of this group. In some of the cebids, i.e., *Cebus*, *Pithecia*, *Cacajao* and *Chiropotes*, each cusp of the upper molars are blunt and less distinct, and the difference in height between the trigonid and the talonid is not clear. Most of the other members of the cebids lack a conspicuous mesostyle except for *Brachyteles* and *Alouatta*. In *Brachyteles*, the paracone and the metacone are elongated antero-posteriorly and situated close together. A tiny mesostyle is present between them. The antero-lingual part of M^1 is truncated so that the molar is not squared. Phylogenetically, *Stirtonia* does not have any relationship with *Brachyteles*. Only *Alouatta* shares the similar morphological characters of molars with *Stirtonia*.

In *Alouatta*, M^1 and M^2 are squared and each cusp of the upper molars is distinct as in *Stirtonia*. Because of the general similar morphological features, it is safe to conclude that

Stirtonia of the late Miocene gave rise to extant *Alouatta*. The morphology of the upper molars of *Alouatta* is different from that of *Stirtonia* in the following features; the mesostyle is situated more posteriorly, closer to the metacone: the paracone is more elongated transversely, especially towards lingually: the preprotocrista runs more straightly towards antero-buccally: a ridge lingual to the metacone on M^1 is more distinct, forming as a metaconule: and, most importantly, the connection between the protocone and the hypocone is seen (discussed more in detail later). The obvious difference in dental morphology between *Stirtonia* and *Alouatta* is found in the premolar structure. The premolars of *Stirtonia* is clearly wider transversely than those of any species of *Alouatta*, especially so than in *A. seniculus* and *A. caraja*. In the latter two species, the premolars are more compressed transversely, and especially P^2 is longer than wide. Even on P^4 , the width is almost the same as the length. In *Stirtonia*, P^2 is clearly wider than long and on P^4 the width is almost twice as much as the length. The premolar structure of *Alouatta guariba* is closer to that of *Stirtonia* than that of *A. seniculus* or *A. caraja*, but even though, the premolars of the former is a little more compressed than in *Stirtonia*. The difference in premolar structures warrants the separation of *Stirtonia* from *Alouatta* in a generic level. Among the species of *Alouatta*, *A. guariba* retains a more primitive feature seen in its antecedent, *Stirtonia* than *A. seniculus* and *A. caraja*.

Stirtonia tatacoensis was originally described by STIRTON (1951) under the name of *Homunculus tatacoensis*. Later, HERSHKOVITZ (1970) separated it from the genus *Homunculus* and based on the species he established a new genus *Stirtonia*. Stirton (op. cit.) believed that the species must belong to the genus *Homunculus*. The holotype of *H. patagonicus*, the genotype of *Homunculus* is a lower jaw fragment with I_2 , C, P_2 , P_3 , P_4 , and heavily worn M_1 and M_2 . It is hard to imagine the exact crown pattern of it, but judging from the outline of the crown base of M_1 and M_2 , the width of the trigonid is almost the same as that of the talonid both on these teeth. This condition is seen in most of the ceboids, both in Callithricidae and Cebidae and hence the condition is regarded as primitive in the South American monkeys. In "*Homunculus*" *tatacoensis*, the talonid is greatly wider transversely than the trigonid and this warrants the separation of "*Homunculus*" *tatacoensis* from *Homunculus* in a generic level as Hershkovitz believed.

The holotype of "*Pitheculus australis*" is a lower jaw fragment with unworn M_2 . The size of M_2 is a little larger than that of extant *Aotus*. In "*Pitheculus australis*", the small but distinct hypoconulid is present on M_2 but except for the presence of this small cusp, the general morphology of M_2 of this form is exactly the same as that of M_2 of *Aotus*. *Pitheculus* was recognized as a distinct genus in the possession of a prominent median buccal cusp in the inflection between the protoconid and the hypoconid. But as Stirton (op. cit., p. 331) stated, this could be a feature in individual variation. Because the holotype of *Homunculus patagonicus* has worn teeth, it is not easy to know the phylogenetic relationship between it and *Pitheculus australis*. As they are contemporaneous, the size of molars is the same and the outline of the crown base of molars is almost identical, they should be very closely related to each other if not conspecific. If this is the case, *Homunculus* should be related to living *Aotus* phylogenetically.

HYPOCONE OR PSEUDOHYPOCONE FOR THE POSTERO-INTERNAL CUSP OF THE UPPER MOLARS

The concept of a pseudohypocone for the postero-internal cusp of upper molars which represents a posterior budding from the main antero-internal cusp or protocone was

introduced by STEHLIN (1916) who originally designated as a pseudypocone. The concept was applied to the North American Eocene *Pelycodus-Notharctus* lineage and the validity has been established for this lineage. Because of the general morphological similarities between *Notharctus* and extant South American Platyrrhines Gregory (1920) believed that the postero-internal cusp of the upper molars of Platyrrhines is “apparently a pseudohypocone”. *Notharctus* possesses a conspicuous mesostyle on its upper molars as in *Alouatta* which is the only member among the ceboids possessing a mesostyle on upper molars with the exception of *Brachyteles* which occasionally has it. GREGORY (1920, p. 220) described, “*Notharctus* also shows certain important special resemblances with the Platyrrhini in the form of the incisors, in the formulae of the adult and deciduous dentitions of evolution of the premolars; this last resemblance is especially striking if we compare the lower premolars of *Notharctus pugnax* with those of *Alouatta*. If the posterointernal cusps of the upper molars of the Platyrrhini be pseudohypocones as the conditions in *Callithrix* apparently indicate, another and very important resemblance must be recorded”.

Thus, the concept that the platyrrhine ceboids may or may not have pseudohypocone on their upper molars was introduced by Gregory. He also wrote (op. cit. , P. 229), “... in spite of the wide structural and paleontological hiatus between the Middle Eocene *Notharctus* on the other hand and the Miocene and recent New World primates on the other, we can feel reasonably confident that although *Notharctus* may not be a direct ancestor of the latter group, it is in general a structural ancestor, *Notharctus* possesses a pseudohypocone.” Unfortunately the direct phylogenetical relationship between them has not been established. Gregory (op. cit.) once believed their phylogenetical relationship but, later, he became skeptical of this matter. He (1922, pp. 220–221) confessed, “But instead of postulating a direct deviation of the modern *Alouatta* from the Eocene *Notharctus crassus*, it seems safer to regard the *Notharctus*-like characters of the *Alouatta* molars as partly homoplastic and secondary, ... we cannot assert that the Notharctidae are the direct ancestors as well as the remote structural ancestors of the Platyrrhinae.”

In the *Pelycodus-Notharctus* lineage, the clear *Nannopithec*-fold runs from the protocone to the pseudohypocone. Thus the connection between these two cusps is seen. In the ceboids, the connection between them and the connection between the postero-internal cusp and the posterior cingulum show a fairly wide range of variation. GREGORY (1922, p. 220) recognized this phenomenon and wrote, “... *Callicebus* seems to be on the whole the most primitive... The hypocones are connected with the posterior slopes of the protocones and are therefore apparently pseudohypocones like those of the Notharctidae.... In *Aotus* on the other hand, the hypocones are quite prominent and appear to be connected with the cingulum. In *Alouatta* they are connected both with the cingulum and with the crest of the protocone; in many or perhaps all of the remaining Cebidae, the hypocones are widely connected with the cingula and well separated from the protocone by a deep cleft. Thus the more primitive genera approach the conditions in the Notharctidae, while the more specialized have lost them.”

The last statement given by GREGORY must be proved by fossil evidences. Unfortunately, no ancestral forms to *Callicebus*, *Aotus* and *Alouatta* have been known. Since the days of Gregory, controversies for and against the GREGORY's opinion were based only on living materials because of the lack of paleontological records. Among them, HÜRZELER's (1948) criticism is worth discussing here. He introduced the concept of the *Nannopithec*-fold for the Tertiary primates. On the upper molars of the Eocene *Nannopithec*, two ridges runs posteriorly from the protocone; one ridge extends towards the base of the metacone so that the

ridge is identified as the postprotocrista, and the other ridge runs postero-buccally between the postprotocrista and the postero-internal cusp. The postero-internal cusp is developed on the posterior cingulum, and the connection between the cusp and the protocone is not pre-est. The ridge from the protocone other than the postprotocrista is called the *Nannopithec*-fold by HÜRZELER.

HÜRZELER recognized a wide range of variation of the structure of the *Nannopithec*-fold on the upper molars of *Necrolemur* cf. *Zittli*; in most of the specimens, the *Nannopithec*-fold does not connect with the postero-internal cusp both on M^1 and M^2 , in some the fold connects with that cusp on M^1 but does not on M^2 , and in some specimens the *Nannopithec*-fold connects with the postero-internal cusp both on M^1 and M^2 . From these evidences, HÜRZELER decided that the *Nannopithec*-fold does not connect with the postero-internal cusp in the primitive form and in some advanced forms the fold migrates lingually to connect with that cusp so that the connection between the cusp and the protocone might be secondary. The secondary connection between these two cusps gives the impression that the postero-internal cusp may be formed by splitting off from the protocone. Thus HÜRZELER denied the validity of the concept of a pseudohypocone itself and concluded that the postero-internal cusp of all the primates is developed on the posterior cingulum and hence the cusp is a hypocone.

Moreover, HÜRZELER recognized the similar morphological variations in extant *Alouatta seniculus* (red howler monkeys) as in *Necrolemur* mentioned above. According to him, in most specimens of *A. seniculus*, the connection between the protocone and the postero-internal cusp is present both on M^1 and M^2 . But in one specimen (Mus. Basel, No. 69422), whereas the connection between these two cusps is present on M^1 , the connection is not seen on M^2 . On M^2 of this specimen, a narrow but deep cleft separates the postero-internal cusp from a ridge running from the protocone. Based on the analogy to the condition seen in *Necrolemur*, HÜRZELER decided that the connection between these two cusps in *Alouatta seniculus* as well is secondary and the postero-internal cusp is undoubtedly a derivation of the posterior cingulum. Thus the postero-internal cusp in *Alouatta* is a hypocone, not a pseudohypocone.

On upper molars of *Alouatta*, only one ridge runs posteriorly from the protocone. On most specimens of *Alouatta*, this ridge connects with the postero-internal cusp both on M^1 and M^2 . HÜRZELER identified the ridge running from the protocone as the *Nannopithec*-fold and in his discussion he did not mention about the presence or absence of the postprotocrista at all. If the ridge should be the *Nannopithec*-fold as HÜRZELER believed, where is the postprotocrista? Is the postprotocrista reduced greatly and vanished completely in *Alouatta*? Careful identification of the ridge running posteriorly from the protocone is inevitable and the discussion on the homology of the postero-internal cusp based on the analogy of the condition in *Alouatta* to that in *Necrolemur* may not be a logical way, because the lingual half of upper molars in *Alouatta* has a different structure from that in *Necrolemur*.

The determination of the homology of the ridge mentioned above must be based on fossil evidences. No upper dentition ancestral to extant *Alouatta* has long been known. But now, the first paleontological record for or against the controversies discussed above is available. As stated above, in *Stirtonia* which is thought to be an ancestral stock to *Alouatta*, the only one ridge runs posteriorly from the protocone and ridge extends between the metacone and the postero-internal cusp both on M^1 and M^2 . The ridge is clearly separated from the postero-internal cusp by a deep entroflexus and the latter cusp is developed on the posterior cingulum. So the ridge must be identified as the postprotocrista. The *Nannopithec*-fold is not

present on the upper molars of *Stirtonia*. The postero-internal cusp is not raised on the *Nannopithecus*-fold but on the posterior cingulum so that the cusp is not regarded as a pseudohypocone but as a hypocone or a euhypocone (REMANE, 1960).

In *Alouatta*, the only one ridge runs posteriorly from the protocone on M¹ and M² as in *Stirtonia*. *Stirtonia* gave rise to *Alouatta* as discussed above so that the ridge on upper molars of *Alouatta* which unites the protocone and the postero-internal cusp is homologous to the ridge posterior to the protocone in *Stirtonia* and hence the ridge must be regarded as the postprotocrista, not as the *Nannopithecus*-fold, as HÜRZELER believed. Moreover, the postero-internal cusp of the upper molars of *Alouatta* is not a pseudohypocone but a hypocone.

In *Stirtonia*, the postprotocrista runs buccal to the hypocone and does not connect with the cusp. Along the course of the evolution from the late Miocene *Stirtonia* to recent *Alouatta*, the postprotocrista migrates more lingually and finally connects with the hypocone. Thus the connection between the protocone and the hypocone in *Alouatta* is surely secondary and the *Notharctus*-like characters of the molars of *Alouatta* is attained by a homoplastic evolution.

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