Introduction

It is increasingly apparent that the Greater Antilles possessed a diverse array of platyrrhine primates during geologically recent times. To date, primate remains have been recovered from cave sites on three of these islands—Jamaica, Hispaniola and Cuba (Ameghino, 1910; Miller, 1916, 1929; Williams & Koopman, 1952; Rimoli, 1977; MacPhee & Woods, 1982; Ford & Morgan, 1986, 1988; Ford, 1990; MacPhee & Fleagle, in press). Some of this material has yet to be formally described and the number of good species represented in existing collections is unclear. However, there were clearly several, all endemic and apparently limited to single islands (for details, see Ford, 1990).

Only one extinct primate has previously been reported from Cuba, the atelid *Ateles anthropomorphus* (Ameghino, 1910; Arredondo & Varona, 1983). In this paper we formally announce the discovery of a second Cuban endemic; this new monkey is also an atelid, but its cladistic affinities lie with howler monkeys rather than spider monkeys.

Systematic paleontology

*Paralouatta Rivero and Arredondo, new genus*

Type Species: *Paralouatta varonai* Rivero and Arredondo, new species.

Type Locality, Associated Fauna, Distribution, and Age: As for type species.

Etymology: *Para*, "beside", + *Alouatta*, the living howler monkey of South and Central America.

Diagnosis: As for the type species.

*Paralouatta varonai Rivero and Arredondo, new species*

Holotype and Only Referred Specimen. Cranium lacking portions of the face and anterior dentition (Figures 1 and 3), Museo Nacional de Historia Natural provisional accession number 90-25 (MNHN 90-25). Discovered 23 August 1987 by Rolando Crespo Diaz, Grupo Espeleológico “Pedro A. Borrás” of the Sociedad Espeleológica de Cuba.
Type locality: Cave deposit in Cueva del Mono Fósil, situated on the south slope of the Sierra de Galeras, Cordillera de Guaniguanico, municipality of Viñales, Pinar del Río province, Cuba.

Associated fauna and distribution: The holotype of Paralouatta varonai was discovered at the bottom of a shaft within Cueva del Mono Fósil, in association with a primate distal humerus and the remains of several other vertebrates (including Solenodon, Geochelone and several species of megalonychid sloths). A second expedition to this cave in February, 1988 failed to recover additional remains, but three fossils of primate-like aspect—a distal tibia, proximal femur (immature) and phalanx—were subsequently discovered in Cueva Alta, a nearby cave on the same hillside. As currently known, therefore, the distribution of Paralouatta varonai is restricted to the area of the type locality in western Cuba.

Age: Of probable late Quaternary age judging by associated fauna.

Etymology: Named after our esteemed colleague and leading student of Cuban mammals, Luis S. Varona.

Diagnosis: A platyrrhine primate with skull size in range of Alouatta and other large Atelinae. Differs from extant Callitrichidae in possessing a combination of: (1) three molars (excepting Callimico), (2) large hypocones on at least M1 and M2 and (3) large face with elongated rostrum. Differs from Cebidae in possessing: (1) low, tapering neurocranium, (2) pronounced lateral expansion of face, (3) more upwardly sloping curve of Spee and (4) three-rooted P3 and P4 with widely furcated buccal roots.

Agrees with Atelidae in: (1) size and relative conformation of molars and premolars and (2) various cranial features (e.g., frontal pneumatization, large face, well developed supra-orbital tori). Within extant Atelidae, the strongest resemblances are to Alouatta; these include: (1) form of hafting of the neurocranium and face, (2) deep malar body, (3) marked lateral flaring of the maxillary root of the zygomatic process and (4) low, posteriorly-tapering cranial vault. The first three traits are strongly derived and represent unique resemblances to Alouatta.

Differs from Alouatta in ways that are probably primitive for the most part, including: (1) foramen magnum more downwardly-directed, (2) nuchal plane less vertically oriented, (3) stylar shelves on molars and premolars inconspicuous and (4) curve of Spee opening less sharply upward. Possesses three-rooted P3 and P4, a ?primitive feature which sporadically occurs in a few extant platyrrhines and the Miocene alouattin Stirtonia.

Contrasts with all other platyrrhines except Aotus in possessing exceptionally large orbits relative to cranial size.

Description

Although it is highly probable that the primate-like postcranials from Cueva del Mono Fósil and Cueva Alta are referable to Paralouatta, their formal assignment must await detailed study, and this report will be limited to an evaluation of the holotype skull. Likewise, comparisons to the much smaller Ateles anthropomorphus are unnecessary, because this taxon is unquestionably a spider monkey (for a detailed description of the latter species, see Arredondo & Varona, 1983).

The higher-level systematics of Platyrhini is in considerable flux at the moment (e.g., Ford, 1986; Kay, 1990; Rosenberger et al., 1990). As we shall not be concerned with fine
PARALOUATTA VARONAI, A NEW QUATERNARY PLATYRRHINE

resolution of cladistic relationships in this paper, we will simply adopt Ford's (1986) concept of the contents of higher level taxa, to which the reader is referred. "Large-bodied platyrrhines" will mean Atelinae (i.e., Alouatta, Brachyteles, Ateles, Lagothrix); the first-named genus is the only member of Tribe Alouattini (informally, alouattins), while the other three are grouped as Tribe Atelini (informally, atelins).

Cranium
The holotype of Paralouatta varonai is well preserved, except in the facial region. The anterior portions of the interorbital region, nasal cavity, and palate have been lost, as have portions of the zygomatic arches and orbital rims. The basicranium, which has not yet been fully cleaned, seems to be intact except for minor damage to the auditory bullae and abrasions to major processes.

The skull is approximately equal in projected length to those of the largest extant atelines, such as Brachyteles and Alouatta (Figures 1 and 2), but differs in proportions and numerous morphological details. Nearly all cranial sutures can be traced. The maxillary third molars are severely worn, so the specimen is assumed to be adult. Measurements of the cranium and dentition are presented in Tables 1 and 2.

Midline structures of the face are mostly lost, including all of the nasal region except the floor and lateral parts of the maxillary paranasal sinuses. However, enough remains of the orbits to be certain that they were large compared to skull size and rather obliquely oriented relative to the Frankfurt plane (c. 50°). The supraorbital tori are rather large and may have extended to the midline, somewhat as in atelines (although in confirmation the best overall match is with Pithecia).

Orbital height, defined as the maximum distance between the superior and inferior orbital rims, could be measured on the right side only (Table 2). Prosthion–opisthocranion length could not be taken because of damage to the face, but it was possible to measure foramen magnum width and the diagonal distance between the superior orbital margin and external occipital protuberance ("modified braincase length"; Table 2). Using these variates, we find that Paralouatta had orbits that were approximately as large, in a relative sense, as those of Aotus (Table 2). Assuming that the orbital margins would have been broadly ovoid in outline when intact, as they are in most extant platyrrhines, we conclude that the external walls of the orbits must have flared outward to a considerable degree.

Although the external surface of the interorbital septum is not present, it was possible to measure septal width within the orbit proper, at the place where the septum is narrowest in most extant platyrrhines. Septal width at this position is approximately 8 mm, which is comparable to the equivalent width in other atelids. Elucidation of the composition of the orbital mosaic and the preserved parts of the nasal cavity will have to await additional cleaning.

Other noteworthy features seen in frontal aspect are the robusticity and depth of the maxillary corpora (orbitale to zygomaxillare, Table 1) and the very low elevation of the frontal bone above the supraorbital tori. In these respects the fossil strongly resembles Alouatta to the exclusion of other large-bodied platyrrhines. There is no sign of a canine fossa on the preserved parts of the maxillae (see Dentition).

The frontal sinus has not been adequately cleaned but it is present and appears to have a honeycombed texture (as defined by Hershkovitz, 1977). Large cellules, judged to be pneumatic chambers connected with the frontal sinus, pass laterally through the supraorbital tori and into the sheared-off lateral walls of the orbital rim. Alouatta has an extensively
pneumatized frontal (Saban, 1964), but other large-bodied platyrrhines also display significant degrees of pneumatization according to Hershkovitz (1977). Whether the pattern of pneumatization is specifically similar to that of any extant platyrrhine, and how pattern may be controlled by body size, remain to be determined.
There are three infraorbital foramina on the specimen’s left side and two on the right. On the better-preserved right side there are three malar foramina, two large and one considerably smaller. Only the ventral half of one malar foramen is preserved on the left side. _Alouatta_ and other atelines normally have one extremely large malar foramen and one or more smaller ones, but there is notable intrageneric and interspecific variability in foraminal size and number (Hershkovitz, 1977; pers. obs.).
Table 1  
Cranial measurements (mm) of *Paralouatta veronai* MNHN 90-25

<table>
<thead>
<tr>
<th>Measurement</th>
<th><em>Paralouatta</em></th>
<th><em>Alouatta villosa</em></th>
<th><em>Alouatta seniculus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Glabella–opisthocranion (estimated)</td>
<td>79.0</td>
<td>4.8</td>
<td>5.1</td>
</tr>
<tr>
<td>Bregma–lambda</td>
<td>31.0</td>
<td>7.6</td>
<td>7.4</td>
</tr>
<tr>
<td>Basion–bregma</td>
<td>47.9</td>
<td>8.1</td>
<td>8.0</td>
</tr>
<tr>
<td>Orbitale–zygomatic line (right side)</td>
<td>21.3</td>
<td>8.2</td>
<td>8.5</td>
</tr>
<tr>
<td>Bizygomatic line</td>
<td>67.1</td>
<td>8.3</td>
<td>8.2</td>
</tr>
<tr>
<td>Staphyline–basion</td>
<td>53.8</td>
<td>7.3</td>
<td>7.0</td>
</tr>
<tr>
<td>Bizygomatic line</td>
<td>57.5</td>
<td>5.4</td>
<td>6.2</td>
</tr>
<tr>
<td>Bimastoid (bieuryion) width</td>
<td>37.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biparietal width</td>
<td>31.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>External acoustic canals, minimum distance between inferior margins</td>
<td>40.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>External acoustic canal, maximum horizontal width</td>
<td>7.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palate, maximum width between alveolar borders at level of P3</td>
<td>31.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palate, maximum width between alveolar borders at level of M1</td>
<td>37.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palate, maximum width between alveolar borders at level of M3</td>
<td>34.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Dentition

<table>
<thead>
<tr>
<th>Tooth</th>
<th><em>Paralouatta veronai</em></th>
<th><em>Alouatta villosa</em></th>
<th><em>Alouatta seniculus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>P4</td>
<td>mesiodistal</td>
<td>5.0</td>
<td>5.1</td>
</tr>
<tr>
<td></td>
<td>buccolingual</td>
<td>8.2</td>
<td>8.2</td>
</tr>
<tr>
<td>M1</td>
<td>mesiodistal</td>
<td>6.8</td>
<td>7.1</td>
</tr>
<tr>
<td></td>
<td>buccolingual</td>
<td>8.1</td>
<td>8.0</td>
</tr>
<tr>
<td>M2</td>
<td>mesiodistal</td>
<td>6.4</td>
<td>7.3</td>
</tr>
<tr>
<td></td>
<td>buccolingual</td>
<td>8.2</td>
<td>8.5</td>
</tr>
<tr>
<td>M3</td>
<td>mesiodistal</td>
<td>5.2</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>buccolingual</td>
<td>7.7</td>
<td>7.7</td>
</tr>
<tr>
<td>M1–M3 length</td>
<td>(24.0, 23.6)</td>
<td>23.8</td>
<td></td>
</tr>
</tbody>
</table>

1Definition of cranio metric points based on Hershkovitz (1977).
2Data for *Paralouatta* presented as (right, left) mean; data for *A. villosa* and *A. seniculus* from Swindler (1976).

On the outer wall of the orbit, a large zone of parietal–zygomatic contact externally prevents the approximation of the frontal and alisphenoid. This arrangement is found in many platyrrhines and is regarded as primitive by Hershkovitz (1977).

The fossil’s outstanding feature in norma lateralis is the markedly oblique hafting of the facial region onto the neurocranium, in the manner of *Alouatta* and (to a lesser degree) atelins, but in sharp contrast to the more vertical orientation found in cebids and callitrichids. Attempts to X-ray the cranium, in order to utilize craniometric points for quantifying the degree of hafting, were unsuccessful.

The mastoid area is rugose and markedly projecting, much as in *Alouatta*. Small defects in the surface of the mastoid, due to breakage, indicate that this area was significantly pneumatized, as it is in many platyrrhines (Saban, 1964).

Of interest is the fact that the occipital condyles are visible in this aspect, projecting below the plane of the auditory bullae. In *Alouatta*, the condyles cannot be observed in norma lateralis because they are backwardly pointing and hidden by the nuchal crest. An additional
**Table 2** Orbital height, modified braincase length and foramen magnum width in *Paralouatta* and selected extant platyrhines

<table>
<thead>
<tr>
<th>Taxon</th>
<th>1. Orbital height</th>
<th>2. Modified braincase length</th>
<th>3. Foramen magnum width</th>
<th>Index 1/2</th>
<th>Index 1/3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paralouatta varonai</em></td>
<td>28.5</td>
<td>73.2</td>
<td>13.4</td>
<td>0.39</td>
<td>2.13</td>
</tr>
<tr>
<td><em>Brachyteles arachnoides</em></td>
<td>23.6 (22.7-24.8)</td>
<td>79.9 (77.5-83.3)</td>
<td>14.8 (14.8-15.7)</td>
<td>0.30</td>
<td>1.59</td>
</tr>
<tr>
<td><em>Ateles geoffroyi</em></td>
<td>21.1 (20.6-21.8)</td>
<td>77.7 (73.6-79.4)</td>
<td>13.8 (12.7-16.0)</td>
<td>0.27</td>
<td>1.54</td>
</tr>
<tr>
<td><em>Lagothrix lagotricha</em></td>
<td>21.6 (19.9-23.3)</td>
<td>75.5 (70.1-81.1)</td>
<td>12.4 (12.1-13.1)</td>
<td>0.29</td>
<td>1.74</td>
</tr>
<tr>
<td><em>Alouatta palliata</em></td>
<td>22.1 (21.3-23.4)</td>
<td>67.7 (62.9-71.8)</td>
<td>12.1 (10.8-12.9)</td>
<td>0.33</td>
<td>1.84</td>
</tr>
<tr>
<td><em>Pithecia monachus</em></td>
<td>18.1 (18.0-18.4)</td>
<td>57.6 (55.2-59.3)</td>
<td>10.4 (9.7-10.9)</td>
<td>0.32</td>
<td>1.74</td>
</tr>
<tr>
<td><em>Cacajao caluus</em></td>
<td>21.0 (20.1-21.9)</td>
<td>67.8 (64.7-70.5)</td>
<td>12.1 (11.2-13.0)</td>
<td>0.31</td>
<td>1.75</td>
</tr>
<tr>
<td><em>Aotus lemurinus</em></td>
<td>18.5 (17.9-19.0)</td>
<td>45.0 (42.5-46.7)</td>
<td>8.3 (8.2-8.5)</td>
<td>0.41</td>
<td>2.23</td>
</tr>
<tr>
<td><em>Aotus trivirgatus</em></td>
<td>19.5 (18.5-20.8)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Callibehus moloch</em></td>
<td>15.2 (14.2-16.3)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Cebus apella</em></td>
<td>20.1 (19.4-21.4)</td>
<td>69.7 (67.8-71.9)</td>
<td>11.8 (11.1-12.4)</td>
<td>0.28</td>
<td>1.70</td>
</tr>
<tr>
<td><em>Callithrix jacchus</em></td>
<td>8.8 (8.5-9.3)</td>
<td>34.6 (33.5-35.7)</td>
<td>5.8 (5.5-6.1)</td>
<td>0.26</td>
<td>1.52</td>
</tr>
</tbody>
</table>

1. *N* = 4 (2 males, 2 females) for each taxon except *Paralouatta varonai* (*N* = 1) and *Brachyteles arachnoides* (*N* = 3, sex not known); data for *Aotus trivirgatus* (*N* = 9) and *Callibehus moloch* (*N* = 9) from Hershkovitz (1974).

2. Maximum distance between superior and inferior sills, in parasagittal plane.

3. Minimum distance between superior sill and external occipital protuberance, diagonal to midsagittal plane.


An unusual feature of the fossil is that the condyles are well separated from surrounding bone, so that from the ventral aspect they appear to be “elevated” above the general basicranial plane. A configuration identical to this is not seen in other platyrhines. The nuchal planum as a whole is sharply inclined rather than subvertical, another point of contrast with *Alouatta*. However, the planum is adorned with rugosities, pits, and crests for muscle attachment, as in *Alouatta* (and many other platyrrhine quadrupedalists) but not like *Ateles* and *Brachyteles* whose nuchal plana are convex outward and less rugged in appearance.

Another noteworthy resemblance to *Alouatta*, best appreciated in lateral and superior aspects, is the rather small size, low profile, and posterior taper of the neurocranium. In atelins and pitheciines, the braincase is more globular, higher, and posteriorly expanded. Maximum biparietal width of the braincase occurs slightly anterior to a coronal plane through the external auditory canals. The temporal lines are sinuous and converge posteriorly to a greater degree than in extant atelids.

The posterior stumps of the zygomatic arches join large, shelf-like suprameatal crests that are posteriorly continuous with the nuchal crest. Suprameatal crests, marking the ventral attachment of the posterior temporalis, are found in most platyrrhine subfamilies, although they are particularly large and sharp-margined only in *Lagothrix*, pitheciines, and *Alouatta*. *Paralouatta* appears to have lacked the upturned outer margin of the zygomatic process of the squamosal distinctive of *Alouatta*, suggesting that the zygomatic arch was not excessively robust. The temporal fossa was probably also relatively smaller than in living howler monkeys. The postglenoid processes are damaged; they were apparently strong and projecting, as in the majority of cebids and atelids, but perhaps less developed than in *Alouatta*.

Also seen best in superior aspect is the conspicuous lateral flaring of the maxillae at the root of the zygomatic process. In platyrhines other than *Alouatta*, the origin of the maxillary root of the zygomatic process is hidden by the lateral rims of the orbits. (Even though the rims are...
incomplete in the fossil, flaring begins anterior to the position of the inferior orbital sill and therefore would still be visible from the superior aspect in an intact specimen.)

As already noted, the position of the foramen magnum is much as it is in other platyrrhines, being more anteriorly placed than in *Alouatta* and facing more downward than backward. Although comparatively low, the auditory bullae do not project as much as in *Pithecia* or *Cebus*, and in this respect resemble *Alouatta* and *Lagothrix*. The flattening of the ventral surface of the bullae, seen in some *Brachyteles*, is not present in the fossil. The rim of the ectotympanic is festooned with a large number of tiny transverse ridges, giving it a denticulated appearance similar to that seen in *Pithecia* and *Alouatta* but not in atelids, callitrichids, or cebids.

**Dentition**

Although the dentition and alveolar borders are not fully preserved (Figures 1 and 3), it appears that the curve of Spee opened upwards to only a moderate degree, as in atelids and pitheciines. The highly derived condition seen only in *Alouatta*, in which the curve opens steeply upwards, is not present.

The palate is in poor condition. The only noteworthy feature of the preserved part is a moderate upward curvature of the palatines, immediately in advance of the choanal openings. *Alouatta* displays a much more marked upward curvature. In other platyrrhines the roof of the mouth is essentially flat, or is canted upward very slightly (e.g. *Callithrix, Brachyteles*).

Remaining elements of the maxillary dentition include part or all of the crowns of the molar teeth on both sides, as well as two premolar crowns on the right side and one on the left. The dental arcades bow outward between M3 and M1, then converge anterior to the first molar. Similar convergence occurs in *Aotus, Callicebus* and callitrichids, but in atelids the cheektooth rows are more parallel.

All of the cheekteeth are worn almost flat and dentine is broadly exposed in each of them. This precludes any detailed assessment of occlusal surface morphology. M1 is broken on both sides, but appears to have been slightly larger than M2; the third molar is by far the smallest.
The molar crowns are wider buccolingually than mesiodistally, and their long axes are somewhat obliquely set. A faint suggestion of a loph (postprotocrista) can be made out on the right M2. Remnants of the three trigon cusps can be detected on M1 and M2; the lingual cingulum supported both a hypocone and a pericone. It is not possible to determine whether hypocones were present on the last premolars; they may have been bicuspid. No enamel remains on the right P3, which is worn through to its roots. There is little or no indication of a lingual cingulum, stylar shelf, or associated cuspules on any of the preserved teeth, although caution is required in interpretation because of wear.

In front of the preserved right P3 is a pair of tandemly-aligned buccal and lingual root sockets, obviously for the absent P2. This indicates that there were three upper premolars in Paralouatta, as in all other known platyrrhines. However, approximately 2 mm in advance of the P2 alveolus, and separated from it by a conspicuous ridge, is yet another socket, this time with a small portion of a tiny root encased within it. We assume that the tooth at this locus must represent either a retained (deciduous) p2 or a diminutive canine. The equivalent area is not preserved on the left side.

In view of the condition of the holotype dentition, comparisons of Paralouatta to other platyrrhines are necessarily inconclusive. As far as may be judged, the strongest phenetic resemblances are with atelids, in the general size and outline of the individual teeth, absence of well developed buccal cingula, and proportions and conformation of the trigon and talon basins. M1 and M2 are slightly mesiodistally narrower and buccolingually longer than in Alouatta villosa and A. seniculus (Table 1).

The protocone seems to have been set more centrally on the lingual aspect of the tooth than is generally found in living platyrrhines (including Alouatta). Despite the level of wear, it is clear that the cheek teeth lacked enamel crenulation, an important synapomorphy of Pithecia, Cacajao and Chiropotes (as most recently discussed by Kay, 1990). Whether cusp relief was high or low cannot be determined, although it is remarkable that wear has produced nearly flat occlusal surfaces. By contrast, even on extremely worn dentitions of Alouatta and atelids, buccal relief on M1 and M2 remains considerably higher than lingual relief, which reflects original disparity in cusp height on these moieties.

One other feature of Paralouatta that may be a nearly exclusive resemblance to some atelids is the conformation of premolar roots. Because of abrasion to the alveolar border, it is possible to determine that both the P3 and P4 possess two large, widely furcated buccal roots. Kay (1990) regards the presence of three roots on upper premolars as a primitive platyrrhine trait because this condition is found in Apidium and Aegytopithecus. Although we do not dispute the primitiveness of three-rooted premolars for Anthropoidea as a whole, this trait is extremely rare in extant platyrrhines. In our survey of extant platyrrhines, we found three-rooted P4s only in specimens of Brachyteles arachnoides and Alouatta palliata; Hershkovitz (1977) has reported two buccal roots on P4s of some specimens of Cebuella and Callithrix.

**Discussion**

**Affinities**

In view of the diagnosis and description of Paralouatta varonai presented in detail above, lengthy discussion of the affinities of this species is not required. In general design, the skull of the Cuban species is phenetically more like that of atelids than either cebids or callitrichids. This is also confirmed by the character analysis, which more specifically groups Paralouatta with atelids, and, within this group, the alouattins. But it is also equally clear that Paralouatta
differs in some important ways from living howler monkeys (e.g. orbit size, position of foramen magnum), and this justifies its separate recognition at the generic level.

Alouattins have a poor fossil record. The only fossil taxon which is persuasively alouattin in affinity is Stirtonia, from the Miocene La Venta Fm of Colombia. Unfortunately, knowledge of the cranial anatomy of this genus is based exclusively on jaw fragments and isolated teeth, and it is the dentition of Paralouatta that we know least about. Nevertheless, it is of some interest that Paralouatta resembles Stirtonia in: (1) conformation of the curve of Spee and (2) presence of three-rooted P3 and P4 with wide separation of buccal roots (S. victoriae only; Kay et al., 1987). Lack of the pronounced curve is undoubtedly primitive; the sharply upturned conformation of Alouatta is clearly an autapomorphy of this alouattin. Outgroup comparisons imply that three-rooted P3s and P4s are also primitive. Whether Paralouatta and Stirtonia share any of the other traits that distinguish the latter genus from Alouatta will have to be determined from better material.

Orbital morphology
One of the most remarkable derived features of Paralouatta is the relatively large size of its orbits, comparable only to those of Aotus among living platyrrhines. This similarity invites the question whether its activity pattern also resembled that of owl monkeys—that is, was Paralouatta a crepuscular/nocturnal monkey?

According to Schultz' (1940) data, the eyeball of Aotus weighs approximately 3.6 cm³, or 0.35% of its body weight. In other platyrrhines for which data are available, eyeballs are always relatively smaller (0.04–0.16% of body weight). We lack information on body weight and eyeball volume for Paralouatta but we note (Table 2) that foramen magnum width compared to orbital height yields a ratio (2.13) that is only slightly less than equivalent ratios for extant species of Aotus (2.24 and 2.19). All other measured platyrrhines exhibit much smaller ratios (1.52–1.84). Indeed, although the skull of Paralouatta is no larger than those of Brachyteles arachnoides, Alouatta palliata and Lagothrix lagotricha for most external dimensions, its orbital height is greater by margins of 17–24% than in other atelids. These observations may qualify as circumstantial evidence for large eyes, but whether they are strong enough to support a hypothesis of crepuscular/nocturnal activity will remain questionable until a skull with complete orbits is recovered.

Conclusion
Much remains to be done before a clear picture of the nature of the platyrrhine efflorescence in the West Indies will emerge. A paramount challenge is to find Tertiary localities that might shed some light on the origin of this and other parts of the Antillean vertebrate fauna. To date, only a few fossils of Tertiary vertebrates have been found (e.g. Poinar & Cannatella, 1987; MacPhee & Wyss, 1990); none of these are mammalian, save for a few hair shafts from Miocene Dominican amber that may belong to rodents (Poinar, 1988). The morphological distinctiveness of some of the Antillean primate taxa could be interpreted as the result of very early isolation or as the consequence of rapid evolution under novel selective pressures—or very possibly as both, depending on the taxon in question. Such issues are difficult to resolve with no fossils of significant antiquity to anchor speculation.

Although the remains of Paralouatta varonai have not yet been radiometrically dated, in view of their faunal associations it is probable that they are of late Quaternary age. While it may be parsimonious to assume that the extinction of the Cuban primates was primarily the
result of anthropogenic effects, it is puzzling that no remains of these mammals have been found in archaeological sites—despite the fact that the early Amerindian residents of Cuba were small-game hunters (Rouse, 1942).

Acknowledgements

The authors wish to thank the members of the Grupo Espeleológico “Pedro A. Borrás” of the Sociedad Espeleológica de Cuba for their exceptional assistance and cooperation in making fossils available for scientific study. We also thank Gilberto Silva de Taboada (Museo Nacional de Historia Natural) for help with the Spanish draft of this paper, and R. D. E. MacPhee, Gina C. Gould, and Audrone Biknevicius (American Museum of Natural History) for translating and revising it. We are especially grateful to Dr MacPhee for providing much of the data in the tables, and to Lorraine Meeker (American Museum of Natural History) for the excellent photographs used in the figures.

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