Chapter 6
Morphology of Howler Monkeys: A Review and Quantitative Analyses

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Abstract Recognition of a particularly derived eco-behavioral strategy for the genus *Alouatta* has been crucial for studying and understanding its equally derived cranial and postcranial morphology. The unique architecture of the skull and mandible has very likely evolved in relation to both masticatory correlates associated with an increasingly folivorous diet as well as the use of vocal communication associated with social behavior and an energy-minimizing strategy. Comparisons of cranial morphology using three-dimensional geometric morphometrics have highlighted significant interspecific shape differences. *Alouatta seniculus* is the most divergent in both cranial and hyoid morphology and exhibits the most pronounced levels of sexual dimorphism in those areas. Cranial variability is expressed in facial prognathism and airorhynchy, basicranial flexure, and zygomatic height. Inter- and intraspecific differences based on these axes of variation are very likely linked to interspecific variations in diet, behavior, and life history. This is further evident in the dental anatomy of the genus, indicating adaptations to a shift to a more folivorous diet. In addition, recent studies provide further evidence for significant inter- and intraspecific variations in hyoid size and shape. *Alouatta seniculus* possesses the largest and most inflated hyoid bulla, and the species that occupy distributional extremes (*A. palliata*, *A. caraya*) are differentiated by highly distinct hyoid shapes. These data indicate a complex relationship between morphology and behavior, with possible biogeographic implications. In terms of postcranial morphology,

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the forelimb bears a mixture of features that favor quadrupedalism with restricted abduction and overhead extension, providing stable contact and support along branches. In contrast, the hind limb appears to allow for a wider range of movement in all joints, with an emphasis on thigh extension and abduction, leg rotation, and powerful grasping with a habitually inverted foot. Interspecific variation reveals traits that can be ultimately related to subtle differences in the frequency of use of different positional modes, associated with variable eco-social factors. These results, deriving from different anatomical regions, provide evidence for understanding morphological variation across howler species in terms of morphofunctional adaptations, environmental pressure, and niche partitioning.

Resumen Reconocer la particular estrategia eco-comportamental del género *Alouatta* ha sido crucial para estudiar y entender su morfología craneal y post-craneal. La arquitectura única de su cráneo y mandíbula indican que muy probablemente evolucionaron en relación con su aparato masticatorio particular que se encuentra asociado a un incremento de una dieta folívora, así como con su comunicación vocal asociada a su comportamiento social y de estrategia de minimización energética. Comparaciones de la morfología craneal utilizando geometría morfométrica tridimensional resaltan diferencias significativas inter-específicas en la forma del cráneo. *Alouatta seniculus* es la especie más divergente en cuanto a la morfología del cráneo y del hueso hioides, exhibiendo los niveles más pronunciados de dimorfismo sexual en esas áreas. La variabilidad craneal es expresada en el prognatismo facial y airorrinchia, flexión basocraneal y altura zigomática. Diferencias inter- e intra-específicas basadas en estos ejes de variación están muy posiblemente vinculadas a variaciones interespecíficas en dieta, comportamiento e historias de vida. Por otra parte, evidencia adicional de la anatomía dental de este género indica adaptaciones de cambio a una dieta más folívora. Además, estudios recientes proporcionan evidencia adicional de variación inter- e intraespecífica significativas en la forma y el tamaño del hueso hioides. *Alouatta seniculus* posee la bula más larga e inflada del hueso hioides y las especies que ocupan los extremos de distribución del género (*A. palliata*, *A. caraya*) se distinguen por diferencias acentuadas en la forma del hueso hioides. Estos datos indican una compleja interrelación entre morfología y comportamiento, con posibles implicaciones biogeográficas. En términos de la morfología craneal, los miembros anteriores muestran una combinación de atributos que favorecen el cuadrupedalismo con abducción restringida y extensión amplia que proporciona contacto estable y soporte en las ramas. En contraste, los miembros posteriores parecieran permitir un mayor rango de movimiento de todas las articulaciones, con énfasis en la extensión y abducción del muslo, rotación de la pierna y una mayor capacidad de asir con una inversión común del pie. Variación interespecífica revela rasgos que ultimadamente podrían estar vinculadas con diferencias sutiles en la frecuencia de uso de diferentes posturas, asociadas con factores eco-sociales. Estos resultados, que derivan de diferentes regiones anatómicas, proporcionan evidencia para entender la variación morfológica a través de las especies de monos aulladores en términos de adaptaciones morfo-funcionales, presiones ambientales y partición de nichos.

Keywords *Alouatta* • Cranium • Hyoid • Morphometrics • Postcranium • Teeth

Palabras clave *Alouatta* • Cráneo • Hueso hioides • Morfometría • Postcráneo • Dientes

6.1 Introduction

The monophyly of atelines as a group is unquestioned, but the interrelationships of the genera within the group remain unclear. The phylogenetic signals from molecular and morphological data disagree on the relationships among *Lagothrix*, *Brachyteles*, and *Ateles*, but all phylogenetic hypotheses distinguish *Alouatta* from the rest: howlers apparently diverged first from the group around 15 MA and evolved unique morphobehavioral adaptations related to increased folivory, energy-minimizing ecological strategies, cautious above-branch quadrupedal positional behavior, and enhanced sound production (Rosenberger and Strier 1989; Hartwig 2005 for a review). The distinctiveness of *Alouatta* was pointed out very early by Lacépède (1799) and was later highlighted by several authors (e.g., Lönnberg 1941; Hershkovitz 1949; Hill 1962). In this chapter, we attempt to point out the unique morphology of the genus *Alouatta* focusing on cranial, dental, hyoid, and postcranial traits. For these purposes, two approaches were adopted: review of the literature on cranial, dental, hyoid, and postcranial characters as well as quantitative multivariate analyses of new data on cranial and hyoid morphology. Reviews will help the reader to appreciate the derived morphology of *Alouatta*, while the analyses of original data will further highlight their remarkably different anatomy from that of other atelines and other platyrrhines and will address issues of intra- and interspecific morphological variations within a functional, phylogenetic, and, where available, biogeographic framework.

6.2 Cranium

6.2.1 The Uniqueness of Alouatta *Cranial Morphology*

Among atelines and other platyrrhines, *Alouatta* can be differentiated by the peculiar form of its skull (Hill 1962): the pyramidal shape of the relatively small brain case, the posteriorly directed nuchal plane, the prognathic face anterior to the braincase, and the extended and unflexed basicranial axis. This morphological organization of the skull has been described as airorhynchy and corresponds to the upward rotation of the functional axis of the splanchnocranium on the neurocranium (see Tattersall 1972; Bruner et al. 2004). The braincase, in comparison to the face, is small (Schultz 1941), a relationship probably related to the early cessation of cranial growth and the obliteration of the cranial sutures (Höfer 1954, 1969). Additionally, the foramen magnum and the occipital condyles face posteriorly, an orientation displaying individual variation, but also undergoing changes during ontogeny (Bolk 1915; Senyurek 1938; Schultz 1955).

The development and form of the face, mandible, and braincase have been interpreted as primitive traits (Anthony et al. 1949). However, a long narrow cranial base with an airorynchous face, a flat, posteriorly facing nuchal plane, and expanded gonial angles of the mandible are most often argued to be associated with opening the subbasal space for an enlarged hyoid (Rusconi 1935; Biegert 1963; Miller and Begun 1998). This functional interpretation is partly supported by the shared airorynchous face and well-developed anatomical structures for sound production in *Alouatta* and *Pongo* (Biegert 1963; Shea 1985; Bruner et al. 2004). Alternatively, this reorganization has been also functionally linked to folivory. For example, in the mandible, the wide bigonial breadth of *Alouatta* appears to both favor folivory and to accommodate the enlarged hyoid bone. The development and posterolateral displacement of the gonial angles is intrinsically related to the enlarged hyoid in males (Watanabe 1982), but their flaring allows the mandible to pass lateral to the enlarged hyoid bone during maximum gape, and their expansion also provides a larger area of attachment for the masseter muscles used during chewing (Herring 1975; Bruner et al. 2004). An airorynchous face and a vertical nuchal plane change the orientation of the head on the neck, which has been suggested to make it easier to crop leaves (Tattersall 1972); this functional link has also been used in interpreting the cranial morphology of the large subfossil lemur *Megaladapis*, other folivorous subfossil lemurs (Godfrey and Jungers 2002), and the folivorous koala *Phascolarctos*.

This reorganization is accompanied by analogous modifications to the arrangement of various cranial muscles. Thus, *Alouatta* is characterized by the pronounced size of the masticatory muscles, which are linked both to the expansion of the hyolaryngeal organs and the mandible. Furthermore, howlers possess a modified insertion of *m. digastricus* on the mandible that does not extend posteriorly, as in other platyrrhines (Leche 1912). The arrangement of facial muscles is comparable to that of the other atelines, but *Alouatta* displays overdeveloped *mm. platysma colli* and *faciei*, which reach the orbitozygomatic plate and are probably linked to the growth of the mandible. The *mm. stylopharyngeus* and the muscles of the pharynx have undergone a large increase in size, especially the pharyngeal middle constrictor and the membranous parts of the pharynx which are implicated in the emptying of the air sacs, as well as the pharyngeal inferior constrictor that is involved in the control of the vocal cords (Schön 1968). *M. pterygoideus medialis* attaches to the enlarged gonial angle and helps elevate and protract the mandible during howling (Schön 1968). Finally, *mm. stylohyoideus*, *genioglossus*, *hyoglossus*, *styloglossus*, *sternohyoideus*, and *thyrohyoideus*, which operate on the hyoid, are all well developed.

These morphological modifications differentiate *Alouatta* from the other atelines. However, their functional link to folivory and sound production, which both vary across howler species and sexes (Di Fiore and Campbell 2007), would imply some degree of intra- and interspecific differences. With this in mind, quantitative analytical approaches were used in this study to examine potential morphological variations.

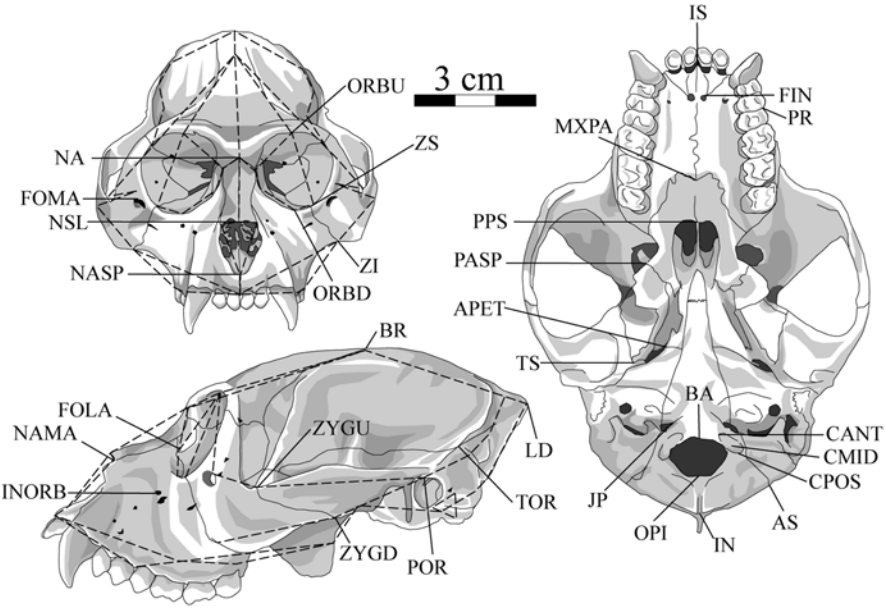

Fig. 6.1 Set of the 55 landmarks defined on the skull. Bilateral landmarks were digitized on the left side only and mirrored (see Table 6.1 for landmark definitions). *Dashed lines* illustrate wireframes used for shape variation visualizations

6.2.2 *Cranial Material and Analyses*

For the current study, we collected data from the skulls of 14 *Lagothrix* (three species), 48 *Ateles* (seven species), 78 *Alouatta* (seven species) adult males and females, and one male *Brachyteles*. For our analysis at the genus level, we did not consider sex or species. In contrast, we considered both variables in our analysis of *Alouatta* cranial diversity at the species level. The *Alouatta* sample was composed of 15 *A. paliatta* (10M, 5F), 4 *A. pigra* (3M, 1F), 9 *A. guariba* (5M, 4F), 14 *A. belzebul* (7M, 7F), 10 *A. caraya* (6M, 4F), 15 *A. seniculus* (8M, 7F), and 11 *A. nigerrima* (6M, 5F). All specimens were wild-shot individuals housed in the Laboratoire des Mammifères et Oiseaux, Muséum national d'Histoire naturelle (Paris, France), Museu Paraense Emílio Goeldi (Bélem, Pará, Brasil), and the American Museum of Natural History (New York, USA). A set of 55 landmarks were used (Fig. 6.1, Table 6.1), identical to those from previous studies and shown to successfully differentiate small shape variations (Couette 2002, 2007). The landmarks were digitized using a MicroScribe G2X (Immersion Corporation, San José, California). Bilateral landmarks have been digitized on the left side only, and mirroring was performed using the R software (2008). Each specimen was digitized twice in order to estimate measurement error, which varied between 1.9 and 2.3 %.

Table 6.1 List of the 55 landmarks used for the analyses of cranial variations (consult Fig. 6.1 for visualizations)

Landmark	Description	Position(s)
IS	Intradental superior	Midline
NASP	Base of the nasal aperture	Midline
NSL	Nasale	Midline
NA	Nasion	Midline
BR	Bregma	Midline
LD	Lambda	Midline
IN	Inion	Midline
OPI	Opisthion	Midline
BA	Basion	Midline
PPS	Posterior point of the palatine suture	Midline
MXPA	Maxillary/palatine point	Midline
FIN	Incisive foramen	Right, left
PASP	Palatine/ sphenoid suture	Right, left
PR	P1/P2 point	Right, left
ZS	Zygomaxillare superior	Right, left
ORBU	Upper point of the orbit	Right, left
ORBD	Lower point of the orbit	Right, left
INORB	Upper point of the infraorbital foramen	Right, left
NAMA	Nasal/maxillary suture on the nasal aperture	Right, left
FOMA	Upper point of the malar foramen	Right, left
FOLA	Lower point of the lachrymal foramen	Right, left
AS	Asterion	Right, left
TOR	Parietal/occipital suture on the occipital torus	Right, left
POR	Porion	Right, left
ZI	Zygomaxillare inferior	Right, left
ZYGU	Jugal/squamosal suture on the upper ridge of the zygomatic arch	Right, left
ZYGD	Jugal/squamosal suture on the lower ridge of the zygomatic arch	Right, left
TS	Temporosphenoidal junction at the petrous	Right, left
APET	Anterior petrous temporal	Right, left
JP	Jugal process	Right, left
CANT	Anterior point of the occipital condyle	Right, left
CMID	Medial point of the occipital condyle	Right, left
CPOS	Posterior point of the occipital condyle	Right, left

For our analysis, we used landmark-based 3DGM methods, such as generalized Procrustes analysis (GPA; Rohlf and Slice 1990), which can involve a great number of variables for the quantification of variation. A good solution to deal with such numerous variables is the use of multivariate statistics such as principal components analysis (PCA). Common parts of variation described by the variables are summarized and expressed by a new series of orthogonal (independent) axes that constitute new morphological variables. Each PC axis describes only a part of the total varia-

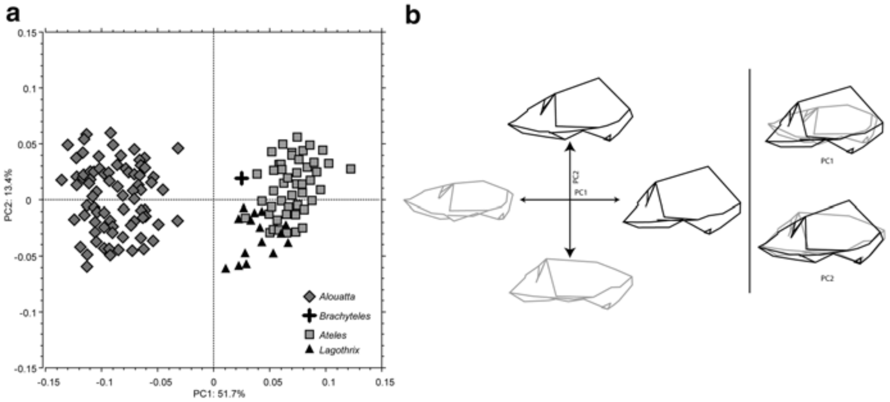

Fig. 6.2 (**a**) PCA results for the analysis of cranial variation at the genus level. *Alouatta* cranial morphology is clearly different from that of the other atelines; (**b**) polarization of the morphologies described by the negative (*gray*) and positive (*black*) values of PC1 and PC2 for the analysis of cranial variation at the genus level (on the *left*). Superimposition of the extreme morphologies of each axis (on the *right*)

tion within the sample, and the contribution of the initial variables on each axis constitutes a key for the understanding of morphological differences between specimens. However, with Procrustes techniques, a great number of variables and the nature of the variables themselves (*X*, *Y*, and *Z* coordinates) usually complicate the polarization of morphological variations described by the PC axes. Therefore, wireframe diagrams and geometric reconstruction of cranial shape are frequently used to visualize PCA results. The GPAs and PCAs were performed using *morphologika*^{2} v. 2.5 (O'Higgins and Jones 2006), which also calculated centroid sizes, PC scores, wireframe diagrams, and the geometric reconstruction of cranial shape. The PAST 1.89 software package (Hammer et al. 2001) was used to perform and output graphical representation of the PCAs. Finally, we used Statistica 7 (Statsoft Inc., USA) for other statistical analyses such as linear regressions to check for allometric effects on the pattern of variation described on each PC axis.

6.2.3 Cranial Variation

In the PCA at the generic level (Fig. 6.2a), the first two PCs accounted for 65.1 % of total variation (51.7 % for PC1 and 13.4 % for PC2). Multivariate regressions (reduced major axis) of the PC scores onto the logarithm of centroid size indicate a significant linear correlation between PC1 scores and size ($a = -0.91$; $b = 5.15$; $R^2 = 0.32$, $p < 0.001$). Size has a significant influence on cranial morphology, and larger specimens lie on the negative side of PC1. Cranial distinction is mainly allometric, with *Alouatta* exhibiting the higher scores ($R^2 = 0.71$; $p < 0.001$), compared to *Ateles* ($R^2 = 0.28$, $p = 0.02$). *Alouatta* are clearly separated from the other atelines and occupy the negative side of the morphospace on PC1 but spread along PC2 with a plot centered at the origin of this axis. *Ateles* and *Lagothrix* overlap on the positive side of PC1 but are distinguishable on PC2. The latter are located on the negative side of the axis, while *Ateles* are mainly on the negative side, with significant overlap in the center.

Regarding morphology, negative values on PC1 are associated with a relatively developed face and a high degree of prognathism, while positive values describe rounded skulls with a relatively small face compared to the neurocranium. On PC1, the main morphological variation is a downward and backward rotation and relative shortening of the face. This rotation implies verticalization of the snout and the orbital plane. The relative volume of the neurocranium increases, and the occipital undergoes a downward and forward rotation, a consequence of an increase in the flexion of the basicranium associated with the facial rotation (Fig. 6.2b). On PC2, the negative values describe skulls with a relatively flattened neurocranium, while the positive values are associated with a high braincase. The main morphological variations are linked to the position of the bregma and the relative height of the braincase and the frontal part of the face (Fig. 6.2b).

The main morphological differences between *Alouatta* and the other atelines are in the degree of prognathism, airorhynchy, the oblique position of the orbital plane, the relative reduction of the neurocranium (essentially in height), the posterior orientation of the occipital condyles and the foramen magnum, the unflexed basicranium, and the robustness of the face and the zygomatic arches of howlers. As described above, functionally, these derived features have been associated with both diet and vocalizations. Although *Alouatta* and *Brachyteles* share dental adaptations to their semi-folivorous diet, the latter have skulls that are most similar to those of their ateline relatives, without an airorynchous face, posteriorly directed occipital, or a relatively small brain case (Rosenberger et al. 2011). Lack of nutrients in the mainly folivorous diet in *Alouatta* may account for a small brain, which may in turn be directly linked to an unflexed cranial base, as the "spatial packing" hypothesis suggests (Biegert 1963; Gould 1977; Ross and Ravosa 1993; Lieberman et al. 2000). Additionally, this morphology may be further associated with the necessity for opening of the subbasal space in order to accommodate the morphological modifications related to sound production. Therefore, it seems that the craniomandibular apomorphies of *Alouatta* are the result of complex adaptations to increased and frequent vocalization and also partly to folivory. However, this is variably expressed within the genus, and size seems to play a significant role suggesting intra- (sexual) and interspecific (phylogeographic) variations.

In the analysis at the species level, the first two PCs accounted for 61.1 % of total variation (37.4 % for PC1 and 23.7 % for PC2; Fig. 6.3a). Morphological variations described by PC1 are very similar to the ones described by PC1 at genus level but with lower intensity. Negative values characterize skulls with a very prognathic face, while positive ones characterize skulls with a less well-developed face. This axis describes a reduction in the degree of prognathism accompanied by a verticalization of the nasal and frontal bones as well as the orbital plane. Variation along

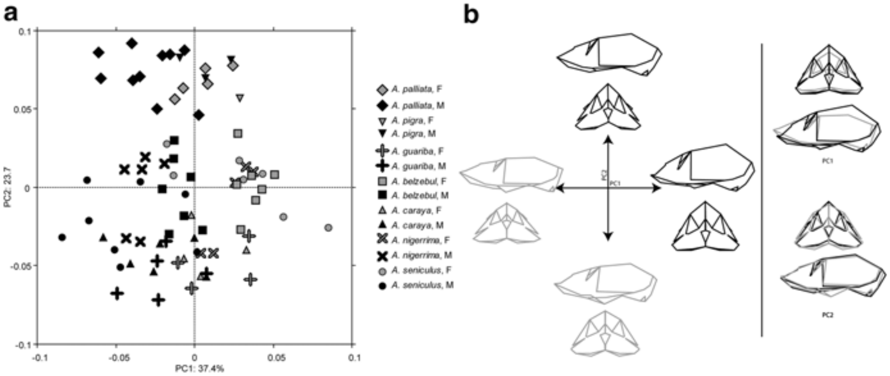

Fig. 6.3 (**a**) PCA results for the analysis of cranial variation at the species level. Morphological variations along PC1 describe differences explained by sexual dimorphism. Differences along PC2 describe geographical differences, distinguishing the Central American (*A. paliatta* and *A. pigra*) from the South American species. (**b**) Polarization of the morphologies described by the negative (*gray*) and positive (*black*) values of PC1 and PC2 for the analysis of cranial variation at the species level (on the *left*). Superimposition of the extreme morphologies of each axis (on the *right*)

PC1 also includes a shortening of the palate, a relative increase of the size of the neurocranium, and a downward rotation of the occipital which leads to increased basicranial flexion (Fig. 6.3b). PC1 also separates males from females. In the morphospace, males occupy the negative side of the axis, while females are clustered in the positive side, with few overlapping. Gender differences and overall variation seem to be more pronounced in *A. seniculus* than for any other species, and are not in accord with body size dimorphism (Ravosa and Ross 1994). These differences in cranial morphological traits do, however, seem to agree with those from previous descriptions of cranial dimorphism [e.g., *A. palliata* (Blanco and Godfrey 2006), *A. arctoidea* (Braza 1980)], although population level differences may be important (Jones et al. 2000). The differences in cranial morphology between the sexes may be related to proximally hypermorphosis during male growth (Ravosa and Ross 1994; Masterson and Hartwig 1998; Jones et al. 2000; Flores and Casinos 2011) but may also be linked evolutionarily to trophic and masticatory functions that are very important for male competition (Flores and Casinos 2011).

Along PC2, the morphological variation represents a difference in the height of the cranial vault associated with a difference in the rotation of the occipital. Compared to the negative side of the axis, positive values are associated with a taller braincase, higher occipital condyles, thicker zygomatic arches, a downward directed muzzle, and a more vertical orientation of the orbital plane. PC2 partly distinguishes between certain species, and the positive side is occupied by the divergent Central American clade (*A. palliata*, *A. pigra*). The rest are rather mixed in the center (*A. belzebul*, *A. seniculus*, *A. nigerrima*), with the southernmost species, *A. caraya* and *A. guariba*, differing slightly. *Alouatta belzebul*, *A. seniculus*, and *A. nigerrima* are distributed widely across the morphospace, displaying higher intraspecific variation (on both PCs). This is noticeable for *A. nigerrima*, with specimens of both sexes positioned on both sides, implying two probable morphological groups for this species. The cranial particularities of the Central American species have been previously reported by Watanabe (1982), and their differentiation within the genus is also supported by molecular data (e.g., Cortés-Ortiz et al. 2003). Watanabe (1982) detected differences between *A. palliata* and *A. seniculus* in basicranium length, height of the nasal bones, bigonial breadth, and the development of the pterygoid wing, which is associated with *m. pterygoideus medialis*, an elevator and a protractor of the mandible (Schön 1968).

6.3 Dental Morphology

In terms of overall proportions, the *Alouatta* dentition can be described as molar centric, where the incisors at the front of the jaw are much smaller than the molars and are often offset from the canines by a diastema (Fig. 6.4). This is the opposite condition seen in many frugivorous primates, including the atelines *Ateles* and *Lagothrix*, which tend to have larger, bladelike incisors for processing the large, potentially tough-skinned fruit into bite-sized pieces (Hylander 1975; Kay and Hylander 1978; Eaglen 1984; Anthony and Kay 1993). In contrast, the narrow width of the incisor row of *Alouatta*, as well as the mediolateral tapering of each incisor itself, reflects the more concentrated force per tooth used to bite and pull leaves (Ungar 1990; Anapol and Lee 1994). The upper incisors are also oriented at an angle due to the howler's airorynchous face and are therefore in an advantageous

Fig. 6.4 Occlusal views of the upper dentition (*left*) and lower dentition (*right*) of male *Alouatta* (third upper molar length = 5.8 mm; third lower molar length = 7.5 mm)

position for cropping leaves off tree branches (Tattersall 1972). *Alouatta* is highly sexually dimorphic in body size, hyoid size, and canine size so male canines are considerably more prominent than those of females of the same species (Ford 1994).

The molars are large and square with complex surfaces made up of long crests of thin enamel (Fig. 6.4); *Alouatta* has the largest postcanine tooth area of all the ateline primates (Rosenberger and Strier 1989). Their distinct morphology is marked by high crowns, deep basins, deep intercuspal notches on the buccal and lingual sides of the crown, and a long cristid obliquid (Fig. 6.4; Cooke 2011). This is particularly clear when comparing the "shearing quotient" of folivorous howler monkeys to frugivorous spider monkeys (Kay 1978; 1984; Anthony and Kay 1993). The high-crested molars of the howlers are adapted to slicing through the tough structural carbohydrates, like cellulose, that make up their leafy diet, while the low-relief molars of the spider monkeys are better suited to mashing up softer fruit pulp (Kay 1975; Rosenberger and Kinzey 1976; Anthony and Kay 1993; Anapol and Lee 1994). More recent analyses of the overall surface relief and topography of the molars, not just shearing crest length, also illustrate this difference between howler monkeys and their more frugivorous relatives (i.e., Cooke 2011).

The shearing capability of *Alouatta* molars has been shown to be convergent upon the superficially similar surface topography of the molars of another ateline, *Brachyteles* (Rosenberger and Strier 1989; Rosenberger 1992). The folivorous woolly spider monkeys also have relatively small incisors and large, high-relief molars that have a high shearing quotient, but the crests appear on a different aspect of the molar surface. *Alouatta*'s shearing crests are concentrated on the buccal side of the molars which exhibit a large paracone, metacone, and ectoloph in the upper tooth row and an elongate talonid and cristid obliquid in the lower (Fig. 6.4; Rosenberger and Strier 1989). *Brachyteles*, on the other hand, shears on the lingual side of the molars with a large protocone and a tall metaconid, which occludes into the gap between the protocone and hypocone; they are also unique among atelines in possessing a strong lingual notch between the metaconid and entoconid (Rosenberger and Strier 1989). Genetic evidence points to a sister-taxon relationship between *Brachyteles* and *Lagothrix*, while skeletal morphology favors a *Brachyteles*-*Ateles* pair; no evidence for a close relationship between *Alouatta* and *Brachyteles* exists besides their shared dental morphology, which has convincingly been shown to be a convergent adaptation to their folivorous diet (Anthony and Kay 1993).

Some differences in relative incisor size have been described between various species of *Alouatta* (i.e., Anthony and Kay 1993), which is to be expected based on their differing degrees of folivory (Di Fiore and Campbell 2007), but no systematic study of interspecific dental morphology exists to date [but see the dissertation work of Orlosky (1973)]. At least one species, *Alouatta palliata*, shows a characteristic species-wide wear sequence as their high-relief molars are flattened over time with use, reducing the shearing crest length but preserving the "angularity," or jaggedness, of the surfaces necessary for processing leaves (Dennis et al. 2004). This is in agreement with Rosenberger and Kinzey's (1976) insights on the ontogenetic maintenance of molar shear in folivores such as *Alouatta*, as well as more insectivorous taxa, like *Callithrix*. The thin enamel and large molar surface area assure that the howler monkey teeth will retain their shearing functions while they wear down (see also Kay 1984; Anapol and Lee 1994).

6.4 Hyoid

6.4.1 A Unique Hypertrophied Hyoid

Alouatta is said to make the loudest vocalizations of any terrestrial vertebrate and has the largest, most inflated hyoid bone within the primate order. While the basic anatomy of the hyoid bone, thyroid and epiglottic cartilages, and air sacs of *Alouatta* have been described by many authors, inter- and intraspecific variations are not as well known, and there is debate about how their morphology relates to diet, vocalizations, body size, respiration, and the functional morphology of the skull. Unlike in humans, the hyoid bone of *Alouatta* is always attached to the cranial base through a chain of cartilaginous, or sometimes even ossified, elements, i.e., the more common "integro-cornuate" condition (Howes 1896). It also sits wedged between the gonial angles of the mandible. The hyoid serves as an attachment point for muscles and ligaments that also serve the mandible, tongue, laryngeal cartilages, pharynx, sternum, and cranial base, hence its proposed functions involving several systems including respiration, swallowing, and vocalizations. In most mammals, the hyoid apparatus lies at or above the entrance to the larynx and consists of two basic parts: inferiorly, the unpaired basihyal and paired thyrohyal "horns" which connect the basihyal to the thyroid cartilage and superiorly, the paired suspensory stylohyoid chains which are made up of four cartilaginous or ossified links, the ceratohyal, epihyal, stylohyal, and tympanohyal, that connect the basihyal to the temporal bone (e.g., Howes 1896; Negus 1949).

It is the size and shape of the basihyal portion that vary across primate species. Some Old World monkeys have a caudally expanded basihyal that covers the top of the thyroid cartilage (Negus 1949; Hilloowala 1975; Nishimura 2003), but none are as extremely modified as that of *Alouatta*. Howler monkeys are the only living primates that have evolved a pneumatized hyoid bone with a large, hollow balloon-like basihyal, which is argued to serve, along with their air sacs, as a resonating chamber (Chapman 1929; Kelemen and Sade 1960; Schön 1971; Hewitt et al. 2002). As the larynx of howlers, and the other nonhuman primates, is positioned so high in the throat, the supralaryngeal dimensions of the pharynx are small, limiting the range of sounds that can be made (Laitman and Reidenberg 2009). The expanded hyoid bone and air sacs positioned above the larynx in *Alouatta* increase the volume of this space and, along with stretching out the neck and manipulations of the lips (Schön 1986; Whitehead 1995), shape the sound and volume of their loud long calls.

The laryngeal cartilages are also enlarged in *Alouatta*, especially the thyroid, cuneiforms, and epiglottis, which are also sometimes ossified (Kelemen and Sade 1960; Hill 1962). The basihyal is joined to the thyroid cartilage with a membranous attachment, and the two are freer to move more independently of one another in *Alouatta* than in other primates (Schön-Ybarra 1995). As mentioned above, the stylohyoid chain is of the common mammalian integro-cornuate type, connecting to the cranial base anterior to the stylomastoid foramen (Howes 1896; Hilloowala 1975). Not enough is known about variation in the associated hyoid musculature, hence how the hyoid may move during howling in the different species, as only a few specimens of *A. seniculus* (Hill 1962; Schön 1968, 1971), *A. palliata* (Kelemen and Sade 1960; Hilloowala 1975), and *A. caraya* (Schön 1971) have been dissected. It is worth emphasizing that the size of the hyoid and the anatomical space it requires in the head are not trivial. For example, an average endocranial volume for a mixed sex sample of 16 *A. belzebul* individuals from the American Museum of Natural History was 55 ml, and the average hyoid volume for four males of that species was 57 mL; in two individuals, hyoid volume was approximately 140 % of their endocranial volume.

The impact of this anatomical specialization on the howler skull has yet to be adequately investigated and synthesized, but various unique aspects of cranial and mandibular morphology in *Alouatta* have been suggested to be related to the large size of these vocal tract structures (e.g., Biegert 1963; Watanabe 1982). While the unique morphology of the bone was mentioned by many early authors (e.g., Grew 1681), variation in hyoid size and shape among the species of *Alouatta* was first systematically described by Hershkovitz in 1949. The morphology of this region has been used as a diagnostic character for species recognition since then by Hill (1962) and many others. This section will quantitatively explore hyoid size and shape within *Alouatta* in order to better understand interspecific differences that in the past have been used as a basis for taxonomic, phylogenetic, and functional interpretations about the genus.

6.4.2 Hyoid Material and Analyses

Over 100 undeformed *Alouatta* hyoids from collections at the American Museum of Natural History (New York, USA), the United States National Museum (Washington, DC, USA), and the Field Museum of Natural History (Chicago, IL, USA) were laser scanned using either a portable Minolta Vivid 910 laser surface scanner or a NextEngine desktop 3D scanner (Table 6.2). As the bony walls of many of the smaller hyoids were too thin to be "seen" properly by the lasers, the hyoid bullae were stuffed with paper towels to make the bone more opaque. The scans were edited using *Geomagic Studio* and ScanStudio HD v. 1.3.0, and a .ply file was created for each specimen (Harcourt-Smith et al. 2008). The *Landmark Editor* program (Wiley 2006) was then used to place homologous landmark points across the superior aspect of the tentorium as well as at the four corners of the posterior opening of the basihyal. These landmarks were used as anchors for drawing automated curves that generate semi-landmarks which quantify the bulbous aspect of the anterior portion of the bone (Bookstein 1997; Gunz et al. 2005; Fig. 6.5). This procedure

Table 6.2 Extant sample for hyoid measurements

Genus	Species	Subspecies[a]	Country	Hyoid	
				M	F
Alouatta	*belzebul*	*belzebul*	Brazil	6	7
			N	6	7
Alouatta	*caraya*		Brazil	7	6
			Bolivia	5	6
			N	12	12
Alouatta	*guariba*	*guariba*	Brazil (NE)	3	2
Alouatta	*guariba*	*clamitans*	Brazil (SE)	4	4
			N	7	6
Alouatta	*palliata*	*palliata*	El Salvador	2	1
Alouatta	*palliata*	*aequatorialis*	Panama	1	–
			N	3	1
Alouatta	*pigra*		Guatemala	2	1
			N	2	1
Alouatta	*seniculus*		Bolivia	2	4
			Brazil	1	–
Alouatta	*seniculus*	*seniculus*	Colombia	26	22
			Peru	3	2
Alouatta	*seniculus*	*straminea*[b]	Guyana	2	2
			N	34	30
Lagothrix	*lagotricha*	*lagotricha*	Colombia	1	–
Lagothrix	*lagotricha*	*lugens*	Colombia	2	–
			N	3	0

[a] Taxonomic allocation and provenance taken from specimen boxes
[b] Currently recognized as *A. macconnelli*

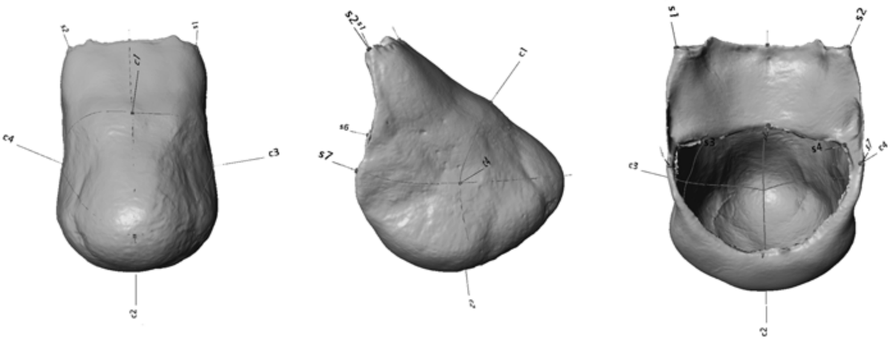

Fig. 6.5 Landmarks recorded on the hyoid. Images are from *Landmark Editor*, showing points and curves on a typical male *A. seniculus* hyoid in (from *left* to *right*) anterior, lateral, and posterior views

captured not only the size of the hyoid, which has been approximated in previous studies by measuring its length and/or width (see, for example, Watanabe 1982; Halpern 1987), but also the bone's contours, which contribute to the unique shape of the hyoid in each species. Several *Lagothrix* hyoids, which are much smaller and less concave than those of *Alouatta*, were also scanned and landmarked, functioning as an "outgroup."

The data were subjected to a GPA (Rohlf and Slice 1990) to translate, rotate, and scale all specimens to unit centroid size using the *morphologika*^{2} v2.5 software program (O'Higgins and Jones 2006). The curves of semi-landmarks on the hyoids were also subjected to a "sliding" protocol using a program implemented in MATLAB in order to minimize Procrustes distance between the specimens and the calculated reference specimen (Bookstein 1997; Gunz et al. 2005). Sliding the semi-landmarks along the outline curves is an extension of the standard GPA superimposition procedure and is necessary to properly account for type III semi-landmarks having fewer degrees of freedom than those of type I or type II (Adams et al. 2004). PCA was then used to visualize the morphological variation in the sample. The PAST 1.89 software package (Hammer et al. 2001) was used to perform and output graphical representation of the PCAs.

6.4.3 Hyoid Variation

The development of the tentorium superiorly and the size and shape of the posterior opening of the basihyal are the most important variables for distinguishing the species from one another (Hershkovitz 1949; Hill 1962; Fig. 6.6a, b). Male *A. seniculus* have the largest, most inflated hyoid bullae with relatively small posterior openings and wide convex tentoria. *A. guariba* has a larger posterior opening with a less inflated tentorium and no cornua. The hyoid of *A. belzebul* is also in a larger size class with the largest posterior opening and a slightly concave tentorium. Of the larger species, *A. caraya* has the smallest tentorium but a very large posterior opening and a uniquely shortened anteroposterior dimension that gives the bone a "snub-nosed" appearance. The hyoid bullae of *A. palliata* are the smallest, with a flared opening, extremely reduced tentorium, and broad attachment sites for the thyrohyal proximally and the stylohyoid ligament distally. While *A. pigra* has been considered a subspecies of *A. palliata* and shares with it a Central American distribution, the female hyoid looks more similar to that of the South American species, while the bone in the male has a very unique, almost two-dimensional appearance.

These qualitative descriptions led Hershkovitz (1949) to divide the genus into three groups: the *seniculus* group which includes *A. seniculus*, *A. belzebul*, and *A. guariba*; the *palliata* group which includes *A. palliata* and *A. pigra*; and the *caraya* group for the snub-nosed *A. caraya*. For Hershkovitz, these groups have evolutionary significance, with *A. palliata* retaining the ancestral condition and *A. seniculus*, especially the males, exhibiting the most derived hyoid shape. Interestingly, while *Alouatta* males do have larger, more inflated hyoid bullae than females of the same species, body size differences between the species do not seem to correspond to differences in hyoid size or the length of the supralaryngeal vocal tract (Hilloowala 1975; Schön-Ybarra 1995). In other words, the species with the largest average body size does not have the absolutely largest hyoid volume

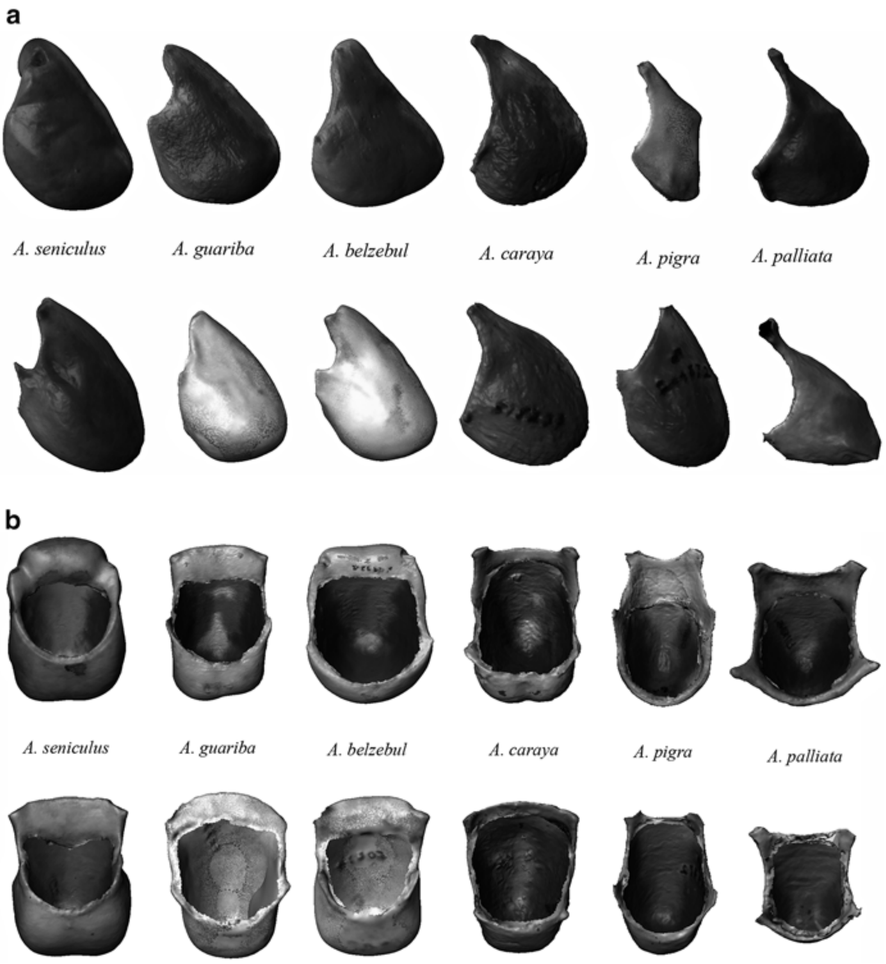

Fig. 6.6 Interspecific variation in hyoid shape across *Alouatta*, lateral (**a**, *top*) and posterior (**b**, *bottom*) views. Images are .ply files created from laser surface scans of individual specimens (see Materials and Methods—ragged edges around the posterior opening of the hyoid are an artifact of the scan editing process) chosen from the hyoid sample as typical representatives of each species and scaled to similar size to emphasize shape differences. *Top row* in each view are males, *bottom row* are females (*A. pigra* female is mislabeled as a male)

(Table 6.3). These differences in howler monkey hyoid size and shape do, however, seem to correlate with various acoustic features of their calls (Table 6.3): *A. palliata* has been shown to vocalize for shorter periods of time over a narrower bandwidth and higher frequency (Sekulic and Chivers 1986; Whitehead 1995), they have the smallest hyoids, and they only have one type of air sac (Schön-Ybarra 1995; Hewitt et al. 2002).

Table 6.3 Relationship between body size, hyoid size, and long call acoustics in *Alouatta*

	Body weight (kg)[a]			Hyoid size[c]				
Taxon	Males	Females	Dimorphism index[b]	Males	Females	Complete rules	Emphasized frequency (Hz)[d]	Call duration (s)[e]
A. belzebul	7.3	5.5	1.327	212	130	1.631	480.6	4.9
A. caraya	6.8	4.6	1.478	164	116	1.414	439.7	–
A. guariba	6.2	4.5	1.378	197	122	1.615	616.6	–
A. palliata	7.1	5.3	1.339	117	74	1.581	413.3	3.5
A. pigra	11.3	6.4	1.766	124	120	1.033	598.9	5–6
A. seniculus	7.2	5.6	1.286	220	131	1.679	475.7	19, 8, 120

[a] Averages taken from Ford and Davis (1992)

[b] Dimorphism index = average male centroid size/average female centroid size (Ford 1994)

[c] Male and female average centroid size calculated in this study

[d] From Whitehead (1995)

[e] From Sekulic and Chivers (1986) and Whitehead (1995)

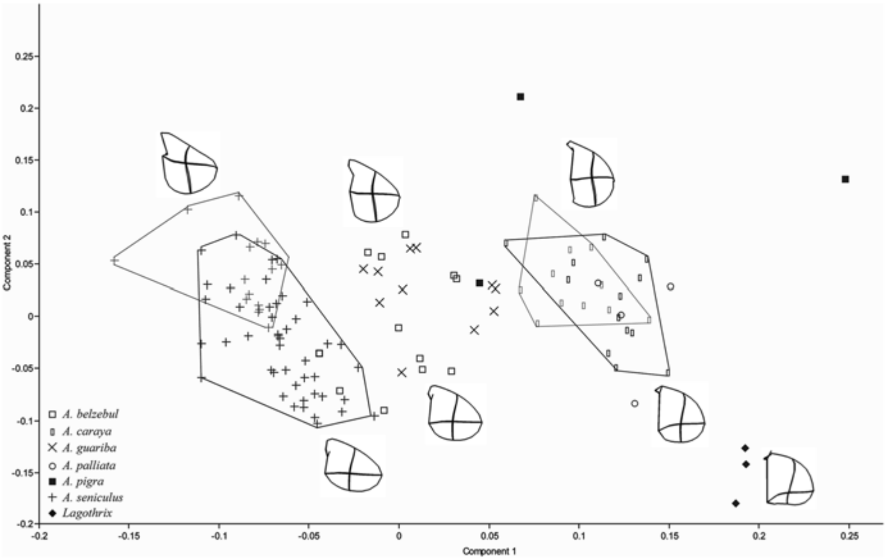

Fig. 6.7 PCA results for the hyoid. Sample includes males and females of all species of *Alouatta* and three *Lagothrix* individuals. PC1 (37 % total variance) separates *A. seniculus* from the other species as the most bulbous with the smallest posterior opening. PC2 (18 %) separates males, individuals towards the positive end of the axis, from females, individuals towards the negative end (also see Fig. 6.8). PC2 is also somewhat related to geographic differences within the *A. seniculus* and *A. caraya* samples. The gray polygon bounds the subset of the *A. seniculus* sample not from Colombia. The *A. caraya* individuals bounded by the *gray* polygon are from Bolivia, while those bounded in *black* are from Brazil. Wireframes show the curves on the basihyal in lateral view with the anterior portion of the bone facing to the right to more easily visualize the shape change along PC1 and the difference between males and females of each species (see Fig. 6.5)

In the PCA results, the *A. palliata* and non-*palliata* groups are not as distinct as one might expect based on the descriptions given above or quantitative studies of interspecific variation of the skull, but this could be due to the much smaller sample size of *A. palliata* compared to the other species (Figs. 6.7 and 6.8). These groupings do, however, generally agree with those described in previous studies of interspecific hyoid variation (i.e., Hershkovitz 1949; Halpern 1987; Gregorin 2006). While having a slightly concave basihyal, the three *Lagothrix* hyoids are clearly separated from the *Alouatta* sample; *Ateles* hyoids look similar to those of *Lagothrix*, but unfortunately none could be laser scanned for this analysis. The anterior-posterior dimensions of the basihyal, along with the position of the four corners surrounding the posterior opening, are the main variables driving separation of the species clusters seen across PC1. The phenetic similarities in hyoid shape suggested by the overlap of the *A. guariba* and *A. belzebul* samples agree with their linkage in molecular phylogenetic studies of the genus (e.g., Cortés-Ortiz et al. 2003). The molecular evidence, however, also suggests a sister-taxon relationship between

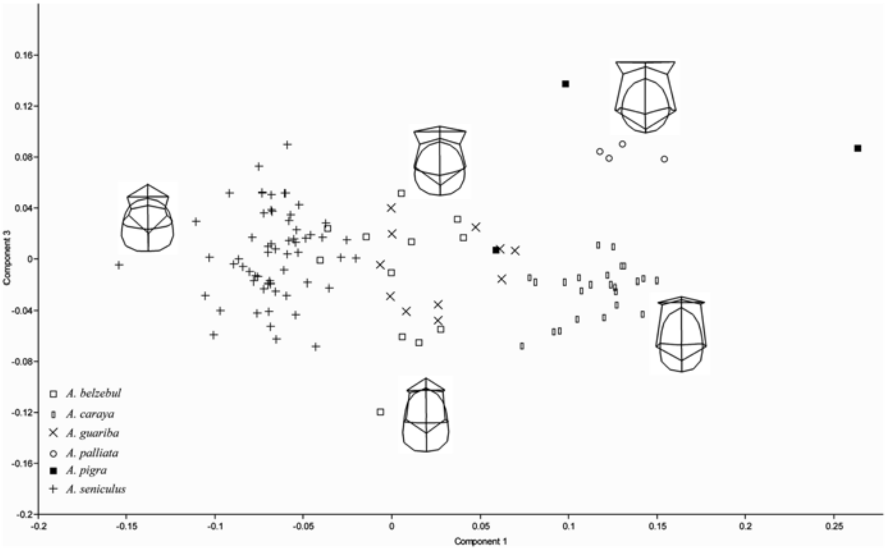

Fig. 6.8 PCA results for the hyoid using the *Alouatta* sample, PC1 vs. PC3. When the *Lagothrix* individuals are excluded from the sample, PC3 (9 % total variance) separates *A. palliata* from *A. caraya*. PC1 (39 %) is still driven by the contours of the inferior portion of the basihyal as well as the dimensions of the posterior opening and tentorium. Wireframes show the hyoid in posterior view, again to visualize the shape differences between the species

A. seniculus and *A. caraya*, two species that are shown here to be quite distinct in their hyoid morphology. Interestingly, there is some suggestion of geographic separation within the *A. caraya* and *A. seniculus* samples; Brazilian and Bolivian *A. caraya* form relatively distinct clusters as do Colombian and non-Colombian *A. seniculus* (Fig. 6.7). Perhaps hyoid size and shape are more influenced by socioecological factors related to long call behavior, like group size and habitat type (e.g., Sekulic and Chivers 1986; Chiarello 1995), rather than phylogenetic relatedness.

PC2 separates *Alouatta* male hyoid shape from female hyoid shape within each species cluster reasonably well, and the dimorphism index calculated by dividing male hyoid centroid size by female hyoid centroid size confirms a relatively high degree of sexual dimorphism in *Alouatta* hyoid size (Fig. 6.9; Table 6.3). The species with the largest hyoids as measured by centroid size, *A. belzebul*, *A. seniculus*, and *A. guariba*, are also the most dimorphic. But as noted above, these are not the species with the largest body sizes nor the highest body size dimorphism indices (Table 6.3). Male hyoid centroid sizes also vary more widely from species to species than those of females. An explanation for this, as well as why there are some males on the "female side" of the clusters in Fig. 6.7, could be that non-dominant but fully adult males are vocalizing less than the dominant males and therefore have smaller musculature moving their smaller, more female-like hyoids.

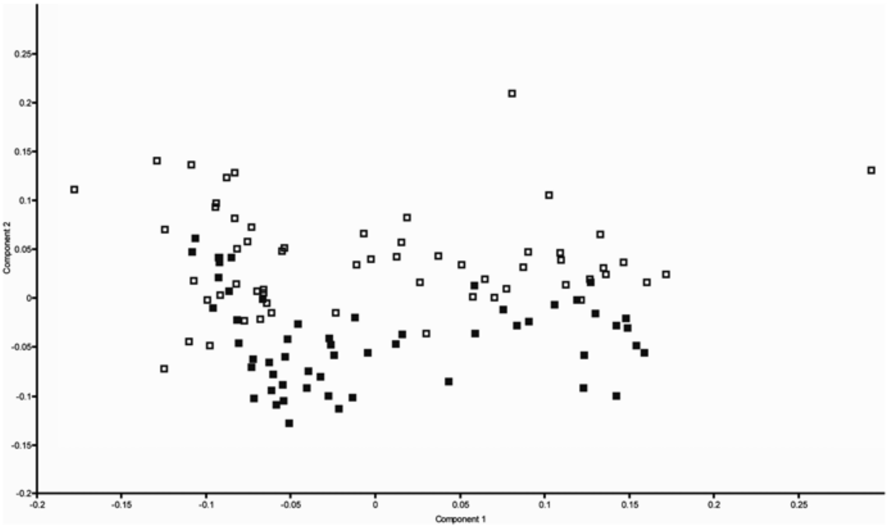

Fig. 6.9 Sexual dimorphism in the *Alouatta* hyoid. This shows the same distribution of specimens as in Fig. 6.6, but with male individuals symbolized by *open squares* and females by *closed squares*. Graphically, the separation between males and females for most species looks distinct, but regressing in centroid size on PC1 scores gives R^2 values for PC1 and PC2 that are both relatively low at 0.4. This would indicate that hyoid shape differs more than hyoid size between the sexes in *Alouatta*

6.5 A Derived Postcranium

This section reviews the current evidence on postcranial apomorphies and provides a functional interpretation of the *Alouatta* skeleton.

6.5.1 Forelimb

In *Alouatta*, the forelimb is relatively short compared to other atelines, representing only 91 % of the length of the vertebral column, whereas it is much longer in *Lagothrix* and *Ateles* (109 % and 150 % respectively, Erikson 1963). However, it is almost equal in length compared to the hind limb, as indicated by the intermembral index (IMI), which ranges between 97 and 99 (Erikson 1963; Youlatos 1994; Jones 2004). A similar condition is encountered in *Lagothrix* (IMI = 97.6), whereas *Ateles* is very different (IMI = 105; Erikson 1963).

The scapula is positioned relatively cranially compared to most other quadrupeds (Youlatos 1994). It is craniocaudally wide and reminiscent of climbing and suspensory mammals, compared to the more dorsoventrally elongated scapular shape of

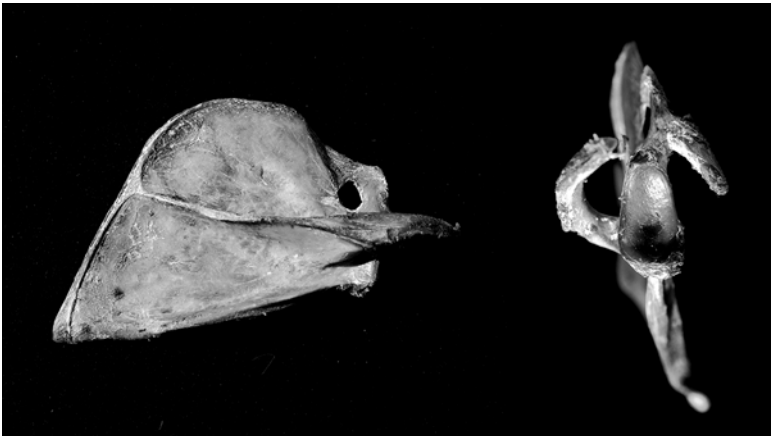

Fig. 6.10 Lateral view (*left*) and proximal view (*right*) of the scapula of *A. seniculus* (glenoid-midaxillary border length is 71.4 mm) showing the enlargement of the suprascapular fossa, the development of the acromion, the distal extension of the coracoid process joining the cranial end of the suprascapular fossa via a large ligament (*left*), and the oblong shape of the glenoid fossa (*right*)

both arboreal and terrestrial quadrupeds (Fig. 6.10; Roberts 1974). The scapular spine is only slightly oblique, compared to the more oblique position in *Lagothrix* and very oblique in *Ateles*, facilitating the rotatory action of the powerful *m. trapezius* during quadrupedal activities (Erikson 1963; Anapol and Fleagle 1988).

The suprascapular fossa is particularly enlarged (Fig. 6.10), a condition also encountered in many climbing and suspensory mammals and associated with the substantial arm raising and abducting action of *m. supraspinatus* (Oxnard 1963; Schön 1968; Larson and Stern 1989; Youlatos 2000). However, the greater relative surface area in *Alouatta* (33–42 % of total scapular surface area) compared to climbing primates (24–33 %, Youlatos 1994) may be related to a more cranial origin and the overdevelopment of *m. atlantoscapularis posterior* providing additional support for the neck (Schön 1968; Youlatos 1994).

The acromion is large and protuberant facing moderately dorsad (Fig. 6.10), whereas it is slightly less prominent and dorsally oriented in *Ateles* (Erikson 1963). This provides a better leverage for *m. deltoideus* during powerful arm protraction and abduction. Medially, the coracoid process is moderately developed, protruding distally over the glenoid fossa in a way reminiscent of *Lagothrix* and arboreal quadrupeds. In contrast, *Ateles* possess an enlarged coracoid, oriented cranio-distally, contributing to a better leverage for *mm. coracobrachialis* and *biceps brachii caput breve* (Schön 1968; Anapol and Fleagle 1988).

The glenoid fossa faces cranially, in contrast to the more lateral and completely lateral direction in *Lagothrix* and *Ateles*, respectively. This is related to the position of the scapula on the dorsoventrally elongated rib cage of *Alouatta*, compared to the more mediolaterally wide ribcage of *Ateles* (Erikson 1963; Rosenberger and Strier

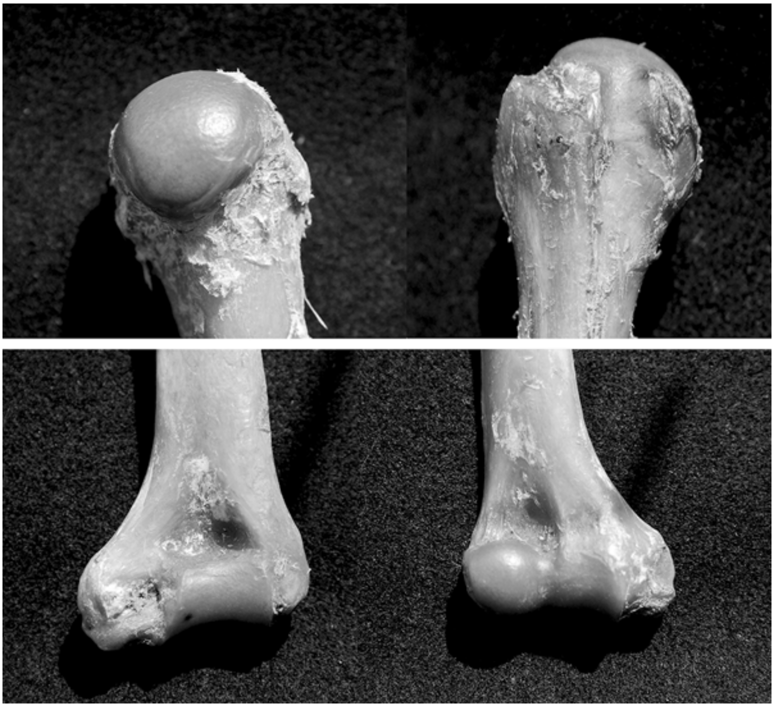

Fig. 6.11 Humeral features of *Alouatta*: narrow proximal humeral head (*top left*), wide bicipital groove and reduced humeral tuberosities (*top right*), protruding medial condyle and shallow olecranon fossa (*bottom left*), wedged trochlea, and ovoid capitulum (*bottom right*) (humeral head width = 16.4 mm; distal epiphysis width = 28.5 mm)

1989; Youlatos 1994). Its shape is oblong in *Alouatta* (Fig. 6.10) with a relatively prominent cranial buttress with dense trabecular bone distribution, unlike the more spherical facet in *Lagothrix* and *Ateles* with a reduced buttress (Schön-Ybarra and Schön 1987; Anapol and Fleagle 1988; Fleagle and Meldrum 1988; Jones 2004; Kagaya 2007).

The humeral head is ovoid in shape, relatively mediolaterally narrow and faces posteriorly (Fig. 6.11; Erikson 1963; Schön-Ybarra and Schön 1987; Kagaya 2007). Its mediolateral convexity is shorter and more pronounced than the anteroposterior one (Schön-Ybarra and Schön 1987; Jones 2004). The head is more circular and larger in *Ateles*, and its surface also expands and faces medially (Erikson 1963; Larson 1988; Jones 2004). This has been metrically expressed by the intertuberosity angle, which is quite reduced in *Alouatta* (63.5°), compared to the intermediate position in *Lagothrix* (76.7°) and the very wide one in *Ateles* (111.2°; Jones 2004). The head projects proximad to the tuberosities (Fig. 6.11). The latter are rather well developed, compared to their reduced development in *Lagothrix* and *Ateles* (Fleagle and Simons 1982; Jones 2004). The lesser tuberosity, the insertion point of *m. subscapularis*, is also well marked, whereas it is quite reduced in *Ateles* and *Brachyteles* and may be related to ample arm rotations (Fleagle and Simons 1982; Jones 2004). This combination of humeral head features allows a greater degree of arm protraction and retraction, as well as increased stability during arm abduction necessary for arm raising movements during climbing and suspensory locomotion, as well as in foraging activities (Fleagle and Simons 1982; Harrison 1989).

The bicipital groove is wide and shallow in *Alouatta* (Fig. 6.11), somewhat more defined in *Lagothrix*, and narrow and deep in *Ateles*; this keeps the tendon of the biceps in place during arm movements (Fleagle and Simons 1982; Schön-Ybarra and Schön 1987; Harrison 1989; Jones 2004). The deltopectoral crest on the humeral shaft is moderately developed and similar to climbing and suspensory forms, unlike the prominent and distally situated crest in more quadrupedal primates (Fleagle and Simons 1982; Schön-Ybarra and Schön 1987; Ford 1988).

Alouatta, and to a lesser extent *Lagothrix*, possesses straight and quite robust humeri (robusticity index = 6.9) similar to most other quadrupedal platyrrhines able to withstand the frequent action of compressive forces (Schön-Ybarra and Schön 1987; Jones 2004). In contrast, *Ateles* and *Brachyteles* are characterized by equally straight but more slender shafts (5.2 and 5.0, respectively; Jones 2004).

The distolateral crest, where *m. brachialis* originates, is noticeable and seems to extend rather proximally on the lateral side of the humeral shaft as in other primates which habitually flex their elbow (Conroy 1976; Fleagle and Simons 1982). The crest is less evident and more distally located in *Ateles* (Jones 2004). At its distal end, the lateral epicondyle is unreduced in *Alouatta*, but small in *Ateles* (Erikson 1963; Rosenberger and Strier 1989).

The humeral trochlea is shallow and spool-like, with a well-developed medial trochlear lip, and is relatively mediolaterally extended (Fig. 6.11), a morphology that facilitates arboreal quadrupedal movements by allowing a certain degree of mediolateral translation (Jenkins 1973; Feldesman 1982; Fleagle and Simons 1982; Schön-Ybarra and Schön 1987; Ford 1988; Rose 1988; Harrison 1989; Jones 2004). In contrast, *Lagothrix* and *Ateles* possess more cylindrical trochlea with relatively reduced medial lips, morphology associated with well-guided elbow flexion and extension during suspensory activities (Jones 2004).

Alouatta possesses a transversely ovoid and proximodistally high capitulum (Fig. 6.11), which seems to be functionally associated with habitual elbow flexion and forearm pronation during arboreal quadrupedal movements (Feldesman 1982; Schön-Ybarra and Schön 1987; Rose 1988; Harrison 1989; Schön-Ybarra 1998). On the other hand, *Lagothrix* and *Ateles* possess a low, well-developed, and more spherical capitulum that provides ample pronosupinatory rotations during elbow excursions (Rose 1988; Jones 2004).

The medial epicondyle of *Alouatta* is well developed and faces slightly posteromedially but is prominent and medially oriented in *Ateles* (Fig. 6.11; Erikson 1963; Feldesman 1982; Schön-Ybarra and Schön 1987; Harrison 1989). The overall projection of the condyle increases the leverage of the forearm flexors and pronators that contribute to arboreal quadrupedal locomotion, and a more posterior direction further enhances the moment of the acting forces in quadrupedalism (Jenkins 1973; Fleagle and Simons 1982; Schön-Ybarra 1998).

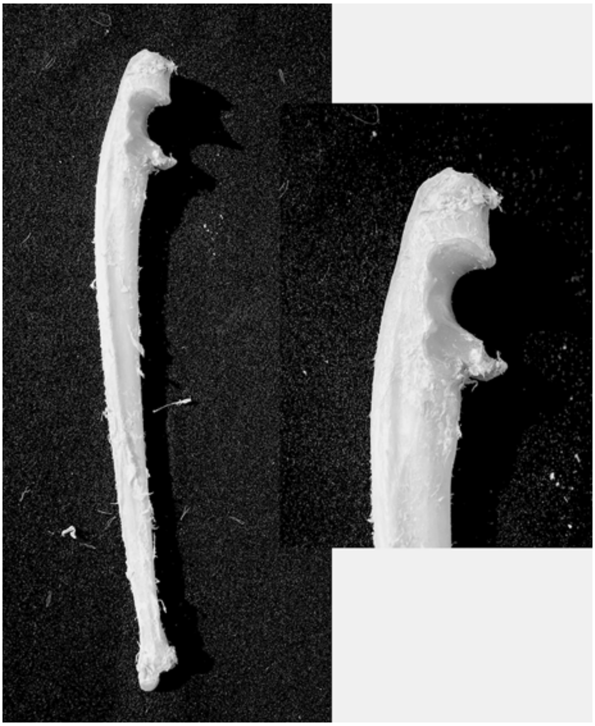

Fig. 6.12 Radial view of the ulna of *Alouatta* (ulna length = 176.3 mm) showing the gentle anterior curvature of the shaft, the robust straight olecranon proximally, and the prominent styloid distally (*left*); the distally inclined shallow sigmoid and the gently concave radial notch in closer views (*right*)

In the ulna, the olecranon is large and faces anteriorly (Fig. 6.12; Youlatos 1994; Jones 2004) providing enhanced mechanical advantage to the action of *mm. triceps* during elbow extension and supporting the weight during habitual elbow flexion (Schön-Ybarra and Conroy 1978; Rodman 1979; Harrison 1989; Schön-Ybarra 1998; Rein et al. 2011; Drapeau 2004). In contrast, it is moderately developed in *Lagothrix* and relatively reduced in *Ateles*, as in most forelimb suspensory mammals (Drapeau 2004).

The sigmoid notch is relatively wide, proximodistally concave and its axis angles medially and distally, with both proximal borders flaring proximally (Schön-Ybarra and Schön 1987; Youlatos 1994). These characters indicate the weight-bearing role of the ulna and elbow excursions that are mediolaterally stable with controlled deviation of the forearm for its placement on arboreal substrates (Conroy 1976; Schön-Ybarra and Conroy 1978; Schön-Ybarra and Schön 1987; Fleagle and Meldrum 1988; Harrison 1989; Schön-Ybarra 1998). Additionally, over the coronoid, the surface is flat and slopes distally; this is related to the habitually flexed postures of the elbows (Fig. 6.12; Schön-Ybarra and Schön 1987; Anapol and Fleagle 1988). The sigmoid of *Ateles* is slightly different, characterized by a weaker angle and being wide, deep, and semicircular with a reduced coronoid process facing anteriorly.

The radial notch is reduced, gently concave, and facing anterolaterally, a condition encountered in most arboreal quadrupedal primates (Fig. 6.12; Youlatos 1994;

Halenar 2011). This morphology allows a certain degree of forearm rotation and provides increased stability during pronation (Rose 1988). In contrast, *Ateles* possess a large concave notch facing anterolaterally, as in other suspensory primates.

In *Alouatta*, and to a lesser extent *Lagothrix*, the ulnar shaft is straight, very robust, and gently concave anteriorly (Fig. 6.12). It is ovoid in section and similar to arboreal quadrupedal platyrrhines (Schön-Ybarra and Schön 1987; Youlatos 1994; Jones 2004). This morphology withstands the action of high compressive forces, resists the action of the elbow flexors, and provides space for radial rotations (Conroy 1976; Fleagle and Meldrum 1988). In contrast, *Ateles* and *Brachyteles* are characterized by quite slender shafts that are T-shaped in section (Jones 2004). Distally, the *Alouatta* ulna is characterized by a robust styloid process, which protrudes distally within the wrist joint. This morphology establishes an extended articulation between the ulna and the lateral part of the wrist, assuring wrist stability and resistance to compressive forces at ulnar deviation during quadrupedal activities (Lewis 1989).

Alouatta, and to a lesser extent *Lagothrix*, possess very robust radii similar to other quadrupedal platyrrhines, implying the action of frequent compressive forces (Schön-Ybarra and Schön 1987; Fleagle and Meldrum 1988; Youlatos 1994; Jones 2004). In contrast, *Ateles* and *Brachyteles* are characterized by quite slender shafts (Jones 2004).

The head of the radius is slightly elliptical with a shallow articular facet that is laterally inclined as in most arboreal quadrupedal primates (Fig. 6.13; Conroy 1976; Rose 1988; Youlatos 1994; Jones 2004). A similar morphology indicates limits to the range of forearm rotation and extended radioulnar and radiohumeral contact during forearm pronation, establishing a locking mechanism for elbow stability (Jenkins 1973; Conroy 1976; Rose 1988; Harrison 1989; Schön-Ybarra 1998). *Lagothrix* and *Ateles* possess horizontal, more cylindrical radial heads with deep facets that permit articular contact throughout a wide range of forearm rotations (Jenkins 1973; Conroy 1976; Rose 1988).

The bicipital tuberosity, that hosts the insertion of *m. biceps brachii*, is distally located as in most quadrupedal platyrrhines (Jones 2004). In contrast, it is rather proximally located in *Lagothrix* and even more so in *Ateles*, indicating a short lever arm, which favors rapid and wider forearm movements (Harrison 1989; Jones 2004).

The distal radioulnar joint is a distally restricted and anteroposteriorly wide facet hosting a syndesmosis that allows a certain range of forearm rotations (Ford 1988; Lewis 1989; Youlatos 1994). In *Ateles*, the facet is practically absent, reflecting the wide range of pronosupination that occurs in the forearm of this suspensory platyrrhine. Distally, *Alouatta* and *Lagothrix* have relatively wide radiocarpal articular surfaces (Fig. 6.13) that provide wide contact for the carpus to withstand compressive forces. Nevertheless, this facet is still narrower than that of other platyrrhines. In contrast, *Ateles* possess very narrow distal articular surface, very likely associated with the reduced presence of compressive forces during their habitual suspensory locomotion (Jones 2004).

Fig. 6.13 Ulnar view of the proximal part of the radius (radial length = 160.9 mm), showing the inclination of the head and the extended articular facet for the radial notch (*left*), proximal view of the ovoid and shallow radial head (radial head length = 12.8 mm) (*right top*), and distal view of the broad radiocarpal facet (*bottom right*)

Alouatta's wrist is rather short and its relative proportions do not depict any functional specializations, other than generalized quadrupedal activities (Godinot 1992). The proximal carpal row, composed of the scaphoid, lunate, triquetrum, and pisiform, is mediolaterally extended and gently curved (Fig. 6.14). In *Alouatta* and *Lagothrix*, the proximal facets of the scaphoid and lunate are similar to most quadrupedal primates and assure an extended contact with the wide distal radial facet allowing flexion and extension movements with limited abduction and adduction (Jenkins and Fleagle 1975; Youlatos 1994, 1996; Kivell and Begun 2009).

The proximal facets of the triquetrum and pisiform are concave and articulate with the corresponding well-developed distal facets of the styloid process of the ulna (Fig. 6.14; Youlatos 1994). This morphology, also encountered in *Lagothrix* and other quadrupedal primates, assures a stable joint during quadrupedal stances when the hand is ulnarly deviated (O'Connor 1975; Beard and Godinot 1988; Lewis 1989). This stability is further enhanced by the long and robust pisiform which is supported by two ligaments that connect with the palmar tubercle of the hamate and the styloid process of metacarpal V (Grand 1968a; Ziemer 1978; Youlatos 1994).

The distal carpal row is composed of the trapezium, trapezoid, capitate, and hamate, which articulate proximally with the distal facets of the proximal carpal row and distally with the metacarpals (Fig. 6.14). At the level of the midcarpal joint, the proximal facets of the capitate and hamate of *Alouatta* and *Lagothrix* are smoothly curved allowing a certain degree of midcarpal rotation (Jenkins and Fleagle 1975;

Fig. 6.14 Radiograph of the hand of *Alouatta*, showing the arrangement of the proximal and distal carpal rows, with the well-developed heads of the capitate and hamate, the well-developed pisiform ulno-proximally, and the extended contact between the distal capitate, and proximal ends of metacarpal II and metacarpal III that accommodate the zygodactylous grasp (metacarpal III length = 33.7 mm)

Kivell and Begun 2009). Additionally, the capitate bears a dorsal expansion of the proximal facet for the os centrale, similar to that found in *Lagothrix*, *Ateles*, and some other suspensory primates, which seem to enhance midcarpal pronosupination (Ziemer 1978). Furthermore, the dorsal facet of the hamate bears a facet for the triquetrum, similar to that of other atelines. This facet allows for the radial rotation of the os centrale over the hamate and increases midcarpal supination (Jenkins 1981; Sarmiento 1988; Kivell and Begun 2009). However, a palmar process on the head of the capitate, non-existent in *Lagothrix* and *Ateles*, would eventually restrain the extended rotations permitted by the above morphology (Youlatos 1994).

The ulnoradial direction and proximodistal elongation of the ulnar facet of the hamate, for the triquetrum, is similar to *Lagothrix* and other quadrupedal primates and is indicative of restricted mobility and enhanced stability for weight bearing (Ziemer 1978; Beard and Godinot 1988; Youlatos 1994). The corresponding facet on the distal surface of the triquetrum is ulnoradially elongated establishing an interlocking mechanism with the hamate in the ulnar side of the wrist (Youlatos 1994).

Intrinsic hand proportions do not show any functional specializations and fall within the ranges of most arboreal quadrupedal primates (Fig. 6.14; Jouffroy et al. 1991; Godinot 1992). *Alouatta*'s metacarpals and phalanges are comparably short and very gently curved, morphology associated with pronograde quadrupedal habits and contrasted with the particularly long and especially curved metacarpals of *Ateles* and other suspensory primates (Erikson 1963; Jouffroy et al. 1991; Hamrick et al. 1995; Stern et al. 1995; Halenar 2011; Rein 2011). *Alouatta* also possess a paraxonal hand with digits III and IV having similar lengths, while the functional axis of the hand usually passes through digit III (Fig. 6.14; Grand 1968a; Youlatos 1999).

The metacarpal I and trapezium facets are rather flat, indicating limited excursions of the pollex (Napier 1961; Rose 1992). The pollex is capable of being positioned against the lateral digits mainly because of the arrangement of digits II–V, but advanced rotatory movements, similar to the ones observed in catarrhines are practically impossible (Rose 1992). However, strong manual prehension upon substrates is achieved by frequent use of a zygodactylous grasp (Fig. 6.14; Grand 1968a). Morphologically, this is assured by the convex joint between the capitate and metacarpal II and between the proximal ends of the latter and metacarpal III, which provide enhanced mobility in both the dorsopalmar and radioulnar planes (Youlatos 1999). Furthermore, the functional separation of the tendons of *m. flexor digitorum profundus and m. extensor digitorum profundus* towards the two pincer arms and the well-developed adductor of digit II probably assure a strong grasp (Youlatos 1999).

6.5.2 Hind Limb

In the pelvis, the iliosacral joint is located cranially in *Alouatta* and the other atelines (Youlatos 1994). The particularly cranial location of the joint increases the distance from the hip joint, providing better leverage for the transmission of the hind limb forces during quadrupedal progression (Rodman 1979). More cranially, the surface of the insertion of *mm. erector spinae* is significantly reduced in *Alouatta*, as in other atelines (Youlatos 1994). A reduced insertion area is functionally associated with the lesser development of these muscles in *Alouatta* and other climbing primates, as these muscles have been shown instead to contribute to pelvic movements during running (Waterman 1929; Stern 1971; Grand 1968b, 1977).

The gluteal surface of the iliac blade is long, wide, concave, and oriented dorsolaterally, presenting an intermediate morphology between the quadrupedal platyrrhines and the more suspensory atelines. The wider and more concave blades in the latter very likely host a well-developed *m. gluteus medius*, which also contributes to hind limb adduction during quadrupedal climbing and frequent suspensory postures (Stern 1971; Zuckerman et al. 1973).

The sciatic area, between the acetabulum and the iliosacral joint, is comparably elongated in *Alouatta*, as in other atelines, and the distribution of trabecular bone is not very dense, as in most quadrupedal primates (Zuckerman et al. 1973; Leutenegger 1974). This condition may be related to the action of tensile forces applied during tail and hind limb hanging postures (Grand 1968b; Zuckerman et al. 1973).

Alouatta possess a large and shallow acetabulum, similar to that found in other atelines and suspensory/climbing mammals, which allows for a wide range of femoral movements (Schultz 1969; Jenkins and Camazine 1977). In addition, it is located rather dorsally and caudally and has equally developed dorsal and ventral buttresses (Youlatos 1994). This morphology very likely reflects resistance to forces applied equally during pronograde quadrupedal actions and hind limb suspension (Fleagle and Simons 1979).

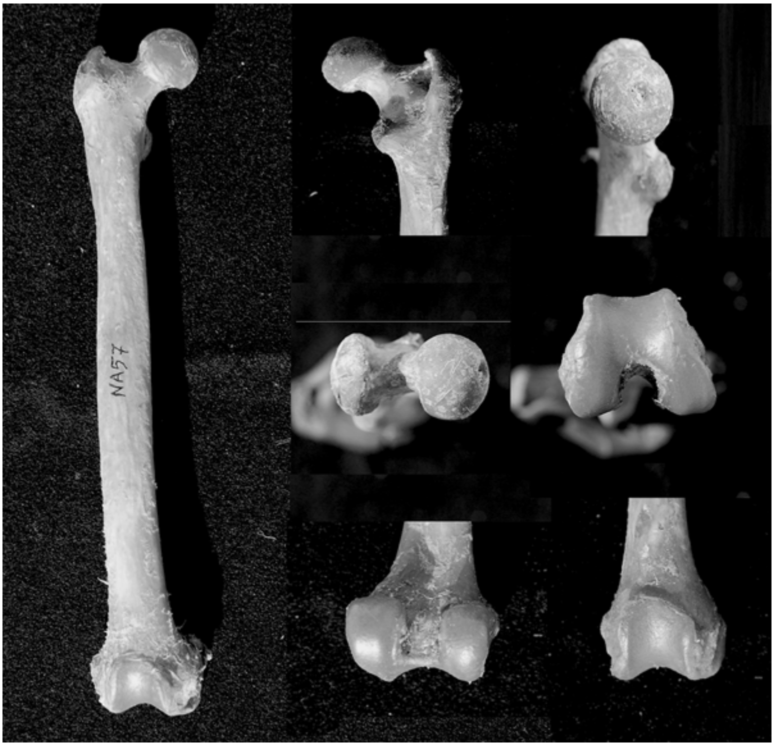

Fig. 6.15 Anterior view of the femur of *Alouatta* (*left*; femur length = 154.2 mm); posterior view of proximal femur showing the head and the greater and lesser trochanters (*top middle*); medial view of the femoral head showing the position of the fovea capitis (*top right*); proximal view of the head and trochanter showing their arrangement (*center middle*); distal view of the knee joint, showing its shape, the depth of the trochlea, and the relative extent and width of the condyles (*center right*); posterior view of the distal femur showing the condyles (*bottom middle*); anterior view of the trochlea showing its shape and its borders (*bottom right*)

The ischium of *Alouatta* is intermediate in length, between the short ischia of the other atelines and the longer ones of quadrupedal platyrrhines. As relatively long ischia provide a better leverage for rapid retraction of the thighs during quadrupedal activities (Smith and Savage 1956), the intermediate condition of *Alouatta* probably reflects slower and more controlled retraction associated with a quadrupedal and climbing repertoire.

The femoral head is more proximally located than the greater trochanter (Fig. 6.15). This condition is encountered in most arboreal mammals and allows a greater range of femoral movements at the hip joint (Dagosto 1983). However, this position is also related to the femoral neck angle which is a variable character among atelines (Ford 1988). In all cases, scansorial and climbing mammals tend to possess higher angles, thus placing the head over the trochanter than more quadrupedal forms (Halaczek 1972; Fleagle 1977; Ford 1988).

The femoral head is semispherical and extends over the neck of the femur (Fig. 6.15). This posterior extension is reduced in *Ateles* and almost lacking in *Lagothrix*, and its expansion in *Alouatta* may be related to its climbing habits as it provides contact between the acetabulum and the head during increased abduction (Jenkins and Camazine 1977; Dagosto 1983). The fovea capitis is large and deep and located either on or near the intersection of the meridian and equator (Fig. 6.15; Schön-Ybarra and Schön 1987; Youlatos 1994). Its morphology and position favor abducted and laterally rotated postures of the hind limb used during climbing and hind limb suspension (Jenkins and Camazine 1977; Rose and Walker 1985).

Alouatta is characterized by a large, deep, and medially oriented trochanteric fossa and a wide intertrochanteric line (Fig. 6.15). This arrangement deviates the tendons of *mm. obturatores* and *gemelli* to an acute angle that favors wide femoral excursions with rotations and abduction (Grand 1968b; Jenkins and Camazine 1977; Schön-Ybarra and Schön 1987; Bacon 1992). Additionally, the increased depth of the fossa enhances the power of the tendons by elongating their lever arm providing controlled and powerful hip rotations (Bacon 1992).

The lesser trochanter is large as in other atelines and is medio-posteriorly directed, as in *Lagothrix* (Fig. 6.15). In contrast, *Ateles* possess a more medially oriented trochanter. This morphology provides a better leverage for the flexion and lateral rotation of the femur by the action of *m. iliopsoas* during climbing activities (Ford 1988, 1990).

The femoral shaft is relatively robust, gently convex anteriorly, and anteroposteriorly compressed (Fig. 6.15; Schön-Ybarra and Schön 1987; Youlatos 1994). This morphology, also shared by the other atelines, is functionally related to the action of forces in various planes, as during climbing and suspensory activities (Halaczek 1972; Godfrey 1988; Ruff 1988; Ruff et al. 1989).

The distal femur of *Alouatta* and the other atelines is mediolaterally wide and oriented slightly laterally (Fig. 6.15; Youlatos 1994). This morphology and deviation is indicative of ample movements in different planes and a more abducted position of the knee joint and is also shared with hominoids and lorisoids (Halaczek 1972; Ciochon and Corruccini 1975; Dagosto 1983; Tardieu 1983). The patellar groove of *Alouatta*, *Ateles*, and *Lagothrix* is relatively deep and wide, similar to that of climbing and suspensory mammals (Fig. 6.15; Schön-Ybarra and Schön 1987; Ford 1988; Youlatos 1994). This morphology allows mediolateral excursions at the knee joint, permitting analogous rotations of the tibia to place the hindfoot on the branches (Rose 1983; Ford 1988; Bacon 1992; Madar et al. 2002).

Both femoral condyles are rather circular in profile implying an extensive range of flexion and extension in contact with the tibial plateau (Rose 1983; Tardieu 1983). However, the medial condyle is slightly longer anteroposteriorly, narrower, and angled medially and posteriorly (Fig. 6.15). This condition reflects the action of stresses through the medial side of the joint and is indicative of mediolateral rotations and a more abducted knee posture (Tardieu 1983; Ford 1988; Bacon 1992; Rafferty and Ruff 1994). Finally, *Alouatta* possesses a very wide and deep intercondylar fossa, a character shared with other climbing primates and mammals. This morphology, in association with the very low intercondylar tibial tubercles, enables

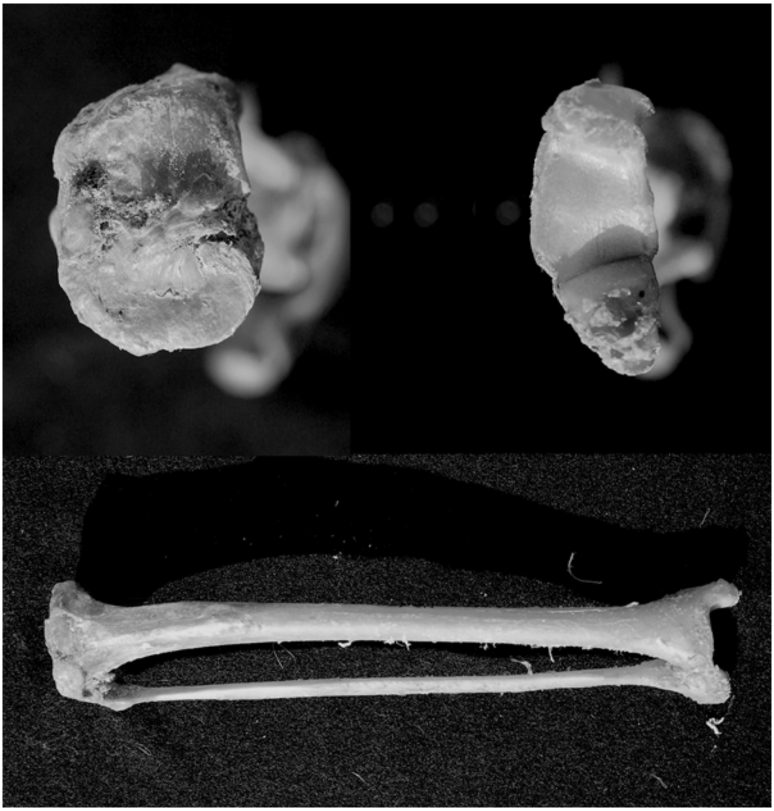

Fig. 6.16 Anterior view of the tibia and fibula of *Alouatta* (left; tibia length = 139.3 mm), proximal view of the rectangular tibial plateau (*top right*), and distal view of the wide talocrural joint and the direction of the medial malleolus (*bottom right*)

mediolateral rotations at the knee joint while keeping the knee flexed (Tardieu 1983; Schön-Ybarra and Schön 1987; Youlatos 1994).

In the tibia, the shape of the plateau is rectangular, similar to arboreal quadrupedal primates and not mediolaterally elongated as in most climbing mammals (Fig. 6.16). The plateau strongly retroflexes and overhangs the shaft posteriorly, a condition indicating habitual flexion of the knee joint (Grand 1968b; Schön-Ybarra and Schön 1987; Youlatos 1994). The tibial facets for the femoral condyles are gently concave with the lateral being longer and narrower than the medial (Fig. 6.16). These features reflect the action of stresses through the medial side of the joint and would favor flexion and medial rotations of the knee (Grand 1968b; Tardieu 1983; Schön-Ybarra and Schön 1987).

Additionally, the anterior tibial tuberosity, insertion of the distal tendon of *mm. vasti* and *rectus femoris*, is relatively reduced and characterized by the presence of dissipated trabecular fibers (Youlatos 1994). This morphology is functionally associated with a controlled role of knee extensors with a reduced lever arm for the tendon's insertion, as well as the presence of multiplanar forces during flexion and extension of the knee joint.

The tibial shaft is straight, relatively robust, and moderately mediolaterally compressed, as in the other atelines (Fig. 6.16). This morphology indicates that major compressive forces act through the medial side of the hind limb and that their action is multidirectional, as encountered during climbing activities (Schön-Ybarra and Schön 1987; Youlatos 1994). The fibula is slender and situated laterally and away from the tibial shaft. This condition is reminiscent of other climbing and hind limb suspensory mammals, providing a wide interosseous membrane for the origin of *mm. flexor digitorum tibialis* and *flexor digitorum fibularis* that flex the pedal digits for powerful hindfoot grasping (Grand 1968b; Youlatos 1994).

The distal tibiofibular facet is low and anteroposteriorly wide as in most platyrrhines (Ford 1988). This condition hosts a synovial articulation that allows a degree of tibiofibular movement that assures a relatively flexible talocrural joint (Ford 1988). The medial malleolus is slightly reduced and fairly medially oriented, similar to the other atelines and most suspensory primates and other mammals (Fig. 6.16; Youlatos 1994; Desilva et al. 2010). Additionally, the anterior surface of the tibiotalar facet is wide and lacks a pronounced distal projection in the middle, as in other atelines (Fig. 6.16). The combination of these features contributes to ample talocrural movements along multiple planes, assuring wide contact with the talus during flexion/extension and inversion/eversion (Ford 1988; Gebo 1989; Harrison 1989; Bacon 1992; DeSilva et al. 2010).

Alouatta has a moderately high talus, higher than *Ateles*, indicating comparably less mobility associated with foot inversion and suspensory habits (Gebo 1986, 1989; Meldrum 1990; Jones 2004). The talar trochlea is large, shallow, and proximodistally wedged as in other atelines. These features provide wide contact of the talus with the tibia throughout flexion, extension, inversion, and eversion of the foot during climbing activities (Dagosto 1983; Langdon 1986; Gebo 1989; Lewis 1989).

The talar neck and head deviate slightly medially, to enable a powerful foot-hold during climbing or pedal suspension against the action of medially directed forces during foot supination (Langdon 1986; Gebo 1989). Furthermore, the talar head exhibits a moderate lateral inclination associated with ample midtarsal movements positioning the navicular and entocuneiform, and thus the hallux, more vertically and enhancing habitual foot supination for powerful foot grasping (Conroy 1976). Powerful grasping is achieved by the leverage of the well-developed *m. flexor digitorum fibularis* (Youlatos 1994), which is evident through the deep groove at the posterior side of the talus and at the plantar surface of the sustentaculum tali of the calcaneus. Additionally, midtarsal supination is further facilitated by the confluent and convex distal talocalcaneal facets on the plantar surface of the head which articulate with the corresponding concave and extended common calcaneal facet on the dorsal surface of the sustentaculum (Dagosto 1983; Ford 1988; Gebo 1989). The proximal talocalcaneal facet is long, wide, and gently curved and associates with a long and equally curved proximal calcaneal facet. This morphology, also shared by the other atelines, facilitates extensive talocalcaneal movements and enhances ankle

Fig. 6.17 Dorsal view of the foot of *A. seniculus* showing the divergent hallux (*bottom*; metatarsal III length = 35.4 mm) and the metatarsal I medial cuneiform joint (*top*)

flexibility during pedal grasping in foot hanging postures (Ford 1988; Gebo 1989; Lewis 1989; Meldrum 1990).

The proximal part of the calcaneus is relatively short, as in most medium-sized arboreal primates, and reflects the leverage for the action of the *mm. triceps surae* (Fig. 6.17; Strasser 1988). Their action is further improved by the elongated tuber calcanei, which further increases their insertion angle for increased power and controlled plantar flexion. Furthermore, the well-developed calcaneal tubercle on the plantar side (Fig. 6.17), where *m. flexor digitorum brevis* originates, reflects its powerful action assisting in digital flexion during foot hanging activities (Sarmiento 1983).

On the medial surface of the calcaneal body, the sustentaculum tali is protruding and medially inclined. These features contribute to frequent subtalar inversion and midtarsal supination related to habitual climbing activities (Gebo 1989). On the lateral surface of the calcaneal body, the peroneal tubercle of *Alouatta* is large, compared to that of other atelines, reflecting the important action of *mm. peroneus longus* and *peroneus brevis*, responsible for foot eversion during quadrupedal activities (Langdon 1986).

Distally, the calcaneocuboid facet is semicircular in shape and relatively shallow, with a well-developed lateral surface. It articulates with a mediolaterally wide calcaneocuboid facet with an equally developed lateral surface on the proximal surface of the cuboid. This morphology enables a certain degree of midtarsal excursions that facilitate mediolateral rotations contributing to foot inversion (Langdon 1986; Ford 1988; Strasser 1988; Gebo 1989).

Alouatta and *Ateles* possess a proximodistally short cuboid, which suggests frequent hindfoot reversal associated with hind limb hanging activities (Gebo 1989; Meldrum 1990; Jones 2004). The proximodistally wide and robust navicular reflects the action of compressive forces on the medial side of the foot during climbing and quadrupedal activities (Langdon 1986). In *Alouatta*, and the other atelines, these two bones articulate via a proximodistally extended facet which enables a wide range of movements between them and contributes to overall midtarsal mobility of the foot (Langdon 1986). On the distal surface of the navicular, the facets reserved for the cuneiforms are transversely arranged, in a manner similar to most quadrupedal primates.

The facet between the medial cuneiform and metatarsal I is similar to most platyrrhines. The dorsomedial part is ovoid in shape reflecting an alignment of the hallux in relation to the lateral digits. Additionally, the plantar part is reduced but retains a saddle-shaped facet that stabilizes the articulation during hallucal prehension (Fig. 6.17; Szalay and Dagosto 1988). This grasping performance is further assured by the relatively elongated and robust metatarsal I, which is achieved by well-developed hallucal musculature, of which the adductors and flexors represent almost 70 % (Youlatos 1994).

6.5.3 Vertebral Column

The vertebral column of *Alouatta* is longer than that of the other atelines in both number of vertebrae in the thoracic and lumbar region, as well as in relative length, and seems similar in these metrics to quadrupedal *Cebus* (Fig. 6.18; Erikson 1963; Johnson and Shapiro 1998). This morphology likely provides more flexibility and lengthens the stride during quadrupedal walking but may also contribute to bridging and clambering maneuvers commonly used by both taxa (Slijper 1946).

Alouatta possesses relatively long lumbar vertebral bodies for their size, contrasting with the rather craniocaudally short vertebrae of *Ateles* (Johnson and Shapiro 1998). Furthermore, the transverse processes of these vertebrae are oriented approximately perpendicular to the sagittal plane, a character shared with other atelines (Ankel 1972; Johnson and Shapiro 1998). These features contribute to a relative firmness and resistance to flexing moments and assure a lumbar region that helps support a hanging animal by the tail and hind limbs (Johnson and Shapiro 1998).

The sacral vertebrae of *Alouatta* are large with wide neural arches, whose proximal and distal openings are more or less the same height, in contrast to most nonprehensile-tailed primates. However, in *Ateles* and *Lagothrix*, the distal opening is even longer than the proximal one, a condition metrically expressed by the sacral index and scoring as high as 112–120 in the latter forms, compared to the 94.4 in

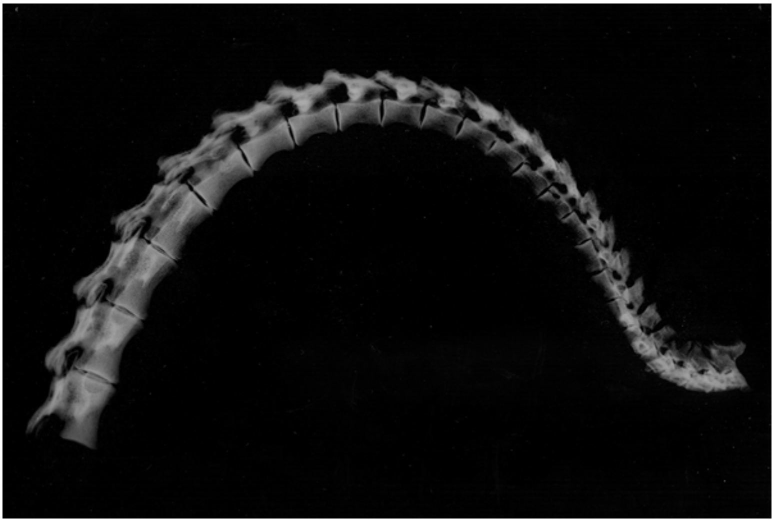

Fig. 6.18 Radiograph of the vertebral column of *Alouatta* showing the different vertebral regions (length of last sacral vertebra = 21.6 mm)

Alouatta (Ankel 1972). This morphology may be associated with the bulkier nerves that provide a fine motor control in the Atelini, compared to that in *Alouatta*, which uses its tail comparatively less (Ankel 1972).

More distally, at the caudal region, *Alouatta* and the other atelines possess several apomorphies that are functionally related to tail prehensility and its extensive use in hanging postures and locomotion. *Alouatta* possesses a very heavy tail, representing ~6 % of total body weight, where caudal vertebrae represent the major component (Grand 1977). Additionally, while atelines have a relatively long tail for their body size, it is least elongate in *Alouatta* (Rosenberger 1983). In effect, howlers have tails that are the same length as their bodies (tail to head body ratio = 0.99 (Youlatos 1994; see also Braza 1980), while there is a gradient to comparably longer tails from *Lagothrix* (1.25) towards *Ateles* (1.38; see also Rosenberger 1983). Interestingly, the relative extension of the naked tactile area shows some variation between atelines. *Alouatta* and *Brachyteles* possess the greatest relative naked areas (0.41 of total tail length) compared to the shorter areas of *Lagothrix* and *Ateles* (0.35 and 0.34, respectively).

In terms of caudal vertebral morphology, *Alouatta* possesses the least number of caudal vertebrae (~25–26) and total caudal vertebral length, compared to *Ateles* (~29–30 (Ankel 1972; German 1982; Youlatos 1994; Organ 2010)). The caudal region is divided into proximal and distal regions, delineated by the transitional vertebra (Ankel 1972). Despite the variability in caudal vertebrae number, all atelines possess a relatively long proximal region characterized by short and high vertebrae articulated by lumbar-like joints that facilitate intrinsic mobility and favor elevation and dorsal flexion of the tail (Ankel 1972). Compared to nonprehensile-tailed primates, the transitional vertebra is located more or less in the same place along tail length in all atelines, indicating a constant relative position (German 1982; Organ 2010). Thus, the relatively long proximal caudal region would favor increased mobility and is associated with its frequent engagement in tail-assisted behaviors (Ankel 1972).

Alouatta, like all atelines and *Cebus*, possess robust caudal vertebrae (German 1982; Lemelin 1995; Organ 2010), a condition also shared by other prehensile-tailed mammals (Youlatos 2003). However, within atelines, *Ateles* has even shorter, more robust vertebrae; this difference is particularly evident in the distal region and more particularly towards the tip of the tail (Ankel 1972; German 1982; Lemelin 1995; Organ 2010). These adaptations reflect the action of frequent and high reaction stresses involving the substrate during extended tail contact and the forces exerted by the powerful *m. flexor caudae longus*.

In effect, *mm. flexor* and *extensor caudae longii* are powerful in prehensile-tailed atelines and span fewer caudal vertebrae (4–7 and 7–9, respectively) compared to nonprehensile-tailed primates. This condition assures greater precision in flexion and extension and more controlled actions (Lemelin 1995). Additionally, the *mm. intertransversarii caudae*, which are the primary lateral tail flexors and rotators, are bulkier in mass and show higher physical cross section area (PCSA) in prehensile-tailed primates, which reflects greater force while maximizing tail contact with the substrate. In *Alouatta*, however, this muscle is not as developed as in other atelines (Lemelin 1995; Organ et al. 2009).

This difference within atelines is skeletally evident in the transverse processes of the caudal vertebrae, whereupon insert *mm. flexor caudae longus* and *intertransversarii caudae*. They are large in atelines compared to those of other platyrrhines, but within the group, *Alouatta* possess the narrowest processes (Ankel 1972; German 1982; Lemelin 1995; Jones 2004). These muscles flex the tail and provide for an enhanced grasp between the distal part of the tail and the substrate while resisting the torsion exerted during tail-assisted locomotion (Lemelin 1995). Their morphology in *Alouatta* may reflect their comparably reduced role in such tail-assisted suspensory activities.

6.6 *Alouatta* Anatomy

The above review of the cranial, dental, hyoid, and postcranial anatomy of *Alouatta* highlights the distinctive morphology of the genus, compared to other atelines and the other platyrrhines as well. The skull of *Alouatta* is quite unique among platyrrhines and reveals strong adaptations to a combination of increased folivory and enhanced sound production. The former is strongly indicated by the arrangement and morphology of the teeth, while the latter is even more prominently evident in the highly modified hyoid bone. Finally, the postcranial skeleton reveals a body plan adapted to above-branch quadrupedal movements with relative arm protraction, abducted forelimbs, and relative stability at the forearm and wrist joints to withstand compressive forces from the substrate. On the other hand, the hind limb reflects adaptations to increased flexion, extension, and abduction, with the capacity for knee rotation and strong flexion and powerful foot grasping. These movements accommodate propulsion as well as a frequent use of suspensory postural behavior, aided by the modifications of the lumbar and caudal parts of the axial skeleton.

This suite of morphological modifications was further substantiated by quantitative analyses of the skull and hyoid bone, which represent the most noticeably derived areas of the skeleton. *Alouatta* is the only extant representative of a group of alouattines that has changed significantly since their divergence from the basal ateline stock at least 15.5 MA, as indicated by molecular and paleontological data (Rosenberger and Strier 1989; Cortés-Ortiz et al. 2003; Hartwig 2005; Jones 2008). This group followed a very distinct evolutionary path from the ancestral stock and the rest of the atelines, which resulted in a very different activity strategy and remarkable morphobehavioral adaptations that currently characterize the genus as a whole. These adaptations are functionally linked to four major behavioral axes: variable but generally increased rates of folivory, enhanced sound production, decreased daily ranges, and emphasis on an above-branch quadrupedal positional repertoire (Rosenberger and Strier 1989; Rosenberger et al. 2011, 2014). These axes are strongly interrelated and very likely evolved in parallel. The simultaneous shift of *Alouatta*'s diet to one focused on leaves, a nutrient-poor food source that imposes important developmental and ontogenetic constraints and also benefits from an energy-minimizing strategy with extended periods of resting for digestion and cautious locomotion, as well as avoidance of costly intergroup violence by the development of an impressive sound production mechanism, probably accounts for the particularly derived skeletal morphology of *Alouatta*. Given the more flexible and ateline-like anatomy and behavior of the last common ancestor of *Alouatta* and the rest of the atelines (Jones 2008; Halenar 2012; Rosenberger et al. 2014), it appears that *Alouatta* evolved a mosaic of cranial and postcranial features that promoted this novel morphobehavioral strategy. Adaptations to these unusual patterns very likely evolved prior to the wide geographic dispersal of howlers in Central and South America and probably contributed to the successful invasion of divergent forested habitats from the northern Mesoamerican wet and dry forests to the seasonal forests of the northern parts of the southern cone (Rosenberger et al. 2009).

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