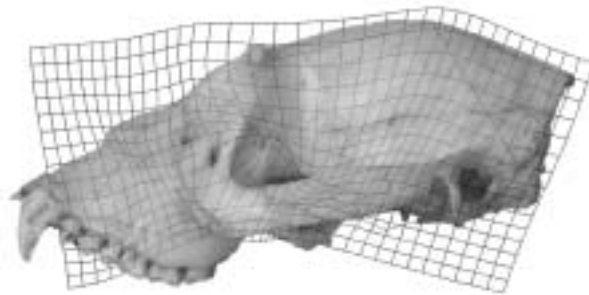


SHAPE MEETS FUNCTION: STRUCTURAL MODELS IN PRIMATOLOGY

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A geometric morphometric approach to airorhynchy and functional cranial morphology in *Alouatta* (Atelidae, Primates)

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Summary – The skull of the howler monkeys (*Alouatta* spp., Atelidae) is characterised by a generalised rotation of the splanchnocranium with respect to the neurocranial antero-posterior axis. This process, referred to as airorhynchy, is the result of a derived structural relationship between basicranium, vault, and facial districts. A number of variables – such as diet and social behaviour – probably co-evolved with the remodelling of the cranial functional matrix. We used a landmark-based analysis to explore the geometrical model of the skull in the genus *Alouatta*. Shape comparisons were performed by using superimposition procedures and the Euclidean distance matrix. In the latter analysis, a method is proposed in order to visualise variations of form through chromatic maps and interpolant functions. The comparison with other genera of Atelidae shows a marked neurocranial flattening in *Alouatta* as well as muzzle projection and enlargement, nuchal flattening, relative basicranial lengthening, and tilting of the occipital foramen. Only minor differences were visible in relation to facial shape, suggesting that significant changes depend on the relationship between splanchnocranium and neurocranium, rather than on localised anatomical variations. The limited vault development constrained by the basicranial structures probably involved the extreme retroflexion of the basal angle. Airorhynchy can be interpreted as an additional adjustment to fit this structural network beyond the biomechanical range of the cranial base hypoflexion. This cranial functional matrix is directly related to feeding and social changes, representing an interesting evolutionary “package”. In *Pongo pygmaeus* a similar process is associated with a different structural pattern, mostly related to the flattening of the upper facial structures, maxillary midsagittal enlargement, and palatal tilting.

Keywords – *Alouatta*, functional craniology, airorhynchy, *Pongo*, geometric morphometrics, Euclidean distance matrix analysis.

Introduction

The genera *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*, are the living representatives of the family Atelidae Gray 1825, forming a monophyletic taxon. Extant howlers are grouped into the Mycetinae subfamily, which includes the fossil genus *Stirtonia* (Szalay & Delson, 1979) and possibly the subfossil genus *Paralouatta* (Rivero & Arredondo, 1991; but see Horovitz & McPhee, 1999). Extant howler monkeys (genus *Alouatta*) represent one of the most distinctive taxa of the Neotropical primatological fauna.

The genus *Alouatta* includes about 10 species and up to 19 subspecies distributed between Mexico and Argentina (see Groves, 2001). They are generally divided into a *palliata* group (mainly Central America) and a *seniculus* group (South America, including *A. caraya*). Despite the controversies on the phylogenetic relationships within the subfamily Atelinae, there is a general agreement about the phyletic independence of *Alouatta* with respect to all the other genera (Rosenberg, 1981; Horovitz & Mayer, 1995; Schneider *et al.*, 1996). According to a mt-DNA analysis, the two subfamilies show a divergence

time close to 16 million years before present (Ma), while the Trans-Andean and Cis-Andean *Alouatta* groups may diverged about 7 Ma (Cortés-Ortiz *et al.*, 2002). The evolutionary patterns are not as clear, because of the mosaic variability expressed in the atelids, which probably includes a large percentage of plesiomorphic characters as well as parallelisms and homoplastic features. *Alouatta* and *Brachyteles* share many dental traits because of the comparable size-related dietary specialisation. *Alouatta* and *Lagothrix* share many postcranial traits, which were influenced by the locomotion patterns (see Szalay & Delson, 1979), and probably some plesiomorphic features like the enlarged zygomatico-faciale foramen displayed by the Oligocenic fossil genus *Parapithecus* (Simons, 2004) and occasionally by *Aotus* (quoted in Osman Hill, 1962: p. 22).

Alouatta displays a set of rather interesting features when compared to the other Atelids, leading early authors to describe this taxon as “the most derived [genus] of the recent Cebidae”, “unmistakable ... on account of its peculiar form”, and with a “bestial appearance” (see Osman Hill, 1962). A trichromatic vision evolved in howlers independently from the catarrhine evolution (see Jacobs, 2004; Heesy and Ross, 2004). The cranial anatomy is very specialised. The hyoid bone is extremely developed, forming large vocal sacs (Schön, 1971) that strongly characterise the howlers communication system accounting for the intense loud calls produced by isolated or grouped individuals. The cranial structure is rather different from the basic morphology of the extant platyrrhini, because of the extreme aiorrhynch. Aiorrhynch can be defined as a dorsoventral rotation of maxillary structures, or the upward rotation of splanchnocranial functional axis onto the neurocranial one. As a consequence of to the subsequent separation between face and braincase, the mandibular ramus enlarges to fill the structural gap between the occlusal plane and the mandibular articulation. In *Alouatta*, the enlargement of the ramus is associated with the development of the masseter, and the development of the hyoid bone. The former morphology is associated with a folivorous diet, while the

latter is associated with the social structure of the howlers. Although the development of the mandible was hypothesised to have the principal role within this structural network (Osman Hill, 1962), it is not possible to split its causes and consequences in an evolutionary perspective, as these processes depend on a general rearrangement of the whole functional matrix of the skull.

Interestingly, aiorrhynch has also been described in *Pongo pygmaeus*, associated — as in *Alouatta* — with the enlargement of the masseter and the development of vocal sacs (Shea, 1985). *Alouatta* also shares some morphological affinities with the cranium of the Oligocene fossil genus *Aegyptopithecus*, mostly in the frontal areas (Simons, 1987). It has also been hypothesised that the two genera share a similar body size and locomotory system (see Rasmussen, 2002). A comparison between *Alouatta* and *Aegyptopithecus* could thus be useful to suggest comments on the evolutionary history of the howlers' morphology.

Although *Alouatta* represents a unique and extremely specialised taxon within the evolutionary radiation of extant primates, the literature on its morphology and anatomy is rather scarce and mostly based on general anatomical descriptions. This explorative analysis is aimed at creating a basic framework for future investigations on this genus, through a “geometric dissection” of its cranial morphology. Different superimposition procedures were used to compare the cranial shape in *Alouatta* with the skull of the other atelids. The process of aiorrhynch in this morphotype was also compared with the analogous changes described in *Pongo*, in order to consider differences and affinities between these two lineages. Finally, we performed a comparison with the cranial shape in *Aegyptopithecus* in order to propose some general considerations on the evolution of the Mycetinae cranial anatomy.

Materials and methods

Sample

In this explorative analysis, Euclidean three-dimensional coordinates were sampled from eight adult *Alouatta* belonging to the *seniculus* group, and averaged in order to compute a mean

configuration of landmarks. Only one adult specimen represents each of the other atelids genus. Unfortunately, the rear vault of the only *Lagothrix* presently available is damaged, and only the facial structures were compared. One *Cebus* was included as non-Atelids morphological outgroup, as well as a cast of the 1966 complete skull of *Aegyptopithecus* (see Rasmussen, 2002). We also considered one adult male *Pongo* and one adult male *Pan* in order to compare the airorhynchy in howlers and orangs. Although this descriptive analysis cannot check the within-genus and between-sexes variability, it is assumed that the intergeneric differences should be larger to allow a generic and explorative morphological comparison. Data were sampled at the Museum of Anthropology Giuseppe Sergi, in Rome (Bruner & Manzi, 2001).

Shape comparison

We used landmark coordinates and superimposition to compare the cranial geometry in different taxa, both in two and three dimensions. A three-dimensional bilateral configuration of 42 landmarks was selected to describe the cranial morphology (Tab. 1; Fig. 1). The entire skull was considered, as well as a sub-configuration including only the facial morphology. Landmarks were sampled with a Microscribe 3DX (Immersion Corporation). Using the three-dimensional dataset, two-dimensional data were computed

with MORPHEUS ET AL. (Slice, 2000) by alignment of the whole sample according to the Principal Component eigenvectors, and subsequently projecting the resulting coordinates on a lateral plane (only the left side was used in the shape comparisons). The coordinate systems were superimposed by Procrustes (both 3D and 2D data) and Bookstein Superimposition (2D data) using MORPHEUS ET AL. (Slice, 2000), and shape differences were visualised using geometrical comparison and thin-plate spline (Bookstein, 1991). The first procedure operates a translation of the coordinate systems to a common centroid, scaling to unitary centroid size, and a rotation between corresponding landmarks using a least-squares approach. The second procedure superimposes the configuration onto a common baseline. Bookstein superimposition was used to compare 2D configurations relatively to the neurocranial length (nasion-opisthocranium). The information available from these two superimpositions is rather complementary: while the first normalises the effect of size differences (i.e. approaching “shape”) the second is useful to compare phenotypic variations with respect to a specific functional/structural reference (the neurocranial axis).

Procrustes distances were computed by TPSSMALL 1.19 (Rohlf, 1998) and visualised according to the unweighted pair-group method using arithmetic averages (UPGMA) cluster pro-

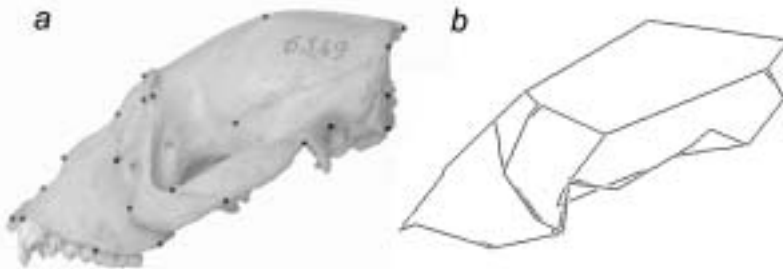


Fig. 1 - Complete three-dimensional configuration of landmarks (42), shown in lateral view (basicranial landmarks are not visible). Landmarks are plotted on the skull of *Alouatta* (a) and linked to produce a geometric reference model (b). See Table 1 for landmarks description.

cedure by SYNTAX 2000 (Podani, 1997), in order to check the main phenotypic affinities.

Euclidean Distance Matrix Analysis (EDMA) was used to perform a further comparison, in order to check form differences regardless of scaling procedures (see Richtsmeier *et al.*, 2002). A subset of 17 lateral-projected landmarks was used to limit the number of interlandmark distances. EDMA were performed using WINEDMA (Cole 2002). Interlandmark distances exceeding 2 standard deviations from the mean value of the whole Form Difference Matrix (FDM) were considered as *determinant interlandmark distances*. Landmarks with a median distance value exceeding 5% of the average median value were considered as *influential landmarks*. The median variation of each landmark from the FDM was used to compute and map an interpolating function in order to visualise the pattern of form differences (*Form Difference Maps*). Maps were computed by SURFER 7.0 (Golden Software, Inc.), using a radial basis function through multiquadric interpolation (Carlson & Foley, 1991), suggested for small samples and scattered data. Interpolations with other common functions gave overall similar results. These maps allow a visualisation of the form differences, describing patterns of increasing/decreasing interlandmark distances. The minimum represents areas of relative shortening, and the maximum value represents areas of relative lengthening. The intermediate value represents a mean size difference between the two forms, expressed as a ratio between each interlandmark value (ratio = 1 means no difference).

Anatomical notes on the cranial structure of the Atelids

The configuration used in this explorative analysis is based almost entirely on type I landmarks (Bookstein, 1991), according to the biological principle of homology. In general, in geometric morphometrics the *operational homology concept* can offer a more useful reference (Smith, 1990), in considering the structural parameters of the anatomical system. The inter-specific variability often makes it difficult to rely on homol-

ogy, and this is the case with the atelids skull (Fig. 2). The inter-orbital area represents a very important source of information, because of its role in convergence, encephalisation, and in the relationship between face and vault. Landmarks from this district were not included in the present study, because of the lack of correspondence between the different taxa. Usually, the maxillary processes reach the frontal suture separating the ipsilateral nasal and lacrimal bones. This pattern allows the recognition of two osteometric points, namely *maxillofrontale* and *dacryon* (see White & Folkens, 2000). This is also the pattern found in *Cebus*. In *Lagothrix*, the maxillary processes meet above the nasal bones, whose lateral borders converge at nasion, while the two *maxillofrontale* converge toward the midsagittal plane. *Brachyteles* shows a marked superior thinning of the maxillary processes, and a tendency to overlap *dacryon* with *maxillofrontale*. In *Ateles* the maxillary processes do not reach the frontal suture, being separated by the lacrimal bones. *Alouatta* displays a pattern similar to *Ateles*, with an almost constant lacrimo-nasal suture that, however, is limited in young specimens (Osman-Hill, 1962). Furthermore, the nasal bones are extremely different in the four genera: broad and short in *Lagothrix*, curved and converging upward in *Brachyteles*, thin and converging in *Ateles*, and almost parallel in *Alouatta*. Other functional areas such as the temporal fossa (Bruner *et al.*, nd) display a similar condition among the Atelids skull. Clearly, further studies are needed to describe the intra-generic and intra-specific variability of these features. It is worth noting the difficulties in considering biological homology in these variable structures. Future analyses must be necessary developed so as to carefully consider the biological correspondence.

Results

Three-dimensional shape comparisons

Figure 3 shows the skull shape 3D comparisons between the *Alouatta* morphology and the other genera considered. In *Alouatta* there is a

Tab. 1 - Landmarks and definitions.

Unpaired	
prosthion	White & Folkens, 2000
nasion	White & Folkens, 2000
rhinion	White & Folkens, 2000
nasospinale	White & Folkens, 2000
sphenobasion	White & Folkens, 2000
posterior nasal spine	White & Folkens, 2000
basion	White & Folkens, 2000
opisthion	White & Folkens, 2000
opisthocranion	White & Folkens, 2000
bregma	White & Folkens, 2000
Paired	
premaxillare	alveolar border of the premaxilla-maxilla suture
premolare	alveolar border between P4 and M1
molare	posterior alveolar border behind M3
zygomaxillare	White & Folkens, 2000
zygoorbitale	White & Folkens, 2000
frontomalare orbitale	White & Folkens, 2000
frontomalare temporale	White & Folkens, 2000
orbitale superior	midpoint on the superior orbital border
nasomaxillare	lowest point of the naso-maxillary suture
sphenoorbitale	lowest point of the zygo-sphenoidal suture
zygomotemporale superior	superior point of the zygomo-temporal suture
zygomotemporale inferior	inferior point of the zygomo-temporal suture
articulare laterale	most lateral point of the glenoid fossa
porion	White & Folkens, 2000
asterion	White & Folkens, 2000
pterion	White & Folkens, 2000

clear midsagittal enlargement of the premaxillary structures and lower face, with *Brachyteles* also showing a more depressed nasal area compared to the other specimens. The maxillary complex widens (mostly when compared with *Ateles*) except when compared with *Brachyteles*. A marked frontal bone flattening is associated with a loss of frontation, i.e. a marked inclination of the orbital surface. Orbits are also relatively narrower. This configuration of the upper face is extreme when compared to the *Cebus* morphology. The cranial base of *Alouatta* is lengthened, because of the backward shifting of the sphenoccipital suture. In *Cebus*, the base is further shortened because of the backward position of the posterior palatal spine. The vault in *Alouatta* is extremely flattened, with the bregma in a relatively forward position. The neurocranium is relatively narrow, mostly com-

pared to *Ateles*, which in contrast has narrower zygomatic arches. Malar bones are relatively widened only in *Cebus*. The whole nuchal plane is rotated upward, and the foramen magnum is consequently tilted backward.

The differences are less marked in considering the superimposition of the facial shape (Fig. 4). *Alouatta* shows a light premaxillary enlargement and upper facial flattening. The midface is also depressed, except when compared with *Brachyteles* that displays an even more flattened profile. The maxilla is relatively narrower in *Ateles* and wider in *Cebus*. The orbital surfaces are no longer inclined, and the frontation is also improved because of a backward shifting of the inferior orbitale with respect to the muzzle area. Orbits are narrower, particularly in comparison to *Ateles* and *Brachyteles*. Because of the maxillary development, malars are relatively shifted backwards.

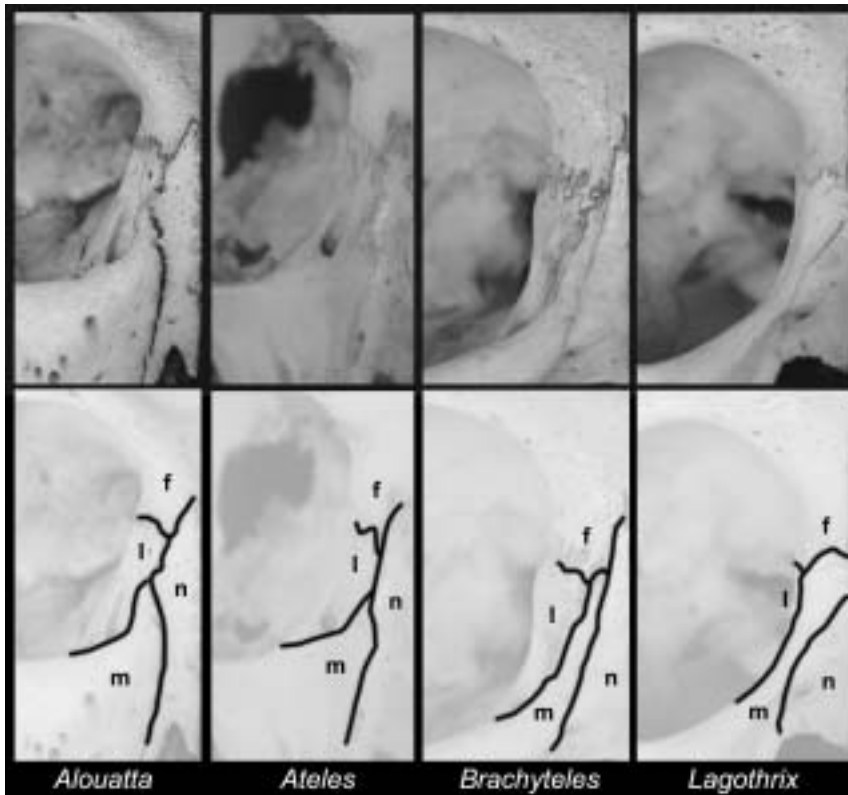


Fig. 2 - The interorbital area in the atelids. *Alouatta* and *Ateles* show a contact between lacrimal and nasal bones. In *Brachyteles* the contact between the maxillary processes and the frontal bone is almost limited to a single point. In *Lagothrix*, the maxillary processes meet above the nasal bones, forming a intermaxillary suture. Labels: m: maxilla; n: nasal bone; l: lacrimal bone; f: frontal bone.

When the overall phenotypic affinity is considered as Procrustes distances, the skull of *Alouatta* differs from the other Atelids (Fig. 5a) more than *Cebus*. In contrast, the facial shape is highly comparable with the *Brachyteles* and *Ateles* configurations (Fig. 5b).

Two-dimensional shape comparisons

In figure 6 the pairwise comparisons between the skull shapes are computed on the 2D projected data (lateral projection, left side). The Procrustes superimposition shows the maxillary enlargement and premaxillary projection in *Alouatta*, and the midfacial flattening in

Brachyteles. Orbits are more verticalised in *Cebus*. In *Alouatta* the entire vault (including the frontal and orbital areas) is extremely flattened, the nuchal structures are tilted backward and upward, and the cranial base (posterior palatal spine to spheno-occipital suture) is lengthened. The malar area varies in each species. *Brachyteles* shows the least amount of shape differences compared to *Alouatta*. The distortion grids stress the neurocranial flattening, nuchal rotation, muzzle enlargement, and basicranial lengthening. Compared to *Cebus*, *Alouatta* shows a vertical facial compression related to the premaxillary rotation, and a coronal structural compression at

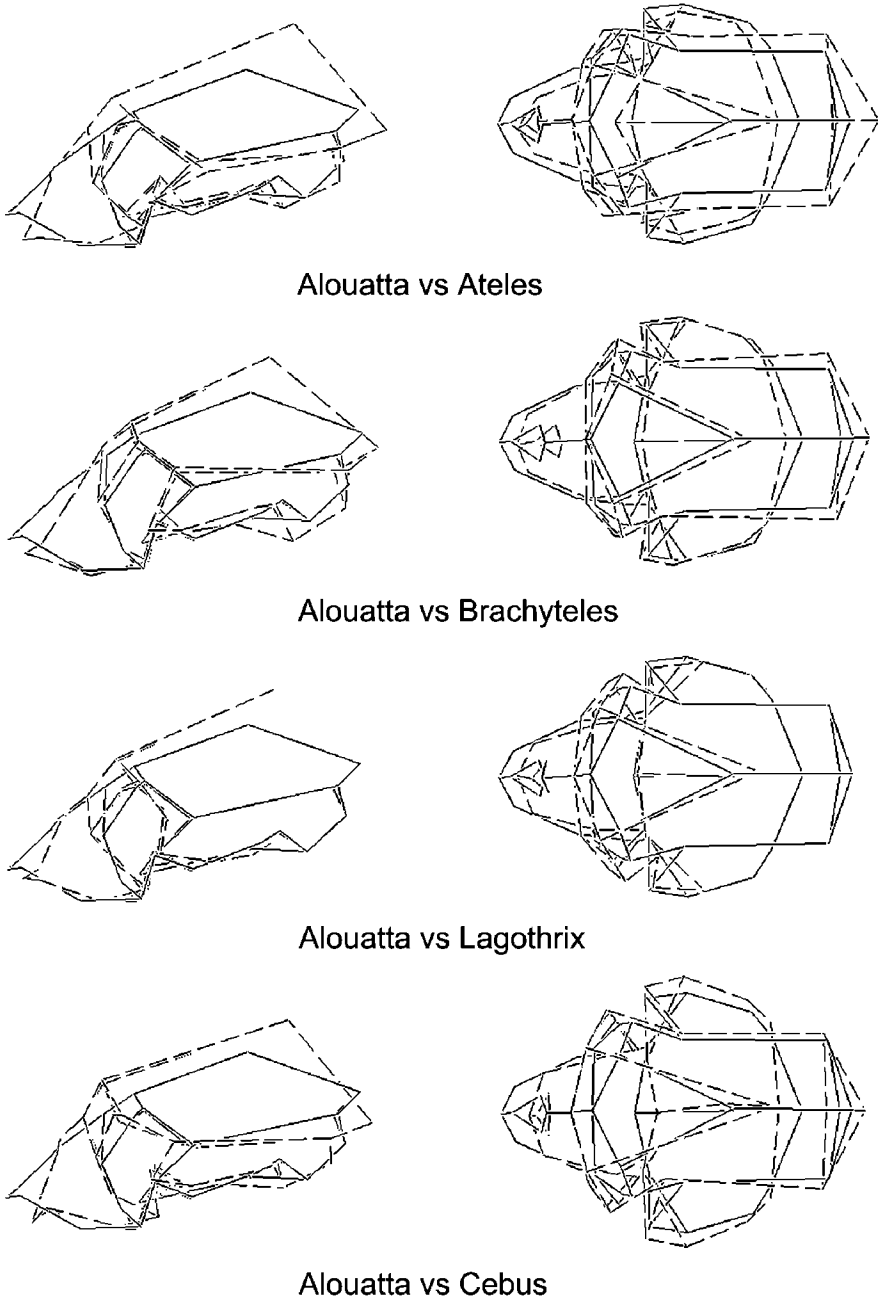


Fig. 3 - Pairwise comparisons of the complete configurations of landmarks after Procrustes superimposition (left lateral and superior views).

the level of the porion. Compared to *Ateles*, the face is rotated on the neurocranial axis but not vertically compressed. The coronal structural compression is localised at the level of the pterion, and the maxilla is significantly enlarged. Compared to *Brachyteles*, there is a marked mid-facial enlargement, and a minor structural compression at the level of the porion. In all cases the flexion of the neurocranial structures onto the facial one is well expressed.

Through the baseline superimposition, it is possible to compare shapes in relation to the same neurocranial length. *Brachyteles* is more similar to *Alouatta* than the other two taxa. The differences concern the upper and midfacial enlargement and neurocranial flattening. *Ateles* and more specifically *Cebus* show a further reduction of splanchnocranium and verticalisation of the orbits. Interestingly, by superimpos-

ing the neurocranial axis, the orientation of the foramen magnum shows a very limited rotation. It is worth noting that while the Procrustes superimposition better describes the overall phenetic affinity, the Bookstein superimposition is suitable to promote structural hypotheses (when the baseline is assumed to represent a functional reference).

Pongo vs Pan

Following the Procrustes superimposition, the main differences identified between the *Pan* and *Pongo* cranial shapes (Fig. 7) concern a marked frontal flattening and maxillary enlargement in the latter. The maxilla-premaxilla complex undergoes a sagittal development without widening, showing a relative inclination of the alveolar border. The orbits are smaller, but there is no loss of frontation. The neurocranium

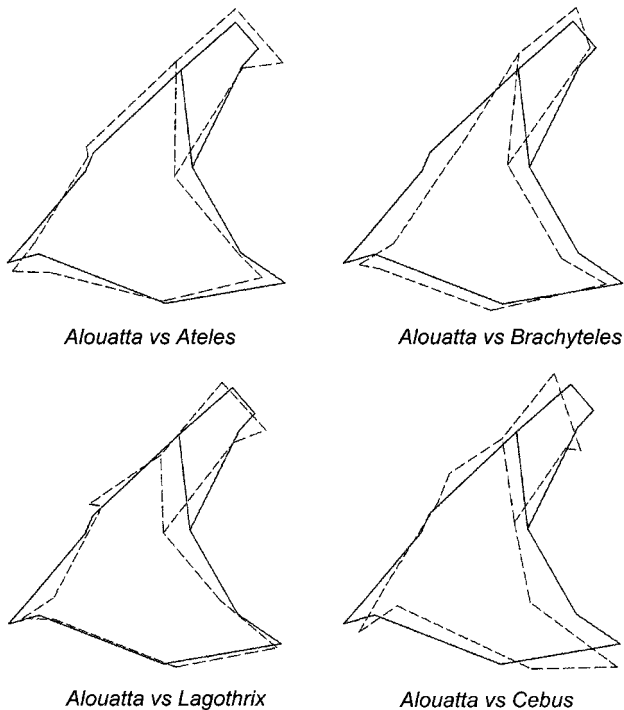


Fig. 4 - Pairwise comparisons of the facial configurations of landmarks after Procrustes superimposition (left lateral view).

widens posteriorly, and the nuchal area becomes shorter and taller. The foramen magnum is slightly tilted backwards. The zygomatic arches enlarge. The cranial base does not lengthen, and the vault does not flatten except at the level of the frontal squama.

Comparing the projected two-dimensional cranial shapes in *Pongo* and *Pan* in lateral view by Procrustes superimposition, the former shows a marked frontal flattening with only a minor relative vertical shortening of the vault. In contrast the nuchal area is relatively taller. The development of the maxilla-premaxilla complex is associated to a rotation of the alveolar border, without changes in the orientation of the lower and midfacial profile. The cranial base is scarcely lengthened, and the foramen magnum is rather tilted backward without a posterior displacement. There is a strong forward shifting of the inferior border of the zygomatic arch, but the malar/pteric areas are quite comparable. There is no clear loss of frontation. The distortion grids are mainly characterised by the zygomatic shifting and by the neurocranial tilting associated to the vault and frontal flattening, and nuchal enlargement.

The neurocranial superimposition emphasises the neurocranial/basicranial vertical development in *Pongo* mainly in relation to the lower areas, and the forward enlargement of the middle and lower face associated to the zygomatic movement. There is a palatal tilting and loss of frontation, without rotation or displacement of the foramen magnum.

Euclidean Distance Matrix Analysis

The Euclidean distance matrix comparison was computed between *Alouatta* and *Brachyteles* and between *Pongo* and *Pan*, to compare the similar airorhynch patterns.

Alouatta/Brachyteles - The FDM shows a similar size for the two specimens (mean and standard deviation for all the interlandmark distances: 0.99 ± 0.13). The influential landmarks show a lengthening at the rhinion (median ratio = 1.10), and shortening at superior orbital rim (0.94), opisthocranion (0.95), and bregma (0.87). The determinant interlandmark distances show a shift of the rhinion from the inferior orbital rim (ratio = 1.73) and a shortening of the distance between porion and the spheno-occipital suture (0.68). Furthermore, there is a general involve-

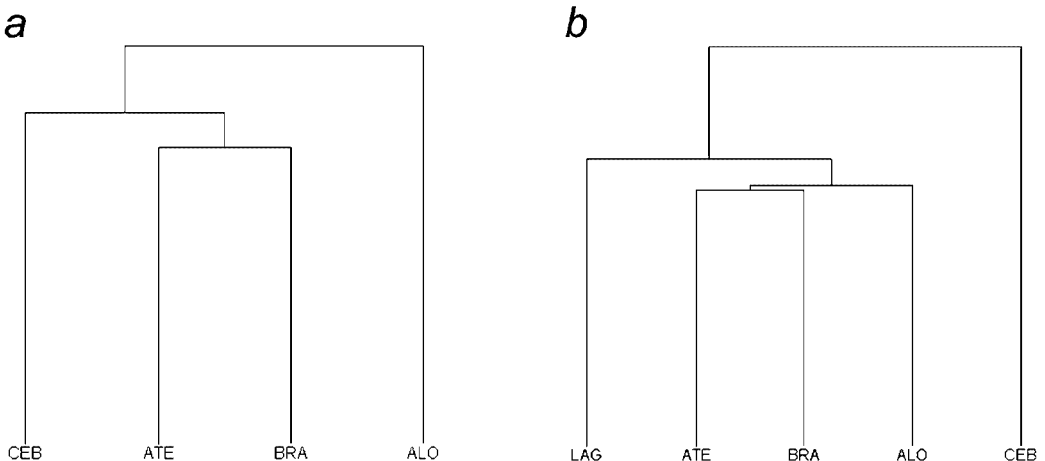


Fig. 5 - UPGMA phenograms computed on the Procrustes distances, considering the complete (a) and facial (b) configurations (Alo: *Alouatta*; Ate: *Ateles*; Bra: *Brachyteles*; Ceb: *Cebus*; Lag: *Lagothrix*).

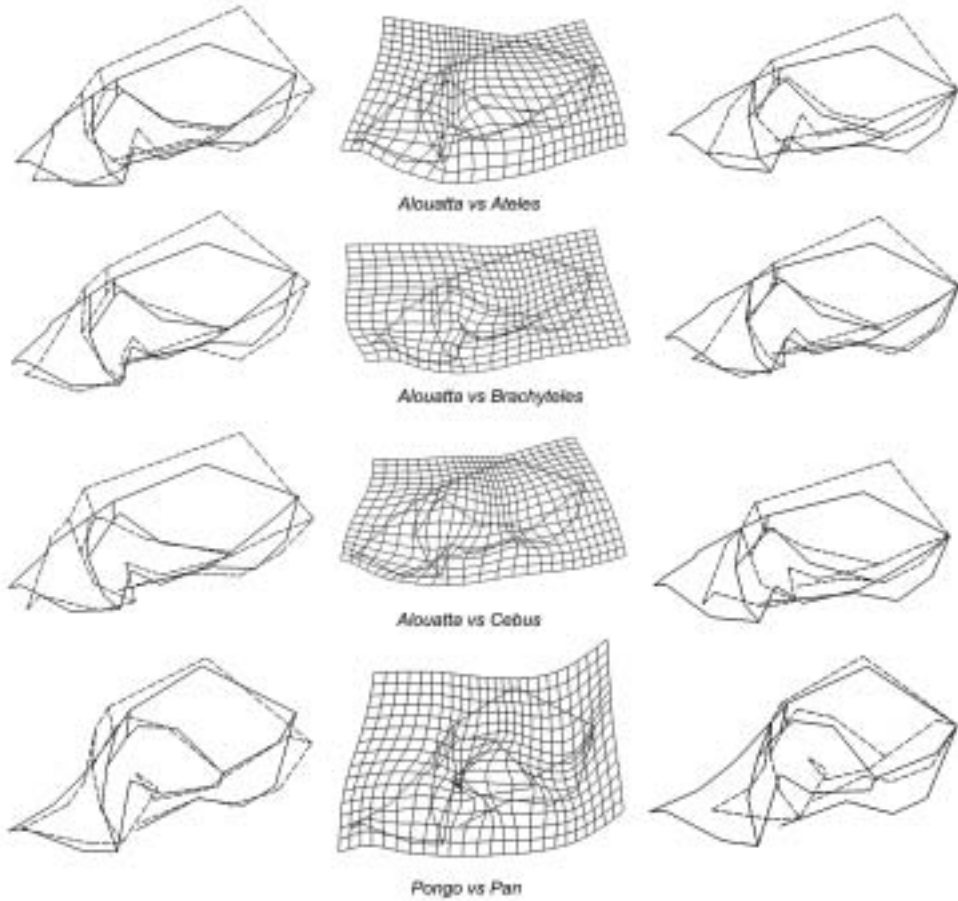


Fig. 6 - Pairwise comparisons of the complete configuration of landmarks after two-dimensional lateral projection (26 landmarks). Comparisons are visualised by Procrustes superimposition of the geometrical model (left), distortion grids and thin-plate spline (middle), and baseline superimposition on the neurocranial length (right).

ment of landmarks in relation to vault and nuchal flattening. The map of the form difference interpolation stresses the flattening of the neurocranium and the muzzle forward development (Fig. 8a).

Pongo/Pan - The FDM shows a larger size for *Pongo* (1.14 ± 0.17). The influential landmarks show a relative lengthening at the prosthion (median ratio = 1.21), premolar (1.26) and

molar (1.23) areas, and basion (1.21), with relative shortening at the orbital rim (1.01-1.06), nasion (1.00), and bregma (1.07). The determinant interlandmark distances again show a shift of the rhinion from the inferior orbital rim (ratio = 2.10), and a relative approaching between the lateral orbital border and nasion (0.65). There is a general involvement of landmarks related to nuchal, vault, and frontal flattening. The map of

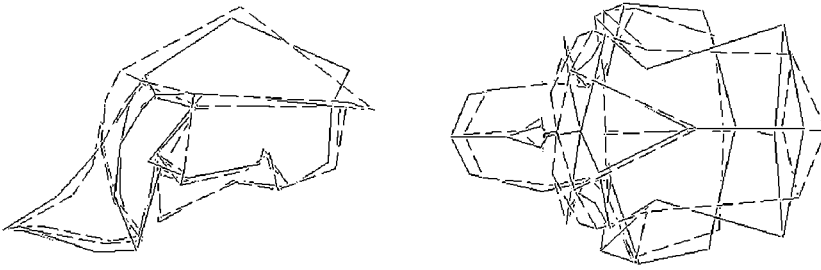


Fig. 7 - Pairwise comparison between Pan and Pongo after Procrustes superimposition (left lateral and superior views).

the form difference interpolation stresses a shortening of the supraorbital landmarks and the downward enlargement of the maxilla (Fig. 8b). *Aegyptopithecus*

Only some landmarks are available on the *Aegyptopithecus* cast, mostly because of the preservation of the specimen. Comparing the *Alouatta* and *Aegyptopithecus* cranial shape by superimposition, a structural affinity is easily recognised mostly because of the muzzle enlargement and because of the similar relationship between facial and neurocranial districts (Fig. 9). The maxillary complex is more developed in the Oligocene taxon, even though it is relatively narrower compared to *Alouatta*. The neurocranium shows similar proportions. The most important difference is observed at the foramen magnum: in both cases it is placed in a posterior position, but in *Aegyptopithecus* is not tilted as in the howler. The distortion grid from the lateral projection stresses the relative splanchnocranial development and the absence of a clear inclination of the occipital foramen in the former.

Discussion

In view of the explorative nature of these results, some comments are provided on the structural craniology in *Alouatta*, on the phylogenetic patterns of the Atelids, and on the parallel evolution of airohynchy in *Pongo pygmaeus*.

Cranial structure and evolution in Alouatta

The shape comparisons between the Atelids genera provide a general description of the structure of the skull in *Alouatta*. The entire neurocranium is extremely flattened, and at the same time narrower than that of the other atelids. It is noteworthy that *Alouatta* shows an early cessation of neurocranial growth related to an early obliteration of all the cranial sutures (quoted in Osman Hill, 1962: p.16), and it is clear that the timing of craniosynostosis had a major role in the evolution of the cranial morphology in this morphotype. The flattening of the frontal bone is associated to a relative posterior shortening of the frontal squama and inclination of the orbits. The subsequent orbital morphology characterises *Alouatta* as probably the least frontated anthropoid (Bruner *et al.*, 2002). It is interesting to note that orbits are inclined with respect to the neurocranial axis, but not considering the facial morphology alone. The morphogenetic processes leading to a generalised flattening of the neurocranial and basicranial structures occur almost entirely during the post-natal growth, with the early ontogenetic stages showing a more typical basikyphosis that is partially preserved in adults along the brainstem (Osman Hill, 1962). Anyway, Jeffery described interesting differences between *Alouatta* and *Macaca* during prenatal ontogeny (Jeffery, 2003). In both species the basicranial retroflexion (i.e. hypoflexion) is correlated with brain growth and development, but in

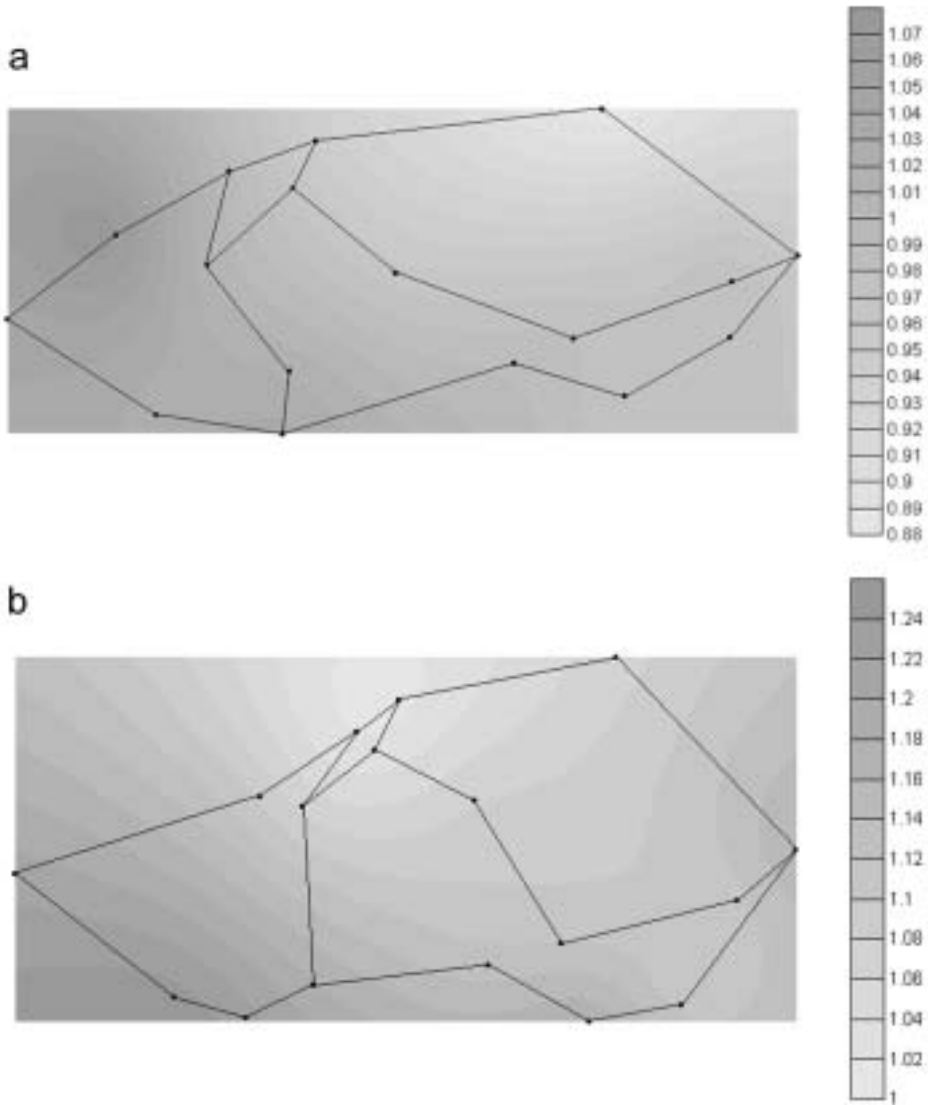


Fig. 8 - Form Difference Maps comparing *Alouatta* versus *Brachyteles* (a) and *Pongo* versus *Pan* (b). The configuration is based on 17 lateral-projected landmarks. The median values from the Form Difference Matrix of each landmark are interpolated using a multiquadric radial basis function (other similar functions do not change the overall pattern). The scale provides a quantification of the processes, referring to the median ratio between the interlandmark distances of the numerator and that of the denominator. In *Alouatta*, a vault vertical flattening associated to a forward muzzle development is observed, while in *Pongo* there is a supraorbital backward flattening associated to a downward premaxilla/maxilla development.

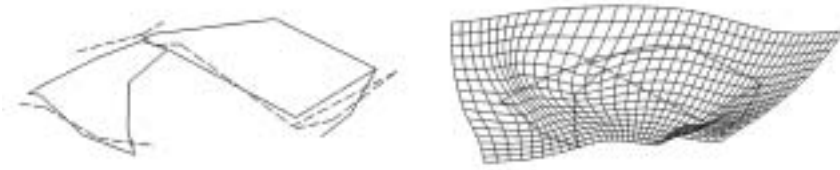


Fig. 9 - Pairwise comparisons between *Alouatta* and *Aegyptopithecus* through Procrustes superimposition of two-dimensional left lateral projections.

Alouatta this process is faster, associated with lower rates of total and posterior cranial base lengthening, and associated with the infratentorial absolute and relative development. Furthermore, in *Alouatta* the volumetric brain expansion is generally slower, but the cranial base angle is always much higher than in macaques of similar maturation quotient, and the infratentorial (i.e. cerebellar) structures are relatively more developed (see details in Jeffery, 2003). All these features must be involved in the final neurocranial morphology of the howler monkeys, and should be carefully considered in terms of structural correlations between cranial parts. The faster retroflexion stresses neurocranial flattening and airorhynchy, which seem to be anyway evident since the earliest fetal stages (at least at the 40% of the total prenatal period). The scarce lengthening of the clivus is probably involved in the basioccipital shortening and nuchal rotation, also necessarily affected by the structural adjustments related to the infratentorial development. The slower rate of cerebral growth leads to a generalised neurocranial limited enlargement.

The basicranium flattens and lengthens through the stretching of the sphenoid body, displacing the sphenoccipital suture and the foramen magnum backward. The pneumatization of the sphenoidal body in *Alouatta* (Osman Hill, 1962) is probably secondarily related to this sagittal development between the vomer and the sphenoccipital suture.

Considering the importance of the basicranium and in particular of the sphenoccipital suture in the development of the cranial functional matrix (e.g. Lieberman *et al.*, 2000), this process has probably a major role within the evolutionary changes described in *Alouatta*. Actually, the pressure along the anterior cranial base can easily involve the rotation of the splanchnocranium and be related to the flattening of the vault. Ross *et al.* (2004) have recently published an extensive analysis on the basicranial flexion in Primates. Species-specific averaged data from Ceboidea and Cercopithecoidea shown the outstanding position of *Alouatta* because of its basicranial length, cranial capacity, and cranial base angle. The basicranium is very lengthened when compared with the small cranial capacity (approximately 50 cc.), probably with a large contribution of its anterior parts (Fig. 10a). Consequently, the encephalisation index relative to the basicranial length is extremely small. The spatial packing hypothesis states that in primates an increase in the relative encephalisation index is associated with a flexion of the cranial base (see Ross *et al.*, 2004). *Alouatta* does not fit the relationship described for the Ceboidea-Cercopithecoidea variation, showing even a less flexed base compared with its low relative encephalisation or, conversely, a small encephalisation index for such cranial base angle (Fig. 10b). Some structural constraints must be involved in this configuration, where the

vault flattening and sphenoid lengthening act directly onto the cranial base flexion and endocranial volume. The howler's base angle is theoretically compatible with a larger encephalisation index, within the Ceboidea-Cercopithecoidea variation. In contrast, the scarce encephalisation index would require an extreme retroflexion of the base, probably out of the available structural range. It is therefore possible to hypothesise that this extremely low encephalisation index has involved the maximum possible retroflexion, plus an additional compensatory adjustment represented by the rotation of the splanchnocranium (namely, airohynchy). The low encephalisation index must be related more to neurocranial flattening and narrowing (i.e. scarce cranial capacity, related to slow rate of cerebral growth, suture fusion, etc.) than to an actual and absolute lengthening of the sphenoid. The Euclidean Distance Matrix Analysis (based onto the ratios between absolute values) largely supports this hypothesis, stressing the neurocranial flattening and midface enlargement, without any localised changes at the cranial base (see Fig. 8).

The same process tilts the occipital foramen backwards, promoting a flattening of the nuchal area and characterising the *in vivo* posture of the howlers. It is worth noting that the foramen magnum is much less inclined with respect to the neurocranial axis.

The premaxilla-maxilla complex undergoes a relevant development, through a general enlargement and forward projection of the midface.

All these features increase the airohynchy, producing a widening of the neurocranial/splanchnocranial axis and a morphological "crease" (Bookstein, 2000) between pterion and porion, which suggests that these surfaces may have a major structural role. The relative position of the occipital foramen onto the neurocranial length and the relative position of the orbits onto the facial morphology stress the hypothesis of different relationships between functional parts (face, base, and vault) without major local rearrangements. The peculiar morphology of the skull in *Alouatta* is actually rather "atelid-like" when the facial shape is considered

alone. *Brachyteles* shows an interesting phenotypic similarity with *Alouatta*, despite a species-specific flattening of the midfacial areas. In addition, the shared interorbital anatomy between *Alouatta* and *Ateles* should be further explored.

These results and the comparison with *Aegyptopithecus* can suggest some comments on the evolution of the howlers' cranial morphology. In the latter, the splanchnocranium is tilted onto the neurocranial axis because of the scarce cranial development and the marked maxilla/premaxilla relative enlargement. The similar morphology displayed by *Aegyptopithecus* and *Alouatta* is probably related to a similar relationship between face and neurocranium, but there is no evidence of shared structural processes. The antero-posterior muzzle enlargement in the specimen of the Oligocene is not associated with a general maxillary widening, and the foramen magnum - although shifted to a posterior position - is not tilted as in *Alouatta*. In considering the muzzle shortening described along the anthropoids evolution and the peculiar nuchal shape in *Alouatta*, it is reasonable to hypothesise a parallelism between a derived condition in the howlers and a plesiomorphic morphology for *Aegyptopithecus*. In the latter, the skull morphology can be easily interpreted as an archaic expression of the volumetric ratio between neurocranium and splanchnocranium. In *Alouatta*, the different relationship between muzzle and cranial base (sphenoidal lengthening and associated shifting of the foramen magnum) suggests that the rotation of the facial axis is probably related to a secondary (i.e. derived) splanchnocranial enlargement associated to with a specific adaptive context (Osman-Hill, 1962).

These inferences do not involve comments on the ancestral morphology of the Atelids themselves, and on the within-group polarity of their characters, including airohynchy. The probable phyletic relationships within the Atelids (Horovitz & Mayer, 1995) is largely characterised by mosaic patterns and a certain amount of homoplasy, as can be possibly hypothesised comparing postcranial and dental traits (Szalay & Delson, 1979). Furthermore, the fossil record is rather scattered (Hartwig & Meldrum, 2002;

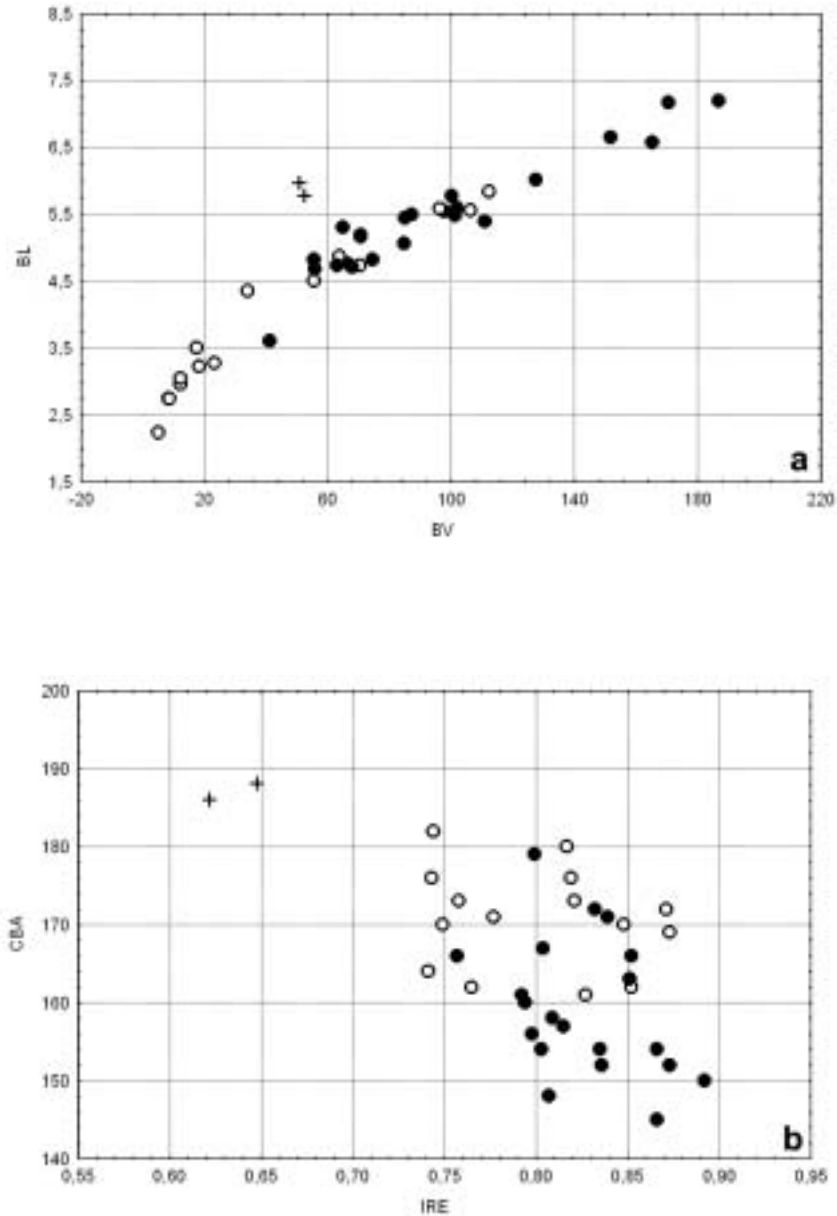


Fig. 10 - Relationship between brain volume (BV; in cubic centimeters), basicranial length (BL: foramen caecum - sella - basion; in centimeters), cranial base angle (CBA; degree), and index of relative encephalisation (IRE; cube root of endocranial volume/BL), in Ceboidea (white circles), Cercopithecoidea (black circles), and Alouatta (*A. belzebul*, *A. palliata*; crosses). Data from Ross *et al.*, 2004 (IRE = IRE5; BL = BL2; CBA = CBA4).

MacPhee and Horovitz, 2002) and the group seems scarcely derived with respect to the Oligocene primates, in relation to size, habits, and locomotion (Conroy, 1990). All these considerations suggest that their interesting evolutionary history is far from being understood.

Airorhynchus in *Alouatta* and *Pongo*

Compared to *Pan*, *Pongo* is mainly characterised by a lower splanchnocranial enlargement, braincase vertical stretching, and supraorbital flattening. The flattening at the supraorbital structures is very stressed, involving loss of frontation with respect to the neurocranial axis but not in relation to the entire skull shape. A minor upper vault flattening is associated with a relevant vertical stretching of the braincase. The nuchal area undergoes a subsequent flattening and relative widening. The foramen magnum is slightly tilted, but not displaced backwards. Interestingly, once more the occipital foramen is angled compared to the whole skull shape, but not considering the neurocranial axis. Similarly, the cranial base does not show a marked lengthening. The premaxilla-maxilla complex shows a sagittal development, mainly in relation to a downward shifting and inclination of the alveolar border. The zygomatic arches are very enlarged and flared. It must be noted that once more the polarity of the structural condition in chimps and orangs has not been discussed, mostly taking into account the phenotypic affinity between *Pongo* and the extinct *Dryopithecinae*.

In *Pongo*, Shea (1985) hypothesised that airorhynchus can be associated to simonathism, supraorbital flattening, orbital shape, mandible enlargement, nasal floor and ethmoid structure, and morphology of the anterior cranial fossa. According to both superimposition and Euclidean distance matrix analysis, there is no evidence of a clear midfacial flattening. The lower and middle facial profile in *Pongo* seems not to differ from the shape expressed in *Pan*, except for a generalised enlargement. Rhinion shows even a further projection considering the overall size increase in *Pongo*. The actual flattening involves the upper face, including the nasion.

On the contrary, in comparing *Pan* and

Pongo, it was also hypothesised that the orbital morphology is independent upon airorhynchus, which was associated to palatal tilting and development of the temporal muscle (Penin & Baylac, 1999). The comparison between *Pan* and *Pongo* shows different superimposition results in the present analysis and the work published by Penin & Baylac (compare Figure 2a in Penin & Baylac, 1999). In both studies there is a frontal and nuchal flattening associated with a palatal tilting. In contrast, Penin & Baylac found a maxillary rotation and relative neurocranial flattening. These differences can be related to the different landmarks considered, or to the use of unilateral vs. bilateral configurations. Anyway, these differences once more stress the need of caution when considering superimposed forms (Richtsmeier *et al.*, 2002), suggesting a complementary use of multiple techniques. Different superimpositions must be compared, and integrated using coordinate-free approaches to "Form" such as the Euclidean Distance Matrix Analysis. This analysis is extremely useful to describe the actual geometrical differences between systems of coordinates, even if results are more difficult to display (Cole & Richtsmeier, 1998). The visualisation method proposed in this paper can improve the interpretation of the interlandmark data, synthesising the information available from the Form Difference Matrix, and allowing a direct comparison of morphological patterns.

When comparing the airorhynchus in *Pongo* and *Alouatta*, some observations can be synthesised to consider this interesting parallel evolutionary process linking anatomy, ecology, and behaviour (Fig. 11). In *Pongo*, Shea (1985) suggested that airorhynchus is probably unrelated to major local rearrangements, but rather depends on a repositioning of the face compared to the neurocranial structure. Interestingly, this also seems to be the case for *Alouatta*. They share a marked flattening of the orbital/supraorbital structures, the orbital shape (tall and narrow), and a consequent mandibular enlargement. In contrast, the maxillary growth is characterised by a general development and forward projection in the howlers, and by a sagittal downward stretch in the orangs. In *Alouatta* and *Pongo* there is a

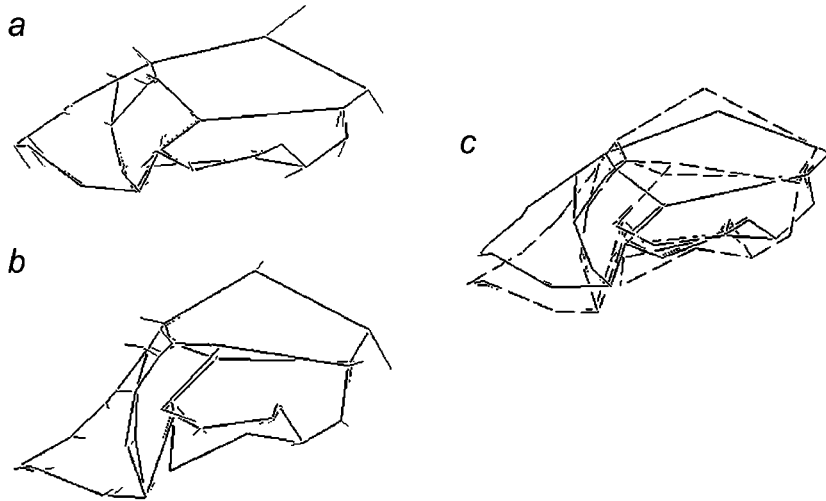


Fig. 11 - Differences between the cranial shape in *Alouatta* and *Pongo*. Vectors display the differences of the three-dimensional configuration between *Alouatta* and a consensus computed from all the other *Atelids* (a), and between *Pongo* and *Pan* (b) after Procrustes superimposition (solid line: *Alouatta* and *Pongo* shapes). The superimposed configurations (c) show a Procrustes comparison between *Alouatta* (solid line) and *Pongo* (dashed line).

nuchal flattening, associated with a rotation of the occipital foramen. In any case, the braincase flattening and narrowing in the previous taxon is not comparable with the braincase vertical stretching and widening of the latter. Furthermore, *Pongo* does not display the relative cranial base lengthening with the consequent nuchal morphology. The frontal flattening itself is oriented downward in *Alouatta* and backward in *Pongo*, with respect to the cranial shape.

In synthesis, in both species airorhynchity is possibly related to changes in the relationship between face and vault, the consequences of which are mainly found at their structural joint. Actually, the supraorbital structures were hypothesised to represent this architectural interface (Lieberman, 2000). Taking into account the anatomical variations of the temporal fossa in the atelids, also the pteric area must be carefully considered. Anyway, the different cranial structure in howlers and orangs required different rearrangements of the whole system.

The complementary role of different approaches should be stressed once again. Geometric morphometrics and EDMA are useful to consider shape and form respectively. Although the theoretical background of these methodologies can be discussed to improve the resolution and power of the morphological analysis (Richtsmeier *et al.* 2002; Rohlf 2003), they can be used simultaneously to increase the range of available models. Differences between their respective results must not be considered necessarily as a bias, but in terms of complementary information. In geometric morphometrics, different superimposition procedures can also contribute to improve the structural knowledge of the morphological systems, optimising the shape comparison (General Procrustes Analysis) or considering specific functional networks (Bookstein Superimposition).

All these explorative and descriptive data on the cranial morphology in *Alouatta* must be further developed through the consideration of the

intra-specific, inter-specific, and inter-generic variability, especially by analysing the possible role of allometry and ontogenetic scaling with respect to airorhynch. Some species of howlers show a sexual dimorphism based on the peramorphic trajectory in males (Zingesser, 1966), probably related to time-dependent differential growth (Couette, 2002). Furthermore, in *Alouatta* there are some indications of a possible female size-related selection, and of a relevant male growth after maturity (Jones *et al.*, 2000). Even more localised differences as the inclination of the foramen magnum show individual variations (Osman-Hill, 1962). All these data make the study of structural cranial morphology in *Alouatta* a quite complex and promising issue.

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