

# Experiments of Nature: Premature Unicoronal Cranial Synostosis in Mantled Howler Monkeys (*Alouatta palliata*)

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In 1960 Adolph Schultz described several cases of plagiocephaly in a collection of mantled howler monkeys (*Alouatta palliata*) from the forests of Central America. Since then several more specimens have been described. These individuals make up one of the largest samples of nonhuman primates that are affected by craniosynostosis. In this study, we used finite element scaling analysis (FESA) to quantify morphologic differences between adult normal (N = 19) and plagiocephalic female howler monkeys (N = 4). FESA utilizes three dimensional coordinate data to provide detailed information on size and shape differences local to biologic landmarks. The relatively large number of plagiocephalic howler monkeys provides a natural means for examining hypotheses concerning patterns of dysmorphology associated with plagiocephaly. Comparison of our results to observations from the clinical literature reveals similarities in neurocranial and facial morphology among plagiocephalic humans and howler monkeys, but the direction and magnitude of local form differences between howler monkeys and humans indicate species-specific responses to sutural constraint. Few cases of craniosynostosis in nonhuman primates are known. The number of plagiocephalic howler monkeys suggests these monkeys may be particularly susceptible to some defect that leads to premature suture closure. If this is the case, then howler monkeys may be a good model to study the cause(s) of craniosynostosis.

KEY WORDS: *plagiocephaly, craniosynostosis, Alouatta palliata, cranial sutures, premature fusion of the cranium*

It is in this dilemma that acute observation is of immense help; for it can register any departure of observable features from their standard norm, and, if we then succeed in pairing this deviation with a corresponding variation in the external circumstances, we immediately come to suspect a causal nexus deserving closer examination.

The dilemma Weiss (1961) refers to is how problems in growth and development can be approached in the absence of precise knowledge of where and when breakdowns in development occur. By examining defects that arise in nature we can make initial hypotheses of possible causes and begin more detailed investigation. The plagiocephalic howler monkeys examined in this study are some of nature's experiments that may provide information on the cause of and morphologic differences in unicoronal synostosis.

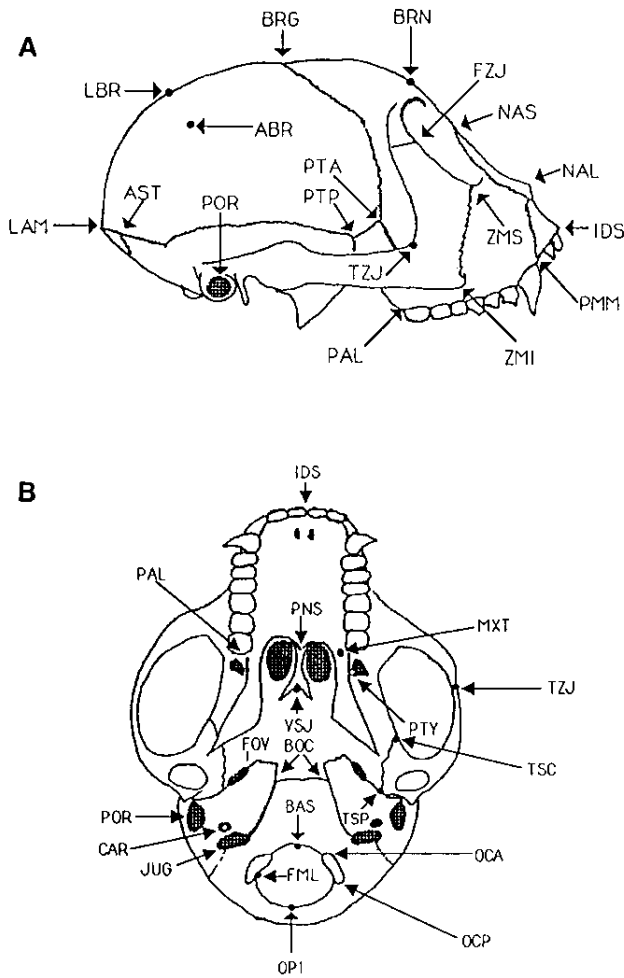
Virchow (1851) published one of the first classifications correlating head shape with specific sites of partial synostosis or premature fusion of the cranium. In Virchow's and more recent classifications (reviewed in Cohen, 1986a), the term plagiocephaly applies to skulls in which dysmorphology arises from premature unicoronal synostosis. Human plagiocephalic skulls are identified by a characteristic bossing of the frontal bone contralateral to the affected coronal suture, and by asymmetries in the orbit, face, basicranium, and vault (Jane and Persing, 1986).

Cohen (1986b) reports an overall frequency of synostosis of approximately .4/1000. The frequency of plagiocephaly, only one of several types of premature suture closure, is lower. Reported cases of cranial synostosis in nonhuman primates are rare. Schultz (1960) identified 11 specimens of *Alouatta palliata* and three specimens of *Ateles geoffroyi* with plagiocephaly in a collection of wild shot monkeys from Panama and Mexico. Smith et al. (1977) describe 10 specimens of *Alouatta palliata* with plagiocephaly obtained during a survey of mammalian fauna from Nicaragua. The relatively high number of *A. palliata* individuals with plagiocephaly prompted us to further examine the nature of this cranial deformity in howler monkeys. In this study, we examine the morphologic differences between normal and plagiocephalic

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**FIGURE 1** A, Lateral and B, inferior views of a howler monkey cranium illustrating the position of landmarks used in analysis. Landmark abbreviations are listed in Table 2.

adult female howler monkey skulls. Our approach utilizes landmark coordinate data (Fig. 1) to quantify local differences between normal and plagiocephalic forms in three dimensions.

**EXPECTED MORPHOLOGIC DIFFERENCES BETWEEN NORMAL AND PLAGIOCEPHALIC HOWLER MONKEYS**

The morphology of skulls with unicoronal synostosis is described in humans (e.g., Kreiborg, 1981; Kreiborg and Björk, 1981; Arvystas et al., 1985; Kreiborg et al., 1985; Fernbach and Naidich, 1986; Marsh and Vannier, 1986; Marsh et al., 1986; Richtsmeier et al., 1991) and in rabbits where suture closure was experimentally produced (e.g., Babler and Persing, 1982; Babler et al., 1982; Persing et al., 1986a,b). From the available data, Jane and Persing (1986) have formulated a general rule governing skull growth following single suture closure.

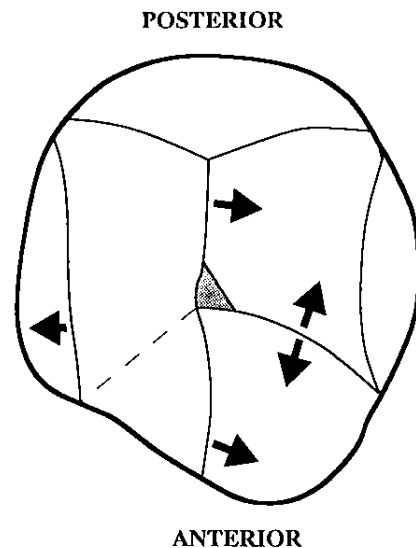
The clinical rule appears to be that when a single suture closes, compensation occurs only at sutures attached to the one undergoing premature synostosis. (p. 313).

Thus, in the case of plagiocephaly, compensatory change should be found on the contralateral side of the metopic and sagittal sutures, on either side of the unaffected coronal suture, and local to the ipsilateral squamous temporal suture (Fig. 2).

Some of the more specific morphologic differences we expected to find in our sample of plagiocephalic howler monkeys included: (1) reduction in the size of the frontal bone on the ipsilateral side, (2) enlargement of the frontal and parietal areas of the vault on the contralateral side, (3) deviation of the orbital axis to the ipsilateral side, (4) decrease in ipsilateral anterior cranial fossa volume, (5) decrease in ipsilateral middle cranial fossa volume, (6) narrowing of anterior cranial width, (7) ipsilateral shortening of the anterior cranial base, and (8) deviation in the face, palate, and cranial base to the affected side.

**MATERIALS**

Our search of the literature resulted in the identification of a total of 21 plagiocephalic skulls (Schultz, 1960; Smith et al., 1977). Specimens noted by Smith et al. (1977) are housed in the Museum of Natural History of The University of Kansas (KMNH). Of the 10 cases of plagiocephaly reported in Smith et al. (1977), only four were identified by museum number (one adult male, one subadult male, and two subadult females). These were requested by our laboratory for examination and analysis. The howler monkeys described by Schultz (1960) are part of the primate skeletal collection in



**FIGURE 2** Superior view of a plagiocephalic human cranium with the right coronal suture prematurely closed. Arrows indicate compensatory changes (after Jane and Persing, 1986).

the National Museum of Natural History (NMNH) (Smithsonian Institutions, Washington, D.C.). Unfortunately, Schultz did not provide museum collection numbers for the plagiocephalic skulls discussed in his study. A search of the NMNH howler skeletal material by one of us (BDC) recovered six of the specimens described by Schultz, and uncovered an additional plagiocephalic individual added to the collection after 1960. Of the seven plagiocephalic specimens from the NMNH, five are female (one subadult and four adults) and two are male (one subadult and one adult). Thus, out of the 21 plagiocephalic howler monkey skulls identified in the literature, 11 were available for study.

Plagiocephalic individuals from the NMNH were initially identified by the general cranial asymmetry that is characteristic of premature unicoronal synostosis. Closer examination of the skulls confirmed this diagnosis, as only one coronal suture was visible in all deformed crania. Clinical studies have demonstrated the involvement of additional sutures (e.g., frontosphenoid) in a high percentage of cases identified with premature unicoronal synostosis (Fernbach and Naidich, 1986). A physical examination of the plagiocephalic individuals in this study did not find any additional prematurely closed cranial sutures.

Because there are more plagiocephalic females than males, we elected to limit our study to the differences between normal and plagiocephalic adult female crania. Table 1 lists the plagiocephalic specimens analyzed in this study. Our normal comparative sample contains 19 adult female crania. A skull was classified as adult if all permanent teeth were erupted and in place.

Museum field records indicate that all plagiocephalic individuals in our sample were of normal adult body size and weight when collected. Examination of the postcranial skeleton of the NMNH specimens revealed no other obvious pathologies (postcranial material for the KMNH specimens was not available for inspection). We therefore conclude we are studying cases of isolated unilateral coronal synostosis.

Three-dimensional coordinates for 58 landmarks were recorded from each normal and plagiocephalic cranium using a Polhemus 3Space digitizer. Landmarks were chosen based on the ease of identification, thus their repeatability, and so that as much of the skull as possible is represented. Table 2 lists the landmarks recorded. Figure 1 illustrates the position of landmarks on a monkey cranium. Note that the neurocranium has far fewer landmarks due to the relative lack of identifiable points on the vault bones.

**METHODS**

Finite Element Scaling Analysis (FESA) is the quantitative comparative method we used to examine form differences between normal and plagiocephalic adult howler monkeys. This method utilizes three-dimensional (3D) coordinate data to obtain a measure of form difference local to the biologic landmarks included in analysis. A brief description of FESA

**TABLE 1 Adult Female Plagiocephalic *Alouatta palliata* Crania Examined**

Museum Number		Coronal Suture Prematurely Closed
NMNH	290562	Left
NMNH	291163	Right
NMNH	315798	Left
NMNH	337858	Right

All specimens are from the National Museum of Natural History (NMNH).

is given below. A detailed description can be found elsewhere (Cheverud et al., 1983; Cheverud and Richtsmeier, 1986; Richtsmeier and Cheverud, 1986; Richtsmeier, 1987).

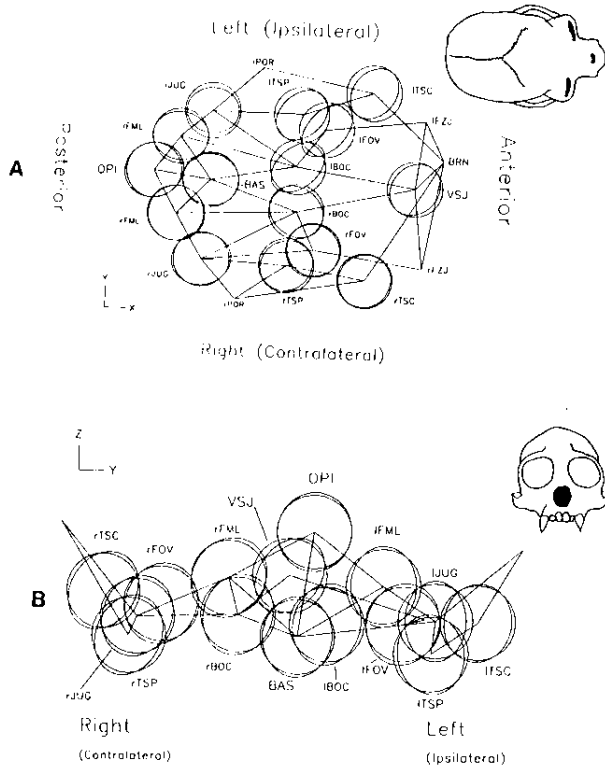
In FESA, the objects of interest are divided into discrete geometric units called finite elements. The vertices of the elements are defined by landmark location. Several 3D element types are available in our FESA computer program (Morris, 1991) including hexahedra, tetrahedra, and wedges. Objects can be modeled using one or a combination of element types. We have selected two types, tetrahedra and wedges, to model the howler monkey cranium.

Finite-element scaling analysis provides numeric and graphic representations of morphologic differences between reference and comparison forms at each landmark consid-

**TABLE 2 Landmarks and Abbreviations Recorded from Plagiocephalic and Normal *Alouatta palliata* Crania**

Abbreviation	Cranial Landmark
AST	Asterion
ABR	1/2 way R. Asterion to Bregma
LBR	1/2 way Lambda to Bregma
BRG	Bregma
BRN	1/2 way Bregma to Nasion
NAS	Nasion
NAL	Nasale
IDS	Intradentale superior
PMM	Premaxilla–Maxilla junction at Alveolus
FZJ	Frontal–Zygomatic junction
ZMS	Zygomaxillare superior
ZMI	Zygomaxillare inferior
TZJ	Temporal–Zygomatic junction
PTA	Pterion Anterior: Zygo–Spheno–Frontal junction
PTP	Pterion Posterior: Fronto–Spheno–Temporo junction
MXT	Maxillary Tuberosity: Maxillary–Palatine junction
PTY	Zygomatic–Maxilla–Sphenoid at pterygoid–palatine
PNS	Posterior nasal spine: Vomer–Palatine intersection
VSJ	Vomer–Sphenoid junction
BAS	Basion
OPI	Opisthion
POR	Porion
JUG	Jugular Process: at occipitomastoid suture
CAR	Carotid Canal: center of canal
TSC	Temporal–Sphenoid suture at crest
TSP	Temporal–Sphenoid junction at petrous
BOC	Basioccipital–Sphenoid synchondrosis
LAM	Lambda
OCA	Occipital condyle, anterior
OCP	Occipital condyle, posterior
FOV	Anterior foramen ovale
FML	Foramen Magnum–lateral midpoint (Occipital condylion)
PAL	Posterior Alveolus–midpoint of last fully erupted tooth





**FIGURE 5** View along superoinferior (A) and anteroposterior (B) axes of the FIESCA graphics illustrating local form differences for basicranial landmarks between normal (reference form) and plagiocephalic (comparison form) female howler monkeys drawn on the comparison form. Landmark abbreviations are listed in Table 2. See Figure 3 for explanation of circles and ellipses.

and basicranium. Table 3 lists the landmarks included in each anatomic region. We report form differences local to these four anatomic regions. The magnitude of size and shape differences for each region is the average of the size and values measured at each landmark within the region. More general facial and neurocranial regions were also defined. The composite facial region includes all the landmarks for the upper and midface regions, and the composite neurocranial region contains all the landmarks found in the calvarial and basicranial regions. Size and shape differences for the composite face and neurocranial regions are average values for the landmarks included in the composite regions. Side-specific size and shape differences between the mean normal adult female and each of the plagiocephalic individuals were calculated for each anatomic region and for the composite regions (Table 4).

**RESULTS**

All our comparisons showed similar patterns of form difference between normal and plagiocephalic individuals, although the magnitude of local size and shape differences varied from individual to individual. We used the most dys-

**TABLE 3** Landmarks Used in Regional Analysis

Region	Landmark Abbreviations
Calvarium	AST,* ABR,* LBR, BRG, BRN, NAS, FZJ*, PTA,* PTP,* PTY,* EAU,* LAM
Basicranium	BAS, OPI, JUG,* TSC,* TSP,* BOC,* FOV,* FML*
Upper Face	NAS, NAL, FZJ,* ZMS,* PTA,* PTY,* VSJ
Midface	NAL, IDS, PMM,* ZMI,* PTY,* PNS, PAL.*

\* indicates bilateral landmarks. Landmarks are listed in Table 2.

morphic individual (NMNH 290562- left coronal synostosis) to describe and graphically characterize the form differences between an extreme plagiocephalic and normal crania. Numeric results from comparisons between the normal sample and the other plagiocephalic crania are also provided (see Table 4).

Table 4 presents the FESA size and shape differences between plagiocephalic and mean normal adult female crania for four anatomic regions, and for the more inclusive composite face and neurocranium regions. The magnitude of size and shape differences are presented separately for the right and left sides of the cranium. Midline landmark values are included in the calculation of size and shape difference for both sides.

Size and shape difference values in Table 4 demonstrated the wide range of dysmorphology displayed in the plagiocephalic crania. From the divergent ipsi- and contralateral size and shape differences in specimens 562 and 798 to the more symmetric values obtained for skulls 858 and 163, the expression of dysmorphology is quite variable. Figures 3 to 5 illustrate the morphologic differences between an extreme plagiocephalic cranium (562) and the normal adult female mean form. Graphic results for the face, neurocranium, and basicranium are presented separately for clarity.

Form differences were less dramatic in the less severely affected crania. Nevertheless, the pattern of form difference was similar in all cases. In the four regions, the magnitude of shape difference was consistently greater for the ipsilateral side (see Table 4). Although the ipsilateral side was more dysmorphic, the contralateral side also differed from normal morphology. Size difference values indicated that the ipsilateral side was comparatively smaller than the contralateral side. The magnitude of size difference in the normal and the plagiocephalic contralateral upper and midface regions indicated that they too are absolutely smaller than the normal. The contralateral basicranium showed relatively little difference in size when compared to the normal, while contralateral size difference values for the calvarial region indicated that the plagiocephalic specimen is slightly larger than that of the normal cranium.

**Composite Face Region**

Local size and shape differences between contra- and ipsilateral facial landmarks were readily seen in Figure 3. Devi-

**TABLE 4** Average Side-Specific Size and Shape Change Values

Region	Side	Average Size Differences				Average Shape Differences			
		562	798	858	163	562	798	858	163
<b>Anatomic</b>									
Upper Face	Contralateral	-.0247	-.1095	.0544	.0433	.1281	.0227	.0854	.0986
	Ipsilateral	-.0530	.0128	.0294	.0459	.1805	.1681	.0990	.0949
Midface	Contralateral	-.0140	-.0072	.0379	.0596	.1386	.1419	.0977	.1116
	Ipsilateral	-.0294	-.0143	.0425	.0488	.1626	.1458	.0949	.0927
Calvarium	Contralateral	.0177	.0351	.0782	.0357	.1430	.1286	.0782	.1211
	Ipsilateral	-.0352	-.0126	.0268	.0151	.1520	.1521	.0827	.1039
Basicranium	Contralateral	.0256	.0069	.0069	.0569	.0857	.0985	.0867	.1008
	Ipsilateral	.0130	.0392	.0392	.0455	.1218	.1165	.0924	.0743
<b>Composite</b>									
Face	Contralateral	-.0158	.0058	.0420	.0526	.1303	.1302	.0820	.1035
	Ipsilateral	-.0374	-.0001	.0445	.0373	.1674	.1509	.0901	.0887
Neurocranium	Contralateral	-.0086	.0305	.0277	.0440	.1137	.1150	.0820	.1117
	Ipsilateral	-.0310	-.0052	.0305	.0278	.1381	.1361	.0876	.0918

Comparison of the mean normal adult cranium (reference form) to each of the four adult female plagiocephalic skulls (comparison forms) by anatomic region.

Composite face and neurocranial regions include average size and shape difference values from landmarks for the upper and midface and for the calvarial and basicranial regions, respectively. Negative size values indicate the reference form is smaller than the comparison form.

ations from the normal female reference form were found among the ipsilateral orbital landmarks (IFZJ, IZMS, IPTA, IPTY). Smaller differences were found local to the inferior border of the zygoma (IZMI), the posterior part of the maxilla (IPAL), and the premaxilla (IPMM). Local differences in size and shape indicated a general strong mediolaterally directed narrowing and slight superoinferiorly directed stretching in the ipsilateral face. With the exception of premaxilla-maxilla intersection (rPMM) and pterygopalatine junction (rPTY), differences from the normal local to the contralateral facial landmarks were relatively small.

In the face, the more superiorly located midline landmarks (NAS, NAL) were strongly shifted ipsilaterally (see Fig. 3), while intradentale superior (IDS), posterior nasal spine (PNS), and vomer-sphenoid junction (VJS) showed little or no deviation from the midline. All the midline landmarks showed some stretching along the superoinferior axis.

### Composite Neurocranium Region

The neurocranium was the site of conspicuous local dysmorphology in the plagiocephalic skull (see Table 4 and Fig. 4). One of the greatest form differences was local to the contralateral asterion (rAST) where there was considerable bulging of the posterolateral portion of the vault (See Fig. 4B). Similarly directed but smaller differences were found in the other contralateral vault landmarks (rABR, rPOR, rPTP, rPTA).

Ipsilaterally, the largest differences in calvarial form between plagiocephalic and normal howler monkeys were local to the more anterior landmarks (IPTA, IPTP, IFZJ, IPTY). These landmarks showed local reduction approximately

along the anteroposterior axis. Midline vault landmarks were deviated toward the synostosed side of the cranium. Landmarks located on the anterior vault (NAS, BRN) displayed a greater amount of deviation than the more posterior positioned landmarks (BRG, LBR, LAM). All midline landmarks displayed some shortening along an oblique anteromedial-posterolateral axis.

Size and shape differences between the normal and plagiocephalic cranial base were found among the ipsilateral landmarks (see Fig. 5A) where a general anteromedial-posterolaterally directed shortening was seen (e.g., IBOC, ITSC, ITSP, IFOV). All basicranial landmarks showed some stretching along the superoinferior axis (Fig. 5B). Deviation of basicranial midline landmarks away from the midline was noticeably less than that seen in midline vault landmarks.

### DISCUSSION

Differences between normal and plagiocephalic facial morphology suggests that the local sutural constraint is most obvious local to landmarks on the ipsilateral side. We expected to find some deviation of midline facial landmarks and a twisting of the orbital axis in plagiocephalic howlers. From our results we hypothesize that the facial asymmetry is possibly a result of reduced ipsilateral development along specific vectors dictated by the synostosis. Reduced facial development may also reflect functional adaptations to changes in the orientation of the muscles of mastication brought about by asymmetry in the temporomandibular joint. Plagiocephalic humans display adaptations in the jaws and musculature to compensate for asymmetry in the cranial base, and to maintain normal occlusal relationships (Kreiborg and Björk, 1981;

Arvystas et al., 1985). Similar adaptations are suggested in the plagiocephalic howler monkeys. Qualitative examination of the plagiocephalic crania indicate other related changes in the masticatory system. These include a shorter (AP) infratemporal fossa, asymmetric development of the ipsilateral pterygoid plate; and an anteroinferior flaring of the ipsilateral inferior border of the zygoma.

Expected changes within the neurocranium include an expansion of the contralateral middle and posterior cranial fossae (Kreiborg and Björk, 1981; Marsh and Vannier, 1986; Marsh et al., 1986). Size differences local to posterior and median contralateral neurocranial landmarks (i.e., rAST, rABR, rPOR, rPTP) demonstrate an anteromedial-posterolateral directed stretching (see Fig. 4B) that suggest a compensatory change in the volume of the cranial fossae. We suspect that this is in response to the local restriction on ipsilateral cranial fossa expansion imposed by the prematurely closed coronal suture (Moss, 1959).

Morphologic differences between normal and plagiocephalic howler monkey calvaria are somewhat different than those found between normal and plagiocephalic humans. Changes from a normal to plagiocephalic vault morphology in the howlers tend to be directed along an anteroposterior or posterolateral axis (e.g., rAST in Fig. 4). In plagiocephalic humans, compensatory change in the vault has a stronger superoinferior component (Arvystas et al., 1985). Differences in direction and magnitude of compensatory changes between normal and synostosed humans compared to those found in howler monkeys likely reflect general species differences in neural mass development (Moss, 1959). Brain growth in humans is directed superiorly and inferoposteriorly (Enlow, 1990). Schultz (1960) demonstrated that vault growth in howler monkeys tends to be directed posteriorly rather than superiorly or inferiorly.

Contralateral expansion of the frontal bone superior to the orbit was an expected morphologic feature in howler monkey plagiocephaly, but was not observed in our sample. Morphologic differences local to the frontal bone in howlers indicates ipsilateral reduction along anteroposterior and mediolateral axes (see Fig. 4, BRN, NAS, FZJ, PTA) rather than a more anteriorly directed contralateral expansion seen in humans. This again likely reflects general species differences in the direction and especially magnitude of neural mass development between humans and howler monkeys. Howler monkeys are very platycephalic and have a flat frontal bone reflecting less development of the anterior portion of the brain compared to humans.

An anteroposteriorly directed shortening local to nasion (NAS) is found in the plagiocephalic howler monkeys (see Fig. 4). A similar result was obtained in experiments involving the coronal suture in laboratory rabbits (Babler and Persing, 1982; Babler et al., 1982). Change at the frontonasal suture reported in Babler and Persing (1982) and in Babler et al. (1982) was obtained from two different experimental manipulations of the coronal suture. In one experiment, the

coronal suture was removed from the rabbits (Babler et al., 1982), and in the other, the coronal suture was fixed using methyl-2-cyanoacrylate adhesive (Babler and Persing, 1982). Both experiments obtained a similar result—reduced growth across the frontonasal suture. This suggests that suturectomy and experimental and naturally occurring restriction of growth across the coronal suture are equivalent with regard to their effect on development at the frontonasal suture.

Differences in cranial base morphology between normal and synostosed skulls have received considerable attention because of the potential link with causes of premature suture closure (Moss, 1959, 1975; Cohen, 1986c). Ipsilateral shortening of the anterior cranial base and the deviation of midline landmarks to the ipsilateral side were expected and observed in our sample. Nearly all of the contralateral and midline basicranial landmarks examined by us are displaced posterolaterally. The mediolaterally directed constriction local to many of the basicranial ipsilateral landmarks studied here may reflect a reduced amount of development due to the synostosis, which could also lead to secondary functional adaptations, or could indicate a primary cranial base defect. However, as noted by others (Cohen, 1986b), we cannot separate the effects of restricted development due to the synostosis from other (potentially primary) basicranial developmental problems.

Studying the differences between normal and plagiocephalic howler monkeys provides an examination of current predictions of the effects of local constraint on cranial morphology. Our observations of dysmorphology in the craniofacial skeleton of plagiocephalic howler monkeys suggests that the general rule of Jane and Persing (1986) generated from human clinical and experimental data applies to howler monkeys as well. Specific differences in the direction and magnitude of morphologic change among humans and howler monkeys brought about by the constraint imposed by unicoronal cranial synostosis most likely reflect differing craniofacial growth patterns in the two species.

The general morphologic result of plagiocephaly may be similar in different animal species, but the underlying primary cause of the defect is still in debate. Three hypotheses have been advanced to explain premature synostosis (reviewed in Cohen, 1986c): (1) a primary defect in the suture (Virchow, 1851); (2) a primary cranial base malformation (Moss, 1959, 1960); and (3) a primary defect in the mesenchymal blastema, which leads to both cranial base deformities and premature synostosis (Park and Powers, 1920).

Which one of the three is the primary cause of plagiocephaly in our study sample cannot be directly determined. Based on our results and our knowledge of howler monkey development, however, we can speculate on the possibilities. First, since no defects are seen in other parts of the skeleton, the possibility of an early generalized embryonic disturbance is low. Second, because howlers tend toward early cranial suture closure compared to other monkeys (Chopra, 1957; Schultz, 1960), a primary defect in the suture itself seems a

plausible explanation for premature closure in our study sample. The rapid rate of closure may make howler monkeys particularly susceptible to biologic circumstances that precipitate premature suture fusion. It may also explain why such a high number of plagiocephalic individuals is found in this species.

This study was limited to an examination of the morphologic differences between normal and plagiocephalic adult female howler monkeys. There are a few subadult plagiocephalic specimens in the KMNH and NMNH skeletal collections. A brief inspection of subadults indicates that the degree of dysmorphology also has an age component. That is, the younger specimens are not as dysmorphic as most of the adult plagiocephalic specimens. Although the degree of actual suture closure is only roughly approximated by exocranial closure, in all subadult specimens the ipsilateral coronal suture was estimated to be one-half to two-thirds closed. Reports indicate an increase in cranial asymmetry with age in humans (Arvystas et al., 1985; Kreiborg, 1986; Richtsmeier, 1987). Whether the progress of the dysmorphology is due to a continued normal growth pattern in a cranium constrained by the synostosed suture, or if there is an underlying growth disorder contributing to the increasing dysmorphology is not known. A comparison of the magnitude of morphologic differences between normal and synostosed subadults to differences between normal and synostosed adults would help clarify the issue. However, a longitudinal study of the prematurely synostosed cranium is the only way to determine the role of growth in the production of a plagiocephalic morphology. Although the differences between normal and synostosed subadult humans have been measured (e.g., Kreiborg, 1986; Richtsmeier, 1987, 1988; Richtsmeier et al., 1991), the rarity of cases of untreated affected adult humans makes quantifying differences between synostosed and normal adults difficult. Quantifying morphologic differences between normal and plagiocephalic subadults, and between normal and plagiocephalic adult howler monkeys is possible. Future work will be directed toward elucidating developmental differences.

The best way to determine the primary cause of craniosynostosis in any group, and to trace its effect on morphology, is to follow its development from conception to adulthood. This would require establishing an animal model for study. Howler monkeys may have a tendency toward craniosynostosis. Based on the number of individuals in museum collections, the frequency of plagiocephaly in howler monkeys is considerably higher than reported for human clinical cases. The frequency of plagiocephaly in the sample described by Smith et al. (1977) is 7.3 percent, lower than the 2.4 percent reported by Schultz (1960). Nevertheless, given the many biases in collection practices, the frequency of plagiocephaly in *Alouatta palliata* is still substantially higher than for other monkey species such as *Ateles geoffroyi* (1.5% [Schultz, 1960]) and *Cebus capucinus* (0% [Schultz, 1960; Smith et al., 1977]), and is considerably greater than the incidence in

humans (Cohen, 1986c). Howler monkeys may provide useful models for the investigation of the one or many primary causes of plagiocephaly.

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