

Cranio-facial sutures of the black-capped squirrel monkey *Saimiri boliviensis* (Primates: Cebidae): gross morphology and postnatal ontogeny

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Abstract

Cranial suture closures in the black-capped squirrel monkey *Saimiri boliviensis* were examined. Sequences in closure and morphological changes during ontogeny were interpreted as indicators of skeletal strains and age. Some sutures seem to be more reliable determinants of skeletal age than others. As found in other species of *Saimiri*, the palatal and rostral portion of the maxillo-premaxillary suture show regular fusion associated with earlier age. The predictable sequence was: (1) maxillo-premaxillary and zygomatico frontal (orbital part), (2) transverse maxillo-premaxillary, (3) sphenoccipital, (4) internasalis, (5) palatal portion of interpremaxillary, denoting a relatively conservative pattern in the genus. However, most sutures were patent still in older specimens. The ontogenetic variation in the suture morphology was pointed to the acquisition of complex interdigitation and overlapping. The general trend detected indicates that the ectocranial sutures of *S. boliviensis* acquire progressively more capacity for strength support because the crescent interdigitation of sutures functionally committed with mastication and growth, as those of vault, rostrum and palate.

Keywords: ontogeny; Primates; skull; suture morphology.

Introduction

In a different way to the appendicular skeleton, which lengthens by endochondral ossification of epiphyseal plates, craniofacial bones grow by bone apposition in sutures (Radhakrishnan and Mao 2004). Sutures are composed of soft connective tissue that articulates cranio-facial bones, defining patterns of mechanical stress resulting from natural activities, such as mastication and growth, as well as exogenous forces (Herring 1972). The structural morphology of cranial sutures is related to mechanical strain caused by tensile and compressive forces (Henderson et al. 2005). When muscles of the cranio-facial complex contract, or when the cranium receives a physical impact, mechanical loading of the skull occurs. In pigs, masticatory strain is suggested as causing new bone formation on cranial sutures (Sun et al. 2004), and Jaslow and Biewener

(1995) suggested that in goats, sutures also function as shock absorbers during impact (i.e., head-butting). Additional evidence (e.g., Mao et al. 2003) indicates that sutures absorb and transmit mechanical stresses generated from functional activities. Patterns of cranial mechanical stress have been detected using strain gages attached over the suture *in vivo*. Strain patterns are known in several mammals, such as Primates (e.g., Behrents et al. 1978, Hylander 1986, Hylander et al. 1991, Hylander and Johnson 1997, Wang et al. 2006), goats (e.g., Jaslow 1990), rodents (e.g., Burstone and Shafer 1959, Moss 1961, McLaughlin et al. 2000, Byron et al. 2004, Henderson et al. 2005) and especially pigs (e.g., Herring and Scapino 1973, Herring and Mucci 1991, Herring et al. 1996, Herring and Teng 2000, Rafferty et al. 2000, Herring et al. 2001).

It is a well-known fact that in Primates many of the craniofacial sutures, or even all of them, tend to disappear completely with advancing age through bony fusion (Chopra 1957). The sequence of fusion could differ widely in cranial regions and among genera in some mammals (see Wilson and Sanchez-Villagra 2009, Sanchez-Villagra 2010). Sutural ontogenetic changes are believed to be associated with extrinsic and intrinsic mechanical forces exerted on the skull and sutures (Massler and Schour 1951, Moss 1957, 1961, Jaslow 1990). At birth, sutures are in general relatively simple, straight-edged structures, but during growth sutural morphology may change with bones overlapping or interdigitating. This assertion, and observations of the morphological variation among sutures, has led researchers to hypothesize ways in which sutures with certain morphologies might respond to particular strains on the skull (e.g., Jaslow, 1990, Herring et al. 1996, Herring and Teng 2000).

The progress of suture closure and morphological changes during postnatal ontogeny, and particularly the sequence of suture closure have been adequately studied in several mammals, such as *Homo* (e.g., Todd and Lyon 1925, Madeline and Elster 1995, Sabini and Elkowitz 2006), *Pteropus* (Giannini et al. 2006), *Puma* (Segura and Flores 2009), hyaenas (Schweikher 1930), hystricognath rodents (Wilson and Sanchez-Villagra 2009), *Dasyurus* (Flores et al. 2006), cervids (Sanchez-Villagra 2010), and several species of otariid seals (Brunner et al. 2004). Two important descriptive works in Primates were made by Chopra (1957) and Bolk (1915), who studied the sequence of closure in several species of New and Old World monkeys (also including man), showing a high frequency of closure in the oldest specimens in most groups. However, the changes of suture morphology through age were not studied in detail. Later, Dolan (1971) studied the detailed sequence of suture closure in *Saimiri*

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Q3: Does Primates need a capital P in every instance?



sciureus (Linnaeus 1758), a closely related congener of *Saimiri boliviensis* (Geoffroy and Blainville 1834).

In this study we analyzed the morphological changes and sequence of sutural closure in a well-represented ontogenetic series of *Saimiri boliviensis*, a species widely distributed in the upper Amazon in Peru, south western Brazil, and north and central Bolivia (Groves 2005). We considered the functional background based in described patterns of cranial strains in *Primates* and other mammal groups (see above). As mentioned, some information exists regarding to the sequence of cranio-facial suture closure in the genus, although discussions of morphological changes on sutures functionally committed were not attended in detail in *S. boliviensis*. Furthermore, the ontogenetic series previously analyzed in the genus were poorly represented in age classes (except Dolan 1971), without the inclusion of this species.

Materials and methods

Taxonomy, sample and age classes

We analyzed an ontogenetic series of 33 skulls of *Saimiri boliviensis* deposited at the Mammal Collection of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (Appendix I). The taxonomy of the species was widely discussed. Several authors (e.g., Hershkovitz 1984, Vandeberg et al. 1990, Groves 2001, 2005) considered the Bolivian populations as separated from *Saimiri sciureus*, a species that occurs farther north. However, other authors (e.g., Cabrera 1958, Thorington 1985, Costello et al. 1993, Anderson 1997) considered that all living *Saimiri* are conspecific, meeting all forms in *S. sciureus*. We follow the criterion considered by Vandeberg et al. (1990) and Groves (2005) in considering *S. boliviensis* as a different species level based in evidence of genetic frequency.

Because captive animals may show alterations in cranial bones and sutures by impaired nutrition and other factors (Duckler 1998, O'Regan 2001, Lieberman et al. 2004), most specimens examined were trapped in the field and may be considered under representative conditions. In our sample, four specimens were juvenile without complete permanent dentition erupted, seven were subadults with a completely erupted permanent dentition without any tooth wear and most sutures patent and 22 specimens with different grades of tooth wear were considered as adults. Then, the frequency reported for juvenile and subadults in Table 1 were based in a small sample size. Since the exact age was unknown, our age classification, like many others, is based in visual observations and comparisons, and therefore remains arbitrary in some aspects. However, age classes based on tooth eruption and wear in primates are commonly used in ontogenetic studies where the real age is unknown (e.g., Ravosa and Ross 1994, Flores and Casinos 2011).

Suture closure analysis and function

We restrict our analysis to the cranium, because the mandible, being without sutures (except for the mandibular

symphysis), does not yield information about the mechanical effects of the arrangement in cranial bones. We follow the suture classification of Chopra (1957) and Dolan (1971), determining six cranial regions: vault, sphenoccipital, circum-meatal, palatal, facial, and cranio-facial region (Table 1). Our classification was modified according to the presence of sutures in the species, which differs respect to ectocranial sutures founded in anthropoid monkeys (see Table 2 of Chopra 1957), identifying 30 ectocranial sutures. Following Chopra (1957, 1957a) classification of *open*, *closing* and *closed* was recorded for sutures on both sides of each skull. *Open* is a condition where the suture is clearly visible and the two adjoining bones have not begun to fuse; a *closing* suture is still visible, and the adjoining bones show partial bony union and *closed* may be described as the complete obliteration of the suture, adjoining bones have united, and the suture line is usually no longer visible. Depending on the shape of the apposed edges, sutures were divided according to the classification followed by Evans (1993): *plane suture*: in which one of the bones meet at an essentially right-angled edge or surface; *squamous suture*: that articulates by overlapping of reciprocally beveled edges; and *serrated suture*: that articulates by means of reciprocally alternating processes and depressions (Figure 1).

Results

In *Saimiri boliviensis* most sutures remain patent in all age stages (Table 1), except those of the occipital plate, metopic (*interfrontalis*) and sphenopterigoid, which were completely closed from earlier age stages. However, changes in structure suture during age occur. In the structural morphology of the sutures of *S. boliviensis*, we observed plane, squamous and serrated types, but no foliated. The general sequence of suture closure reflects in part those reported by Dolan (1971) for *Saimiri sciureus*: (1) maxillo-premaxillary and zygomatico frontal (orbital part), (2) transverse maxillo-premaxillary, (3) sphenoccipital, (4) internasalis, (5) palatal portion of interpremaxillary (Table 1), denoting a relatively conservative pattern, at least in the genus. We report suture closing as a description of the general trends in the six suture groups defined in Materials and methods, for young, subadults and adults.

Vault group

The metopic suture is absent in almost all specimens examined, as reported by Dolan (1971) for *Saimiri sciureus*. However, in two of the younger specimens, a short plane suture is observed on the anterior portion, at the interorbital level. The frontoparietal suture, also called coronal, close first anteriorly and then continues posteriorly, becoming strongly serrated in older specimens, ~~but always visible.~~ The interparietal suture is clearly open in younger specimens, especially in their medial and posterior portion. In adults, this suture becomes closed and strongly serrated, showing also a



Table 1 Ectocranial suture conditions and sample percentage of closure in the three defined age stages of *Saimiri boliviensis*. Suture type is indicated as Serr (serrated), Sq (squamosal) and Pl (plane). Parentheses indicate sample size.

Region	Suture	Young (4)			Subadult (7)			Adult (22)					
		%Open	%Closing	%Closed	Suture Type	%Open	%Closing	%Closed	Suture Type	%Open	%Closing	%Closed	Suture Type
Vault	Coronal	75	25	0	Sq/Pl	35.7	64.3	0	Sq/Serr	0	43.7	56.2	Sq/Serr
	Sagittal	75	25	0	Serr/Pl	38.5	61.5	0	Sq/Serr	0	93.7	6.2	Sq/Serr
	Lambdoid	75	25	0	Serr/Sq	30.2	69.2	0	Sq/Serr	0	75	25	Sq/Serr
Spheno-occipital	Spheno-occipital	100	0	0	Pl	57.1	21.4	21.4	Pl	4.5	22.7	72.7	Pl
	Basisphenoid-presphenoid	100	0	0	Pl	100	0	0	Pl	0	100	0	Pl
	Parieto-squamosal	100	0	0	Sq	35.7	64.3	0	Sq/Serr	0	81.2	18.7	Sq/Serr
Circum-meatal	Occipito-mastoid	75	25	0	Sq/Pl	25	75	0	Sq/Pl	0	100	0	Sq/Pl
	Occipito-petrosal	75	25	0	Sq/Pl	25	75	0	Sq/Pl	0	100	0	Sq/Serr
	Spheno-temporal	100	0	0	Sq	35.7	64.3	0	Sq/Serr	0	68.7	31.2	Sq/Serr
	Spheno-parietal	100	0	0	Sq	35.7	64.3	0	Sq	0	68.7	31.2	Sq/Serr
	Parieto-mastoid	75	25	0	Sq/Pl	25	75	0	Sq/Pl	0	81.2	18.7	Sq/Serr
Palatal	Transverse maxillo-palatine	100	0	0	Pl	64.3	35.7	0	Serr	0	68.7	31.2	Serr
	Transverse maxillo pre-maxillary	0	100	0	Sq	0	85.7	14.3	Sq	0	62.5	37.5	Sq
	Interpremaxillary	75	25	0	Serr/Pl	35.7	64.3	0	Pl/Serr	50	43.7	6.2	Pl/Serr
	Intermaxillary	75	25	0	Serr	64.3	35.7	0	Serr	0	68.7	31.2	Serr
	Interpalatine	75	25	0	Pl	42.9	57.1	0	Pl/Serr	12.5	81.2	6.2	Pl/Serr
Facial	Internasal	50	50	0	Pl	21.4	78.6	0	Pl	0	18.7	81.2	Pl
	Maxillo-premaxillary	0	75	25	Pl	0	0	25	Fused	0	0	0	Fused
	Naso-maxillaris	75	25	0	Pl	35.7	64.3	0	Pl	0	25	75	Pl
	Naso-frontalis	75	25	0	Pl	35.7	64.3	0	Pl	0	25	75	Pl
	Zygomatiko-maxillary (anterior)	75	25	0	Sq	42.8	57.1	0	Sq	0	50	50	Sq/Serr
	Zygomatiko-maxillary (posterior)	75	25	0	Sq	21.4	64.3	14.3	Sq	0	43.7	56.2	Sq/Serr
	Maxillo-lacrimal	75	25	0	Sq	71.4	28.6	0	Sq	0	81.2	18.7	Sq/Serr
	Spheno-orbital	75	25	0	Serr/Sq/Sq	42.9	57.1	0	Serr	43.7	31.2	25	Sq/Serr
	Spheno-zygomatic	75	25	0	Sq/Serr	35.7	64.3	0	Sq	0	62.5	37.5	Sq/Serr
	Zygomatiko-frontal (facial)	75	25	0	Sq/Serr	42.9	57.1	0	Sq/Serr	0	75	25	Sq/Serr
Cranio-facial	Zygomatiko-frontal (orbital)	75	0	25	Sq	35.7	64.3	0	Sq/Serr	0	75	25	Sq/Serr
	Fronto-maxillary	100	0	0	Sq	35.7	64.3	0	Sq	0	56.2	43.7	Sq
	Fronto-lacrimal	66.6	33.3	0	Sq	57.1	42.9	0	Sq	0	93.7	6.2	Sq
	Spheno-zygomatic	75	25	0	Sq/Serr	57.1	42.9	0	Sq/Serr	0	68.7	31.2	Sq/Serr
	Spheno-palatine	75	25	0	Sq	64.3	28.6	7.1	Sq/Serr	0	13.3	86.7	Sq/Serr
	Spheno-ptyergoid	75	25	0	Sq	64.3	28.6	7.1	Sq/Serr	0	13.3	86.7	Sq/Serr
	Zygomatiko-temporal	75	25	0	Sq	64.3	35.7	0	Sq	0	100	0	Sq
Zygomatiko-parietal	75	25	0	Sq	42.9	57.1	0	Sq/Serr	0	75	25	Sq/Serr	

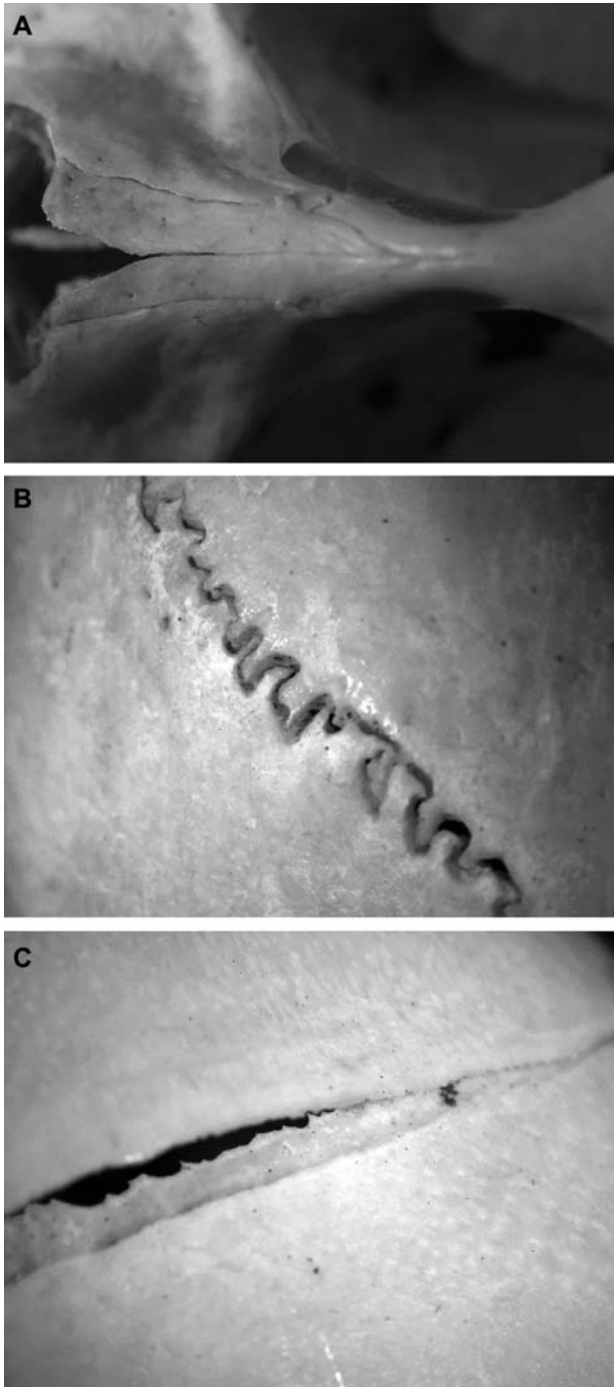


Figure 1 Examples of the three sutural morphologies observed in *Saimiri boliviensis*. (A) Plane, e.g., internasal. (B) Serrated, e.g., sagittal. (C) Squamosal, e.g., coronal in young. Not to scale.

high degree of overlapping, forming a squamous and interdigitated suture. The occipito-parietal (or lambdoid) suture in most young and subadult is closing and anteriorly squamous but posteriorly serrated. In older specimens, although still visible, the suture becomes strongly serrated and closing. As indicated by Chopra (1957), all sutures of the vault are visible in older specimens (Table 1).

Spheno-occipital group

This region is composed only of the spheno-occipital syncondrosis, which separates the basioccipital from the basisphenoid bone, and the basisphenoid-presphenoid suture. The syncondrosis is a useful character for age determination in some mammals (e.g., García-Perea 1996 for *Lynx*). In *Saimiri boliviensis*, the syncondrosis is open in young and becoming closing in most subadults (Table 1). In adults, it becomes closed and in just five cases completely fused. Contrary to observations in *Saimiri sciureus* (Dolan 1971), there is no evidence of sexual dimorphism in the timing of fusion in *S. boliviensis*. However, the basisphenoid-presphenoid suture remains open in all young and subadult specimens, becoming closing in all adults examined.

Circum-meatal group

All sutures of this group remain visible in all age stages. The parieto-squamosal, spheno-mastoid, parieto-mastoid and occipito-mastoid sutures are completely closed in several older specimens, although the most common condition is a closing but clearly visible bone limit (Table 1). Commonly, the sutures of this group are plane or squamous in young and subadult specimens, but become notably serrated in adults. The spheno-temporal suture becomes dorsally fused in senile specimens, but remains serrated in its ventral portion, on the anterior tip of the glenoid fossa.

Palatal group

Sutures in this group remain visible also in older specimens, but the transverse maxillary-premaxillary suture is squamous in its palatal portion in young, subadults and adults, although tends to be fused in senile specimens (Table 1). The same occurs in the intermaxillary suture, which is serrated in early stages, but it is completely closed in several older specimens. The sutures interpremaxillary and interpalatine remain plane and closing from young to adult. Finally, the transverse suture maxillo-palatine is plane in young and becomes serrated and closing in adults.

Facial and cranio-facial groups

Similar to observations in *Saimiri sciureus* (Dolan 1971), the fusion of the facial and palatal portions of the maxillary and premaxillary bones are coordinated in *Saimiri boliviensis*, i.e., the closing starts laterally to mesially in the palate, and inferiorly to superiorly in the face. The internasalis suture is open and plane from early stages, although in adult specimens it tends to close superiorly and rarely inferiorly, as evidenced for *S. sciureus* (Dolan 1971). The naso-maxillaris and naso-frontalis sutures are plane from young to adult stages, without evident changes during ontogeny. The zygomatico-frontal suture is already serrated in young specimens in their facial part, becoming closing and strongly serrated in adult and senile specimens, specially in the orbital region. The lacrimal is a small bone in *S. boliviensis*, always with well-defined

limits from early stages. In subadults and adults, their limits with the maxillary become strongly serrated and closing. The zygomatico-maxillaris suture is closing in subadults and adults. The general trend of this suture is the acquisition of a serrated morphology, especially in the inner part of the zygomatic arch. The alisphenoid bone is clearly exposed in lateral and ventral view, with their sutures marked and plane from early stages, but becoming serrated and squamous in subadult and adult specimens. However, the sphenopalatine and sphenopterygoid sutures are completely closed in subadult and adult specimens. As in the general pattern of the cranio-facial sutures, those of the internal region of the orbit (i.e., sphenoorbital, sphenozygomatic and the orbital part of the zygomatico-frontal suture) are closing and serrated from early stages, and becoming more complex in adult specimens, but visible in all age stages considered.

Finally, as reported by Chopra (1957), the mandibular symphysis becomes completely obliterated very early. In all mandibles examined it was found that the symphysis was fully obliterated.

Discussion

The *in vivo* relationship between bone strain and muscle function in the mammalian skull was investigated empirically (e.g., Hylander et al. 1991, Hylander and Ravosa 1992, Herring et al. 1996, Ross and Hylander 1996, Herring and Teng 2000, Henderson et al. 2005). The *in vivo* strains documented for the pig rostrum are among the largest recorded for mammalian sutures (Rafferty and Herring 1999). Such information in *Primates* and other mammals allows a clear relation between ontogenetic changes of sutures with growth and functional processes. According to the patterns described, we made special emphases in sutures and areas subjected to tensile and compressive forces as vault, temporal region and rostrum. Most cranial sutures of *Saimiri boliviensis* are patent until later age stages, where they become strongly serrated (Table 1, Figure 2). In general, mammals born with relatively simple sutures which may remain simple, increase their interdigitation allowing an efficient load transmission from one bone to another, or mineralize to fuse two adjacent bones. The mechanical properties of the sutures and bones in rostrum and vault are highly variable (Jaslow 1990), generating a composite structure in which energy is absorbed through sutural deformation (Behrents et al. 1978, Jaslow 1990, Persson 1995, Herring and Teng 2000, Rafferty et al. 2003). Open cranial sutures, as observed in all young and several subadult specimens of *S. boliviensis* (Table 1), are necessary to permit normal and rapid growth during early development (Herring 1972). Several studies in *Primates* demonstrated that the loads imposed by muscle forces causes complex patterns of stress, including sagittal and transverse bending, and deformation (e.g., Hylander 1979, 1984, Hylander and Johnson 1994, Wang et al. 2006). In such models, the maxillary and premaxillary bones receive loads primarily from forces generated by occlusion. In this way, the maxillo-premaxillary suture of *S. boliviensis* is already closed from an earlier age (Table 1).

The *in vivo* analyses on pigs and some primates (e.g., Herring 1972, Herring and Mucci 1991, Herring et al. 1996, Hylander and Johnson 1997, Herring and Teng 2000) reveal that the masseter muscle action opens anteriorly and closes posteriorly the midline suture (interfrontalis and interparietalis), and also tensed the coronal suture. However, the temporalis action caused strains in the midline suture in the reverse direction, i.e., opening posteriorly and closing anteriorly, compressing the coronal suture (Behrents et al. 1978). Although such findings were made specifically in pigs, they are relevant to the present study on *S. boliviensis*, because *Primates* and pigs use similar muscle coordination to produce the power stroke of mastication (Weijs 1994). Indeed, the torsion detected in the supraorbital regions in Old World Primates (as *Macaca* and *Papio*, Hylander et al. 1991) may originate from the same coupling of muscles, the masseter and its opposite temporalis, as in pigs. However, the early fusion of the interfrontal (metopic) suture in primates implies small changes in the transmission of forces in the vault. In this sense, the strongly serrated interparietal (sagittal) and coronal sutures of *S. boliviensis* is tensed and compressed by temporal and masseter muscles. The actions of these muscles will increase with age, a situation that is suggested by the increased interdigitation with age (Table 1, Figure 2).

Suture morphology is important in mechanical strain since properties of different kinds of sutures can support specific levels of tension and compression during mastication and growth (Rafferty and Herring 1999). Suture interdigitation (or serrated), as commonly found in the cranio-facial regions of most adult and subadult specimens of *Saimiri boliviensis* (Table 1, Figure 2), supports strains usually higher than the adjoining bones (Herring and Mucci 1991, Jaslow and Biewener 1995) dissipating loads and modifying its orientation (Behrents et al. 1978, Jaslow 1990, Herring et al. 1996, Herring and Teng 2000). Interdigitation adds strength to compromising structures as rostrum and vault (Herring 1972, Byron et al. 2004, Sabini and Elkowitz 2006), which is observed in *S. boliviensis* from early age stages (Table 1). Jaslow (1990) and Henderson et al. (2005) demonstrated that energy absorption by the sutures is positively correlated with increased sutural interdigitation, which enlarges the area of the adjoining bone surfaces and the number of collagen fibers crossing the suture (Herring 1972). The highly serrated sutures of the braincase, palate and rostrum of *S. boliviensis* should exhibit greater strengths than those less interdigitated sutures. In this sense, the crescent complexity of the patent vault sutures observed in the ontogeny in adults of *S. boliviensis* is in agreement with Henderson et al. (2005), who identified a structural role for the fibrous tissue in the sutures during cranial development: any increase in the volume of the brain, intracranial blood, or cerebrospinal fluid results in an increase in intracranial pressure, which in turn, results in increased sutural strain and complexity.

When the jaw opens, the coronal suture is tensed by contraction of neck muscles, but during jaw closing polarity depends on the muscle contracted (masseter tense the coronal suture whereas the temporalis cause compression, Herring and Teng 2000). Because these two muscles have almost opposite

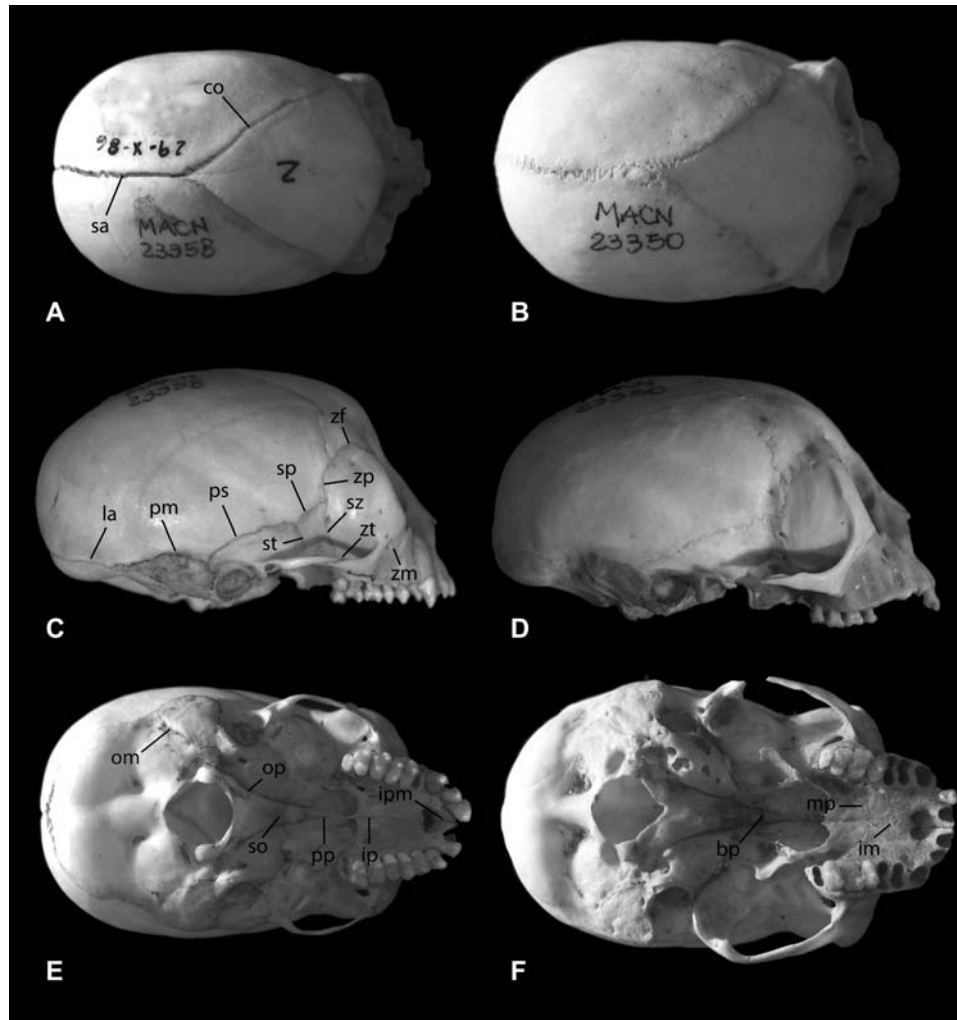


Figure 2 Dorsal, lateral and ventral views of the skull of *Saimiri boliviensis* showing exposed ectocranial sutures. (A, C, E) Young, condylo-insicive length 52.6 mm. (B, D, F) Adult condylo-insicive length 59.5 mm. Abbreviations of sutures: bp, basisphenoid-presphenoid; co, coronal; im, intermaxillaris; ip, interpalatine; ipm, interpremaxillaris; la, lambdoid; mp, maxillo-palatine; om, occipito-petrosal; pm, parieto-mastoid; pp, pterygoid-presphenoid; ps, parieto-squamosal; sa, sagittal; so, spheno-occipital; sp, spheno-parietal; st, spheno-temporal; sz, spheno-zygomatico; zf, zygomatico-frontal; zm, zygomatico-maxillaris; zp, zygomatico-parietal; zt, zygomatico-temporal.

effects on the vault, strain patterns during mastication consist in alternating reversals of right masseter/left temporalis vs. left masseter/right temporalis. However, unilateral bite is common in primates, causing contralateral joint loads and torque of the braincase and rostrum during chewing, alternating tension and compression depending on the chewing side (Hylander 1979; Greaves 1985, Hylander and Johnson 1997, Rafferty et al. 2003). Such actions were not directly correlated with any additional change in the rostral sutural morphology of *Saimiri boliviensis*, except the already mentioned general crescent interdigitation, and the early closing of premaxillar-maxillar suture (Table 1).

Although the braincase is subjected to endo- and ectocranial strains, frontal and parietal bones support low strains compared with sutures of the vault in pigs (Herring and Teng 2000), rats (Rawlinson et al. 1995) and anthropoid Primates (Hylander et al. 1991), whose magnitude are comparable to

those measured in the zygomatic suture (Herring and Mucci 1991). This fact explains the thin and weak bones of the braincase in young of *Saimiri boliviensis* and its strongly interdigitated and overlapped sutures from early age stages (Table 1). The disparity between strain magnitudes in braincase sutures and adjacent bones probably diminishes with maturity and partial suture closing the vault, which occur more commonly than in facial sutures of *S. boliviensis*, where they remain visible longer (except premaxillar-maxillar suture). Our observations of the age-dependent change in the complexity of the sagittal suture of *S. boliviensis* (Table 1), suggest also an improved capacity of adults to incorporate harder food. Byron et al. (2004), found that increasing masticatory muscle mass and bite force, increase sagittal suture complexity, explained as tissue adaptation to a particular mechanical regime achieved by bone growth at the suture. A similar pattern in *Cebus* explain why some species that exploit tough fruits have more

complex sagittal sutures than closely related congeners that do not feed on these foods (Byron et al. 2004). Such observations (in addition to experimental data), suggest a functional relationship between masticatory muscle strength and cranial suture complexity, and that suture interdigitation could not be strictly correlated with growth or age (Rafferty and Herring 1999, Byron et al. 2004).

In adult *Saimiri boliviensis*, almost all sutures remain visible, but reach high complexity in the pattern of overlap and interdigitation (Table 1). The fact that most sutures observed as a simple contact (plane or squamous) among cranial bones in young becomes complex (serrated) but always visible in adults, suggests a response to mechanical stress caused by muscular activity. This is pointed to maintain the dynamic of energy absorption of strain and compression in specific areas, such as vault, rostrum and zygomatic arch. Future research about sequence transformations of sutures could be directed in a phylogenetic context, through the exploration of patterns in related groups, and its evolution according to mechanical demands in different clades, as well as the comparison with sutural gross morphology detected in fossil Primates.

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Appendix I

Specimens examined of *Saimiri boliviensis* deposited at the Mammal Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (MACN). 12981; 13.23; 14210; 17.35; 17.36; 17.37; 2.53; 2.54; 23336-7; 23339-47; 23349-51; 23353-5; 23357-8; 3.37; 4.28; 50.15; 50.16; 50.16; 50.17.

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