COMPARATIVE ANALYSIS OF CRANIAL SUTURE COMPLEXITY IN THE GENUS *Caiman* (CROCODYLIA, ALLIGATORIDAE)

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(With 3 figures)

ABSTRACT

The variation in degrees of interdigitation (complexity) in cranial sutures among species of *Caiman* in different skull regions was studied by fractal analysis. Our findings show that there is a small species effect in the fractal dimension of cranial sutures, but most variation is accounted for by regional differentiation within the skull. There is also a significant interaction between species and cranial regions. The braincase sutures show higher fractal dimension than the facial skull sutures for all three species. The fractal dimension of nasal-maxilla suture is larger in *Caiman latirostris* than in the other species. The braincase sutures show higher fractal dimensions in *C. sclerops* than in the other species. The results suggest that different regions of the skull in caimans are under differential functional stress and the braincase sutures must counteract stronger disarticulation forces than the facial sutures. The larger fractal dimension shown by *C. latirostris* in facial sutures has probably a functional basis also. *Caiman latirostris* is known to have preferences for harder food items than the other species.

Key words: cranial sutures, fractal analysis, osteology, *Caiman*.

RESUMO

Análise comparativa da complexidade de suturas cranianas no gênero *Caiman* (Crocodylia, Alligatoridae)

A variação no grau de interdigitação (complexidade) em suturas cranianas entre espécies de *Caiman* em diferentes regiões cranianas foi estudada por análise fractal. Os resultados mostram que há um pequeno efeito atribuível a diferenças interespecíficas na dimensão fractal das suturas, mas a maior parte da variação na dimensão fractal é causada por diferenças entre regiões cranianas. Há também uma interação significativa entre espécies e regiões cranianas. As suturas da caixa craniana apresentam dimensão fractal mais alta que as suturas craniofaciais nas três espécies. A dimensão fractal da sutura nasal-maxilar é maior em *Caiman latirostris* que nas outras espécies. As suturas da caixa craniana apresentam maior dimensão fractal em *C. sclerops* que nas outras espécies. Os resultados sugerem que diferentes regiões cranianas nas espécies de *Caiman* se encontram sob estresse funcional diferenciado. As suturas da caixa craniana precisam suportar maior força de desarticulação que as suturas craniofaciais. A maior dimensão fractal nas suturas craniofaciais de *C. latirostris* provavelmente é causada por uma demanda funcional. *Caiman latirostris* apresenta preferência por itens mais duros em sua dieta que as outras espécies.

Palavras-chave: suturas cranianas, análise fractal, osteologia, *Caiman*.

INTRODUCTION

The study of suture complexity (interdigitation) patterns is an important tool in functional analysis. There is evidence that stress caused by tension influences the interdigitation of sutures. The increased interdigitation of sutures improve resistance to shearing and increase the area for attachment of connective ligaments, which counteract tensile forces that attempt to disarticulate the skeletal elements (Herring, 1972).

In the last decade, the use of fractal analysis as a tool for quantifying complexity in natural structures and patterns has become popular (Slice, 1993). The fractal dimension (D) can be interpreted as a measure of suture complexity in the sense that the more interdigitated (i.e., deviant from a straight line) sutures will present larger fractal dimensions. Several studies successfully attempted to characterize cranial suture complexity by fractal analysis.

Long (1985) first showed that sutures in biological structures (deer skulls and ammonite shells) could be characterized as fractal curves. Hartwig (1991) studied the fractal dimension of the sagittal cranial suture in humans, and developed a method to discriminate between interfingering (large scale interdigitation) and interlocking (small scale interdigitation) of sutures. Alados *et al*. (1995) used the fractal dimension of the sagittal suture of two deer species as a measure of fitness to assess the effects of inbreeding depression. Gilbert & Palmqvist (1995) compared the fractal dimension of cranial sutures from a skull fragment with that of several vertebrate species and found it to be a hominid. However, there is a need for studies that objectively use fractal analysis in the functional analysis of cranial sutures.

The species of the South American alligatorid genus *Caiman* (*C. latirostris*, *C. sclerops*, and *C. yacare*; sensu Medem, 1983) have similar habits and food preferences (fishes, mollusks, crustaceans, and insects; Carvalho, 1951), but it is known that *C. latirostris* has a major preference for gastropods with hard shells (Diefenbach, 1979). Our goal is to assess whether species differences and regional differences in the skull do raise differential functional stresses that may influence suture complexity, as quantified by their fractal dimension.

MATERIAL AND METHODS

The sample of 32 specimens used (16 *Caiman latirostris*, 6 *C. sclerops*, and 10 *C. yacare*), is housed in the Museu Nacional do Rio de Janeiro. We photographed four cranial sutures (Fig. 1) in each skull: the suture between premaxilla and maxilla (suture 1), the suture between maxilla and nasal (suture 2), the suture between postorbital and squamosal (suture 3), and the suture between squamosal and parietal (suture 4). Sutures 1 and 2 are important in maintaining stability and integrity of facial skull elements during feeding. Sutures 3 and 4 are important in maintaining braincase integrity. The photographs were digitized by a desk scanner and the coordinates of points along the sutures were captured for the fractal analysis.

The fractal dimension of biological structures has been widely used in the characterization of morphological complexity (Slice, 1993). In this study, we used the program Fractal-D (Slice, 1994) to calculate the fractal dimension (D) of the cranial sutures. This program uses the divider method (Monteiro & Reis, 1999), which consists in measuring the suture length several times by steps of decreasing lengths. The regression slope of log (suture length) on log (step length) is used to calculate D in the formula $D = 1 - b$, where *b* is the regression slope (Long, 1985; Slice, 1993). The process can be visualized in Fig. 2. A suture between postorbital and squamosal (suture 3) is depicted (Fig. 2A) as *x* and *y* coordinates of an open contour. The suture length is measured several times using rulers of different sizes (step lengths). Intuitively, we expect that, unless the suture is a straight line, smaller steps will capture the contour curves, and therefore, measure larger suture lengths, producing a relationship with negative slope. The slope of the regression of log suture length on log step length (Fig. 2B) yields the fractal dimension of the suture by the formula referenced above. This process was repeated for the four sutures in the 32 specimens.

To analyze variation of the fractal dimension among species and among sutures, we used a two-way (species, sutures) ANOVA (Sokal & Rohlf, 1995). We also tested the correlation between the fractal dimension and skull size (Basicranial Axis Length) for the species.

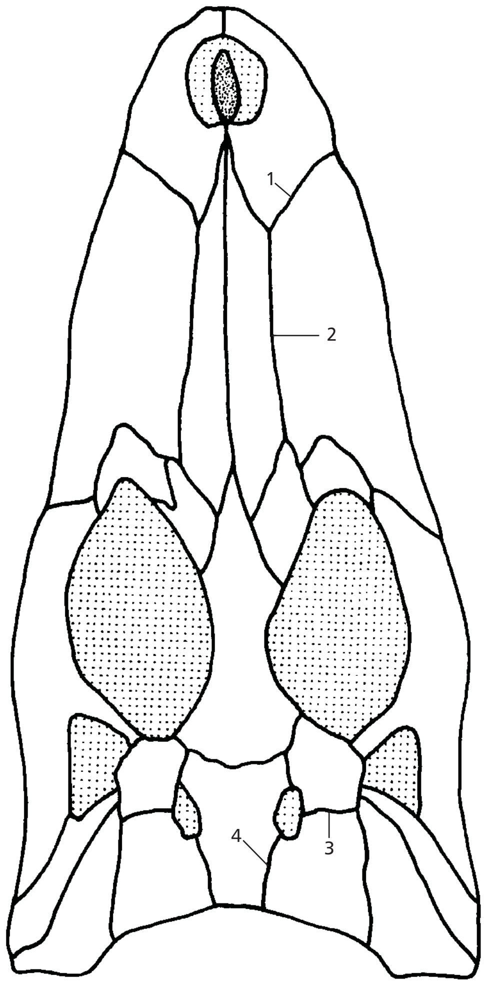

Fig. 1 — Schematic *Caiman* skull in dorsal view showing the sutures studied. See anatomical descriptions in text.

This measure of skull size was chosen because it is a good indicator of general size for the species studied (Monteiro & Soares, 1997).

RESULTS AND DISCUSSION

No significant correlation between skull size and the fractal dimension ($P > 0.05$) was observed. Herring (1972) studied interespecific and ontogenetic variation in suture closures and interdigitation of pigs and also did not observe any ontogenetic variation in suture complexity.

The two way ANOVA (Table 1) was significant for suture and the interaction between species and suture. There is a small difference in overall suture complexity among species, and the interaction between factors indicates that certain sutures are more complex in certain species than others. In Fig. 2, we see the summary of variation patterns among species and sutures. Sutures 1 and 2 (facial sutures) are generally less complex than the braincase sutures (3 and 4), which have larger fractal dimensions.

It would be interesting to compare these findings with other animal groups, but most studies to date (Long, 1985; Hartwig, 1991; Alados *et al.*, 1995; Gilbert & Palmqvist, 1995) have only dealt with single braincase sutures.

Anyway, reported values for the fractal dimension of braincase sutures in mammals (Long, 1985; Hartwig, 1991) are generally larger than those found by us for the braincase of reptiles.

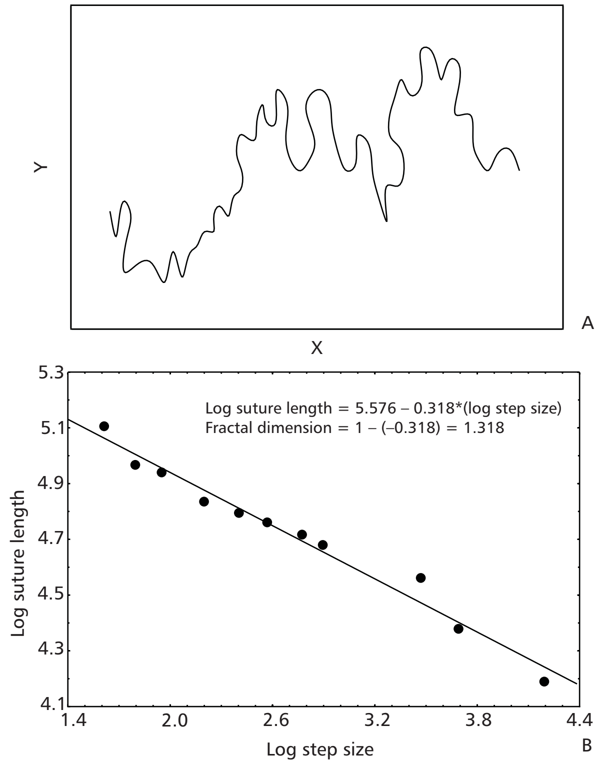

Fig. 2 — A) Suture 3 of specimen *Caiman latirostris* MNRJ 1019, depicted as an open contour. **B)** Regression between suture length and step length used to calculate the fractal dimension.

TABLE 1

Two-way ANOVA table for the fractal dimension variation among species and sutures.

	d.f. effect	**MS effect**	**d.f. error**	**MS error**	***F***	***P***
Species	2	0.003359	116	0.001360	2.46962	0.089056
Suture	3	0.023788	116	0.001360	17.49093	< 0.00001
Species × Sutures	6	0.003048	116	0.001360	2.24143	0.043989

The larger fractal dimension of braincase structures might indicate that there is a larger functional stress in the braincase, and the sutures respond to these loads by increasing interdigitation. The main directions of shearing stresses in the facial skull and the braincase might also be inferred from the fractal analysis. Suture 3 shows a larger fractal dimension than suture 4 for all three species. This indicates that the braincase supports stronger shearing forces in the lateral axis than in the longitudinal axis. However, in the facial skull, the directions of functional stress on the sutures are not so clear, because the fractal dimension is low for both sutures. However, in *C. latirostris*, there might be stronger longitudinal stresses than lateral ones in the facial region.

Examining interespecific variation in each suture separately, we see that suture 1 shows little variation among the three species. *Caiman latirostris* shows the largest mean fractal dimension in suture 2, whereas *C. sclerops* and *C. yacare* show similar ranges of variation. A possible functional interpretation for this difference is that because *C. latirostris* has a broader snout and eats harder prey (hard-shelled mollusks) than the other species, the suture between nasals and maxillas has to support a stronger loading and resist a stronger shearing stress when the animals bite. In sutures 3 and 4, *C. sclerops* shows the largest mean and the widest range of variation. The other two species show similar smaller means and ranges of variation. As a result, *C. sclerops* is shown to have more intrincate (hence more resistant) braincase sutures than other species in the genus; however, it is not entirely clear which factors could be influencing this pattern. The fractal dimension of cranial sutures in *C. yacare* are similar to *C. sclerops* in the facial region, and similar to *C. latirostris* in the braincase.

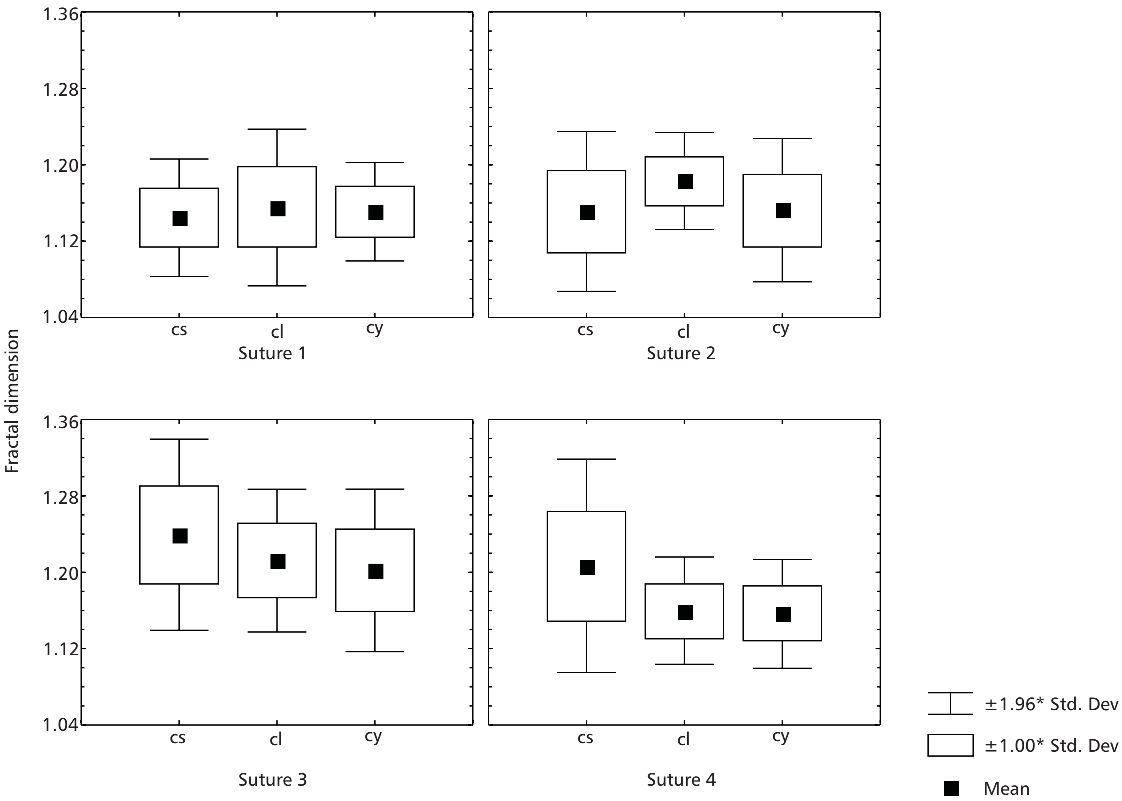

Fig. 3 — Box plot of variation of the fractal dimension among sutures and species. Acronyms used for species are: cs – *Caiman sclerops*; cl – *C. latirostris*, cy – *C. yacare*.

The study of suture complexity is a very important tool. It might give insights on the forces acting on certain morphological structures, in studies such as this one and that of Herring (1972), and might be interesting indicators of genetic stability (Alados *et al.*, 1995), as a measure of fitness, in cases where the function of larger or smaller fractal dimension of sutures is clearly established.

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REFERENCES

ALADOS, C. L., ESCÓS, J. & EMLEN, J. M., 1995, Fluctuating asymetry and fractal dimension of the sagittal suture as indicators of inbreeding depression in dama and dorcas gazelles. *Can. J. Zool.*, *73*: 1967-1974.

CARVALHO, A. L., 1951, Os jacarés do Brasil. *Arqu. Mus. Nac.*, *42*: 127-152.

DIEFENBACH, C. O. C., 1979, Ampullarid gastropod – staple food of *Caiman latirostris*? *Copeia*, *1979*: 162-163.

GILBERT, J. & PALMQVIST, P., 1995, Fractal analysis of the Orce skull sutures. *J. Human Evol.*, *28*: 561-575.

HARTWIG, W. C., 1991, Fractal analysis of sagittal suture morphology. *J. Morphol.*, *210*: 289-298.

HERRING, S. W., 1972, Sutures – a tool in functional cranial analysis. *Acta Anat.*, *83*: 222-247.

LONG, C. A., 1985, Intricate sutures as fractal curves. *J. Morphol.*, *185*: 285-295.

MEDEM, F., 1983, *Los Crocodylia de Sur America*. Colciencias, Bogotá, Colombia, 2 vol.

MONTEIRO, L. R. & SOARES, M., 1997, Allometric analysis of the ontogenetic variation and evolution of the skull in *Caiman* Spix, 1825 (Crocodylia: Alligatoridae). *Herpetologica*, *53*: 62-69.

MONTEIRO, L. R. & REIS, S. F., 1999, *Princípios de morfometria geométrica*. Holos Editora, Ribeirão Preto, 188p.

SLICE, D. E., 1993, The fractal analysis of shape, pp. 161-192. *In*: L. F. Marcus, E. Bello & A. García-Valdecasas (eds.), *Contributions to morphometrics.* Monografias, Museo Nacional de Ciencias Naturales, Madrid.

SLICE, D. E., 1994, *Fractal-D*. Exeter Publishing Ltd., Setauket, New York, 55p.

SOKAL, R. R. & ROHLF, F. J., 1995, *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman and Co., New York, 887p.