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Author(s): Leandro R. Monteiro and Marcelo Soares

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ALLOMETRIC ANALYSIS OF THE ONTOGENETIC VARIATION AND EVOLUTION OF THE SKULL IN CAIMAN SPIX, 1825 (CROCODYLIA: ALLIGATORIDAE)

LEANDRO R. MONTEIRO¹ AND MARCELO SOARES²

¹Depto de Zoologia, UNESP caixa postal 199 cep: 13506-900, Rio Claro, SP, Brasil

²Setor de Herpetologia, Museu Nacional do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, Rio de Janeiro, RJ cep: 20940-040, Brasil

ABSTRACT: We studied ontogenetic variation in the shape of the skull among species of *Caiman* using principal component analysis. Comparison of multivariate allometric coefficients and ontogenetic trends between size and shape reveals that *C. sclerops* and *C. yacare* have similar ontogenetic processes, and they are more related to each other than either is to *C. latirostris*. Allometric relationships of the characters measured are similar in all species studied. The greater differences were in the width measurements, with higher coefficients in shape (second principal component) for *C. latirostris*, and length measurements with higher coefficients in shape for *C. yacare* and *C. sclerops*. The ontogenetic process leading to change in skull shape in the group seems to be plesiomorphic for elongation and derived for broadening. Statistical comparison of the ontogenetic trends with models of allometric heterochrony suggests that *C. latirostris* has diverged from the other species by a neotenic process, and that *C. sclerops* is separated from *C. yacare* by ontogenetic scaling (progenesis).

Key words: Allometry; Heterochrony; *Caiman*; Skull ontogeny

THE species of *Caiman* (*C. latirostris*, *C. sclerops*, and *C. yacare*, sensu Medem, 1983) are widely distributed through South America. *Caiman latirostris* ranges from northern to southern Brazil along the Atlantic Coast, west into Paraguay and into the northern part of Argentina; *C. yacare*

occurs in swampy areas of the midwestern part of Brazil, and *C. sclerops* is widespread in the Amazon Basin (Brazaitis, 1973; Carvalho, 1951; Groombridge, 1987). These species have similar habits and food preferences. They eat fishes, mollusks, crustaceans, and insects, and larger indi-

viduals also prey on birds and mammals (Ayarzaguena, 1983; Carvalho, 1951; Vanzolini and Gomes, 1979).

The study of growth in crocodylians is an interesting subject, which has received little attention. These animals are thought to have unlimited growth (Jacobsen and Kushlan, 1989) and, consequently, have a large range of size during their lifespans. Because the crocodylian skull is solid, it is an appropriate subject for studies of variation in shape in relation to size. Most morphometric studies of crocodylians deal with a single species or compare the skulls of unrelated species. Studies on allometric growth have been carried out on *Alligator mississippiensis* (Dodson, 1975), *Caiman crocodilus* (Ayarzaguena, 1983; Gans, 1980; Vanzolini and Gomes, 1979), *Paleosuchus trigonatus* (Vanzolini and Gomes, 1979), and *Crocodylus novaeguinae* (Hall and Portier, 1994). None of these compared the allometries of different species. However, the embryonic growth of unrelated species of crocodylians was studied and quantified by Deeming and Ferguson (1990), and morphometric analyses were performed on *Crocodylus porosus* by Webb and Messel (1978).

Herein we compare the allometric relationships of several cranial characters in three species of *Caiman* using multivariate allometric coefficients, and ontogenetic trends between size and shape. Such an approach is important to evolutionary studies, because it allows a study of the evolutionary process (allometric heterochrony) that leads to a given phylogenetic pattern (Kluge, 1988; Reis, 1988). If we consider the statement of McKinney (1988), that heterochronic processes play a major role in evolution (at least in small scale), the models developed for the study of heterochrony deserve special attention (Kluge, 1988). However, these are rarely applied to real problems, as in Reis et al. (1988).

MATERIALS AND METHODS

Sample

The sample was composed of 46 skulls from the collections of the Museu Nacional

do Rio de Janeiro and the Department of Zoology—UNESP—Rio Claro. This included 11 specimens of *Caiman sclerops* (basicranial axis length range 31.15–236.00 mm), 13 specimens of *C. yacare* (BAL range 29.10–306.00 mm), and 22 specimens of *C. latirostris* (BAL range 42.95–284.00 mm). The specimens of *C. latirostris* (with geographic data) are mainly from the states of Espírito Santo and Rio de Janeiro (very close populations in southeastern Brazil). The specimens of *C. sclerops* are from the states of Mato Grosso and Roraima, respectively, in western and northern Brazil, and those of *C. yacare* are from the state of Mato Grosso. However, most skulls are from old specimens (collected >40 yr ago) that lack data.

Measurements

Nineteen measurements, designed to reflect skull shape (Fig. 1), were as follows: basicranial axis length (BAL, measured from the tip of the snout to the occipital condyle), rostral width at the level of the fourth premaxillary tooth (RWP), rostral width at the level of the ninth maxillary tooth (RWM), orbital width (OW), orbital length (OL), cranial roof width (CRW), frontal width (FW), palatine length (PL), palatine width (PW), nasal length (NL), palatine fenestra length (PFL), palatine fenestra width (PFW), cranial width at quadrate level (CWQ), external mandibular fenestra height (MFH), external mandibular fenestra length (MFL), dentary dorsal length (DDL), mandibular arch length (MAL), retroarticular process length (RPL), and mandibular height at the external fenestra level (MH). The paired measurements were taken on both sides (whenever possible) and averaged.

Statistical Analysis

Cranial ontogenetic variation was assessed by a principal component analysis (PCA) of the variance-covariance matrix of log-transformed values. This technique summarizes the variation within a data set and presents it as eigenvectors that contain all the important information (Neff and Marcus, 1980). The first principal component corresponds to the major axis of

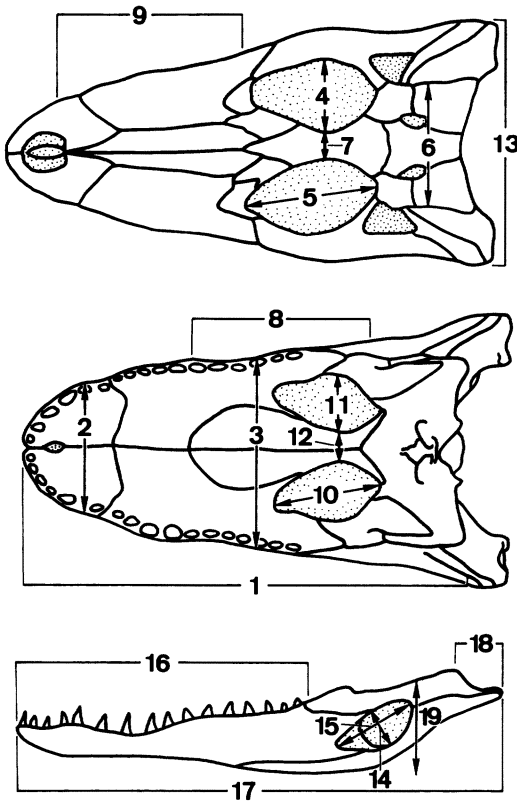


FIG. 1.—Schematic alligatorid skull and mandible showing the measurements taken for the analysis: 1—BAL, 2—RWP, 3—RWM, 4—OW, 5—OL, 6—CRW, 7—FW, 8—PL, 9—NL, 10—PFL, 11—PFW, 12—PW, 13—CWQ, 14—MFH, 15—MFL, 16—DDL, 17—MAL, 18—RPL, 19—MH.

variation within a set of variables, and the subsequent components (number of components = number of variables) account for decreasing amounts of variance within the sample. The coefficient of a given variable on a principal component is the cosine of the angle that variable forms with the component (or the eigenvector of the variance-covariance matrix). Therefore, the larger the coefficient of a variable, the larger the contribution of that variable to the variance of the component (Marcus, 1990). The sign of the coefficients denotes the direction of variation of a variable on a given component.

The analysis assumes that the direction of maximum variation is the same among groups in the case that heterogeneous groups are being examined. This assump-

tion can be tested by calculating the vector-correlation coefficients between the within-group first principal components (Strauss and Fuiman, 1985). These coefficients are calculated as the inner product of the matrix containing two columns of coefficients of the first within-group principal components. As common correlation coefficients, these may be calculated only for two groups at a time, and values near 1.0 indicate coincidence of the vectors, whereas values near zero indicate orthogonality of the vectors (Reis et al., 1988).

When the coefficients of the first principal component have the same sign, it can be interpreted as a general size factor (because all variables have the same direction of variation). If the remaining components have coefficients with positive and negative signs, they can be interpreted as shape factors (because the variables have different directions of variation, giving information about ratios of the diverse characters) (Marcus, 1990). If these conditions are true for an analysis, we can obtain multivariate allometric coefficients from the first principal component (Jolicoeur, 1963). The multivariate allometry coefficient of a character in relation to general size is the standardized first principal component coefficient of that character divided by $\sqrt{1/p}$, where p is the number of variables (Cavalcanti and Lopes, 1993; Cheverud, 1982). This is equivalent to dividing each coefficient by the grand average of the coefficients. Values >1.0 indicate positive allometry, whereas values equal to 1.0 indicate isometry, and values <1.0 indicate negative allometry (Gould, 1966; Shea, 1985). We performed four analyses, one for each species and one combining all samples.

Heterochrony Models

The scores obtained from the projection of the eigenvectors on the logarithmically transformed data of the combined sample were plotted on the space of the first two principal components and the ontogenetic trajectories estimated for each species by linear regression between them.

Kluge (1988) reported a way in which ontogeny can be characterized by pure al-

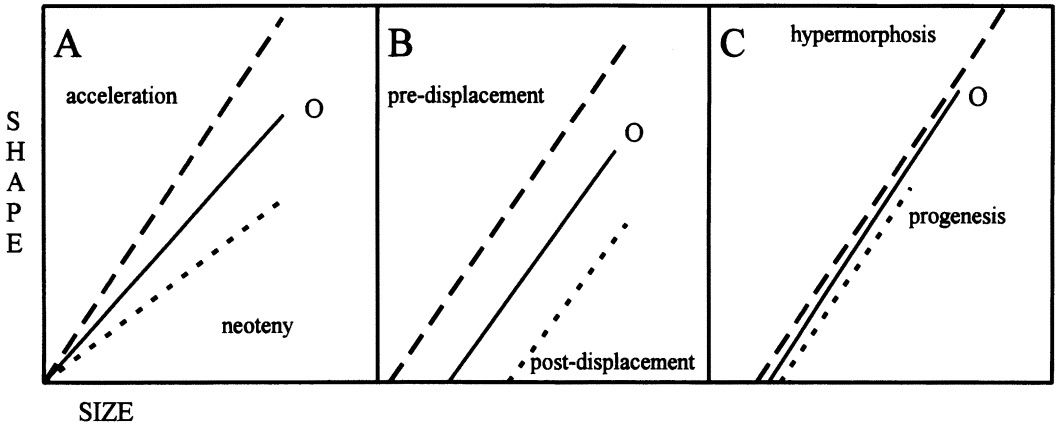


FIG. 2.—Pure heterochrony models for the comparison between ontogenetic trajectories. Dotted lines correspond to paedomorphic processes, dashed lines correspond to peramorphic processes. Continuous lines (O) correspond to the trajectory of the outgroup. A = differences in slope, B = differences in Y-intercept, C = differences in cessation of growth.

lometric heterochrony models developed by Alberch et al. (1979). This model states that ontogenetic trajectories between size and shape factors can be compared by three parameters (Fig. 2); the differences in these parameters are used to test hypotheses about allometric heterochronic processes. Allometric heterochrony is the term used for heterochronic processes when studied by size, rather than age. The parameters are slope (differences in slope being linked to neoteny or acceleration), onset of growth or Y-intercept (accounting for post or pre-displacement), and cessation of growth or extent of ontogeny (relating to hypermorphosis or progenesis). Differences in these parameters can be tested by simple statistical procedures. Slopes and Y-intercepts are tested for equality by analysis of covariance (ANCOVA). Differences in extent are tested by an analysis of variance (ANOVA) on the first principal component or size factor. The ANOVA is recommended because any hypothesis testing requires at least three species (one in the outgroup and two in the ingroup: Kluge, 1988).

The multivariate analyses were performed on PCA software written by Pe Dr. J. S. Moure. Univariate analyses (ANOVA, ANCOVA, and linear regressions) were performed following the procedures explained in Sokal and Rohlf (1981).

RESULTS

The vector correlation coefficients indicated a high level of coincidence between the first eigenvectors in the pairwise comparison of samples (>0.98), satisfying the assumption that the direction of maximum variation is the same in the three groups studied.

The two first principal components account for 98.5% of the variation in the combined sample, 98.2% for *Caiman latirostris*, 99.5% for *C. sclerops*, and 99.5% for *C. yacare*. The remaining eigenvectors were not considered, because their eigenvalues were too low. The first principal component was interpreted as a size factor in each individual sample and in the combined one, because all the characters had positive loadings and high correlation coefficients ($P < 0.0001$). Following the assumption above, the multivariate allometric coefficients were calculated for the characters measured, separately for each species (Table 1).

Common features among the species were (1) positive allometry of rostral width at the level of the premaxilla, frontal width, nasal length, external mandibular fenestra height, retroarticular process length, and mandibular height and (2) negative allometry observed in the orbital width and length, cranial roof width, and length of

TABLE 1.—Coefficients (PCI) of the first principal component for 19 measurements taken for each species. Also provided are the correlation coefficient of each character with the first principal component (r) and the multivariate allometric coefficients for each measure (k).

Character	<i>C. latirostris</i>			<i>C. sclerops</i>			<i>C. yacare</i>		
	PCI	r	k	PCI	r	k	PCI	r	k
BAL	0.2173	0.94	0.959	0.2285	0.99	1.009	0.2322	0.99	1.025
RWP	0.2467	0.99	1.089	0.2463	0.99	1.087	0.2444	0.99	1.078
RWM	0.2234	0.99	0.986	0.2023	0.99	0.893	0.2034	0.98	0.898
OW	0.1560	0.98	0.688	0.1580	0.99	0.698	0.1598	0.91	0.705
OL	0.1554	0.97	0.686	0.1557	0.99	0.687	0.1673	0.95	0.738
CRW	0.1848	0.99	0.815	0.1749	0.99	0.772	0.1701	0.96	0.751
FW	0.2882	0.96	1.272	0.2475	0.99	1.093	0.2400	0.89	1.059
PL	0.1971	0.98	0.870	0.2383	0.99	1.052	0.2109	0.50	0.931
PW	0.2210	0.94	0.975	0.2142	0.98	0.946	0.2288	0.93	1.010
NL	0.2708	0.98	1.195	0.3036	0.99	1.340	0.2941	0.95	1.298
PFL	0.2018	0.99	0.890	0.2096	0.99	0.925	0.2203	0.96	0.972
PFW	0.2080	0.97	0.918	0.1961	0.99	0.866	0.1838	0.91	0.811
CWQ	0.2454	0.99	1.083	0.2334	0.99	1.030	0.2251	0.98	0.993
MFH	0.2698	0.96	1.191	0.2551	0.98	1.126	0.2508	0.84	1.107
MFL	0.2394	0.98	1.056	0.2202	0.99	0.972	0.2483	0.85	1.096
DDL	0.2266	0.99	1.000	0.2488	0.99	1.098	0.2399	0.94	1.059
MAL	0.2371	0.99	1.046	0.2433	0.99	1.074	0.2458	0.90	1.085
RPL	0.2597	0.97	1.146	0.2673	0.98	1.180	0.2732	0.96	1.206
MH	0.2569	0.99	1.134	0.2597	0.99	1.147	0.2671	0.96	1.179

palatine fenestra. Also shared is the isometry of the basicranial axis length and palate width. *Caiman sclerops* and *C. yacare* share more common features than either does with *C. latirostris*. Slight differences in some allometric coefficients between *C. sclerops* and *C. yacare* do not account for divergence in ontogenetic patterns, except that the positive allometry of the palatine in *C. sclerops* might indicate that the skull is proportionally longer in this species than in *C. yacare*. However, skulls of adult *C. yacare* and *C. sclerops* are hardly distinguishable by shape, although they do differ in some osteological characters and absolute size. The main difference between *C. latirostris* and the other species is the positive allometry of the cranial width between the quadrates in *C. latirostris* and isometric in the others. Also, variation of rostral width at the maxilla level (RWM) is isometric in *C. latirostris*, but negatively allometric in the other species. The mandibular characters have similar allometric trends in all three species. Adults have thicker mandibles than the newborns, because the height-related characters have a highly positive allometry and the length characters are isometric.

Analysis of the combined sample indi-

cates that the major interspecific differences are in shape, because the onset and extent of growth (size variation) is similar (although skulls of adult *Caiman sclerops* are smaller than of the other species). During ontogeny, the head of *C. latirostris* becomes stout, increasing greatly in cranial width; this is reflected in the fact that the most significant coefficients for this species are in the width variables (positive eigenvectors of variables increasing upwards in the shape component-PCII) (Table 2, Fig. 3). The skulls of *C. sclerops* and *C. yacare* elongate; the larger coefficients for these species are in the length variables (negative coefficients of variables with negative directions of variation in the shape component-PCII). The mandible variables seem to differ little among the species; their coefficients in the shape component are low, and the allometric coefficients are similar in each of the species. Examination of the principal component scatter reveals that *C. latirostris* and *C. yacare* differ greatly from *C. sclerops* with respect to size range, whereas *C. yacare* and *C. sclerops* differ from *C. latirostris* primarily in shape.

The regressions between size and shape factors (ontogenetic trends) yielded sig-

TABLE 2.—Coefficients (PCI and PCII) of the principal component analysis for 19 measurements taken for the combined sample of the species of *Caiman*. Symbols as in Table 1.

Character	PCI	PCII	r
BAL	0.2257	-0.0948	0.99
RWP	0.2501	0.1873	0.99
RWM	0.2150	0.3600	0.96
OW	0.1575	-0.0376	0.98
OL	0.1622	-0.0876	0.98
CRW	0.1743	0.0220	0.99
FW	0.2565	0.1211	0.97
PL	0.2087	-0.4877	0.80
PW	0.2241	-0.4949	0.92
NL	0.2838	-0.2011	0.98
PFL	0.2083	0.0715	0.98
PFW	0.1969	0.4534	0.98
CWQ	0.2352	0.1322	0.99
MFH	0.2610	0.0193	0.97
MFL	0.2371	0.1039	0.98
DDL	0.2380	-0.1592	0.99
MAL	0.2420	-0.0257	0.99
RPL	0.2682	0.1164	0.99
MH	0.2641	0.0006	0.99

nificant results for all species (Fig 4). The homogeneity test between the regression slopes did not show a significant difference between *C. sclerops* and *C. yacare* ($F = 0.031, P = 0.861$), but the slopes were significantly different between these two species and *C. latirostris* ($F = 8.715, P = 0.006$). The ANCOVA was used only to test for differences between the Y-intercepts of the regressions for the two former species (because of the slope equality). The difference was also insignificant ($F = 1.052, P = 0.318$). The ANOVA performed on the size component (PCI) to test for differences among the species in the extent parameter of the ontogenetic trends showed significant results ($P < 0.05$) only separating *Caiman sclerops* from the other species.

DISCUSSION

The comparison of the ontogenetic trends revealed that the skulls of three species of *Caiman* have similar shapes at birth but that differences appear early in the ontogenetic process. The final adult shape (particularly in *C. latirostris*) is often evident in young animals, and the shape of the skull changes little with subsequent development. The ontogenetic trends of *C.*

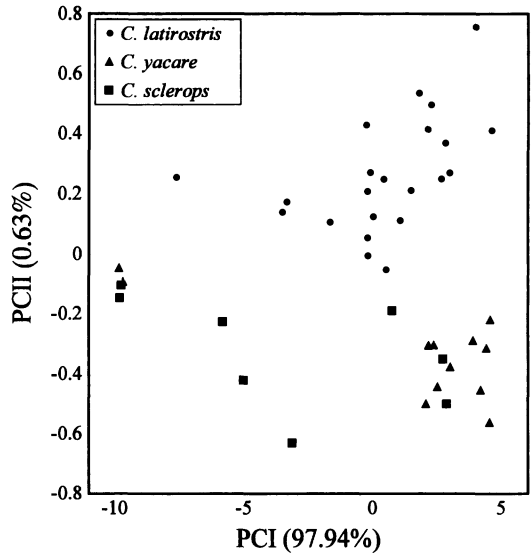


FIG. 3.—Scatterplot of the combined sample in the space of the first two principal components. The numbers in parentheses are the percentage of contribution of each component to the total variance in the sample.

sclerops and *C. yacare* lead to similar skull shapes in the adults.

Dispersion of the specimens in the space of the size and shape components suggests

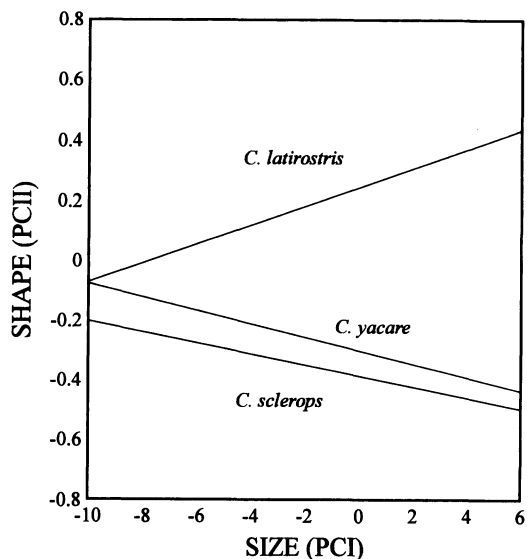


FIG. 4.—Ontogenetic trends of the species studied. The regression equations, correlation coefficients (r), and significance probabilities (P) are: *Caiman latirostris* ($Y = 0.228 + 0.052X, r = 0.592, P < 0.01$); *C. yacare* ($Y = -0.298 - 0.023X, r = -0.664, P < 0.05$); *C. sclerops* ($Y = -0.439 - 0.027X, r = -0.720, P < 0.05$).

that a heterochronic mechanism was involved in the evolution of *Caiman latirostris*. The mechanism might be neoteny (a paedomorphic process), a model in which the ontogenetic trajectory of a given species is not as steep as those of a sister species and the outgroup (Kluge, 1988). Retention of juvenile characters in adults and posterior ontogenetic re-patterning (Wake, 1989) is the only way to explain such divergence found in the ontogenetic trajectory of *C. latirostris*. The ontogenetic process involving the elongation of the skull (observed in *C. sclerops* and *C. yacare*) probably is the plesiomorphic condition in the group, because it occurs also in *Melanosuchus niger* (Monteiro, unpublished data), which may be considered as an outgroup to the species of *Caiman*. The process that forms a broader skull (and a divergent trajectory from the other species) probably is the derived condition and an apomorphy of *C. latirostris*. The allometric pattern observed in this species is unique among crocodylians.

Whereas *Caiman sclerops* and *C. yacare* have similar ontogenetic trajectories in the parameters slope and Y-intercept, they differ significantly in extent (cessation of growth). As the outgroup for this species (*C. latirostris*) has a greater size range than *C. sclerops* and is not significantly different from *C. yacare*; *C. sclerops* probably differentiated from *C. yacare* by a heterochronic process of progenesis (another paedomorphic process). Thus, it seems that diversification of skull shape in this group has been achieved by paedomorphic processes—i.e., neoteny and progenesis—with the former occurring before the latter.

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