

Cranial ontogeny of *Caluromys philander* (Didelphidae: Caluromyinae): a qualitative and quantitative approach

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The ontogeny of skull allometry has been the subject of research in didelphid, microbiotheriid, and dasyurid marsupials. We described and compared postweaning stages of cranial development in the woolly opossum *Caluromys philander*, a member of a distinct lineage of didelphids. We identified 31 qualitative morphological changes between juveniles and adults, many related to the trophic apparatus. Early development of the paracanine fossa in the snout, correlated with the presence of well-developed canines in juveniles, represents a remarkable difference between the ontogeny of *C. philander* and other marsupials. We performed bivariate and multivariate analyses of allometry on a data set composed of 14 cranial measurements and 45 specimens. Allometric scaling showed that braincase is relatively small in adulthood, whereas other neurocranial components, particularly the orbit, grew isometrically along its length. The palate becomes elongated by the combination of the isometry of its length and the negative allometry of its width. The rostrum lengthened, but its height remained proportionally constant. In relative terms the temporal fossa expanded inward following the marsupial model that combines the negative allometry of the braincase and the isometry of the zygomatic breadth. The mandible increased in robustness. The skull ontogeny of *C. philander* shares 4 allometric trends with 2 didelphids (*Didelphis albiventris* and *Lutreolina crassicaudata*) and two australidelphians (*Dromiciops gliroides* and *Dasyurus albopunctatus*). Three of these trends, breadth of palate, breadth of braincase, and height of occipital plate, were allometrically negative, whereas height of the dentary was positive. These common allometric trends may be interpreted as symplesiomorphic for marsupials, suggesting a high degree of conservatism in the skull development of *Caluromys* and other marsupials. DOI: 10.1644/09-MAMM-A-291.1.

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Recent studies on cranial ontogeny in several groups of marsupials were focused on functional interpretations from both a qualitative and quantitatively approach (Abdala et al. 2001; Flores et al. 2003, 2006; Giannini et al. 2004). Such studies detected complex modifications occurring in the skull during postweaning ontogeny, accompanying the critical changes of diet (from milk-fed to the adult trophic function) during this period. Ontogenetic pattern of 2 related ameridelphians (the didelphids *Didelphis albiventris* and *Lutreolina crassicaudata*) and 2 australidelphians (the microbiotheriid *Dromiciops gliroides* and the dasyurid *Dasyurus albopunctatus*—Abdala et al. 2001; Flores et al. 2003, 2006; Giannini et al. 2004) showed some cranial trends common to all taxa and

presumably to the groups to which they belong, whereas other trends appeared clearly distinct in each of the studied taxa. The latter probably represent ontogenetic characteristics of different marsupial lineages. Interactions between growth of neurocranial and splanchnocranial components modify functions of the skull linked to the transition to the specific diet of adults, through developmental stages. In a comparative sense the common patterns of skull growth in postweaning stages in taxa studied to date may represent plesiomorphies in the



marsupial clade (e.g., isometry of the muzzle height, negative allometry of the breadth of braincase and the height of occipital plate, and positive allometry of the height of the mandible); i.e., a common developmental pattern inherited from ancestors at the marsupial root.

On the basis of comparisons of the 2 didelphid species analyzed to date, we advanced the existence of general cranial growth trends in the family (Flores et al. 2003). For instance, the basic ontogenetic plan of skull growth in Didelphinae would consist of an interaction between neurocranial and splanchnocranial growth trends that provide a wide space for the large temporal muscles (Flores et al. 2003). Thus the detection of patterns of cranial growth in groups closely related to didelphines, such as caluromyines, is essential to assess a common plan in the growth pattern of didelphids in a more inclusive phylogenetic context.

Caluromys, along with *Caluromysiops* and *Glironia*, is one of the most basal groups in the Didelphidae. An apparent consensus exists on its phylogenetic position, on the basis either of morphological data (Flores 2003, 2009), DNA–DNA hybridization data (Kirsch et al. 1995), DNA sequence data (Jansa and Voss 2000; Palma and Spotorno 1999), or a combination thereof (Creighton 1984; Flores 2009; Reig et al. 1987; Voss and Jansa 2003, 2009). All studies agree in the significant divergence between caluromyines and the remainder of Didelphidae. Thus the comparative study of development in this taxon is of special importance for understanding the evolution of the family (Astúa de Moraes and Leiner 2008). The postweaning cranial development observed in *Caluromys philander*, and those of didelphids, dasyurids, and microbiotheriids, allowed us to test and expand previous hypotheses of cranial ontogeny in basal marsupials and improve our prior generalizations made for Didelphidae (Flores et al. 2003).

MATERIALS AND METHODS

Caluromys philander is a common marsupial of neotropical rainforests, with well-developed arboreal habits (Atramentowicz 1982, 1986, 1995; Charles-Dominique et al. 1981; Julien-Laferriere 1991; Julien-Laferriere and Atramentowicz 1990). As are most didelphids, the species is omnivorous, with some marked preference for fruits (Astúa de Moraes et al. 2003; Charles-Dominique et al. 1981; Julien-Laferriere 1999; Julien-Laferriere and Atramentowicz 1990; Leite et al. 1996).

Caluromys philander is one of the three species of woolly opossums living in Central and South America, with body mass of adult males and females ranging from 300 to 400 g (Atramentowicz 1995). Breeding patterns and correlation between absolute age and tooth eruption sequence are well known (Astúa de Moraes and Leiner 2008; Atramentowicz 1986). At birth each young is approximately 0.2 g and remains attached to the teat for about 80 days. Young start eating solid food at this stage but still depend on milk until approximately day 120 postpartum, when young become independent (Atramentowicz 1982, 1995).

Study specimens.—We studied an ontogenetic series of 45 specimens of *C. philander* of widely different ages housed in the mammal collection of the American Museum of Natural History (AMNH). The specimens examined were AMNH 5943-50, 5953, 16955, 16967, 76969, 93529, 94895, 94898, 95525, 95527-8, 95530-5, 95537, 95972, 96623, 96631, 96640, 96650, 96651-2, 139815-6, 169668, 169762, 171380, 174001, 174004, 174006, 203351-2, 208994-5, and 234989. We focused the study of qualitative changes on the contrast between juveniles and adults, but we also observed subadults for anatomical transformations that occur throughout the range of ages available.

In our sample 14 specimens were collected before achieving the stage of full adult dentition. Other individuals were adults of different sizes. The smallest specimen (AMNH 16955, sex undetermined, condylobasal length of 31.6 mm) has the third lower (m3) and second upper (M2) molars erupting, and the third lower (dp3) and upper (dP3) deciduous premolars present. The largest specimen (AMNH 93529, male) measured 60.1 mm for condylobasal length and exhibited severely worn cusps. Thus in our sample the smallest individual was only about one-half the maximum adult size. On the basis of known sequences of tooth emergence and wear (Astúa de Moraes and Leiner 2008; Atramentowicz 1986), our youngest specimen is approximately 5 months old, whereas the largest specimen probably was 2 years old (or older).

Study of growth.—In this study we took two descriptive approaches. First, we contrasted developing features in the skull of the youngest specimens with those of the oldest on a qualitative basis (Flores et al. 2006; Table 1). Anatomical terminology follows primarily Wible (2003). Second, we followed previous studies on marsupials using a series of 14 linear measurements to estimate allometric growth of skull components (Abdala et al. 2001; Flores et al. 2003, 2006; Giannini et al. 2004). These variables represent length, width, or depth of major skull structures (Fig. 1).

For the quantitative analysis we took 2 methodological approaches: bivariate and multivariate allometry. In bivariate studies the scaling of any individual measurement can be affected strongly by the choice of the independent variable (Smith 1981; Wayne 1986). In most previous works (Abdala et al. 2001; Emerson and Bramble 1993; Flores et al. 2003; Giannini et al. 2004; Wayne 1986) researchers have taken the total length of the skull, or the condylobasal length, as a proxy of size for use as an independent variable in allometric studies. Instead, we used as independent variable one with the least departure from isometry in our multivariate analyses. This resulted in an unconventional choice, the length of palate, which nevertheless guarantees the best approximation to isometry in the data set. For comparative purposes we also report results using the condylobasal length as proxy of size. Bivariate coefficients of allometry can be extremely useful because they are less affected by sample completeness (Giannini et al. 2004) and are more directly interpretable in terms of size-dependent functional relationships (Jungers and German 1981). In addition, bivariate coefficients can be

TABLE 1.—List of morphological changes detected in a comparison of smallest versus largest specimens of *Caluromys philander*.

Characters	Figure	Juvenile	Adult
Rostrum			
1. Anterior portion of the nasals	3	Wide	Narrow
2. Level of upper alveolar line	2	At zygomatic root	Ventral to zygomatic root
3. Paracanine fossa	2	Poorly developed	Large
4. Incisivomaxillary suture in lateral view	2	Near the anterior margin of the paracanine fossa, adjacent to last incisor	In the middle of the paracanine fossa, well separated from last incisor
Palatal region			
5. Upper postcanine rows	4	Posteriorly divergent	Parallel
6. Major palatine foramen	4	Inconspicuous	Small
7. Minor palatine foramen	4	Notch opening laterally	Enclosed foramen
8. Postpalatine torus	4	Slightly curved	Strongly curved
Orbitotemporal region			
9. Postorbital border of frontal	3	Absent	Well developed
10. Postorbital constriction	3	Absent	Well developed
11. Base of zygomatic process of squamosal	3	Oriented anteriorly	Oriented laterally
12. Temporal fossa in dorsal view	3, 4	Narrow	Wide
13. Dorsal profile of the skull	2	Higher than level of orbit	Level with orbit
14. Temporal line	3	Absent	Converging to the caudal tip
15. Anterodorsal portion of the jugal, at the orbit base	4	Not laterally extended	Laterally extended
16. Masseteric line of the jugal	2	Absent	Present
17. Anterior edge of the orbit	2	Between P2 and dP3	Between P3 and M1
Occipital region			
18. Nuchal crest	3	Absent	Well developed
19. Occipital condyles	2	Not caudally extended	Caudally extended
20. Paracondylar process	2	Small	Elongated to the level of the ventral edge of foramen magnum
Basicranial region			
21. Postglenoid process	2	Small	Well developed
22. Transverse sinus canal	4	In line with anterior end of tympanic bulla	Anterior to the tympanic bulla
23. Glenoid fossa	4	Narrow	Laterally expanded
Mandible			
24. Angular process	6	Slightly oriented medially	Strongly oriented medially
25. Mandibular foramen	5	Large	Small
26. Coronoid crest	5	Robust	Weak
27. Dorsal margin of the coronoid process	5	Short anteroposteriorly	Long anteroposteriorly
28. Posterior shelf of the masseteric fossa	5	Incipient	Well developed
29. Ventral margin of mandibular body	5	Straight	Convex
30. Diastema between p1-p2	5	Absent	Present, long
31. Articular condyle	6	Narrow	Laterally expanded

derived from simple growth models of each measurement (Laird 1965; Wayne 1986).

To estimate the change in size of each cranial variable we used the linear (\log_{10}) transformation of the power equation of growth $y = x^{b_1} b_0 e$, where y is the variable of interest, b_0 the y -intercept, x the size proxy, b_1 the slope parameter or bivariate coefficient of allometry, and e the error term. We tested deviations from isometry by means of 2-tailed t -tests, as the independent variable was normally distributed (Shapiro Wilk test, $w = 0.98$, $P = 0.79$). Allometric coefficients are taken to be isometric whenever they cannot be distinguished statistically from unity, with α fixed at 0.01. Statistically significant deviations from isometry represented cases of negative allometry if $b_1 < 1.0$ and positive allometry if $b_1 > 1.0$. We report allometry coefficients calculated by ordinary least-squares regression (hereafter LS) and reduced major axis regression (RMA—Abdala et al. 2001; Flores et al. 2003). The

response of each cranial variable to our chosen proxy of size, the length of palate, was evaluated by the r^2 coefficient.

In multivariate analysis of allometry size is a latent variable affecting all measured variables simultaneously. As in our previous studies, multivariate coefficients of allometry are obtained from a principal components analysis (PCA) based on a variance–covariance matrix of all variables (Jolicœur 1963). This was followed by a resampling strategy using jackknife pseudovalues of coefficients to generate confidence intervals (CIs) for the coefficients so obtained (Flores et al. 2006; Giannini et al. 2004). The CI may be inclusive of a matrix-specific isometric value that depends only on the number of variables, p , and therefore be statistically indistinguishable from isometry, or may exclude such value and therefore be considered significantly allometric. The isometric value for 14 variables is 0.267 (calculated as $1/p^{0.5}$), so instances of allometry included all coefficients whose

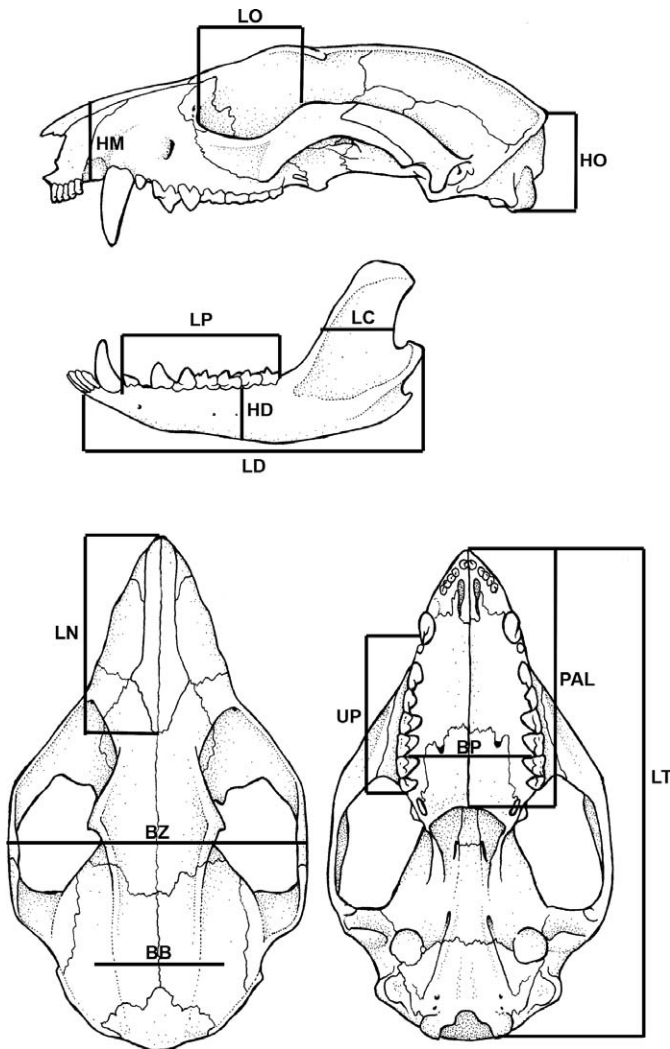


FIG. 1.—Cranial measurements of *Caluromys philander* used in this study. Abbreviations: BB, breadth of braincase; BP, breadth of palate; BZ, zygomatic breadth; HD, height of mandibular body; HM, height of muzzle; HO, height of occipital plate; LC, length of coronoid process; LD, length of mandible; LN, length of nasals; LO, length of orbit; LP, length of lower postcanine row; LT, total length of the skull; PAL, length of palate; UP, length of upper postcanine row.

intervals excluded this value (positive if >0.267 , negative if <0.267).

Giannini et al. (2004) and Flores et al. (2006) followed Manly's (1997) suggestion of using trimmed pseudovalues as an alternative for the calculation of the *CI*. Trimming the *m* largest and *m* smallest jackknife pseudovalues for each variable can significantly decrease width of the *CI* and yield more realistic allometric estimations (Giannini et al. 2004). If untrimmed and trimmed *CI*s differ greatly in width, this can be interpreted as an indication of extreme pseudovalues affecting the standard errors. Here we report untrimmed and trimmed calculations. For the bivariate analyses the computer program PAST (Hammer et al. 2001) was used. For the multivariate statistical analysis (PCA + jackknife resampling) the R-script (R Development Core Team 2008) of Giannini et al. (2009) was used and is available from the authors.

RESULTS

Qualitative trends.—We identified 31 structures exhibiting ontogenetic changes between youngest and oldest specimens of *C. philander* (Table 1). These included changes in the rostrum (4 characters), palatal region (4), orbitotemporal region (9), occiput (3), basicranial region (3), and mandible (8). Seven of those changes represented the appearance of structures absent in juveniles (characters 6, 9, 10, 14, 16, 18, and 30 in Table 1), whereas 11 of them imply completion or enlargement of structures already present in juveniles (characters 3, 7, 12, 19, 20, 21, 23, 24, 27, 28, and 31). Three changes indicated the relative decrease in size of some structures with age (characters 1, 25, and 26). Finally, 10 more or less complex reorganizations occurred (characters 2, 4, 5, 8, 11, 13, 15, 17, 22, and 29).

Similar to previous results in morphological analyses of marsupial ontogeny, several modifications observed in the skull of *C. philander* were related to trophic function, including changes related to the development of masticatory muscles and safety of the temporomandibular joint at occlusion. For instance, the paracanine fossa is present but not well developed in juveniles, and it enlarges considerably toward adulthood (character 3 in Table 1; Fig. 2). Linked with this change is the placement of the suture between the premaxilla and maxilla. In juveniles this suture is located at the anterior margin of the paracanine fossa, close to the last upper incisor. In adults the suture has migrated to a position in the middle of the paracanine fossa (character 4 in Table 1; Fig. 2). The upper dental series showed a diastema between the first and second premolars that is present in all the ontogenetic stages (Fig. 2). By contrast, the first and second lower premolars are in contact in juveniles and separated by a large diastema in adults (character 30).

Important morphological changes correlated with the development of the temporalis muscle include the widening of the temporal fossae (character 12; Figs. 3 and 4), change in orientation of the zygomatic process of the squamosal from anterior to lateral (character 11; Fig. 3, arrow), and the strong development of the postorbital process (character 9; Fig. 3) and the sagittal and nuchal crests (character 18; Figs. 2 and 3). Of these structures, the nuchal crest experienced the most extreme transformation, perhaps because of its dual condition of origin and insertion of muscles of the mandible and the neck, respectively. Associated with this change is the widening of the dorsal margin of the coronoid process of the mandible (character 27; Fig. 5).

The development of the masseter muscle also was evident in several characters, specifically the masseteric line of the jugal (character 16; Fig. 2), site of origin of the superficial masseter and present only in adults, and the masseteric fossa of the mandible, represented as an incipient shelf in juveniles and a strong and well-developed structure in adults (character 28; Fig. 5). In correlation with the development of the cranial crests, the dorsal margin of the coronoid process is extended more craniocaudally in adults (character 27; Fig. 5). Finally, the angular process of the mandible becomes remarkably more

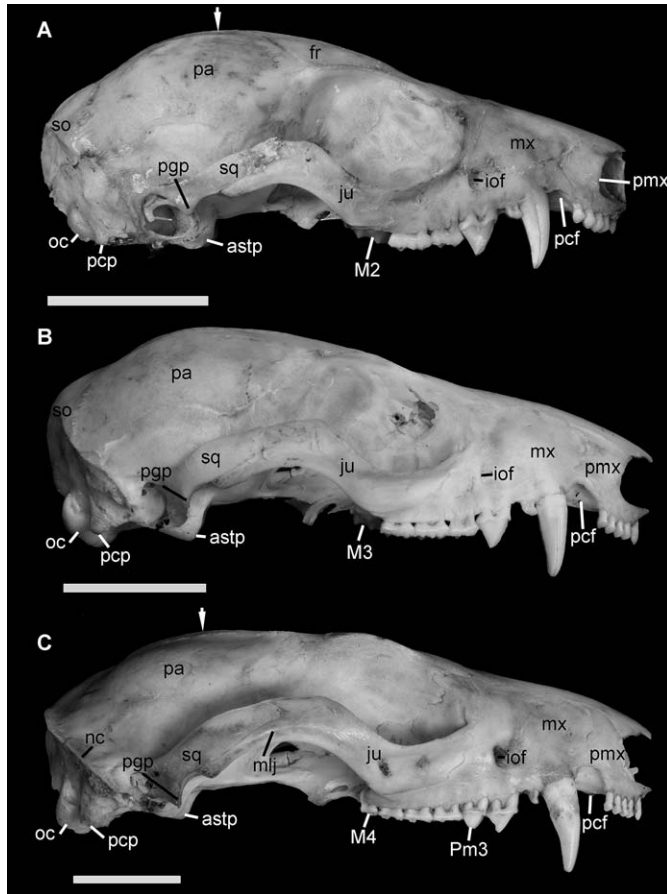


FIG. 2.—Lateral view of the skull of A) a juvenile, AMNH 96652; B) subadult, AMNH 203352; and C) adult, AMNH 95529 of *Caluromys philander*. Abbreviations: astp, alisphenoid tympanic process; fr, frontal; iof, infraorbital foramen; M2, second upper molar; M3, third upper molar; M4, fourth upper molar; mlj, masseteric line of jugal; mx, maxilla; nc, nuchal crest; oc, occipital condyle; pa, parietal; pcp, paracondylar process; pgp, postglenoid process; Pm3, third upper premolar; pmx, premaxilla; pcf, paracanine fossa; so, supraoccipital; sq, squamosal. Arrows in juvenile and adult indicate change on the dorsal profile of the braincase. Scale bars = 10 mm.

robust and mesially extended in adults, increasing the surface for the insertion of the superficial masseter and the internal insertion of the medial pterygoid muscle (character 24; Fig. 6).

Modifications related to adjustments of occlusion included the displacement of the upper alveolar line, which is leveled with the zygomatic root in juveniles and ventral to the root in adults (character 2; Fig. 2). Changes also occurred in the orientation of the upper postcanine row. In ventral view the rows are posteriorly divergent in juveniles and subparallel, with a slight labial convexity, in adults (character 5; Fig. 4). The adult condition in *C. philander* in this trait represents a remarkable difference from other marsupials sampled (Abdala et al. 2001; Flores et al. 2003, 2006; Giannini et al. 2004). Development of the bony palate involves the closure of the minor palatine foramen (character 7; Fig. 4), with its function

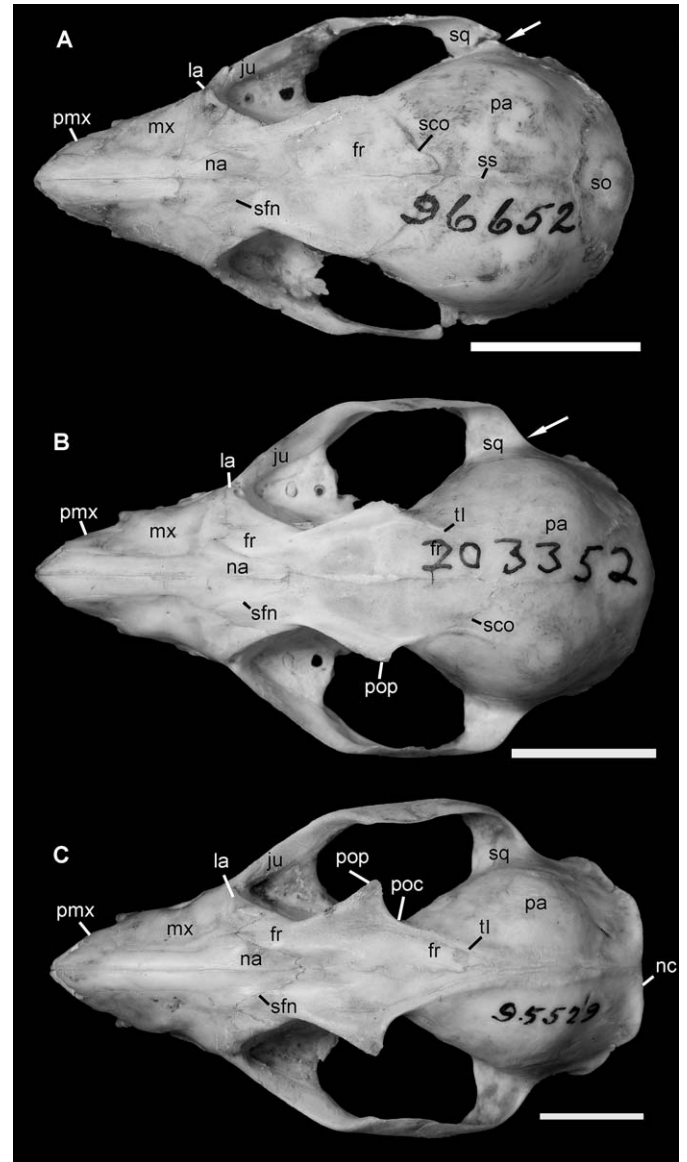


FIG. 3.—Dorsal view of the skull of A) a juvenile, AMNH 96652; B) subadult, AMNH 203352; and C) adult, AMNH 95529 of *Caluromys philander*. Abbreviations: fr, frontal; la, lacrimal; mx, maxilla; na, nasal; nc, nuchal crest; pa, parietal; pmx, premaxilla; poc, postorbital constriction; pop, postorbital process; sco, sutura coronalis; sfn, sutura frontonasalis; sq, squamosal; so, supraoccipital; ss, sutura sagittalis; tl, temporal line. Arrows in juvenile and subadult indicate change of flexure of the zygomatic process of the squamosal. Scale bars = 10 mm.

probably replaced by the opening of a small major palatine foramen (character 6; Fig. 4) and the increasing curvature of the postpalatine torus (character 8; Fig. 4).

Also related to the trophic function is the development of the paracondylar process of the exoccipital, from which the posterior belly of the digastric muscle originates and whose action is depressing the jaw, thus opening the mouth. The knob present in juveniles was transformed in adults into a strong process extended ventral to the level of the basioccipital (character 20; Fig. 2).

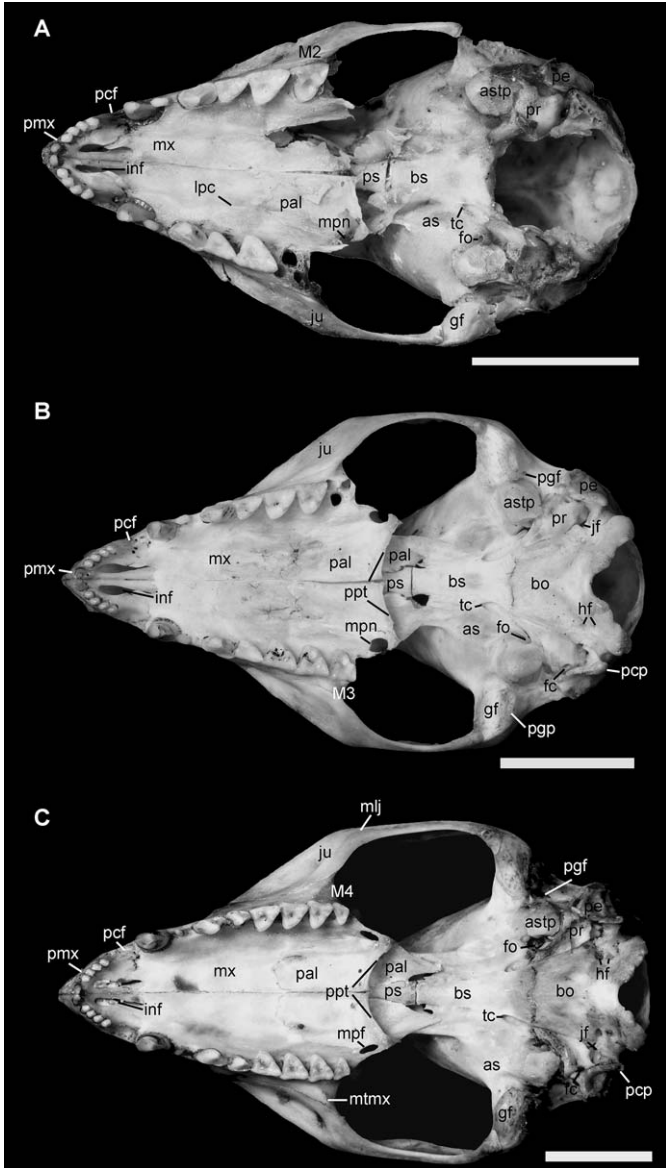


FIG. 4.—Ventral view of the skull of A) a juvenile, AMNH 96652; B) subadult, AMNH 203352; and C) adult, AMNH 95529 of *Caluromys philander*. Abbreviations: as, alisphenoid; astp, alisphenoid tympanic process; bo, basioccipital; bs, basisphenoid; fc, fenestra cochleae; fo, foramen ovale; gf, glenoid fossa; hf, hypoglossal foramen; inf, incisive foramen; jf, jugular foramen; ju, jugal; lpc, lateral palatine crest; M2, second upper molar; M3, third upper molar; M4, fourth upper molar; mlj, masseteric line of jugal; mpf, minor palatine foramen; mpn, minor palatine notch; mtmx, masseteric tuberosity of maxilla; mx, maxilla; pal, palatine; pcf, paracanine fossa; pcp, paracondylar process; pe, periotic; pgp, postglenoid process; pmx, premaxilla; ppt, postpalatine torus; pr, promontorium; sq, squamosal; tc, transverse canal. Scale bars = 10 mm.

Some ontogenetic changes reshape the temporomandibular joint and the mandibular body resistance. These include the lateral expansion of the articular condyle of the dentary (character 31; Fig. 6) and the concomitant change of the glenoid fossa of the squamosal, with an increased contribution of the jugal (character 23; Fig. 4) and the enlargement of the

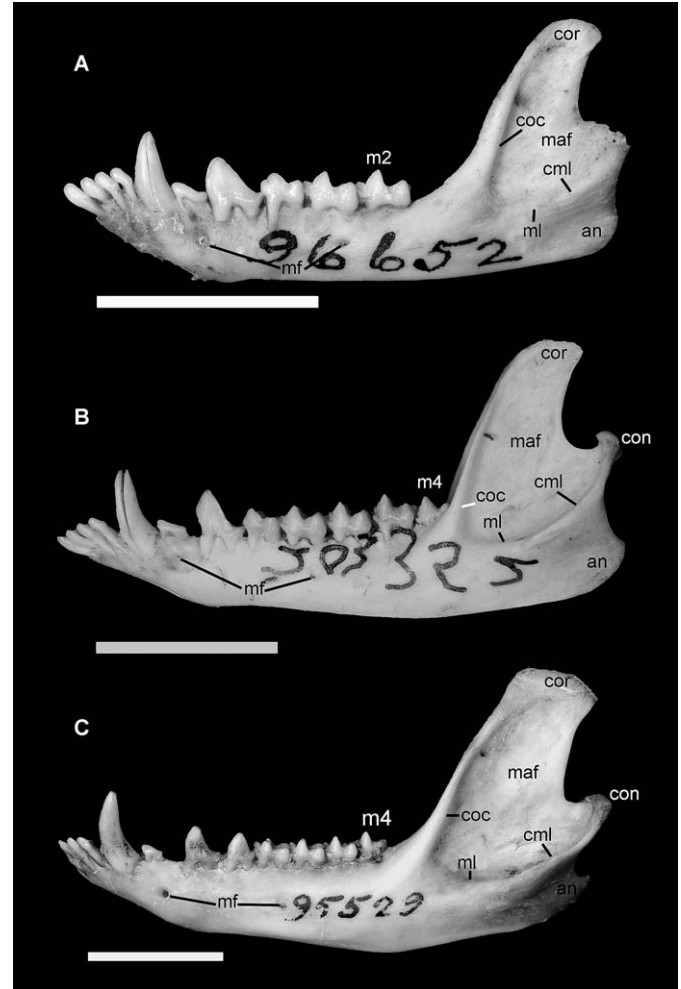


FIG. 5.—Lateral view of the lower jaw of A) a juvenile, AMNH 96652; B) subadult, AMNH 203352; and C) adult, AMNH 95529 of *Caluromys philander*. Abbreviations: an, angular process; cml, crest of masseteric line; con, condylar process; cor, coronoid process; m2, second lower molar; m4, fourth lower molar; maf, masseteric fossa; mf, mental foramen; ml, posterior shelf of masseteric line. Scale bars = 10 mm.



FIG. 6.—Occlusal view of the lower jaw of A) a juvenile, AMNH 96652, and B) adult, AMNH 95529 of *Caluromys philander*. Abbreviations: an, angular process; con, condylar process; m2, second lower molar; m4, fourth lower molar. Scale bars = 10 mm.

TABLE 2.—Summary of bivariate regressions using the length of palate as proxy of size (independent variable, see text) in *Caluromys philander*. Abbreviations: r^2 , adjusted coefficient of correlation; b , coefficient of allometry under least squares (LS) or reduced major axis (RMA); t_{iso} , 2-tailed Student’s t -value under null hypothesis of isometry (expected coefficient of allometry under isometry = 1; $df.$ = 43); P_{iso} , P -value for t_{iso} . Symbols indicate isometry (=), positive allometry (+), and negative allometry (–). When in parentheses, the symbol indicates a marginally nonsignificant allometric trend ($0.01 < P < 0.04$). Other abbreviations (variable acronyms) as in Fig. 1.

Variable	Range (mm)	r^2	LS			RMA			Allometric trends	
			b_{LS}	t_{iso}	P_{iso}	b_{RMA}	t_{iso}	P_{iso}	LS	RMA
UP	10.9–18	0.97	0.93	–1.42	0.16	0.98	–0.26	0.79	=	=
BP	9.1–17.6	0.94	0.78	–3.37	0.001	0.89	–0.26	0.10	–	=
BB	14.5–20.3	0.96	0.50	–16.00	<0.001	0.54	–14.69	<0.001	–	–
BZ	18.9–35.9	0.98	1.01	0.32	0.75	1.05	1.2	0.24	=	=
LN	13.3–25.3	0.98	1.14	2.72	0.009	1.18	3.66	<0.001	(+)	+
HO	8.9–13.9	0.95	0.6	–9.42	<0.001	0.66	–7.98	<0.001	–	–
LO	9.3–15.9	0.95	0.96	–0.69	0.49	1.05	0.71	0.48	=	=
HM	6–11.3	0.91	0.97	–0.26	0.80	1.18	1.75	0.086	=	=
HC	10.1–20.2	0.94	1.11	1.23	0.23	1.25	2.82	0.007	=	(+)
LP	11.2–19.8	0.97	0.94	–1.23	0.23	0.99	–0.23	0.82	=	=
HD	3.3–7.7	0.91	1.29	2.18	0.03	1.55	4.18	<0.001	=	+
LD	24.3–43.6	0.98	0.96	–0.87	0.39	1.00	0.05	0.96	=	=
LT	31.6–60.1	0.99	1.04	1.93	0.06	1.05	2.36	0.023	=	=

postglenoid process (character 21; Fig. 2). Also important is the strengthening of the mandibular body (Fig. 5).

The cranium exhibited two remarkable differences between juveniles and adults: the development of a postorbital constriction absent in juveniles (character 10; Fig. 3) and the flattening of the skull roof by which the domed calvaria of juveniles is leveled with the interorbital surface in adults (character 13; Fig. 2, arrows). The latter trend could be linked to changes in the deflection of the rostrum with respect to the basicranium during ontogeny (Lieberman et al. 2008).

Bivariate allometry.—The fit of the cranial variables examined to the proxy of size, the length of palate, as evaluated by the r^2 coefficient in bivariate regression (Table 2), varied between 91% (height of mandibular body and height of muzzle) and 99% (total length of the skull). LS and RMA showed the same allometric trends in 10 of 13 variables. The 2 methods found isometric trends in 7 variables, positive allometry in length of nasals, and negative allometry in breadth of braincase and height of occipital plate (Table 2). RMA differed from LS in 3 variables (breadth of palate, height of coronoid process, and height of dentary; Table 2). These discrepancies are more apparent than real: given that RMA slopes are always equal to or higher than LS slopes by definition ($RMA = LS/r$, with $r \leq 1$), a negative trend in LS may become isometric under RMA (e.g., breadth of palate), and isometric slopes may become positive (e.g., height of coronoid process). Results using total length of the skull as proxy of size differed in 3 variables when using the least-squares method, and in only 1 (breadth of palate) under RMA (Table 3).

Multivariate allometry.—The first principal component includes 87.8% of the total variance. Observed multivariate coefficients of allometry varied widely across variables (Table 4). Two variables, length of palate and length of mandible, showed the least observed departure from isometry (–0.001). Therefore, we used the cranial variable, length of

palate, as the proxy of size in bivariate allometry (see above). Breadth of braincase exhibited the largest departure from isometry (–0.131). Average estimated bias (using absolute jackknife values) across coefficients calculated from trimmed and untrimmed values were both small (0.002 and 0.008, respectively). Extreme pseudovalues did affect jackknife estimates given that isometry could be rejected in only 4 skull variables using the untrimmed set, as compared with 6 variables if the trimmed set of pseudovalues was used. This strongly suggests that the breadth of *CIs* could have been affected seriously in some variables by those extreme values. Taking the results from the ($m = 1$) trimmed analysis, 3

TABLE 3.—Comparison of allometric trends using least-squares (LS) versus reduced major axis (RMA) regression methods for the length of palate (PAL) versus the total length of the skull (LT) as independent variable (proxy of body size) in *Caluromys philander*. Symbols indicate isometry (=), positive allometry (+), and negative allometry (–). When in parentheses, the symbol indicates a marginally nonsignificant allometric trend. Abbreviations for variables as in Fig. 1. N/A = nonapplicable.

Variable	LS		RMA	
	PAL	LT	PAL	LT
UP	=	–	=	=
BP	–	–	=	–
BB	–	–	–	–
BZ	=	=	=	=
LN	(+)	=	+	+
HO	–	–	–	–
LO	=	=	=	=
HM	=	=	=	=
LC	=	=	(+)	+
LP	=	–	=	=
HD	=	+	+	+
LD	=	–	=	=
PAL	N/A	–	N/A	–
LT	=	N/A	=	N/A

TABLE 4.—Results of the multivariate analysis of cranial allometry in *Caluromys philander*. The first three data columns show results using all specimens. The remainder of the columns show jackknife results calculated with untrimmed and ($m = 1$) trimmed sets of pseudovalues (see Materials and Methods). Allometry coefficient is the corresponding element of the first (unit) eigenvector per variable. The expected coefficient is the value under isometry (0.267, same for all variables). The observed coefficient is the value obtained with all specimens included ($n = 45$). The resampled coefficient is the first-order jackknife value. Bias is the difference between the resampled and observed coefficients. The jackknifed 99% confidence interval (CI) is provided; allometric variables are those whose CIs exclude the expected value under isometry (0.267). Symbols indicate isometry (=), positive allometry (+), and negative allometry (-). When in parentheses, the symbol indicates a marginally nonsignificant allometric trend. Abbreviations (variable acronyms) as in Fig. 1.

Variables	Expected allometry coefficient	Observed allometry coefficient	Observed departure	Untrimmed values				Trimmed values			
				Resampled allometry coefficient	Bias	99% CI	Growth trend	Resampled allometry coefficient	Bias	99% CI	Growth trend
LT	0.267	0.2808	0.013	0.280	-0.0005	0.258-0.303	=	0.288	0.007	0.276-0.300	+
PAL	0.267	0.2668	-0.001	0.266	-0.0010	0.246-0.285	=	0.268	0.001	0.254-0.282	=
UP	0.267	0.2497	-0.017	0.251	0.0009	0.206-0.295	=	0.249	-0.001	0.222-0.276	=
BP	0.267	0.2217	-0.044	0.224	0.0018	0.152-0.295	=	0.232	0.010	0.196-0.267	-
BB	0.267	0.1366	-0.131	0.136	-0.0005	0.107-0.165	-	0.133	-0.003	0.117-0.150	-
BZ	0.267	0.2830	0.014	0.281	-0.0016	0.251-0.312	=	0.271	-0.012	0.252-0.290	=
LN	0.267	0.3034	0.036	0.303	-0.0005	0.250-0.356	=	0.292	-0.011	0.266-0.318	(=)
HO	0.267	0.1596	-0.107	0.160	0.0008	0.111-0.210	-	0.167	0.008	0.138-0.197	-
LO	0.267	0.2409	-0.023	0.244	0.0033	0.175-0.313	=	0.266	0.025	0.224-0.307	=
HM	0.267	0.2838	0.017	0.284	0.0002	0.222-0.346	=	0.275	-0.009	0.237-0.313	=
LC	0.267	0.3252	0.055	0.322	-0.0033	0.268-0.375	(+)	0.317	-0.008	0.276-0.359	+
LP	0.267	0.2602	-0.009	0.258	-0.0024	0.221-0.295	=	0.255	-0.005	0.227-0.284	=
HD	0.267	0.3957	0.122	0.390	-0.0061	0.293-0.486	+	0.377	-0.019	0.304-0.450	+
LD	0.267	0.2657	0.001	0.268	0.0023	0.223-0.313	=	0.263	-0.003	0.230-0.297	=

variables (breadth of the palate, breadth of braincase, and height of the occipital plate) were negatively allometric, whereas 3 variables (total length of the skull, length of coronoid process, and height of mandibular body) were positively allometric. Notably, the set of allometric variables in the trimmed analysis also includes the total length of the skull, although this variable includes the expected value under isometry in the 99% CI of the untrimmed set (Table 4). A brief comparison of bivariate and multivariate allometry (Table 5) indicated that the latter shared all but 1 trend (breadth of palate) with RMA and all but 2 trends (height/length of coronoid and height of dentary) with LS.

DISCUSSION

Skull modeling in Caluromys philander.—As a basis for comparison with other marsupials we collated the various results from allometric analyzes to interpret the modeling of the skull in *C. philander*. The braincase is relatively smaller toward adulthood, as indicated by the strong negative trend in breadth of the braincase and height of the occipital plate. By contrast, another neurocranial component—the orbit—increases its length isometrically, thus keeping the relative size of the eye socket almost constant in the anteroposterior dimension. The palate becomes slender as a consequence of the isometry of its length and the negative allometry of its width. The upper and lower tooth rows are isometric, despite tooth emergence in the upper postcanine row being delayed with respect to the lower row—during ontogeny, tooth count in the lower row exceeds in 1 element the upper row (Astúa de Moraes and Leiner 2008). Taken together, the positive allometry of the

nasal length and the isometry of the height of the muzzle show that the rostrum elongates while keeping its height proportionally constant. In relative terms the temporal space expands inward given the braincase negative allometry and the zygomatic breadth isometry. The mandible changes essentially by increasing its robustness because the thickness (height) of mandibular body and the length of the coronoid process showed a positive trend, whereas the length of the mandibular body and the lower postcanine row were isometric. The strong positive allometry of measurements of the mandible is correlated with the change of diet after weaning to reach an active mastication in adults, producing critical adjustment in the mandibular structures committed with the occlusion and its mechanic demands. For instance, the lateromesial development of the mandibular condyle and the positive allometry of the height of the mandibular body confer great strength and resistance to the mandible during the postweaning period, permitting an active mastication of solid food (Figs. 4 and 6). Although the sagittal crest does not develop to a great extent in adults, the nuchal crest does develop to a remarkable degree (Figs. 3 and 4), suggesting the importance of the posterior fibers of the temporalis muscle acting as part of a lever that transmits the strongest force component to the canines (Flores et al. 2003, 2006). This crest also might reflect the presence of powerful neck muscles (Radinsky 1981).

Comparative cranial ontogeny and allometry.—As in large-sized marsupials previously studied (*Didelphis*, *Lutreolina*, *Dasyurus*), most of the ontogenetic changes observed in *C. philander* are indicative of a general strengthening of the masticatory apparatus and cervical musculature. However, the pattern of development of some features in *C. philander* is

TABLE 5.—Comparison of results across methods used to estimate cranial allometry in *Caluromys philander*. Symbols indicate isometry (=), positive allometry (+), and negative allometry (−). When in parentheses, the symbol indicates a marginally nonsignificant allometric trend. Abbreviations: LS, least-squares method; RMA, reduced major axis method. Other abbreviations (variable acronyms) as in Fig. 1. Multivariate trends are based on trimmed values under jackknife resampling.

Variable	LS	RMA	Multivariate
UP	=	=	=
BP	−	=	−
BB	−	−	−
BZ	=	=	=
LN	+	+	(=)
HO	−	−	−
LO	=	=	=
HM	=	=	=
LC	=	(+)	+
LP	=	=	=
HD	+	+	+
LD	=	=	=
LT	=	+	+

somewhat different from that of the marsupials previously studied. Here we interpret selected aspects of qualitative change and allometry in the comparative context of marsupials so far studied.

The early development of the paracanine fossa in *C. philander* (Fig. 2) contrasts with the condition observed in *Lutreolina* and *Didelphis*, in which the fossa is absent in juveniles of comparable developmental stage (Abdala et al. 2001; Flores et al. 2003). In the australidelphian *Dasyurus*, juveniles larger than those of *C. philander* (~39 mm—Flores et al. 2006) and in a similar stage of dental eruption do not show any evidence of a paracanine fossa, whereas it is clearly present in adults. The paracanine fossa is absent altogether in the small-sized *Dromiciops gliroides*. The early development of the paracanine fossa in *C. philander* (Fig. 2) is correlated with large canines already present in young. This is suggestive of an active use of canines early in the life of individuals, which perhaps incorporate adult food items into their diet earlier in life than other marsupials studied (adults of *C. philander* are omnivorous with some preference for fruit—Astúa de Moraes et al. 2003; Charles-Dominique et al. 1981; Julien-Laferriere 1999; Julien-Laferriere and Atramentowicz 1990; Leite et al. 1996). This is also correlated with changes in the temporomandibular joint that progressively limit the rostrocaudal displacement and the transverse rotational movement of the mandible, thereby reducing mandibular movements to the dorsoventral plane (Abdala et al. 2001).

The development of a P1-P2 diastema (Fig. 2) also has been reported in *Didelphis albiventris* (Abdala et al. 2001) and *L. crassicaudata*, in which the spacing appears comparatively larger (Flores et al. 2003). Two small interdental spaces appear in adults of *Dromiciops gliroides* in both the upper and lower tooth rows, i.e., a small diastema between c and p1 and p1 and p2, and also between C and P1 and P1 and P2 (Giannini et al. 2004). The pattern of dental spacing is different in

Dasyurus albopunctatus given that the interdental space is between p2 and m1 (p3 is absent in this species), and this diastema is present in all the ontogenetic stages observed (see Flores et al. 2006).

The changes in the orientation of the upper postcanine row, which becomes nearly parallel in adults (Fig. 4), and the strongly curved postpalatine torus (Fig. 4) reflect a complex remodeling during postweaning. Such changes were not detected in the ontogeny of any of the marsupial species studied to date, likely representing ontogenetic patterns unique to Caluromyinae, as inferred from palate morphology in other members of the subfamily (*Caluromysiops irrupta* and *Glironia venusta*; D. A. Flores, pers. obs.).

Results from allometric analyses of the skull development in the didelphids *Didelphis albiventris* (Abdala et al. 2001), *L. crassicaudata* (Flores et al. 2003), and *Caluromys philander* (this contribution), and the australidelphians *Dasyurus albopunctatus* (Flores et al. 2006) and *Dromiciops gliroides* (Giannini et al. 2004) allow for a basic comparison of allometric trends among representatives of different marsupial lineages (Table 6). Four variables show the same trends in the 5 marsupial species sampled: breadth of palate, breadth of braincase, height of occipital plate (negatively allometric), and the height of dentary (positively allometric). These 4 variables seem to conform to a basic growth plan shared at the level of marsupials (Flores et al. 2006). The negative allometry of the breadth of palate detected in all groups implies that the posterior palate is wide in juveniles. This condition is most likely related to its function as a platform for the tongue in the suckling opossum (German and Crompton 1996) and therefore can be extended to other species of marsupials. Pump suckling is an essential function during the early life of marsupials and determines many other structural traits in the skull of neonates (Clark and Smith 1993; Maier 1993). In turn, neurocranial components such as braincase dimensions are negatively allometric as in most mammals (Emerson and Bramble 1993). Sensory capsules are in general expected to scale negatively (Emerson and Bramble 1993). In almost all vertebrates accelerated differentiation of the central nervous system and sensory capsules produces embryos and neonates with large braincases, eyes, and auditory regions relative to trophic components of the skull (Emerson and Bramble 1993). However, in marsupials virtually all neurogenesis occurs after birth and during lactation (Smith 1997). In our studies inspecting marsupial ontogeny after weaning, and in all the species sampled, the rate of growth of neurocranial components such as breadth of braincase and height of occipital plate shows pronounced negative allometry.

Some allometric trends are specific to 1 of the marsupial representatives sampled, but most trends are common to 2 or more taxa. *Caluromys* shares specific growth trends with *Didelphis* or *Lutreolina*, but no allometric trend is shared by the 3 didelphids to the exclusion of australidelphians (Table 6). Likewise, *C. philander* shares no allometric trend with the 2 australidelphians to the exclusion of didelphids (Table 6).

Three variables exhibit the most remarkable differences between *C. philander* and the other didelphids (Table 6). First, the development of the orbit is isometric in *Caluromys*, as is in *Dromiciops* and *Dasyurus*, and negatively allometric in the other 2 didelphids (Table 6). Second, the lengths of the upper and lower postcanine rows are isometric in *C. philander* and negatively allometric in the other didelphids (Table 6). In adult *D. albiventris* and *L. crassicaudata*, the lengths of both postcanine series are nearly the same, but during ontogeny the emergence of the lower postcanines is usually advanced in 1 element with respect to the upper postcanines (Astúa de Moraes and Leiner 2008). This sequence of emergence leads to allometric differences between upper and lower rows, with the coefficient of the lower postcanine row being smaller than that of the upper row. However, the upper and lower rows exhibit similar allometric coefficients in *C. philander* (isometric in all of methods applied), but the lengths of the lower and upper tooth rows are equally involved in the mutual adjustment of the postcanine rows during growth.

The space for temporal musculature in adults is provided by the interaction between the pattern of growth of the braincase and zygomatic arches. In didelphids the breadth of zygoma is isometric, whereas the breadth of the braincase is negatively allometric (Table 6). Therefore, the space for the temporalis muscle increases principally inward in relative terms (Abdala et al. 2001). In *Dasyurus* the space for the temporalis also increases by lateral expansion (i.e., the positively allometric zygomatic breadth; Table 6), as observed in large felids as *Puma concolor* (Giannini et al. 2009). This extra space for masticatory musculature is likely associated with carnivorous habits (Flores et al. 2006).

The comparison of quantitative cranial trends and the pattern of morphological changes in the ontogeny of *C. philander* and the other marsupial taxa considered herein indicates a series of common developmental trends and some trends restricted to specific groups. Just as in other mid- and large-sized marsupials, most of the ontogenetic changes in *C. philander* indicate strengthening of the masticatory system and cervical musculature. However, several morphological characters observed that appear in late ontogenetic stages in the other marsupials were already present in young specimens of *C. philander*, indicating precocial development of such traits independent of the final adult size. In addition, specific changes occur in the palate of *C. philander*, such as the shift of orientation between the upper postcanine rows and the development of a strongly curved postpalatine torus, which are not known in any marsupial studied to date. *Caluromys* shares ontogenetic trends with both didelphids and australidelphians. The cranial growth patterns obtained from multivariate analysis in *C. philander* show some unexpected trends, such as the isometry of the orbit and of the upper postcanine row, which are trends partially shared only with some studied australidelphian marsupials. The exploration of the allometric trends in a representative of the caluromyine clade to the previously studied taxa reveals that no less than 4 ontogenetic trends could be interpreted as plesiomorphic relative to the

TABLE 6.—Comparison of allometric trends in *Caluromys philander* (this study), the didelphids *Didelphis albiventris* (Abdala et al. 2001) and *Lutreolina crassicaudata* (Flores et al. 2003), and the australidelphians *Dromiciops gliroides* (Giannini et al. 2004) and *Dasyurus albopunctatus* (Flores et al. 2006). Symbols indicate isometry (=), positive allometry (+), and negative allometry (−). When in parentheses, the symbol indicates a marginally nonsignificant allometric trend. The trends for *Caluromys* are a composite of results from LS, RMA, and multivariate methods. In the cases of *Didelphis albiventris* and *L. crassicaudata* bivariate methods were used with skull length as the independent variable; therefore, allometric trend of skull length is unknown (marked ?). The number of allometric cranial variables in each species is listed in the last row. *n* is sample size for each species. Other abbreviations (species acronyms) as in Fig. 1.

Variable	<i>Caluromys philander</i>	<i>Lutreolina crassicaudata</i>	<i>Didelphis albiventris</i>	<i>Dromiciops gliroides</i>	<i>Dasyurus albopunctatus</i>
UP	=	−	−	(=)	−
BP	(−)	−	−	−	−
BB	−	−	−	−	−
BZ	=	=	=	=	(+)
LN	(+)	(−)	+	+	=
HO	−	(−)	−	−	−
LO	=	−	−	=	−
HM	=	−	(−)	(=)	=
LC	(+)	=	+	(=)	+
LP	=	(−)	−	−	−
HD	+	+	+	(+)	+
LD	=	=	+	(=)	=
PAL	=	=	=	=	−
LT	(+)	?	?	+	−
<i>n</i>	45	32–43	52–61	43–51 (37)	31
Allometric trends	7	7	11	7	11

marsupial clade, likely representing part of the basic developmental plan of Metatheria. Future interpretations of the postweaning ontogenetic changes in additional neotropical marsupials phylogenetically distinct, such as *Metachirus*, *Monodelphis*, and some mouse opossums, could reveal patterns of growth in a phylogenetic context. Finally, the comparison of the specific patterns detected in neotropical marsupials with those of additional Australasian clades with different life history (e.g., Diprotodontia) is essential to increasing our understanding of the evolution of cranial postweaning ontogeny in the group.

RESUMEN

La ontogenia craneana ha sido estudiada desde una perspectiva alométrica cuantitativa en marsupiales didélfidos, microbiotéridos y dasyúridos. En continuación con trabajos previos, describimos y comparamos el desarrollo craneal postdestete en la comadreja lanosa *Caluromys philander*. Identificamos 31 cambios morfológicos cualitativos entre juveniles y adultos, la mayoría relacionados con el aparato trófico. El temprano desarrollo de la fosa paracarina, relacionado con la presencia de caninos bien desarrollados

en juveniles, es una marcada diferencia en la ontogenia de *C. philander* en relación a otros marsupiales estudiados. Realizamos un análisis de alometría bivariado y multivariado sobre una matriz compuesta por 14 medidas craneales en 45 especímenes. El escalamiento alométrico mostró que la caja cerebral es relativamente pequeña en adultos, mientras que otros componentes neurocraneales, particularmente la órbita, crecieron isométricamente. El paladar se torna elongado por la combinación de la isometría de su largo y la alometría negativa de su ancho. El rostro se alarga mientras su altura permanece proporcionalmente constante. En términos relativos, la fosa temporal se expande interiormente siguiendo el modelo marsupial, que combina la alometría negativa de la caja cerebral y la isometría del ancho cigomático. La mandíbula se hace más robusta. La ontogenia craneana de *C. philander* comparte cuatro tendencias alométricas con dos didélfidos (*Didelphis albiventris* y *Lutreolina crassicaudata*) y dos australidelfos (*Dromiciops gliroides* y *Dasyurus albopunctatus*) previamente estudiados. Tres de estas tendencias, ancho del paladar, ancho de la caja craneana y altura de la placa occipital fueron alométricamente negativas, mientras que la altura del dentario fue positiva. Estas tendencias alométricas comunes pueden ser interpretadas como simpleiomórficas en marsupiales, sugiriendo un alto grado de conservación del desarrollo craneal de *Caluromys* y otros marsupiales.

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