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Comparative Postnatal Ontogeny of the Skull in *Dromiciops gliroides* (Marsupialia: Microbiotheriidae)

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ABSTRACT

Dromiciops gliroides is the single extant representative of the marsupial family Microbiotheriidae. The importance of *D. gliroides* stems from its peculiar cranial anatomy (specifically the configuration of the tympanic region) and dentition and from its controversial position in the phylogenetic tree of marsupials—a South American form more closely related to Australasian marsupials. We studied the postnatal ontogeny of the skull in *D. gliroides* by analyzing qualitative and allometric aspects of the development of cranial structures. We compared recently weaned young individuals with adults and described the bivariate and multivariate allometric trends of 14 cranial dimensions for a sample of 37–51 specimens. Most cranial components develop in a way similar to didelphids studied so far. However, some trends (e.g., growth of the orbit) seem particular to *D. gliroides*. The microbiotheriid bulla of *D. gliroides*, a structure to which five basicranial bones contribute parts, is already present in its highly derived condition in the youngest specimens of our series. We conclude that except for the bulla, most of the cranial development in *D. gliroides* is highly conservative and that some peculiarities may be shared with other marsupials of similarly small body size. Data on australidelphians and small-size didelphids are needed to contrast these patterns.

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INTRODUCTION

The marsupial *Dromiciops gliroides*, a small South American endemic, is the single survivor of the Microbiotheriidae, cohort Microbiotheriomorpha Ameghino, 1887. The other 5 (Marshall, 1982) to 13 (HersHKovitz, 1999) forms of microbiotheres are fossils from the Tertiary of Patagonia, Argentina (Marshall, 1982), and Seymour Island, Antarctica (Goin et al., 1999). *Dromiciops gliroides* occurs in Chiloé Island, continental Southern Chile, and adjacent parts of Argentina (Marshall, 1978). Reig (1955) first recognized the affinities of *D. gliroides* with microbiotheres, primarily on the basis of the structure of the tympanic bullae and molar shape. Microbiotheres were considered by Reig et al. (1987) and HersHKovitz (1992, 1999), among others, to be closely related to didelphoids—members of the family Didelphidae and allies. By contrast, Szalay (1982), who examined ankle-joint morphology, proposed the inclusion of *D. gliroides* in the cohort Australidelphia—a monophyletic group including all Australasian marsupials. In most recent studies, *D. gliroides* consistently appears more closely related to australidelphians than to didelphoids (e.g., Rougier et al., 1998; cf. Colgan, 1999). However, there is disagreement with regard to the exact placement of this form. *D. gliroides* is either the sister taxon of all australidelphians (Retief et al., 1995 [part]; Palma and Spotorno, 1999 [part]; Amrine-Madsen et al., 2003), or it is nested within australidelphians, usually as sister to Diprotodontia (Kirsch et al., 1991; Retief et al., 1995 [part]; Palma and Spotorno, 1999 [part]; Jansa and Voss, 2000; Horovitz and Sánchez-Villagra, 2003).

Most studies on *Dromiciops gliroides* have emphasized the anatomical differences of this form with other South American marsupials. In a detailed study of the middle ear, Segall (1969) found support for Reig's (1955) contention that the bulla of *D. gliroides* is microbiotheriid-like. Marshall (1982), in his systematic revision of microbiotheres, included a diagnosis of *D. gliroides* with a brief account of anatomical features of the skull and dentition, and he reported morphological differences between *D. gliroides* and *Microbiotherum*. HersHKovitz (1992, 1999)

carried out two anatomical revisions discussing the phylogenetic position of *D. gliroides* (although not on the basis of a numerical character analysis), reporting putative autapomorphies and symplesiomorphies in osteology, dentition, soft anatomy, and serology.

In spite of this body of anatomical work, little is known about the ontogeny of *D. gliroides*. However important in itself, the phylogenetic and biogeographic relevance of *D. gliroides* makes the understanding of development in this species particularly significant. In this work, we report postnatal ontogenetic data on skull morphology, a part that provides some of the most distinctive anatomical features of *D. gliroides* (Reig, 1955; Segall, 1969; Marshall, 1982; HersHKovitz, 1999). To our knowledge, this also represents the first study of an australidelphian for which data on skull ontogeny are approximately comparable to those available on didelphids (cf. Moeller, 1973). Qualitative and allometric analyses of growth allowed us to explore how distinctive the skull development of *D. gliroides* is in a context of comparative ontogeny. On the basis of our previous work on large-sized didelphids (Abdala et al., 2001; Flores et al., 2003), we show that the overall pattern of skull growth in *D. gliroides* is highly conservative. In turn, we contend that a minority of the observed developmental trends may be uniquely derived, but this remains to be contrasted with yet unknown ontogenetic patterns of small-sized didelphids and australidelphians.

MATERIALS AND METHODS

STUDY SPECIMENS

We analyzed a sample of 51 specimens of *Dromiciops gliroides* from Chile and Argentina housed at the following U.S. and Argentinian collections: American Museum of Natural History, New York (AMNH); Centro Regional Universitario Bariloche, Bariloche (CRUB); Colección Mamíferos Lillo, Tucumán (CML); Field Museum of Natural History, Chicago (FMNH); Instituto Argentino de Investigaciones en Zonas Áridas, Mendoza (IADIZA); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN); and National Museum of Natural History, Smithsonian Institution,

Washington, D.C. (USNM). The specimens examined were AMNH 92147; CML 1869, 6217–8; CRUB 11, 12; FMNH 22671, 22673, 22675, 50073–5, 127436–8, 127440, 127443–8, 127450, 127451, 127453–5, 127457–65, 129803, 129804, 129806–8, 134556, 134624; IADIZA 2526; MACN 48.26, 13308, 19142–5; and USNM 391772.

Seventeen specimens in our sample do not have a fully adult dentition, whereas the remaining individuals were adults of varying sizes. The young specimens were in an age stage in which, according to Mann-Fischer (1978) and Muñoz-Pedreros and Palma (2000), they could move outside the mother's pouch. The smallest individual (CML 6217; total length of skull 20.1 mm) has I5 and M2 in the process of eruption, with the latter having the protocone not yet totally emerged. The difference in size between CML 6217 and the largest specimen (AMNH 91147; total length of skull 29.8 mm) implies that the smallest specimen had achieved only approximately two-thirds of its maximum adult size, suggesting that the size range of our sample is appropriate for an analysis of postweaning growth.

QUALITATIVE DESCRIPTIONS AND ALLOMETRY

In this study, we took two descriptive approaches. First, we contrasted developing features in the skull of smallest (youngest) specimens with those of the largest (oldest) on a qualitative basis. Anatomical terminology follows primarily Wible (2003) and also Sánchez-Villagra and Wible (2002). Second, we used a series of quantitative linear measurements (fig. 1) to estimate allometric growth of skull components. We took two approaches to study allometry: bivariate and multivariate. For the bivariate treatment, we used total length of the skull as a measure of overall size (Abdala et al., 2001; Emerson and Bramble, 1993). In order to estimate the change of each of the other cranial variable with respect to overall size, we used the log transformation of the power growth equation $y = b_0x^{b_1}e$, where y is the focus variable, b_0 is the y -intercept, x is the total length of the skull, b_1 is the slope of the line or coefficient of allometry, and e is the error term. We assessed deviations from isometry by testing

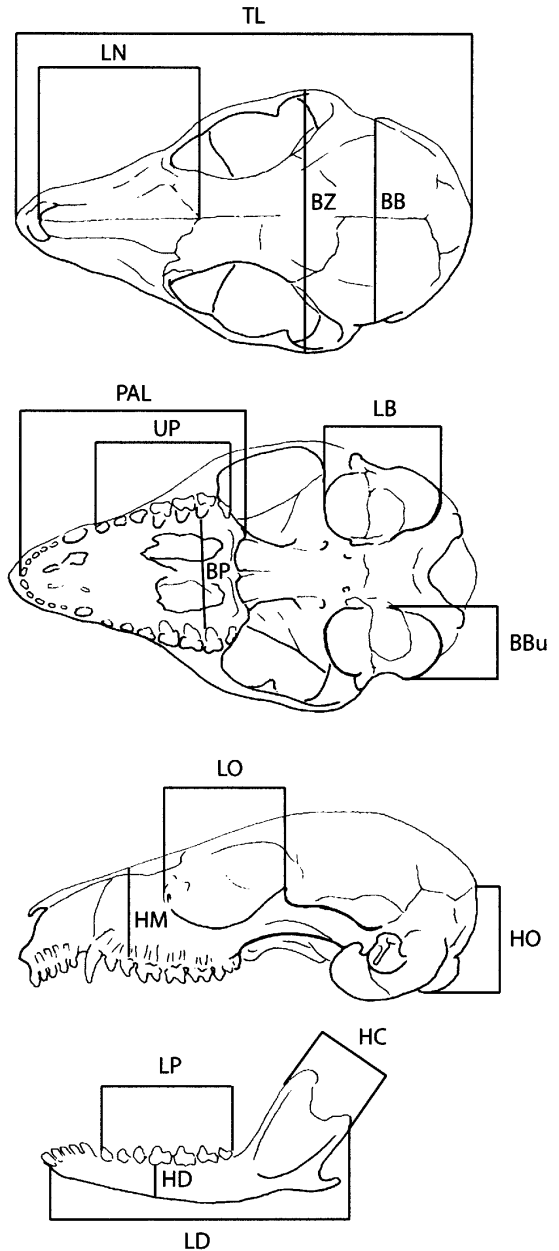


Fig. 1. Cranial measurements of *Dromiciops gliroides* used in this study. Abbreviations: BB, breadth of braincase; BBU, breadth of bulla; BP, breadth of palate; BZ, maximum breadth of the skull, or zygomatic breadth; HC, height of coronoid process; HD, height of mandible; HM, height of muzzle; HO, height of occipital plate; LB, length of bulla; LD, length of mandible; LN, length of nasals; LO, length of orbit; LP, length of lower postcanine row; PAL, length of palate; TL, total length of the skull; UP, length of upper postcanine row.

the significance of the allometry coefficients (two-tailed t -tests) under the null hypothesis $b_1 = 1.0$ fixing type I error rate at $\alpha = 0.01$ (for decreasing the chance of multiple comparisons errors). Additionally, we considered marginally significant those coefficients that yielded $0.05 > P > 0.01$. Isometry is the condition in which an allometry coefficient is statistically indistinct from unity. Statistically significant deviations from unity represent cases of “negative” allometry if $b_1 < 1.0$ and “positive” allometry if $b_1 > 1.0$. Following Abdala et al. (2001), we used two ways to calculate b_1 . Under the first approach—least-squares regression (hereafter LS)—an independent variable x , chosen to represent overall size, is assumed to be measured without error, therefore transferring the full error component to the response variable y . Under the second approach—reduced major axis regression (hereafter RMA)—the two variables involved in a bivariate relationship, now y_1 and y_2 , are interchangeable. That is, the dependence relationship on size is not explicit; residuals are oblique components representing variation in both y_1 and y_2 . LS and RMA coefficients are arithmetically related through the correlation coefficient r (Niklas, 1994). Due to this relationship, differences between LS and RMA are mere scale shifts along the variation of b_1 whose magnitude depends on the amount of variation explained by size (i.e., on the size of the r value). As a consequence, we interpret bivariate allometry depending on the strength of the relationship found in both methods.

Our multivariate approach to allometry is based on the generalization of the allometry equation proposed by Jolicoeur (1963a, 1963b; see applications in Voss et al., 1990; Voss and Marcus, 1992). In bivariate allometry, one variable is set apart representing size, and allometry of all other variables is estimated one by one with respect to that chosen variable. By contrast, in multivariate allometry, size is regarded as a latent variable affecting all original variables simultaneously. The various allometric relationships of all variables with the latent size can be expressed in the first eigenvector of a principal components analysis, with this vector extracted from a variance-covariance matrix of log-transformed variables and scaled to

unity (i.e., with all elements scaled so that the sum of squared elements equals 1; Jolicoeur, 1963a). Allometry is, in this approach, a deviation with respect to a hypothetical isometric eigenvector that represents pure size change. Under isometry, all variables respond the same way to growth; the elements of the isometric unit eigenvector are equal to an expected value calculated as $1/p^{0.5}$ with p equal to the number of variables. The value of an element of the sample eigenvector represents the observed multivariate coefficient of allometry of the corresponding variable. We were specifically interested in the deviations from multivariate isometry of each of the skull variables used in our bivariate analyses (bullar dimensions excluded). For that purpose, the first unit eigenvector was extracted from a variance-covariance matrix calculated on values of the 14 variables (including total length of the skull) transformed to the natural logarithms. Because principal components analysis requires a complete design (i.e., no missing data), we performed our analysis with the subset of 37 specimens having measurements for all 14 skull variables.

The elements of the hypothetical isometric vector are equal to 0.267 since $p = 14$. Comparison of each of the empirical elements of the first-unit eigenvector with the isometric eigenvector allows to detect negative (<0.267) and positive (>0.267) departures from isometry in each original variable. However, multivariate coefficients of allometry are single values that come from a one-sample estimation. As such, deviations from isometry can only be assumed. The number of *D. gliroides* specimens is too limited to draw adequate subsamples and calculate standard confidence intervals for multivariate coefficients, which would allow for an isometry test. Instead, we adopted a resampling strategy based on the jackknife (Tukey, 1958). This technique transforms any problem of estimation into the estimation of a sample mean (Manly, 1997). As applied to our study, a set of pseudovalues (surrogates of the true coefficients of interest) are calculated by successively removing one specimen at a time from the sample (first-order jackknife) and calculating the subsample unit eigenvector as established above. Specific-

ly, one pseudo-value \hat{e}_{-j}^* , corresponding to the removal of specimen j from the sample of size n , is calculated as

$$\hat{e}_{-j}^* = n \hat{e} - (n - 1) \hat{e}_{-j},$$

where \hat{e} is the observed element of the unit eigenvector that corresponds to the multivariate coefficient of allometry of the skull variable x , and \hat{e}_{-j} is the value of the coefficient obtained with specimen j removed (terminology follows Manly, 1997). Then, the set of 1 to n pseudo-values ($n = 37$, the number of specimens in our sample) is used for two purposes. First, for a given variable, the mean of the corresponding pseudo-values represents the jackknife estimate of the multivariate allometry coefficient of that variable, and the difference between that mean and the observed coefficient of allometry is an estimate of the sampling bias that may be present in the one-sample coefficient derived from the analysis including all specimens (Quenouille, 1956; Manly, 1997). Second, the set of pseudo-values can be used to calculate a standard deviation, and then a confidence interval, for each coefficient of allometry. We considered as a departure from isometry the case when the 99% confidence interval for a coefficient did not include the expected value under isometry (0.267).

Further considerations are necessary. When standard deviations are calculated by resampling, confidence intervals may be severely influenced by extreme values (Manly, 1997). This is particularly true when the total number of resampled values is not large, as in the first-order jackknife. Trimming the m largest and the m smallest values tends to ameliorate this problem (Manly, 1997: 44). The justification of this practice lies in the observation that, as in any sampling problem, if the m pseudo-values are not especially large or small in magnitude, trimming has a negligible effect on standard deviations and hence on the breadth of confidence intervals. But if the extreme pseudo-values are indeed unduly influential, trimming the m pseudo-values effectively prevents large standard deviations and exceedingly wide confidence intervals. Manly (1997) reported that taking out of the pseudosample even the minimal number of extreme pseudo-values yielded satisfactory results. We report 99% confidence

intervals for each multivariate coefficient of allometry based on all pseudo-values (untrimmed set) and in a set taking $m = 1$ pseudo-values out (trimmed set; table 2). In all analyses, we assume that there are no growth-independent shape differences among sexes and localities. In support of these assumptions are the facts that *D. gliroides* lacks sexual dimorphism (Hershkovitz, 1999) and that all but one specimen in our sample (FMNH 127465, from Chiloé) were collected in continental localities. That specimen may be influential only in the breadth of palate (see fig. 4A). For our analysis of multivariate allometry, we used the program NTSYS-pc 1.6 (Rohlf, 1990). The jackknife procedure was done partly manually and partly with the help of a NTSYS batch file.

Finally, we compared both our quantitative and qualitative results in *D. gliroides* with the developmental trends known from two didelphid marsupials, *Didelphis albiventris* (Abdala et al., 2001) and *Lutreolina crassicaudata* (Flores et al., 2003). Unfortunately, there are no published studies dealing with skull allometry in australidelphian marsupials in a similar way, so our comparisons must be restricted to didelphids. To our knowledge, only a single study of cranial allometry in australidelphians exists, specifically on dasyuromorphans (Moeller, 1973). However, in that study, the independent variable selected for the bivariate estimation of skull allometry was atypical—the length of the brain cavity—thus complicating comparisons with our results.

RESULTS AND DISCUSSION

QUALITATIVE TRENDS

OSSIFICATION: In the youngest specimen (CML 6217), part of the zygomatic arch, the lateral side of the braincase, the mastoid portion of the petrosal, the lacrimal, part of the alisphenoid, and the orbitosphenoid are poorly ossified. Most of these are neurocranial components, so our observations are in agreement with the model of delayed growth (both in timing of onset and in rate of ossification) proposed for marsupial neurocranial development by Clark and Smith (1993).

TEETH: Most of the teeth in our juvenile sample are contiguous. Only a small diaste-

ma appears between the last upper incisor (I5) and the canine (C). In adults, there are enlarged diastemata between I5 and C and among the upper and lower premolars (fig. 2). Therefore, the spacing among several teeth modestly increases with age in response to the continuing growth of the supporting bone.

SPLANCHNOCRANIUM: The mandible shows important modifications in the development of coronoid and angular processes (fig. 2, cf. D and H). In adults, the bone in the pars molaris of the mandible is thicker, the coronoid process is higher, and the angular process is longer than in younger individuals, both in relative and absolute terms (see also Allometry below). The caudal margin of the mandibular symphysis in the young specimens is at the level of the canine (fig. 2D); in the adult, that margin is slightly displaced caudally to the level of p1 (fig. 2H).

In young animals, the angular process of the mandible closely fits in the globular shape of the bulla. This mandible-otic connection was interpreted in functional terms by Maier (1987, 1990), who proposed that the pouch young might first hear sounds transmitted by the mandible. However, Sánchez-Villagra and Smith (1997) rejected this hypothesis on the basis of measurements of the auditory capacity of developing young, but they did not provide an alternative hypothesis. In *D. gliroides*, the developing mandible soon detaches from the ear region, so that in adults the contact between the bulla and the angular process is lost, causing the isolation of the bulla from the mechanics of the mandible. According to Sánchez-Villagra and Smith (1997), this developmental process is common to all known marsupials.

In adults, an excavated mandibular notch notably separates the articular condyle from the coronoid process. The condyle of adults is more laterally expanded than in juveniles (fig. 2, cf. D and H). The postglenoid process, weak in juveniles, is enlarged in adults (fig. 2, cf. C and G). Abdala et al. (2001) and Flores et al. (2003) observed these changes in two didelphids and proposed that the adjustment of the jaw articulation through the expansion of the condyle facilitates the safety of the mandibular movements during strenuous bites. A functionally related

change is the development of the masseteric line in adults, for insertion of the deep masseter muscle (based on *Didelphis marsupialis*; Turnbull, 1970).

NEUROCRANIUM: The foramen magnum is bordered by the basioccipital ventrally, the exoccipitals laterally, and the supraoccipital dorsally, in all observed growth stages (fig. 3). This condition is also present in all small-sized didelphids (*Gracilinanus*, *Marmosa*, *Marmosops*, *Micoureus*, *Thylamys*, *Monodelphis*, and *Lestodelphis*; Flores, 2003). In contrast, in large-sized didelphids (e.g., *Didelphis*, *Lutreolina*), there is an ontogenetic exclusion of the supraoccipital so that only exoccipitals contribute to the dorsal rim of the foramen magnum in adults (Abdala et al., 2001; Flores et al., 2003). Therefore, the condition in *D. gliroides* may be correlated with its small size. Alternatively, this may represent a plesiomorphy, given that in adults of the Paleocene metatherian *Pucadelphys andinus*, also a small form and sister to Marsupialia (Horovitz and Sánchez-Villagra, 2003; Rougier et al., 1998), the supraoccipital forms the dorsal margin of the foramen magnum (Marshall and De Muizon, 1995).

In adult *D. gliroides*, the sphenorbital fissure is virtually coalesced with the foramen rotundum; only a tiny bony wall deep inside the fissure, not apparent in lateral view, barely separates the two openings. Unfortunately, the condition in the youngest specimens cannot be assessed due to poor preservation of the bone in the pterygopalatine fossa. By contrast, in most adult didelphids, these openings are close together, but the bony wall that separates them is noticeable in lateral view (personal obs.). All basicranial foramina (the foramen ovale, carotid, jugular, and hypoglossal foramina, and the transverse canal) are already in place in the juvenile. *Dromiciops gliroides* lacks secondary foramen ovale; there is only a sulcus for the exit of the mandibular ramus of trigeminal nerve (V^3), located in the anterior part of the tympanic wing of alisphenoid. The sulcus is present in juveniles.

Dromiciops gliroides is unique among marsupials in having a sphenoid crest—a ventral, median ridge of the presphenoid and basisphenoid in the basipharyngeal duct (this structure, however, is widely distributed

among eutherians; Hershkovitz, 1992). The sphenoid crest is already present in juveniles, although less marked in comparison with the adult condition.

AUDITORY BULLA: The bulla of *D. gliroides* is illustrated in Hershkovitz (1999: fig. 7A)⁴ and in Sánchez-Villagra and Wible (2002: fig. 11). In adult *D. gliroides*, the bulla is a ventrally closed, globular structure formed by four components: the ectotympanic (lateral), the tympanic process of the alisphenoid (anterior), the caudal tympanic process of the petrosal (posterolateral), and the rostral tympanic process of the petrosal (mesial and ventral; Sánchez-Villagra and Wible, 2002). Additionally, two small processes, one from the basioccipital and another from the exoccipital, complete the sealing of the bulla at its contacts with the basicranium—sutures only interrupted by the jugular foramen. The young specimen features two main differences with the adult in relation to the bulla. First, the opening of the external acoustic meatus in the young is delimited only by the ectotympanic. Toward adulthood, the tympanic process of the alisphenoid and the caudal process of the petrosal grow over the ectotympanic as the pneumatization of the bulla increases, so the opening of the external acoustic meatus is smaller than in young individuals in absolute size. The ectotympanic is then partially concealed in adults, its ventral portion being no longer visible externally. Second, the surfaces of the rostral and caudal tympanic processes of the

petrosal are not distinct in the youngest specimens. This may suggest that both processes are actually a single unit that becomes separated with age. In the adult, the suture coincides with the location of the internal septum of the bulla that overlies the bullar floor (likely homologous to the rostral tympanic process of the petrosal of other marsupials given its position rostral to the cochlear fenestra; see fig. 6 in Wible, 2003). An embryological study is necessary to fully understand the homology of the bullar floor.

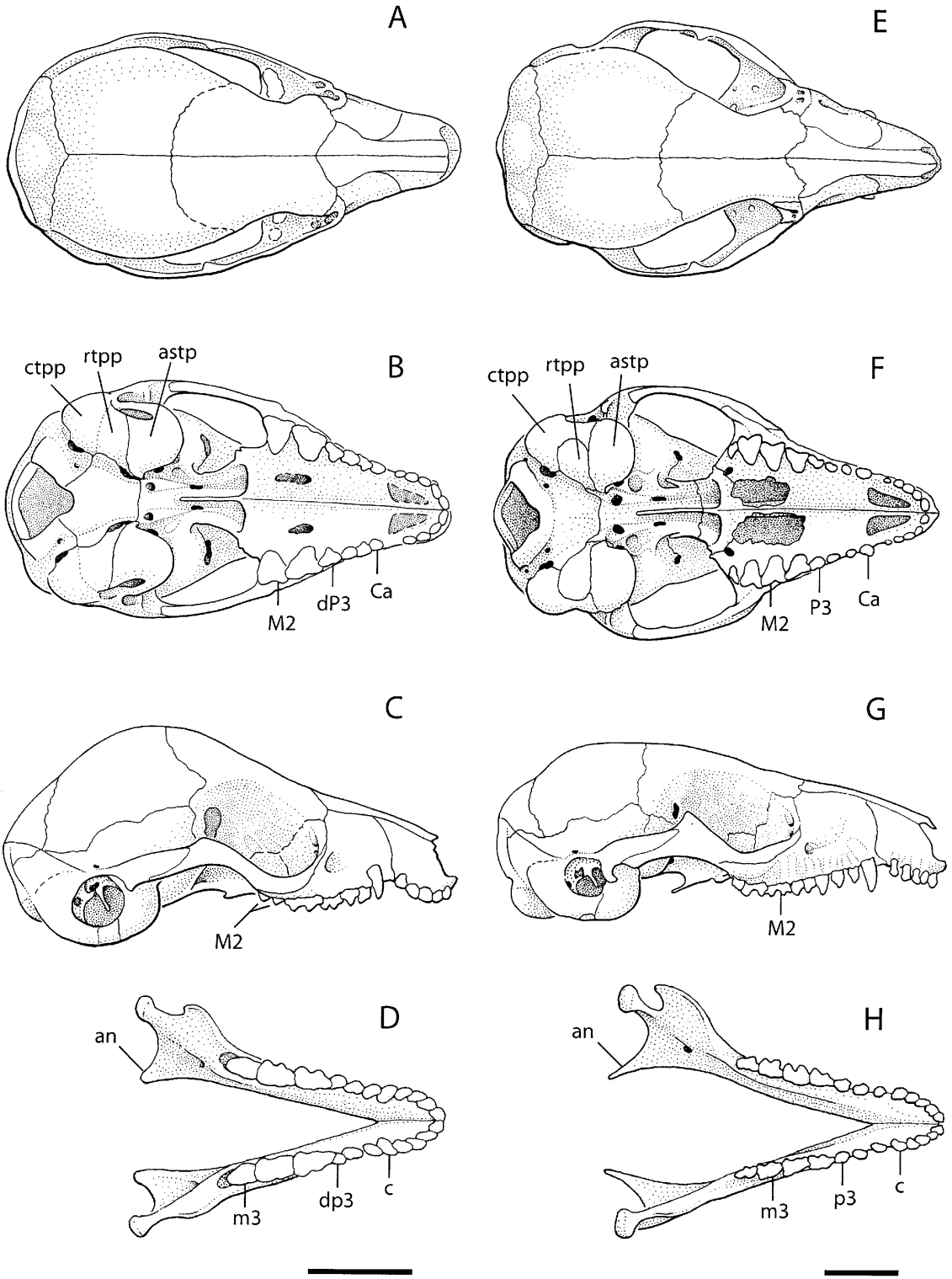
The mastoid exposure of the petrosal, which covers the semicircular canals posteriorly, is poorly ossified in the youngest specimen (CML 6217). All other specimens have already formed a thick wall of bone that is continuous with the caudal tympanic process of the petrosal (see fig. 3A, ref. a).

ALLOMETRY

BIVARIATE ALLOMETRY: The rate of change (allometric analysis) of each quantitative variable with respect to size (total length of the skull) is shown in table 1. The fit of the variables examined, as evaluated by the adjusted R^2 (coefficient of determination adjusted by $df = N - 2$), varied widely between 29 and 89% (fig. 4). In 8 out of 13 variables (not including the bullar dimensions), LS and RMA showed the same allometric trends. Specifically, both methods tended to reject isometry in the case of length of nasals (positively allometric), breadth of palate, breadth of braincase, length of lower postcanine row, and height of occipital plate (negatively allometric; table 1). Both methods led to acceptance of isometry in the length of palate, length of orbit, and breadth of zygomatic (table 1). The allometric trends in the remaining variables were as follows: the lengths of the upper postcanine row and mandible and the heights of the mandible and coronoid process were positive (or marginally so) under RMA and marginally positive or isometric under LS, whereas the height of muzzle was marginally negatively allometric under LS and isometric under RMA (table 1).

MULTIVARIATE ALLOMETRY: Observed multivariate coefficients of allometry varied widely across variables (table 2). Two variables, the total length of the skull and the

⁴ In Hershkovitz's illustration of the *Dromiciops*' basicranium, nomenclature of referred structures is either incorrect or inconsistent with Sánchez-Villagra and Wible (2002), Wible (2003), or the *Nomina Anatomica Veterinaria* (1994; N.A.V.) in the following cases: reference 14 is the sphenoid crest, not presphenoid (crista) or basisagittal crest of figure 8 in the same study (since the crest is also formed by the basisphenoid, the term crista sphenoidalis of the N.A.V. [1994] seems more appropriate); reference 19 is the caudal tympanic process of the petrosal, not tympanic process of petrotic; reference 22 is exoccipital, not supraoccipital or exoccipital; reference 24 is rostral tympanic process of petrosal, not entotympanic; reference f is suprameatal foramen, not postglenoid foramen; reference h is carotid foramen, not foramen ovale; reference k + m is jugular foramen, not jugular foramen (k) separate from hypoglossal foramen (m); reference l is hypoglossal foramen, not stylomastoid foramen; reference n is foramen ovale, not carotid foramen.



breadth of zygoma, showed the smallest departure from isometry values. Average estimated bias (using absolute jackknife values) across coefficients calculated from trimmed and untrimmed values were both small and similar to each other (0.016 and 0.017, respectively). Conversely, trimmed pseudovalues did affect jackknife estimates of confidence intervals; the average standard deviation across coefficients from untrimmed pseudovalues was 3.2 times higher than from trimmed pseudovalues, and this difference is not attributable to outlying coefficients. The fact that only two skull variables can be characterized as allometric using an untrimmed set of pseudovalues is another suggestion that the breadth of confidence intervals may have been seriously affected. Extreme pseudovalues occurred mainly in pseudosamples in which the smallest specimen of the sample (CML 6217) was removed (46% of the 28 pseudovalues trimmed from the pseudovalues of the 14 variables used). This strongly suggests that, in order to obtain reasonable allometry estimates, the youngest specimen is indispensable, reinforcing the need for more specimens in that size range.

Considering then the ($m = 1$) trimmed analysis, which ignores all cases in which CML 6217 (and/or few other young specimens) were removed, several variables can be safely characterized as allometric (table 2). The breadth of palate, breadth of braincase, length of lower postcanine toothrow, and height of the occipital plate were negatively allometric, whereas the length of the nasals and the height of the mandible were positively allometric. Notably, the set of allometric variables may also include the total skull length, but we must interpret this departure cautiously given that the upper limit of the 99% confidence interval for this variable almost includes the expected value under isometry.

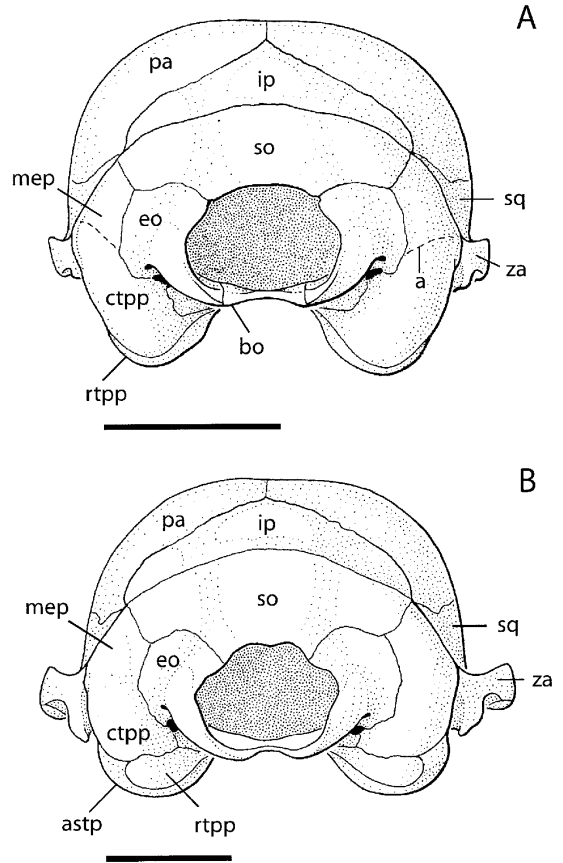


Fig. 3. Comparison of the occipital plate of young (A) and adult (B) *Dromiciops gliroides*. Abbreviations: **a**, schematic line indicating approximate limit of mep and ctp (see below); **astp**, tympanic process of the alisphenoid; **bo**, basioccipital; **ctpp**, caudal tympanic process of petrosal; **eo**, exoccipital; **ip**, interparietal; **mep**, mastoid exposure of the petrosal; **pa**, parietal; **rtp**, rostral tympanic process of petrosal; **sq**, squamosal; **za**, zygomatic arch. Scale bars: 5 mm.

A comparison of bivariate and multivariate allometry (table 3) indicated that 8 out of 13 variables showed the same trend in multivariate and both methods of bivariate allom-

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Fig. 2. Comparison of skull shape in young (A–D) and adult (E–H) *Dromiciops gliroides*. Dorsal (A, E), ventral (B, F), lateral (C, G), and mandible (D, H). Abbreviations: **an**, angular process; **astp**, tympanic process of the alisphenoid; **c**, lower canine; **Ca**, upper canine; **ctpp**, caudal tympanic process of petrosal; **dp3**, lower deciduous third premolar; **dP3**, upper deciduous third premolar; **M2**, upper second molar; **m3**, lower third molar; **p3**, lower third premolar; **P3**, upper third premolar; **rtp**, rostral tympanic process of petrosal. Scale bars: 5 mm.

TABLE I
Results of Bivariate Allometric Analyses on *Dromiciops gliroides*

Variables	N	Range	R ²	Least squares			Reduced major axis		
				b ₁ ^a	t _{ISO}	P _{ISO}	b ₁	t _{ISO}	P _{ISO}
Cranial dimensions									
Length of nasals	49	6.4-12.4	0.71	1.23	2.02	0.049	1.46	4.04	<0.001
Height of muzzle	47	4.4-6.1	0.60	0.79	-2.17	0.036	1.02	0.25	0.800
Length of palate	49	10.0-15.2	0.86	1.04	0.64	0.523	1.12	2.00	0.051
Breadth of palate	45	5.0-6.5	0.29	0.43	-5.80	<0.001	0.80	-2.07	0.044
Length of upper postcanine row	51	5.5-9.3	0.66	1.09	0.79	0.435	1.34	3.06	0.004
Length of lower postcanine row	48	7.6-9.9	0.35	0.44	-6.51	<0.001	0.75	-2.94	0.005
Length of mandible	49	13.2-20.8	0.76	1.04	0.46	0.651	1.19	2.28	0.027
Height of mandible	44	1.5-2.6	0.63	1.28	1.87	0.034	1.61	4.11	<0.001
Height of coronoid process	47	5.1-8.5	0.84	1.15	1.97	0.028	1.25	3.37	0.002
Breadth of zygoma	47	11.6-17.3	0.89	0.94	-1.20	0.118	1.00	-0.04	0.966
Breadth of braincase	51	9.7-13.3	0.67	0.60	-6.83	<0.001	0.73	-4.59	<0.001
Height of occipital plate	47	5.7-7.6	0.53	0.49	-7.42	<0.001	0.68	-4.72	<0.001
Length of orbit	43	5.6-7.5	0.63	0.87	-1.28	0.107	1.10	0.96	0.345
Bullar dimensions									
Length of bulla	47	5.9-7.6	0.50	0.61	-4.47	<0.001	0.86	-1.63	0.111
Breadth of bulla	47	2.9-4.7	0.61	1.06	0.46	0.326	1.35	2.85	0.006

Abbreviations: N, sample size; R², adjusted coefficient of determination; b₁, coefficient of allometry; t_{ISO}, t-value under the null hypothesis of isometry; P_{ISO}, P-value under the null hypothesis of isometry. Range is given in millimeters.

^a3.59 ≤ t ≥ 19.34 and P < 0.001 under null hypothesis of b₁ = 0.

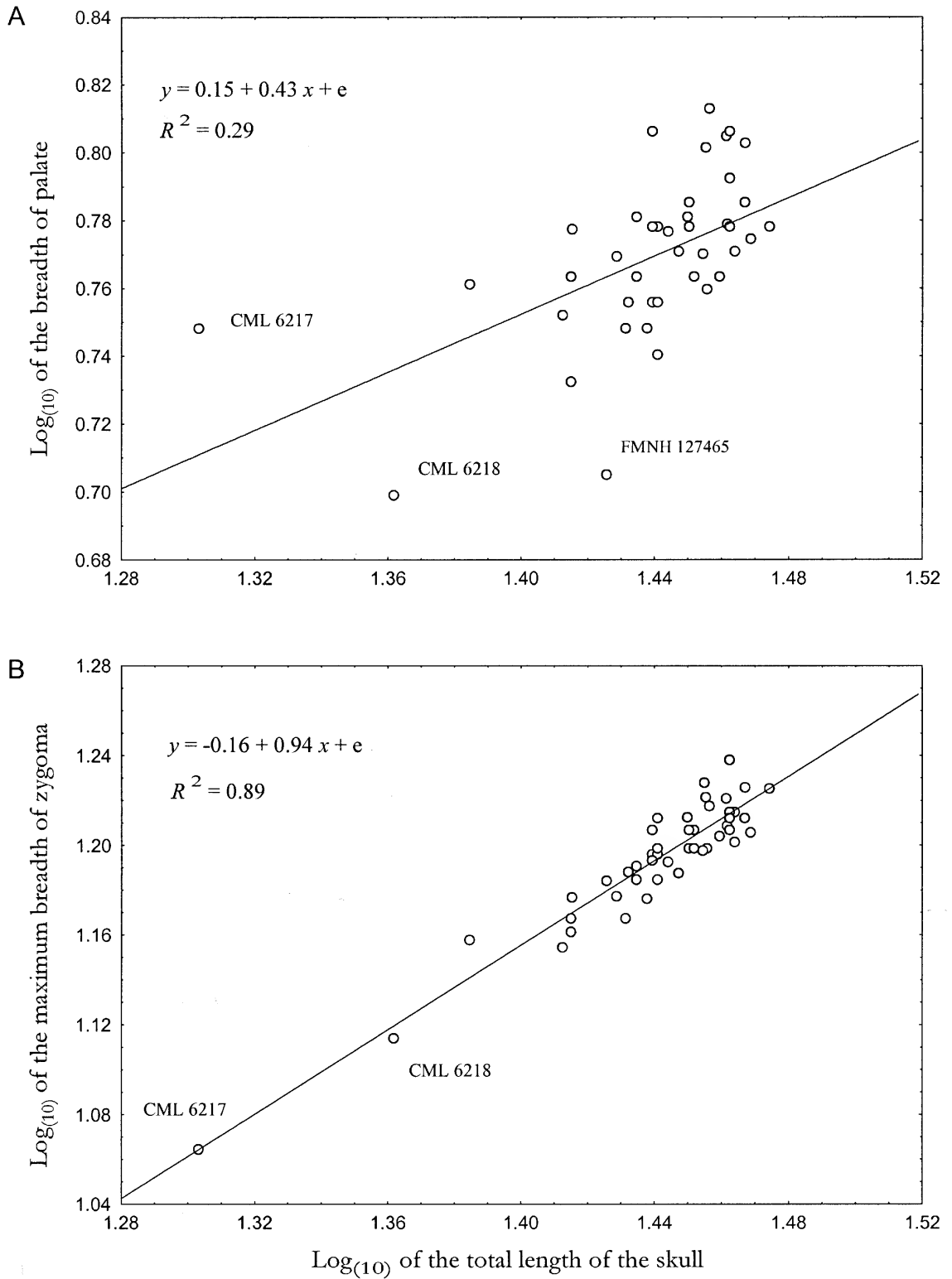


Fig. 4. Examples of allometry trends in *Dromiciops gliroides*, showing (A) worst fitted and (B) best fitted regressions on the total length of the skull. Inset: least-squares regression model and coefficient of determination.

TABLE 2
Results of Multivariate Analysis of Cranial Allometry in *Dromiciops gliroides*^a

Variables	Untrimmed values						Trimmed values					
	Expected allometry coefficient	Observed allometry coefficient	Observed departure	Resampled allometry coefficient	Bias	99% confidence interval	Growth trend	Resampled allometry coefficient	Bias	99% confidence interval	Growth trend	
Total length	0.267	0.273	0.006	0.286	0.013	0.214-0.359	=	0.253	-0.020	0.242-0.264	+	
Length of nasals	0.267	0.367	0.100	0.395	0.028	0.202-0.588	=	0.329	-0.038	0.287-0.370	+	
Height of muzzle	0.267	0.229	-0.038	0.222	-0.007	0.137-0.307	=	0.222	-0.007	0.174-0.270	=	
Length of palate	0.267	0.292	0.025	0.304	0.012	0.222-0.386	=	0.227	-0.015	0.243-0.312	=	
Breadth of palate	0.267	0.133	-0.134	0.110	-0.023	-0.087-0.308	=	0.145	0.012	0.098-0.192	-	
Length of upper postcanine row	0.267	0.299	0.032	0.318	0.019	0.203-0.432	=	0.284	-0.015	0.206-0.362	=	
Length of lower postcanine row	0.267	0.127	-0.140	0.127	-0.001	0.079-0.174	-	0.120	-0.008	0.094-0.146	-	
Length of mandible	0.267	0.297	0.030	0.291	-0.006	0.206-0.376	=	0.290	-0.007	0.240-0.339	=	
Height of mandible	0.267	0.387	0.120	0.360	-0.026	0.117-0.603	=	0.402	0.015	0.337-0.467	+	
Height of coronoid process	0.267	0.326	0.059	0.349	0.023	0.219-0.479	=	0.291	-0.035	0.264-0.318	=	
Breadth of zygoma	0.267	0.272	0.005	0.279	0.007	0.238-0.320	=	0.262	-0.010	0.246-0.278	=	
Breadth of braincase	0.267	0.169	-0.098	0.195	0.025	0.024-0.365	=	0.131	-0.039	0.107-0.154	-	
Height of occipital plate	0.267	0.145	-0.122	0.157	0.012	0.068-0.246	-	0.132	-0.013	0.098-0.167	-	
Length of orbit	0.267	0.249	-0.018	0.231	0.018	0.078-0.384	=	0.258	0.008	0.227-0.289	=	

^aThe first three data columns show results using all data. The rest of the columns show jackknife results calculated with untrimmed and trimmed sets of pseudovalues (see text). Allometry coefficient is the correspondent element of the first (unit) eigenvector per variable. The expected coefficient is the value under isometry (equal for all variables). The observed coefficient is the value obtained with all specimens included ($N = 37$). The resampled coefficient is the first-order jackknife value. Bias is the difference between the resampled and observed coefficients (e.g., the untrimmed value of 0.013 for total length is 0.286 minus 0.273). The jackknife 99% confidence interval is provided; allometric variables are those whose confidence intervals exclude the expected value under isometry (0.267). Growth trend is the summary allometry of each variable presented in symbols: = isometry, - negative allometry, + positive allometry.

TABLE 3
Gross Comparison of Results Across Methods Used
to Estimate Cranial Allometry in
Dromiciops gliroides

Variables	Multivariate	RMA	LS
Length of nasals	+	+	(+)
Height of muzzle	=	=	(-)
Length of palate	=	=	=
Breadth of palate	-	(-)	-
Length of upper postcanine row	=	+	=
Length of lower postcanine row	-	-	-
Length of mandible	=	(+)	=
Height of mandible	+	+	=
Height of coronoid process	=	+	=
Breadth of zygoma	=	=	=
Breadth of braincase	-	-	-
Height of occipital plate	-	-	-
Length of orbit	=	=	=

Symbols: =, isometry; +, positive allometry; (+), positive allometric trend (see text); -, negative allometry; (-), negative allometric trend (see text).

Abbreviations: RMA, coefficient of allometry under reduced major axis method; LS, coefficient of allometry under least squares method.

etry. The remaining variables were consistent with either RMA or LS estimates, and there was no case of a multivariate coefficient different from both RMA and LS estimates. In 11 cases the multivariate trend is the same as in the least-squares regression, and in 10 cases the trend is the same as in reduced major axis regression (table 3). The small differences between the multivariate and bivariate results are almost certainly due to the fact that, besides stochastic causes, bivariate allometry assumes isometry of the independent variable (total length of the skull), which is somewhat questionable in light of the trimmed jackknife analysis. Other variables, like the breadth of zygoma, may represent a more appropriate x -variable, if a bivariate analysis is desired.

We conclude that multivariate allometry is preferable, on grounds discussed in the methods, over bivariate approaches. However, the latter are still useful principally because they are less affected by sample completeness, provided that the independent variable of choice is the closest possible to isometry. In

our analysis, a variable-wise sample size reduction of 14–27% in the multivariate analysis was caused by missing data in specimens. This is especially critical in fossils and in extant species in which specimens may be fragmentary as a consequence of their fragility. Also, examination of bivariate plots is highly useful.

QUANTITATIVE SKULL MODELING IN *DROMICIOPS GLIROIDES*: On the basis of the multivariate analysis with trimmed jackknife estimates of allometry, we describe the quantitative trends in the modeling of the skull in *D. gliroides* as follows. The braincase is relatively smaller in adulthood, as indicated by the negative trend in breadth of the braincase and height of the occipital plate. By contrast, another neurocranial component—the orbit—increases its length at a pace comparable to the increase in latent size, thus keeping the relative size of the eye socket constant. The palate becomes elongated in shape as a consequence of the isometry of its length and the strong negative allometry of its width. The upper toothrow is isometric, while the lower toothrow grows at a markedly slower rate than the latent size, likely because tooth emergence in the upper postcanine row is phased out with respect to the lower row—the lower row has one more tooth than the upper row, and so it shows a slower growth rate as to yield approximately the same absolute length in adults. In the other dimensions involving the muzzle, the nasals slightly increase their length whereas the height of the muzzle is isometric. Therefore, the entire muzzle grows isometrically except the palate, which decreases in width toward adulthood. The temporal space expands only a little given that the braincase is negatively allometric while the zygomatic breadth is isometric. The mandible changes essentially by increasing its robustness, since the height of mandible shows a positive trend, whereas the other two dimensions considered (length of mandible and coronoid process) are isometric.

On the basis of bivariate allometry, the bulla tends to grow with negative allometry along its length (b_1 varying from 0.61 to 0.86 depending on the regression method; table 1) and with a positive allometry along its width (b_1 varying from 1.06 to 1.35). In relative

terms, the trend is toward a lateral enlargement and longitudinal shortening of the bulla, which is consistent with our qualitative observations.

COMPARATIVE ALLOMETRY: Bivariate allometric values from Abdala et al. (2001) for *Didelphis albiventris* ($N = 61$) and Flores et al. (2003) for *Lutreolina crassicaudata* ($N = 43$) allow us to attempt a comparison of allometric pattern with those didelphids. Fortunately, the youngest specimen of our sample (CML 6217) exhibits a stage of tooth eruption roughly similar to the youngest specimens both in *D. albiventris* and *L. crassicaudata*. However, one aspect compromises the direct comparability of our results; although in Abdala et al. (2001), Flores et al. (2003), and the current work, total length of the skull was chosen as the estimator of overall size, this measurement does not exactly correspond in the three studies and is therefore not properly homologous. At any rate, dimensions spanning the entire length of the skull are known to be highly correlated, so an approximate comparison is still possible.

The coefficients for *D. gliroides* are concordant with either or both *D. albiventris* and *L. crassicaudata* in 11 of the 13 compared measurements (table 4). Of those 11 measurements, 6 show the same tendency in the three species. These are the isometric length of palate and zygomatic breadth; the negatively allometric breadth of palate and braincase and the height of the occipital plate; and the positively allometric height of mandible. *Dromiciops gliroides* shares slightly more allometric trends with *L. crassicaudata* (9 variables overall, 3 variables exclusively) than with *D. albiventris* (8 variables overall, 2 variables exclusively; table 4).

Two variables define the most striking differences in coefficient values between *D. gliroides* and both *D. albiventris* and *L. crassicaudata*. First, the development of the orbit is isometric in *D. gliroides* and strongly negatively allometric in the two didelphids (Abdala et al., 2001; Flores et al., 2003). This difference goes beyond this interspecific comparison, since the “negative” allometry of the orbit is a virtually general pattern in vertebrates (Emerson and Bramble, 1993). Second, the length of the upper postcanine row is isometric in *D. gliroides*, while it is

TABLE 4
Allometric Comparison of *Dromiciops gliroides* (this study, multivariate results) with *Didelphis albiventris* (Abdala et al., 2001) and *Lutreolina crassicaudata* (Flores et al., 2003)

Variables	<i>Dromiciops</i>	<i>Didelphis</i>	<i>Lutreolina</i>
Length of nasals	+	+	(-)
Height of muzzle	=	(-)	=
Length of palate	=	=	=
Breadth of palate	-	-	-
Length of upper postcanine row	=	-	-
Length of lower postcanine row	-	-	? ^a
Length of mandible	=	+	=
Height of mandible	+	+	+
Height of coronoid process	=	+	=
Zygomatic breadth	=	=	=
Breadth of braincase	-	-	-
Height of occipital plate	-	-	(-)
Length of orbit	=	-	-

Symbols for isometry, negative allometry, and positive allometry are =, -, and +, respectively. Parentheses indicate allometric trends; i.e., situations in which only one of the two regression methods used (least squares and reduced major axis) led to rejection isometry. For instance, in *Lutreolina*, the length of nasals is negatively allometric under least squares and isometric under reduced major axis.

^aValue under LS (-), under RMA +.

negative in the didelphids. In fact, *D. gliroides* shows a greatly accentuated trend already present in *D. albiventris* and *L. crassicaudata*: the upper tooththrow elongates much faster than the lower tooththrow in order to reach roughly the same length in both rows toward adulthood—a necessary compensation because the upper row always bear one tooth less than the lower row until the dentition is completed (Abdala et al., 2001).

In *D. albiventris* and *L. crassicaudata*, the breadth of zygoma is isometric and the braincase width is extremely negatively allometric (Abdala et al., 2001; Flores et al., 2003). Therefore, in relative terms, the space for the temporal muscles increases principally inwards. The condition in *D. gliroides* is the same but somewhat less marked, implying that the braincase of young *D. gliroides* will leave relatively less space to hold the temporal muscles. We speculate that this growth pattern may be shared with small-sized *Mar-*

mosa-like species of marsupials, which have similar braincase size and shape.

CONCLUSIONS

Most of the developmental trends seen in *D. gliroides* are similar to those found in didelphids studied so far (*Didelphis albiventris* and *Lutreolina crassicaudata*) in spite of the marked size difference, corroborating a common ground of therian development in the sense advanced by Flores et al. (2003) for didelphids (see also Abdala et al., 2001; Maunz and German, 1996). For instance, growth in most neurocranial components were typically negatively allometric, whereas coefficients of splanchnocranial components varied widely in a complex but consistent manner (Abdala et al., 2001; Flores et al., 2003). The six variables that show the same trends in *D. gliroides*, *D. albiventris*, and *L. crassicaudata* define much of the overall shape of the skull, so the three species arrive ontogenetically at their adult proportions in roughly the same way. Other aspects, like the isometry of orbit, development of bulla, and the extremely different allometry shown by the postcanine tooththrows, indicate, so far, ontogenetic patterns probably unique to *D. gliroides*. An interesting comparison of *D. gliroides*' postnatal ontogeny would be with other small-sized marsupials, both South American and Australasian.

A combination of qualitative observations and allometry continues to provide insightful results in comparative ontogeny of marsupials. We found a highly conservative pattern of skull growth in *D. gliroides* being remarkably similar to that of the two didelphids studied so far. Inasmuch as *D. gliroides* is a member of the australidelphian clade, comparisons with didelphids alone are not satisfactory, but this study represents indeed the first ameridelphian-australidelphian comparison. Therefore, future contributions need to incorporate more australidelphians, for which no data are currently available, in order to expand our understanding of the comparative cranial ontogeny of marsupials as a group.

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