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POSTWEANING ONTOGENY OF THE SKULL OF *DIDELPHIS ALBIVENTRIS*

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Postweaning development of the skull of *Didelphis albiventris* was studied in juveniles (3.5–8 months), subadults (7.5–9.5 months), and adults (>9.5 months). Analysis of allometry of 15 skull measurements was performed on a continuous growth series of 52–61 specimens to evaluate quantitative ontogenetic changes. Complex modifications occurred in cranial bones or regions such as the palate, processes for origin and attachment of jaw muscles, mandibular joint, frontal region, braincase, occipital bones, and petrosal. All measurements except zygomatic breadth were either positively or negatively allometric. Neurocranial components grew with strongly negative (<1) coefficients of allometry. Adult proportions of the masticatory apparatus arose from the counteraction of developmental trends; for example, the space for large temporal muscles was provided by isometric growth of the zygomatic breadth versus slower growth of the braincase. We interpret most of the postweaning developments as a function of the shift from milk suckling to active mastication.

Key words: allometry, *Didelphis albiventris,* marsupials, ontogeny

Among mammals, marsupials undergo the greatest change during postnatal ontogeny. The gestation period is short, after which the individual is born with minimal anatomical development (Lillegraven 1976; Russell 1982). The neonate experiences the change from an intrauterine to an external environment while in an embryonic condition (Clark and Smith 1993; Smith 1994). Marsupials have very different requirements for development compared with placental mammals (Smith 1997). Moreover, their reproductive pattern was considered as an alternative to, rather than a primitive stage of, the pattern observed in eutherians (Atramentowicz 1995; Hayssen et al. 1985). This makes the postnatal ontogeny an es-

pecially interesting aspect of the biology of metatherians.

Some studies dealing with growth in American marsupials have being oriented toward age estimation via the establishment of morphometric or dental parameters (Bergallo and Cerqueira 1994; Gardner 1973; Lowrance 1949; Pine et al. 1985; Regidor and Gorostiague 1990; Tribe 1990; Tyndale-Biscoe and Mackenzie 1976), predictive curves of growth (Atramentowicz 1995), or assessment of maternal investment during lactation (e.g., Atramentowicz 1995). In *Monodelphis domestica,* Maunz and German (1996) compared craniofacial growth between sexes and functionally different regions of the skull.

We examined the postnatal development of cranial structure in *Didelphis albiventris,*

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an omnivorous Neotropical opposum. We investigated how cranial configuration of this species changes from juveniles of about 3.5 months age to individuals of >20 months age. During this period, individuals just weaned develop morphologies needed to achieve definitive feeding habits and an existence independent from their mother. We took a descriptive approach by successively comparing structures in skulls of juveniles, subadults, and adults. However, some other traits were better understood by studying their continuous transformations as they age, for which we applied an analysis of allometry.

Allometry of growth explicitly considers timing of changes throughout the life of an individual (Kunz and Robson 1995; Maunz and German 1996; Prestrud and Nilssen 1995; Stern and Kunz 1998). Alternatively, allometry of size compares changes against overall size along a growth series; the time frame is implicitly incorporated but not specified. Allometry of size may in turn be interspecific with the purpose of studying functional changes from an evolutionary perspective within a lineage (Davis 1962; Hayssen and Kunz 1996; Radinsky 1981a, 1981b; Silva 1998), or intraspecific with an aim similar to the allometry of growth (Nelson and Shump 1978), that is, to describe relative modifications in structures as the animal grows. We took the latter approach in the present study. We interpreted allometry coefficients as growth rates, but in truth, they represented size rates (Gould 1966; Nelson and Shump 1978; Simpson et al. 1960). Thus, we ultimately assumed that intraspecific allometry of size closely reflected true allometry of growth.

Taken together, qualitative and allometric analyses allowed us to study relative growth of the different cranial components. We further interpreted our findings on functional grounds during a period in which critical changes in habits of developing young occur.

MATERIALS AND METHODS

We studied 61 skulls of *D. albiventris* from individuals of different ages (Appendix I). Age stages (juveniles, subadults, and adults) were estimated from dental formulae following Regidor and Gorostiague (1990). Juveniles (3.5–8 months) retained the deciduous premolars (sensu Luckett 1993), subadults (7.5–9.5 months) showed the successional last upper premolar but lacked the last molar, and adults (9.5–≥20 months) showed a definitive adult dentition. Additional information on age stages was obtained from Lowrance (1949), Petrides (1949), and Gardner (1982), who studied *Didelphis virginiana*. We focused study of qualitative changes of the skull on the contrast between juveniles and adults, but we also observed subadults for anatomical transformations implied throughout the range of ages available.

We used 15 cranial variables to study allometry (Fig. 1). Overall size was estimated by the total length of the skull (Emerson and Bramble 1993; Radinsky 1981a, 1981b; Simpson et al. 1960). The relation of each variable with overall size (total length of the skull) was examined with the equation of allometry: $\log y = \log b_0 + b_1 \log x + \log e$. That equation was derived from the power growth function, $y = b_0 x^{b_1} e$, by taking the (base 10) logarithms on both sides (Alexander 1985; Silva 1998). The y-intercept was b_0, and b_1 was the slope of the line or coefficient of allometry. We assumed that the error term e was multiplicative, that is, it interacted with x, as expressed in the 2nd equation, so log transformation allowed the function to take the form of the 1st equation. Significance of allometry coefficients was evaluated by means of 1-tailed t-tests. Significance level was set to $P = 0.0036$; that P-value represented the usual 5% alpha level divided by the number of statistical tests (14 regressions) performed over the same sample units (Bonferroni correction—Hair et al. 1995).

Deviations from isometry were assessed by comparing the allometry coefficient with that expected under geometric similarity (Alexander 1985). Expected coefficients under isometry are equal to 1.0 for variables involved, because they all are linear measurements. Consequently, we used 1-tailed t-tests with the null coefficient set at 1.0 to assess significant deviations from isometry. Negative allometry refered to the case of a coefficient significantly less than expected by
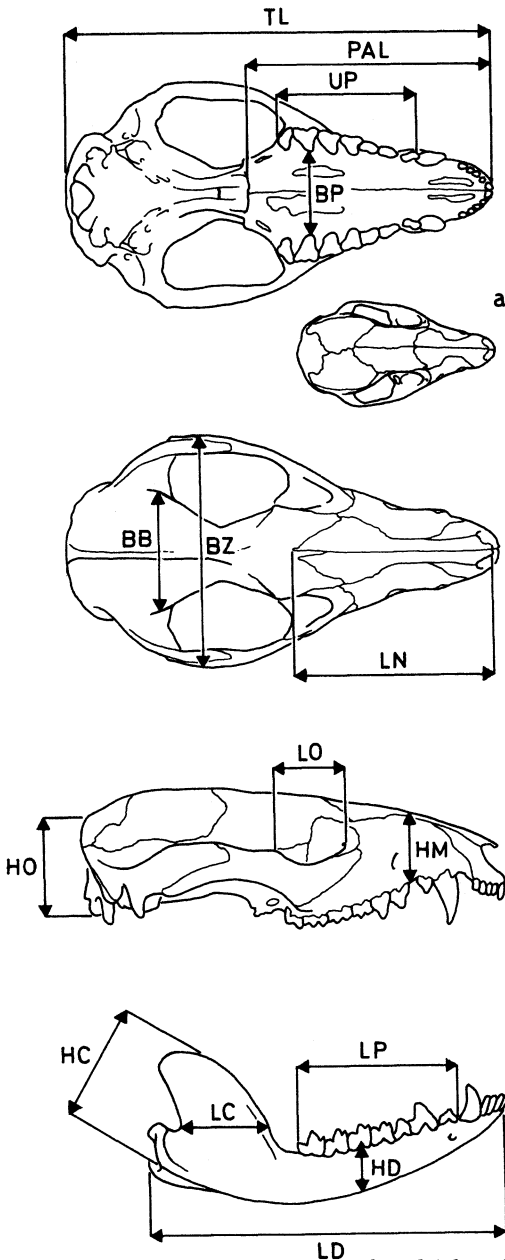
FIG. 1.—Cranial measurements of *Didelphis albiventris* used in our study of allometry. TL, total length of skull; PAL, length of palate; UP, length of upper postcanine row; BP, breadth of palate; BZ, breadth of zygoma; BB, breadth of braincase; LN, length of nasals; HO, height of occipital plate; LO, length of orbit; HM, height of muzzle; HC, height of coronoid process of the dentary; LC, length of coronoid process of dentary; LD, length of dentary; HD, height of dentary at the level of 2nd lower molar; LP, length of lower postcanine row (scale 1:0.7). a) Skull of young at the same scale.

isometry, and as positive when it was significantly higher (Emerson and Bramble 1993). At that stage, the significance level was reset because 14 additional tests were to be performed, so Bonferroni corrected value for rejecting the null hypothesis of isometry was 0.05/28 = 0.0017. Significance of other tests was set at 0.01 alpha level.

Least squares regression assumes a clearly identifiable independent variable with neither measurement error nor natural variation (Hair et al. 1995; Zar 1996). Although it could be argued that all variables are size-dependent, our estimator of overall size (the "independent" total length of the skull) was obviously subjected to variation and measurement error. Therefore, we also calculated reduced major axis (RMA) coefficients of allometry for all variables (Niklas 1994; Radinsky 1981a, 1981b). The RMA method allowed variation in both dimensions, so residuals were oblique with a component that also represented variation in size. RMA coefficients were arithmethically obtained from least squares coefficients by dividing them by the Pearsons product-moment correlation coefficient r, and standard errors were the same for both coefficients (Niklas 1994). We informally compared least squares coefficients with the more appropriate RMA coefficients to ensure reliability of estimators of the relation of each variable with overall size.

RESULTS

Qualitative traits.—Observed differences in neurocranial components between juveniles and adults (Fig. 2) included those that involved appearance of structures absent in juveniles (first 4 characters in Table 1), completion or enlargement of structures already present in juveniles (next 2 characters), relative decrease of structures (next 3 characters), and reorganizations (last 5 characters). Most pronounced rearrangements occurred in the occipital and basicranial regions, for example in the foramen magnum (Fig. 3) and the alisphenoid area.

In relation to splanchnocranial components, differences between juveniles and adults implied the strong development of crests and processes and modifications of
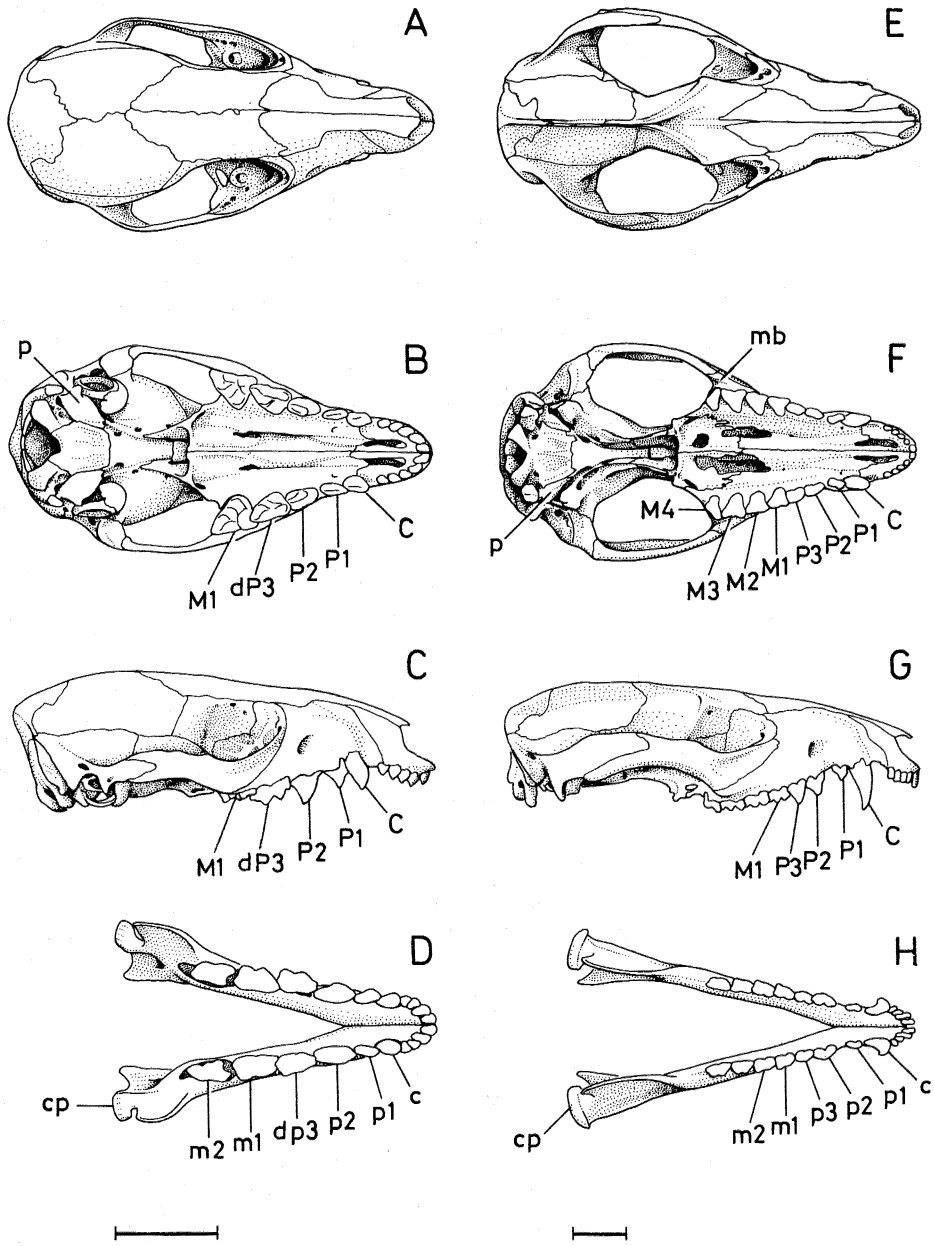
FIG. 2.—Comparison of skulls of (A–D) young and (E–H) adult *Didelphis albiventris*. Dorsal (A and E), ventral (B and F), and lateral (C and G) view of the skull, and dorsal view of the mandible (D and H). Abbreviations: mb, maxillary boss; cp, condyloid process of the dentary; dP3, upper deciduous 3rd premolar; dp3, lower deciduous 3rd premolar. Scale bars represent 1 cm.

nasals, palate, and condyloid process of the dentary (Fig. 2; Table 2).

Allometry.—All variables were related significantly to total length of the skull (Table 3). Overall size explained a large frac-

tion of total variation in all dependent variables (R^2-values ranged from 0.59 to 0.99, most >0.90; Table 3). Neither outliers nor systematic trends were apparent in residual plots. Coefficients of allometry obtained by

TABLE 1.—Differences in qualitative traits of the neurocranium between juvenile and adult *Didelphis albiventris.*

Characters	Juveniles	Adults
Supraorbital border of frontal	Absent	Present
Postorbital constriction	Absent	Present
Secondary foramen ovale	Absent	Present
Groove for petrosal sinus	Absent	Present
Gyrus of anterior semicircular canal	Narrow	Wide
Cavum supracochlear floor	Incomplete	Complete
Petrosal, promontorium, and tympanic process of the petrosal	Relatively large	Relatively small
Fossa subarquata	Relatively large	Relatively small
Internal acoustic meatus	Relatively large	Relatively small
Dorsal margin of foramen magnum formed by	Interparietal	Exoccipitals
Exoccipital–basioccipital	Partially fused	Entirely fused
Relation of petrosal to squamosal	Completely fixed	Loosely attached
Sphenorbital fissure and foramen rotundum	Almost adjacent	Separated by a wall of alisphenoid
Sphenorbital fissure and foramen ethmoidal	Almost adjacent	Separated by a wall of orbitosphenoid

least squares (b_1) were very similar to those calculated by the RMA (b_{rma}; Table 3). An exception was height of muzzle, for which b_1 (0.77) was allometric (Table 3) and b_{rma} (0.97) was isometric ($t = -0.44$, *d.f.* $= 55$, $P = 0.333$). Seven variables showed negative allometry (coefficients less than expected by isometry), and 5 were positively allometric. For 2 variables, nonsignificant departures from isometry occurred (length of the palate and breadth of zygoma; Table 3).

Coefficients ranged from 0.44 for maximum breadth of the braincase to 1.56 for length of the coronoid process of the dentary. Coefficients for neurocranial components tended to be lower (0.44–0.85) than those for splanchnocranial components (0.58–1.56). Some obviously related structures showed distinct coefficients. For instance, the coefficient of length of the lower postcanine row (0.79) tended to be different from length of the upper postcanine row (0.88; 1-tailed *t*-test for differences between slopes—Zar 1996; $t = 2.32$, *d.f.* $= 113$, $P = 0.011$). In the same line, the palate changed isometrically along its length (b_1 $= 0.98$), but its width was strongly negatively allometric ($b_1 = 0.58$).

DISCUSSION

Most observed modifications can be associated directly to functional changes in neurologic and trophic complexes. In nearly 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). After weaning (our study period) in *D. albiventris,* rate of growth of neurocranial components slows, showing pronounced negative allometry, which is easily observed in characters treated here as qualitative. In the auditory region, the petrosal itself (Figs. 2B and 2F), promontorium, and tympanic process of the petrosal are comparatively larger in juveniles. Similarly, the fossa subarcuata, which accommodates the paraflocculus of the cerebellum (Wible 1990), is relatively large in petrosals of ju-
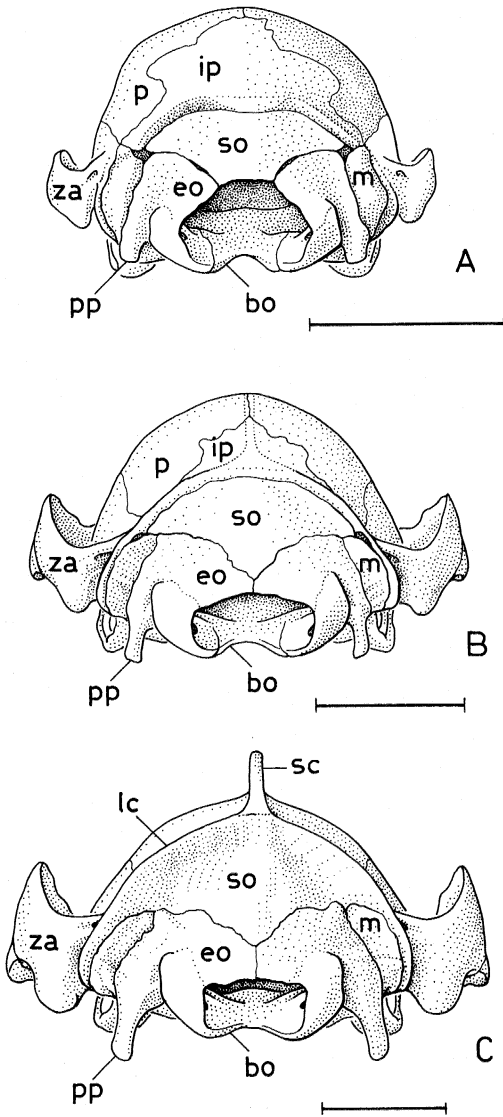
FIG. 3.—Comparison of the occipital plate of A) young, B) subadult, and C) adult *Didelphis albiventris*. Abbreviations for bones: p, parietal; ip, interparietal; so, supraoccipital; eo, exoccipital; bo, basioccipital; pp, paroccipital process; za, zygoma; m, mastoid process of the petrosal; sc, sagittal crest; lc, lambdoid crest. Scale bars represent 1 cm. Interparietal and supraoccipital are fused and cannot be distinguished as separated bones in C) adults.

veniles. Consequently, the gyrus of the anterior semicircular canal is narrower compared with adults. The petrosal in juveniles also shows the osseous floor of the cavum supracochlear incomplete, which probably means that the geniculate ganglion was not totally enclosed by bone at this stage.

The tight attachment of the petrosal to squamosal in juveniles may conform with the general robustness and rigidity of the skull in young that is needed for permanent suckling (Clark and Smith 1993; Maier 1987, 1989, 1993; Smith 1997). In adults, the petrosal becomes detached, likely to provide isolation of the inner ear, improving acoustic and vestibular function during chewing, mastication, or head movements. Many mammals have the petrosal in contact with adjacent bones only through connective tissues, with this isolation being extreme in acoustic specialists such as bats, cetaceans, and sirenians (Moore 1981; Novacek 1993).

The supraoccipital (fused to interparietal—Clark and Smith 1993) is excluded from the foramen magnum by growth of exoccipitals (Fig. 3). We also observed this characteristic in *Lutreolina crassicaudata*, indicating a pattern not unique to *D. albiventris*. A close examination of contours (Fig. 3) reveals more than a mere displacement of the supraoccipital by the exoccipitals but also an overlap and thickening of growing exoccipitals over the supraoccipital. This overlap is widespread in the sutures among several cranial bones in *Didelphis* (Gardner 1973). Occipitals are the 1st endochondral elements that ossify in the skull of *D. virginiana* (Nesslinger 1956), which also holds for *M. domestica* and *Macropus eugenii* (Clark and Smith 1993). This early development was interpreted as a response to mechanical stress imposed by cervical musculature (i.e., for supporting the head during migration immediately after birth and the attachment to the teat—Clark and Smith 1993).

Radinsky (1968) pointed out that the neurocranial structure is affected by the

TABLE 2.—Differences in qualitative traits of the splanchnocranium between juvenile and adult *Didelphis albiventris*.

Characters	Juveniles	Adults
Sagittal and lambdoidal crests	Absent	Well developed
Paroccipital process	Small, close to the tympanic process of petrosal	Well developed, extended below the occipital condyles
Boss for the origin of superficial masseter	Absent, last teeth close to the zygoma	Developed, separated from the tooth series
Palate	Almost completely ossified	Palatal vacuities
Condyloid process	Narrow and rounded	Laterally expanded
Nasals	Wide	Narrow

brain and sense organs, and also by its relationships to the splanchnocranium and functional demands of the jaw mechanism. Negative allometry of the braincase leads to a postorbital constriction, which is absent in the very enlarged braincase of the juveniles (Fig. 2A). In combination with the isometry of the zygomatic breadth, the braincase negative allometry also provides a wide temporal space that enlarges inward as the animal grows. Because this increasing space accommodates temporal, masseter, and pterygoid muscles, this pattern of growth gradually permits animals to achieve and maintain adult trophic function (e.g., prey–predator relationships—Emerson and Bramble 1993) and offensive–defensive behaviors.

Other changes also suggest an increasing importance of the occlusal musculature. The positive allometry of the coronoid process can be associated easily with the noteworthy

TABLE 3.—Summary of regressions on the total length of the skull of *Didelphis albiventris*. Abbreviations: n, sample size; R^2, adjusted coefficient of determination; log b_0, y-intercept; b_1, coefficient of allometry (least squares); t, 1-tailed Student's t-value for b_1 ($d.f. = n - 2$); t_{iso}, 1-tailed Student's t-value under null hypothesis of isometry (expected coefficient of allometry under isometry is 1; $d.f. = n - 2$); P_{iso}, P-value for t_{iso}; b_{rma}, coefficient of allometry (reduced major axis). Last 3 variables are neurocranial components.

Variables	n	R^2	log b_0	b_1	t[a]	t_{iso}	P_{iso}	b_{rma}
Length of nasals	60	0.98	−1.41	1.16	60.12	8.42	<0.001	1.17
Height of muzzle	57	0.69	−1.03	0.77	11.16	−3.33	<0.001	0.97
Length of palate	59	1.00	−0.42	0.98	113.91	−2.22	0.015[b]	0.98
Breadth of palate	61	0.90	0.71	0.58	23.79	−17.50	<0.001	0.61
Length of upper postcanine row	58	0.94	−0.57	0.88	29.95	−4.14	<0.001	0.92
Length of lower postcanine row	59	0.94	−0.06	0.79	31.17	−8.40	<0.001	0.83
Length of dentary	61	1.00	−0.49	1.07	113.74	7.77	<0.001	1.07
Height of dentary	60	0.98	−3.81	1.37	48.32	13.21	<0.001	1.39
Height of coronoid	60	0.96	−2.28	1.23	37.66	6.97	<0.001	1.27
Length of coronoid	59	0.97	−4.13	1.56	44.59	16.00	<0.001	1.62
Breadth of zygoma	52	0.97	−0.80	1.04	40.17	1.54	0.130[b]	1.06
Breadth of braincase	61	0.64	1.17	0.44	10.30	−13.33	<0.001	0.55
Height of occipital plate	57	0.96	−0.89	0.85	35.56	−6.25	<0.001	0.87
Length of orbit	61	0.59	0.28	0.52	9.36	−8.73	<0.001	0.68

[a] All significant at Bonferroni corrected $P < 0.0017$.

[b] Nonsignificant at $P > 0.0017$.

development of the sagittal and lambdoidal crests, the posterior border of the frontal bone, and the prominent maxillar boss. These modifications represent enlargements and improvements of surfaces for either origin or insertion of jaw musculature: specifically, the maxillary boss for the origin of the superficial masseter (Fig. 2F), the sagittal and lambdoid crests for the origin of different sections of the temporal muscles (Figs. 2E and 3C), and the coronoid process for the attachment of both muscles (Hiiemae and Jenkins 1969).

The mandible also is thickened, and the condyloid process of the dentary, which is rounded and narrow in juveniles, is profoundly modified (compare Figs. 2D and 2H). The condyloid process expands lateromedially, which likely reduces lateral rotation of the mandible and augments safety of the mandibular joint under stress, such as while biting prey (Crompton and Hylander 1986).

Particularly noticeable is that the relative length of the postcanine row in young specimens (75% of the length of the jaw) contrasts with the proportion in adults (57%; Figs. 2D and 2H). This is explained by the negative allometry of the tooth series, which is not an unusual condition in mammals (e.g., for the horse, *Equus*—Radinsky 1983, 1984). Teeth are discrete units, but their emergence is gradual, so length of the tooth row increases in an approximately continuous manner. The last tooth is added to the row at about 10 months (dental class 5 in Tyndale-Biscoe and Mackenzie [1976]); Regidor and Gorostiague (1990) report this condition at 9–13 months. After completion of the dentition, no further growth occurs, but the entire skull continues to grow well beyond this age (perhaps >20 months). This accounts for the negative allometry of the postcanine series but also indicates that the rate is not constant and that our estimation is only approximate.

Lower and upper postcanine rows are about the same length in adults. However, we found that the lower row grows at a slower rate. This can be interpreted in relation to the mode of dental eruption in *Di-*

delphis. Normally, the lower postcanine row has 1 more tooth than the upper row at a given time, until the final number is completed (Gardner 1982; Petrides 1949; Regidor and Gorostiague 1990; see also Figs. 2B and 2D). Therefore, this difference is compensated by a slower rate of growth to maintain the same length in upper and lower tooth row as an individual progresses toward adulthood. Conversely, the upper tooth row, having started with fewer teeth, may grow faster to reach its final length. Complex compensation of growth among interrelated structures were reported by Maunz and German (1996) for the palate and the mandible of *M. domestica*.

Length of the palate is isometric, but its breadth is strongly negative allometric ($b_1 = 0.58$). Therefore, the posterior palate is wide in juveniles (Fig. 2B). This is related to the importance of the palate as a platform for the tongue in intraoral transport and swallowing processes in suckling opossums (German and Crompton 1996). Disposition of the palate in relation to the tongue determines feeding and breathing. Consequently, pump-suckling is one of the most important functions during the early life of marsupials and determines many other traits that are structural adaptations of the skull of neonates (Clark and Smith 1993; Maier 1993). Palatal vacuities originate by bone resorption (compare juvenile and adult in Figs. 2B and 2F).

Splanchnocranial (=viscerocranial) components in *M. domestica* grew slightly faster and decelerated later than the neurocranium (Maunz and German 1996). However, results of Maunz and German (1996) seem to indicate more pronounced differences between sexes than between cranial regions, because of the strong dimorphism in the genus (cf. Pine et al. 1985). Splanchnocranial components in *D. albiventris* also showed a tendency to grow faster than neurocranial components. However, a generalization cannot be made because some coefficients for the neurocranium (e.g., height of the occipital plate with $b_1 = 0.85$) are greater than

some coefficients of the splanchnocranium (e.g., breadth of the palate with $b_1 = 0.58$). Even interrelated structures showed heterogeneous rates of growth, implying a complex pattern of changes, especially in the splanchnocranium. For instance, in the lower jaw, length of dentary was only slightly positively allometric ($b_1 = 1.07$), length of coronoid process (1.56) and its height (1.37) were strongly positive, and length of the lower postcanine series was negative (0.79).

Our analysis of qualitative and allometric changes in *D. albiventris* showed that neurologic and trophic complexes are affected in several different but mutually related ways. From morphology, we attempted to infer functional changes that are known to occur (i.e., the shift from lactating to predatory habits). This allowed us to link morphologic and behavioral processes on descriptive grounds. Further, *Didelphis* is a generalized basal genus that has been used as a model to understand various aspects of evolution of the mammalian skull (Crompton 1989; Crompton and Hiiemae 1970; Crompton and Hylander 1986). Therefore, our examination of its ontogeny may provide a comparative frame for the postweaning ontogeny in all marsupials. Differences that may be found in more specialized forms may be regarded as departures from the basic plan of a conservative didelphid such as *D. albiventris*.

RESUMEN

Examinamos el crecimiento del cráneo de *Didelphis albiventris* despues del destete. Los aspectos cualitativos se estudiaron comparativamente en jóvenes (3.5–8 meses de edad), subadultos (7.5–9.5 meses), y adultos (>9.5 meses). Para evaluar cambios ontogenéticos cuantitativos, se hizo un análisis de alometría de medidas craneales en una serie continua de crecimiento de 52–61 ejemplares. Desde juveniles a adultos pueden detectarse modificaciones complejas en la mayoría de los huesos o regiones craneales. Éstas incluyen el paladar, procesos para el origen e inserción de la musculatura mandibular, la articulación mandibular, las regiones frontal y occipital, la caja cerebral, y el petroso. Todas las medidas, excepto el ancho zigomático, resultaron alométricas. El crecimiento de los componentes neurocraneales tienen coeficientes de alometría fuertemente negativos (<1). Las proporciones del aparato masticatorio en el adulto surgen por tendencias de desarrollo contrapuestas. Por ejemplo, el espacio para los grandes músculos temporales se origina por la isometría del ancho zigomático versus la tasa menor de crecimiento de la caja cerebral. Interpretamos la mayor parte del desarrollo posterior al destete como una función del cambio desde la succión de leche a la masticación activa.

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APPENDIX I

Specimens examined.—Specimens of *Didelphis albiventris* studied are stored in Argentina at Colección Mamíferos Lillo, Universidad Nacional de Tucumán (CML); Museo Argentino de Ciencias Naturales (MACN); Museo de La Plata (MLP); and in Brazil at Fundacão Zoobotânica (MCN), Porto Alegre. List of specimens examined: MACN 2797, MACN 17262, MACN 30222, MACN 30348, MACN 36299, MACN 36300, MACN 36301, MACN 36302, MACN 36303, MACN 36304, MACN 36305, MACN 36306, MACN 36307, MACN 36729, MACN 36730, MACN 36731, MACN 36732, MACN 36734, MACN 36735, MACN 36737, MACN 36753, MACN 36757, MACN 36808; CML 20, CML 447, CML 463, CML 469, CML 471, CML 472, CML 476, CML 473, CML 474, CML 480, CML 519, CML 652, CML 1181, CML 1354, CML 1559, CML 5482, CML 3172, CML 5481; MLP 6-IX-95.1, MLP 6-IX-95.2, MLP 6-IX-95.3, MLP 6-IX-95.4, MLP 6-IX-95.5, MLP 6-IX-95.6, MLP 6-IX-95.7, MLP 5513, MLP 5515; MCN 69, MCN 336, MCN 337, MCN 338, MCN 373, MCN 389, MCN 411, MCN 451, MCN 456, MCN 458, MCN 459, MCN 505, MCN 506, MCN 510, MCN 511, MCN 512, MCN 513. Specimens of *Lutreolina crassicaudata* are stored at Colección Boliviana de Fauna in La Paz, Bolivia (CBF 2926, CBF 2925, and CBF 2118).