

Comparative Postnatal Ontogeny of the Skull in the Australidelphian Metatherian *Dasyurus albopunctatus* (Marsupialia: Dasyuromorpha: Dasyuridae)

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ABSTRACT We describe the cranial ontogeny of an australidelphian marsupial, *Dasyurus albopunctatus*, using a combination of qualitative and quantitative approaches. We examined in detail qualitative morphological changes of just-weaned individuals as compared to old adults; specifically, changes in 31 morphological structures (e.g., processes, foramina) and 38 changes in cranial joints. We also interpreted growth-invariant structures in terms of their functional relevance. We performed a multivariate allometry analysis based on 14 cranial measurements taken from 31 specimens encompassing the entire postweaning period. Three variables (height of occipital plate, breadth of braincase, and height of mandible) showed the same allometric trends in *D. albopunctatus* and the three marsupial species studied previously in the same framework (*Didelphis albiventris*, *Lutreolina crassicaudata*, and *Dromiciops gliroides*). In addition, *D. albopunctatus* shared allometric trends in two variables (length of the upper postcanine row and length of the orbit) with the microbiotheriid *D. gliroides*. Most of the growth trends observed are interpreted as linked to the predominantly carnivorous dietary habit of adult *D. albopunctatus*. Because dasyuromorphians are most likely basal to the major Australasian radiation of marsupials, knowledge of ontogenetic changes in *D. albopunctatus* may shed light on the evolution of ontogeny in the highly diverse Australasian marsupial fauna. *J. Morphol.* 267:426–440, 2006. © 2006 Wiley-Liss, Inc.

KEY WORDS: *Dasyurus*; marsupials; skull; ontogeny; allometry

The postweaning cranial ontogeny of two closely related didelphid species, *Didelphis albiventris* and *Lutreolina crassicaudata*, and the microbiotheriid, *Dromiciops gliroides*, has recently been studied in detail (Abdala et al., 2001; Flores et al., 2003; Gianni et al., 2004). Based on comparisons of the two didelphid species, we hypothesized the existence of general cranial growth trends in the family (Flores et al., 2003). These trends indicated that neurocranial and splanchnocranial components interact in a complex way, producing morphological arrangements with important relationships to trophic func-

tions, particularly the transition from suckling to mastication of solid food (Flores et al., 2003). In general, neurocranial components grew at a slower pace than the skull as a whole, while splanchnocranial components exhibited a range of growth rates from strongly negative allometry to strongly positive allometry. A subsequent study of the South American australidelphian *Dromiciops* confirmed most of the allometric trends seen in didelphids, but also showed some surprising differences, such as the isometry of the orbit, a typically negatively allometric structure (Gianni et al., 2004). Six variables (out of 14 analyzed) that define much of the skull proportions showed the same allometric trends in the three species studied, regardless of the adult size differences involved. Therefore, a common pattern of growth in marsupials seemed to emerge. However, the existence of this putatively plesiomorphic pattern has not been tested in Australasian forms, which in fact constitute the largest fraction of extant marsupial diversity.

Previous ontogenetic studies of Australasian marsupials have focused on developmental description and age estimation (e.g., Fleay, 1935; Hill and Hill, 1955; Shield and Woolley, 1961; Sharman et al., 1964; Nelson and Smith, 1971; Inns, 1982; Merchant et al., 1984). To our knowledge, only one study

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(Moeller, 1973) approached allometry in australidelphians, but an unfortunate choice of measurements makes these results noncomparable with other studies. With 61 currently recognized species (Groves, 1993), Dasyuridae is a highly diverse clade that represents the principal insectivore-carnivore radiation in the recent Australasian mammal fauna (Wroe, 1997). Dasyurids are relatively conservative in cranial shape (e.g., Wroe, 1997, and citations therein), and are currently considered as either sister-group to the remaining Australasian marsupials (Horowitz and Sánchez Villagra, 2003), or sister to the highly diverse diprotodontian clade (Asher et al., 2004; Kavanagh et al., 2004). As part of an ongoing effort to document comparative cranial ontogeny in marsupials, we analyzed the postweaning cranial development of *Dasyurus albopunctatus* in the same methodological framework previously used for didelphids and microbiotheriids (Abdala et al., 2001; Flores et al., 2003; Giannini et al., 2004). The postweaning cranial ontogeny of a dasyurid may provide an important comparative context for the understanding of cranial ontogeny in derived australidelphians. Comparisons of the cranial development found in *D. albopunctatus* with that of didelphids and microbiotheriids allow us to test and expand previous hypotheses of cranial ontogeny in marsupials, as well as to refine prior generalizations in the light of new data.

MATERIALS AND METHODS

Study Specimens

For this study, we chose the New Guinean quoll *Dasyurus albopunctatus* on the basis of the availability of specimens of widely different ages. *Dasyurus albopunctatus* is the smaller of the two New Guinean species of quoll; its natural prey includes small mammals, birds, and reptiles, as well as insects (Flannery, 1990; Menzies, 1991). There is little information about the reproductive biology of New Guinean quolls, although their Australian congeners have been well studied in this respect (e.g., Fleay, 1940; Hill and Hill, 1955; Collins, 1973; Settle, 1978; Godsell, 1982, 1983; Edgar, 1983; Merchant et al., 1984; Bryant, 1988; Burnett, 2000). According to Menzies (1991), *D. albopunctatus* gave birth to 1–6 neonates that spent 2 months in the pouch and another 2 months in the den before dispersing; the lifespan is about 2 years (an indication of high mortality).

We analyzed an ontogenetic series of 31 specimens of *Dasyurus albopunctatus* in the mammal collection of the American Museum of Natural History (AMNH). The specimens examined were: AMNH 104044-5, 109407, 109410, 109416, 109418-20, 109424, 151971-6, 157081-4, 190924-9, 194704-7, 194709, and 221650. In our sample, nine specimens do not have a fully adult dentition, whereas the remaining individuals were adults of different sizes.

The smallest specimen (AMNH 190927; condylo-basal length 35.6 mm) has the lower (m3) and upper third molar (M3) erupting, and the lower (dp3) and upper deciduous premolar (dP3) present. The largest specimen (AMNH 151976, male) has a condylo-basal length of 66.2 mm. Although no temporal ontogenetic data are available for *D. albopunctatus*, some inference about the age of the specimens is possible based on data from *D. viverrinus* (Hill and Hill, 1955; Merchant et al., 1984). In *D. viverrinus*, tooth eruption begins at ~90 days and is completed at ~177 days (Nelson and Smith, 1971; Collins, 1973; Bryant, 1988). Our younger specimens, then, are clearly older than 90 days.

Study of Growth

Following previous studies (Abdala et al., 2001; Flores et al., 2003; Giannini et al., 2004), we took two descriptive approaches. First, we compared qualitative features of the skull of young specimens with those of fully adult specimens and described observed differences using anatomical terminology defined by Wible (2003). Second, we used 14 linear measurements representing important skull dimensions (Fig. 1) to estimate allometric growth of skull components (Giannini et al., 2004). Adult males of *Dasyurus albopunctatus* tend to be larger than adult females, but the difference is not statistically demonstrable at conventional α levels ($t = 1.81$, d.f. = 19, $P = 0.087$). Therefore, we pooled males and females in a single sample. For the study of allometry, we took a multivariate approach based on the generalization of the allometry equation proposed by Jolicoeur (1963a,b). In multivariate allometry, size is regarded as a latent variable affecting all measured variables simultaneously. The first eigenvector of a principal components analysis (PCA) expresses various allometric relationships of all variables with the latent size, provided that this vector is 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). For this purpose, we used a matrix of 14 variables by 31 specimens that had reliable measurements for all variables (no missing data). For a given variable, allometry is the statistical deviation of its corresponding eigenvector element with respect to a hypothetical isometric value that represents pure size change. That expected value under isometry is calculated as $1/p^{0.5}$ with p equal to the number of variables; i.e., 0.267 for the current study based on 14 variables.

Statistical departures from isometry were estimated using the application of jackknife (Que-nouille, 1956; Tukey, 1956; Manly, 1997) developed by Giannini et al. (2004; see Weston [2003] for a bootstrap alternative). Briefly (but see Giannini et al., 2004), the goal of the technique is to generate

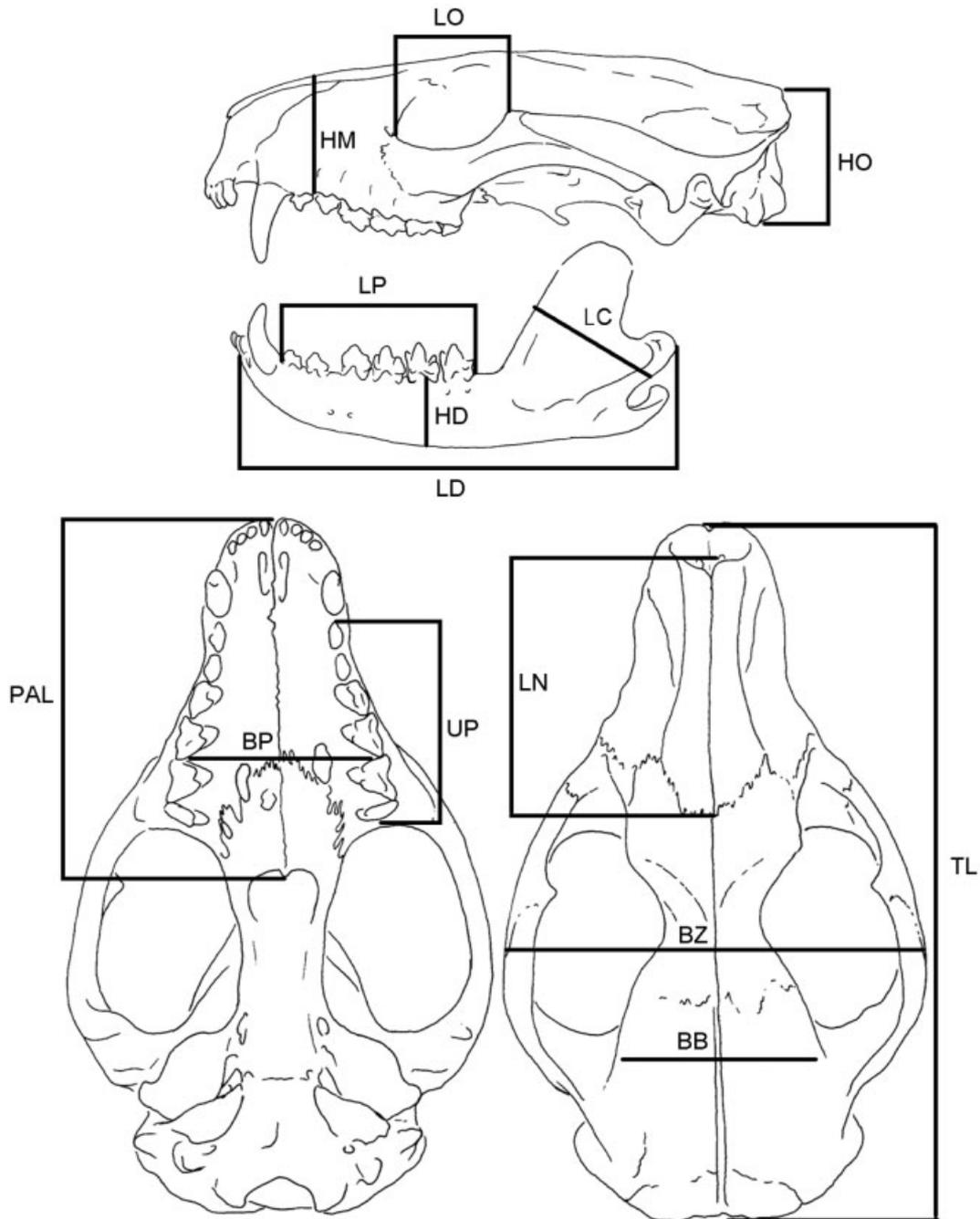


Fig. 1. Cranial measurements of *Dasyurus albopunctatus* used in this study. BB, breadth of braincase; BP, breadth of palate; BZ, zygomatic breadth; HD, height of mandibular body; HM, height of muzzle; HO, height of occipital plate; LC, length of coronoid process; LD, length of mandible; LN, length of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

confidence intervals for the empirically derived eigenvector elements. The confidence interval may be inclusive of the null value 0.267 and therefore indistinguishable from isometry, or may exclude such value and therefore can be considered significantly allometric: either positive if the observed element is >0.267 , or negative if the observed element is <0.267 . To that end, pseudosamples are generated

such that a new first unit eigenvector is calculated from a matrix with one individual removed at a time. Each time a pseudovalue for each element is calculated using the traditional formulation for the first-order jackknife:

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

where one pseudo-value $\hat{\epsilon}_{-j}^*$ corresponds to the removal of specimen j from the sample of size n , $\hat{\epsilon}$ is the observed element of the unit eigenvector that corresponds to the multivariate coefficient of allometry of the skull variable x , and $\hat{\epsilon}_{-j}$ is the value of the coefficient obtained with specimen j removed (terminology follows Manly, 1997). From the collection of 31 pseudo-values per variable, a mean is calculated for each variable, representing the jackknife estimate of the multivariate allometry coefficient for that variable. The difference between that estimate and the actual value from the complete sample is a measure of bias. The standard deviation and the corresponding 99% confidence interval (for $n - 1$ degrees of freedom) are calculated for each allometry coefficient.

Giannini et al. (2004) followed Manly (1997) in using trimmed values for the calculation of pseudo-values. For *Dromiciops gliroides*, trimming the m largest and m smallest pseudo-values (with $m = 1$) for each variable significantly decreased the standard deviations and allowed for more realistic allometric estimations (see Giannini et al., 2004). Here we report untrimmed as well as ($m = 1$) trimmed calculations, opting for the results with either lower average standard deviation or bias (see Allometry in Results and Discussion). The jackknife procedure was done partly manually and partly with the help of an NTSYS-pc 1.6 (Rohlf, 1990) batch file.

RESULTS AND DISCUSSION

Qualitative Trends

We identified 31 structures exhibiting ontogenetic changes between youngest and oldest specimens (summarized in Table 1). These include changes in the rostrum (4 characters), palatal region (5), orbitotemporal region (6), occiput (2), basicranial and auditory region (7), and mandible (7). Almost a third of those changes represent the appearance of structures absent in juveniles (characters 3, 6, 10, 12, 13, 15, 16, 18, 20, and 30 in Table 1). Another third of the changes imply completion or enlargement of structures already present in juveniles (characters 5, 8, 11, 17, 19, 21, 23, 25, 26, 27, and 28). A few changes imply the relative decrease in size or disappearance of some structures or relationships with advancing age (characters 2, 7, 9, 14, 31). Finally, some reorganizations occur (characters 1, 4, 22, 24, and 29).

A series of changes are indicative of an ontogenetic strengthening of the masticatory apparatus towards adulthood. These include changes related to the dentition, to the masticatory muscles, and to the temporomandibular joint (see in Table 2 and changes in articulations, below). For example, the paracanine fossa enlarges to receive the lower canine (character 3 in Table 1, Fig. 2B). When this tooth is fully emerged it barely diverges from the vertical and therefore must fit in the paracanine

fossa. The upper alveolar line is below the level of the root of the zygomatic arch (character 4, Fig. 2B), whereas a rearrangement occurs in the lower alveolar line: the lower molars are elevated with respect to the lower premolars (character 29, cf. Fig. 3A,B), the latter no longer occluding with the upper premolars (character 31). The canine is clearly the most developed element in the anterior dentition of the adult and there exist small spaces between canine and first premolar and also between the premolars. Osteological changes related to the muscle system are basically enlargements of areas of origin and insertion of the temporalis, masseter, and pterygoid muscles. In relation to the origins of the temporalis, the postorbital process appears in adults (character 10, Fig. 4B), as well as the sagittal (Figs. 2B, 4B), nuchal (Figs. 2B, 4B), and infratemporal crests (Fig. 5B; characters 15, 16, and 12, respectively). Of these, the nuchal crest experiences the most extreme change. This likely reflects the significance of the canine bite in *Dasyurus*, as the posterior fibers of the temporal muscle (which originate in the nuchal crest) are more important than anterior temporal fibers (which originate in the sagittal crest) in generating forces transmitted to the canines—a pattern only comparable to *Lutreolina* among the marsupials hitherto described by us (Flores et al., 2003). In relation to the masseter, its origin along the masseteric line of the jugal becomes strongly marked (character 13, Fig. 2B). Its insertion in the mandible is on the widened shelf of the masseteric fossa (character 27, Fig. 3B), which is reinforced by a lateral crest that becomes prominent in adults (character 28, Fig. 3D). Finally, the angular process markedly increases its robustness in adults, thereby increasing the surface for the insertion of the superficial masseter and internal insertion of the medial pterygoid muscles (character 25, cf. Fig. 3C,D). Also related to the feeding function, the paracondylar process of the exoccipital, origin of the posterior belly of the digastric muscle, becomes increasingly prominent in adults (character 17, Fig. 2A,B).

Modifications in the palate are noteworthy. First, the palatine openings (also known as “vacuities”) either appear (character 6 in Table 1, palatine fenestra, cf. Figs. 5B, 6B), increase in size (character 5, major palatine foramen, cf. Fig. 6A,B), or are reshaped into an almost closed structure (character 7, minor palatine foramen, cf. Fig. 6A,B) with advancing age. In general, the palatal openings are not as developed as in many marsupials (e.g., *Didelphis albiventris*; Abdala et al., 2001). Second, the palate is greatly strengthened caudally in adults by the development of a thickened postpalatine torus (character 8, Fig. 6).

We detected ontogenetic changes in most sutures, synchondroses, and synovial joints (Table 2). Precociously mature joints exhibit no change from the juvenile to the adult, presumably because their function is attained early in ontogeny. Precociously

TABLE 1. List of morphological changes detected in a comparison of smallest (youngest) and largest (oldest) specimens of *Dasyurus albopunctatus*

Characters	Figure	Juveniles	Adults
Rostrum			
1. Caudal extension of nasals	4	Reaching the lacrimal	Surpassing the lacrimal
2. Lacrimal foramen		Proportionally large	Proportionally small
3. Paracanine fossa	2	Absent	Large
4. Level of upper alveolar line	2	At zygomatic root	Ventral to zygomatic root
Palatine region			
5. Major palatine foramen	6	Rounded, small	Elongated, enlarged
6. Palatine fenestrae	6	Absent	Present, irregular
7. Notch for minor palatine nerve and vessels	6	Widely open	Notch almost closed ventrally
8. Postpalatine torus	6	Smooth	Sculptured ridge
9. Nasal spine	6	Prominent	Reduced
Orbitotemporal region			
10. Postorbital process	4	Absent	Prominent
11. Ethmoidal foramen		Incompletely enclosed by the frontal ventrally	Completely enclosed by the frontal
12. Infratemporal crest	5	Absent	Present
13. Masseteric line of jugal	2	Absent	Marked
14. Suprameatal foramen	2	Large	Minute
15. Sagittal crest	2, 4	Absent	Well developed
Occipital region			
16. Nuchal crest	2, 4	Absent	Well developed
17. Paracondylar process	2, 7	Blunt and short	Prominent
Basicranial and auditory regions			
18. Posttympanic process	2	Absent	Prominent
19. Basioccipital crest	7	Faint	Marked
20. Muscular tubercles on basicranium	7	Absent	Strong
21. Ectotympanic	7	Not widened laterally	Widened laterally
22. Alisphenoid-ectotympanic contact	7	Both bones juxtaposed	Alisphenoid abuts ectotympanic ventrolaterally
23. Alisphenoid strut	5	Present, thin	Present, well developed
24. Contact between postglenoid process and ectotympanic	7	Absent	Present
Mandible			
25. Angular process	3C, D	Thin	Robust
26. Mandibular foramen		Near caudal edge of ramus	In middle of ramus
27. Posterior shelf of the masseteric fossa	3C, D	Narrow	Greatly expanded laterally
28. Masseteric line of mandible	3A, B	Low, not marked	Forming a prominent ridge
29. Alveolar line of mandible	3A, B	Molars placed ventral to premolars	Molars displaced dorsally with respect to premolars
30. Retromolar space	3	Absent	Present
31. Occlusion of upper and lower premolars		Present	Absent

The characters are grouped by skull regions and numbered successively. When available, a reference is made to the figure(s) of the present study that show the structure.

mature joints are those designated as 3, 4, 12, 16, 17, 20, and 36 in Table 2. The overall trend of the ontogenetic transformations in the sutural pattern is obviously to increase structural strength and rigidity. First, in the cranium the synchondroses either fuse or their components come to a closer contact (joints 31–35), and the plane sutures form high crests (joints 5 and 7) or become serrated in the border (joint 1). Second, in the rostrum the border of the squamous sutures changes from simple to serrated (joints 22), and the plane sutures become serrated (joints 9, 10, 21, 24, 25, and 26). The palatine sutures (sutura palatina mediana et transversa) are a remarkable example of the latter (cf. Fig. 6A,B). And

third, in the union of rostrum and cranium (Fig. 4), the sutures involved become either serrated (joints 9, 10, and 23) or with serrated borders (joints 11 and 30). Finally, components of synovial joints (37 and 38) are reshaped to provide a firmer anchorage via transverse (in 37, Fig. 3C,D) or longitudinal (in 38, Fig. 2) enlargement of the mandibular condyles.

The changes in the temporomandibular joint (number 37 in Table 2) are noteworthy. The glenoid fossa is reshaped such that the contribution of the jugal to the fossa greatly increases in adults, whereas the postglenoid process and the mandibular condyle expand laterally (cf. Fig. 7A,B, Fig. 3C,D). In our interpretation, these changes in the temporomandibular joint, as well

TABLE 2. Ontogenetic changes in skull joints between smallest (youngest) and largest (oldest) specimens of *Dasyurus albopunctatus*

Joints	No.	Juveniles	Adults
Sutures			
occipitomastoidea	1	plane	slightly serrated
occipitoparietalis	2	plane	squamous
coronalis	3	squamous	squamous
squamosal	4	squamous	squamous
sagittalis	5	plane	raised in crest
sphenoparietalis	6	plane	squamous
interfrontalis	7	plane	raised in crest caudally
sphenofrontalis	8	slightly squamose	squamous
frontonasalis	9	plane	serrated
frontomaxillaris	10	plane	serrated
frontolacrimalis	11	squamous	squamous, caudal border foliate
frontopalatina	12	squamous	squamous
sphenopalatina	13	squamous, little overlap	squamous, large overlap
pterygosphenoidalis	14	squamous, little overlap	squamous, large overlap
temporozygomatica	15	squamous, little overlap	squamous, large overlap
incisivomaxillaris	16	foliate	foliate
nasoincisiva	17	plane	plane
vomeroincisiva	18	foliate, unfused	fused
interincisiva	19	plane, loose contact	plane, close contact
internasalis	20	plane	plane
nasomaxillaris	21	plane	serrated
lacrimomaxillaris	22	squamous, border simple	squamous, border serrated
zygomaticomaxillaris	23	foliate, border simple	foliate, border serrated
palatomaxillaris	24	plane	serrated
intermaxillaris	25	plane	serrated
palatine transversa	26	plane	serrated
vomeropalatina dorsalis	27	squamous, loose contact	squamous, close contact
pterygopalatina	28	squamous, unfused	squamous, fused
palatolacrimalis	29	squamous, border simple	squamous, border serrated
zygomaticolacrimalis	30	squamous, border simple	squamous, border serrated
Synchondroses			
spheno-occipitalis	31	unfused	fused
petro-occipitalis	32	unfused	close contact
intersphenoidalis	33	loose contact	close contact
intraoccipitalis	34	close contact	seamlessly fused
squamolateralis			
intraoccipitalis	35	close contact	seamlessly fused
basilateralis			
intermandibularis	36	close contact	close contact
Synovial joints			
Temporomandibular	37	Mandibular condyle rounded Glenoid process of jugal small Postglenoid process tapering to a point	Mandibular condyle laterally expanded Glenoid process of jugal large, contributing up to one-third of joint surface Postglenoid process greatly expanded mediolaterally
Atlanto-occipital	38	Lateral notch of postglenoid process absent Occipital condyle not elongated caudally	Lateral notch of postglenoid process present Occipital condyle elongated caudally

Articulations are grouped into sutures, synchondroses, and synovial joints, and numbered for reference in the text. Articulation names are in Latin following NAV (1994).

as the presence of the paracanine fossa, limit the rostrocaudal displacement and the transverse rotational movement of the mandible. A similar but less marked pattern has been reported for the large didelphids (e.g., *Didelphis* [Abdala et al., 2001] and *Lutreolina* [Flores et al., 2003]).

Allometry

The results of our multivariate analysis of allometric coefficients are given in Table 3. The mean difference in standard deviations of jackknife estimates between untrimmed (0.091) and trimmed

(0.071) appears to be negligible. However, the mean difference in absolute bias clearly favors untrimmed over trimmed values, with 0.004 average absolute bias for the former, and 0.017 for the latter (4.25 times higher). Therefore, as the jackknife was originally intended as a technique for bias removal (Quenouille, 1956; Manly, 1997), our interpretations are based on untrimmed values (cf. our results for *Dromiciops gliroides*; Giannini et al., 2003).

Three variables (length of palate, breadth of braincase, and height of occipital plate) are negatively allometric; three (length of coronoid process, height of mandible, breadth of zygoma) are posi-

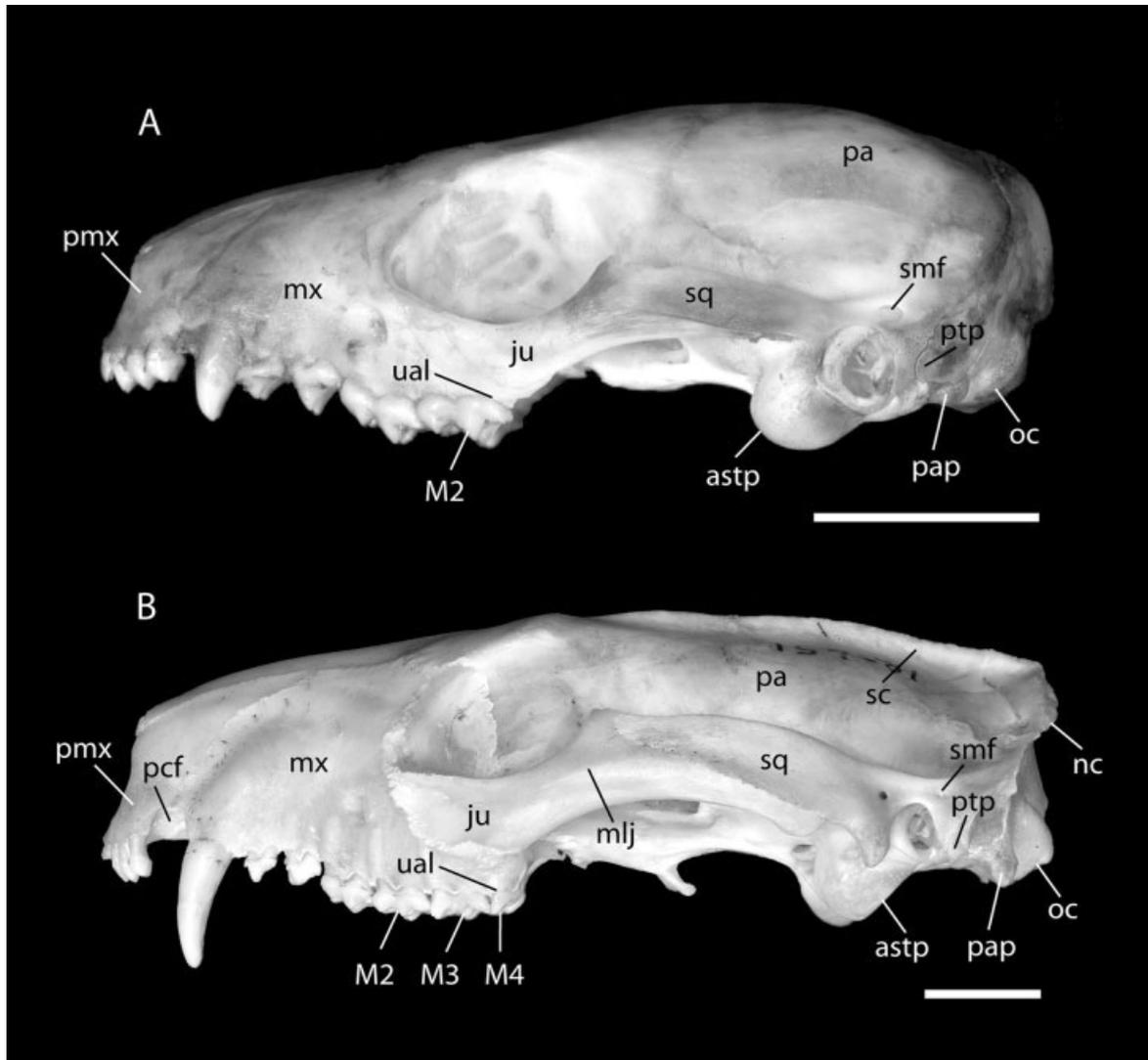


Fig. 2. Lateral view of the skull of young *Dasyurus albopunctatus* AMNH 151982 (A) and adult AMNH 157081 (B). astp, alisphenoid tympanic process; ju, jugal; M2, second upper molar; M3, third upper molar; M4, fourth upper molar; mlj, masseteric line of jugal; mx, maxilla; nc, nuchal crest; oc, occipital condyle; pa, parietal; pap, paracondylar process; pcf, paracanine fossa; pmx, premaxilla; ptp, posttympanic process; sc, sagittal crest; smf, suprameatal foramen; sq, squamosal; ual, upper alveolar line. Scale bars = 10 mm.

tively allometric; and the remaining eight variables scale isometrically with increasing general size. On the basis of these trends, we describe the postnatal skull growth in *Dasyurus albopunctatus* as follows.

Condylbasal length, a commonly employed index of cranial size, is ontogenetically isometric. The braincase grows at a slower pace than the skull, as do other measured neurocranial components, such as the height of the occipital plate. Thus, the two main dimensions of the braincase (height and breadth) share a markedly negative allometric growth of similar magnitude (jackknife coefficient for breadth of braincase is 0.111, and for height of occipital plate is 0.164, as compared with the null isometric value, 0.267). By contrast,

length of the orbit scales isometrically (see below; note that the orbit is negatively allometric when considering trimmed values; Table 3). The temporal space, which contains the temporalis muscle, expands both inward and outward, by the combination of the positive allometry of the zygomatic breadth with the negative allometry of the braincase breadth (cf. Fig. 4A,B). In relative terms, the palate shortens as the animal grows as the result of isometric width scaling and negative length scaling. However, two other dimensions of the facial skeleton, rostral height and length of nasals, scale isometrically. Both tooth rows grow at about the same relative rate as the skull, as does mandibular length. By contrast, vertical dimensions of the mandible grow relatively faster than the skull;

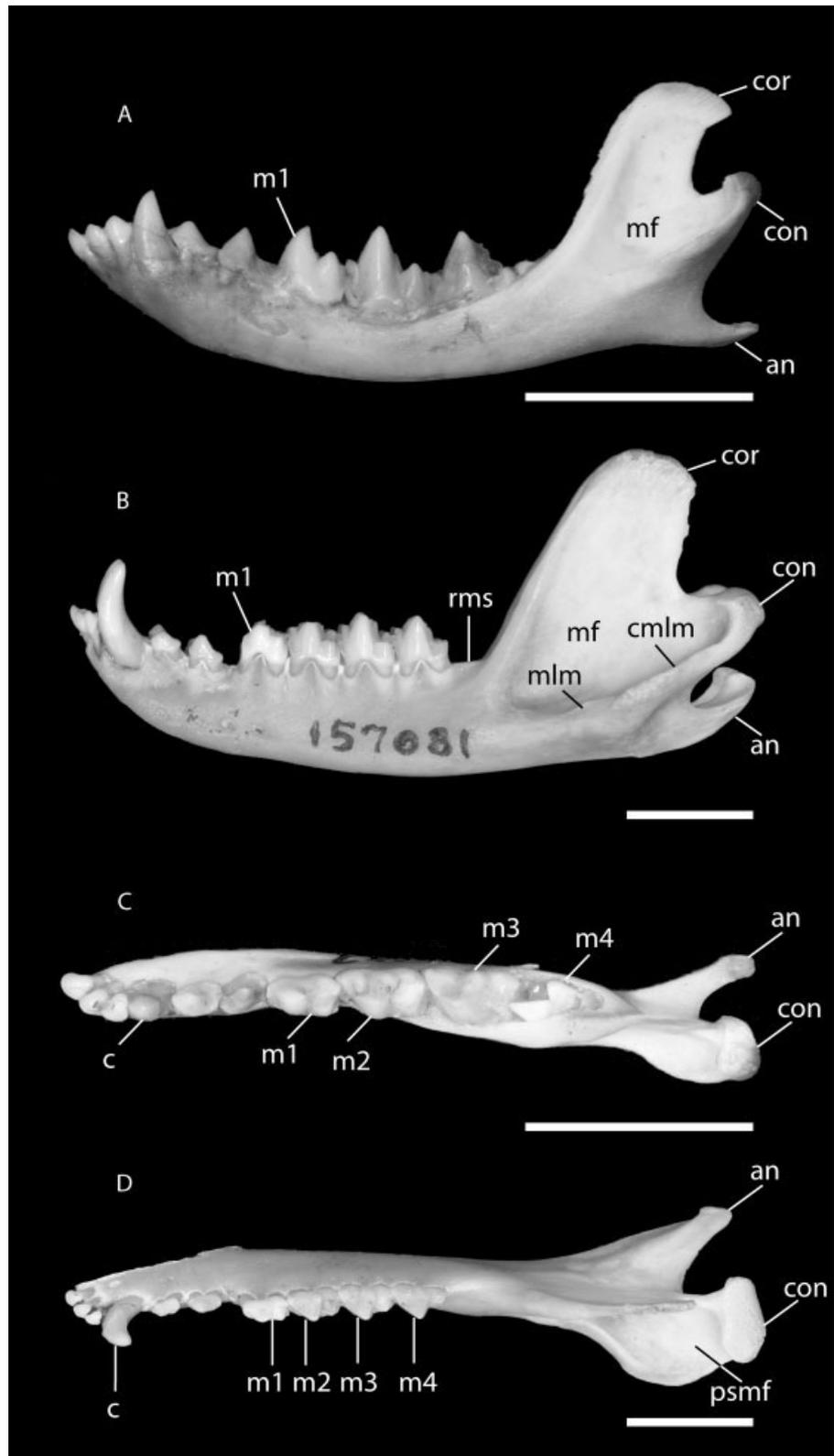


Fig. 3. Mandible of young *Dasyurus albopunctatus* AMNH 151982 in lateral (A) and occlusal view (C), and mandible of adult AMNH 157081 in lateral view (B), and occlusal view (D). an, angular process; c, lower canine; cmlm, crest of masseteric line of mandible; con, mandibular condyle; cor, coronoid process; m1, first lower molar; m2, second lower molar; m3, third lower molar; m4, fourth lower molar; mf, masseteric fossa; mlm, masseteric line of mandible; psmf, posterior shelf of masseteric fossa; rms, retromolar space. Scale bars = 10 mm.

in particular, the mandible becomes relatively more robust, and the coronoid process relatively longer (cf. Fig. 3A,B) in larger animals.

Although sexual dimorphism is statistically non-significant in our small sample (see Materials and Methods), adult males tend to be larger than adult

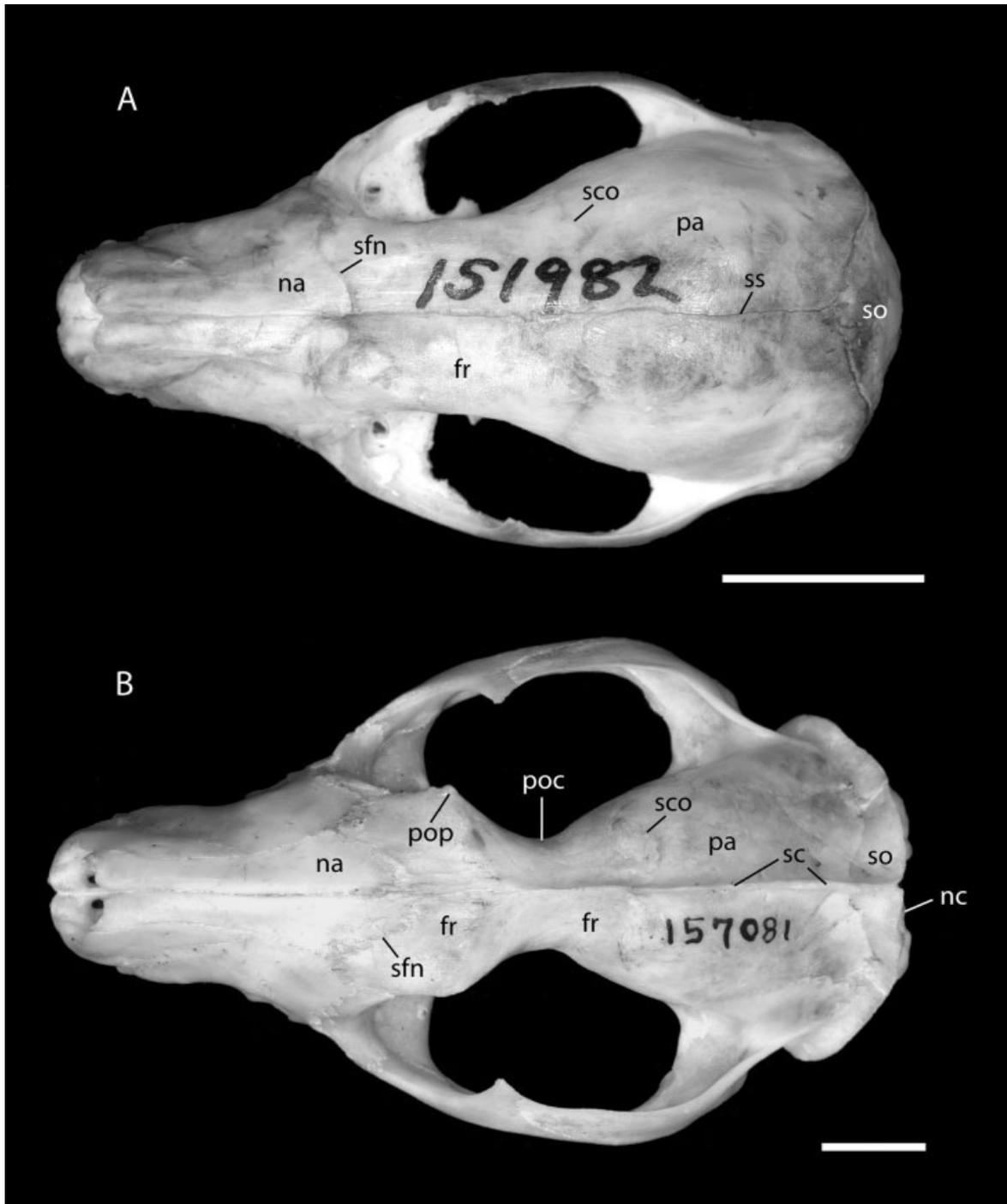


Fig. 4. Dorsal view of the skull of young *Dasyurus albopunctatus* AMNH 151982 (A) and adult AMNH 157081 (B). fr, frontal; na, nasal; nc, nuchal crest; pa, parietal; poc, postorbital constriction; pop, postorbital process; sc, sagittal crest; sco, sutura coronalis; sfn, sutura frontonasalis; so, supraoccipital; ss, sutura sagittalis. Scale bars = 10 mm.

females (Fig. 8). We deemed it unnecessary to statistically test for a change in slope or position between curves for males and females given, first, the close fit of the common curve to the data points from the pooled sexes and, second, our limited sample size. In effect, we assume that *Dasyurus albopunc-*

tatus exhibits parallel growth trajectories for both sexes without vertical curve displacement (i.e., identical y-intercept), such that there are no growth-invariant shape differences between males and females. Of course, there may be differences in average shape between like-aged males and fe-

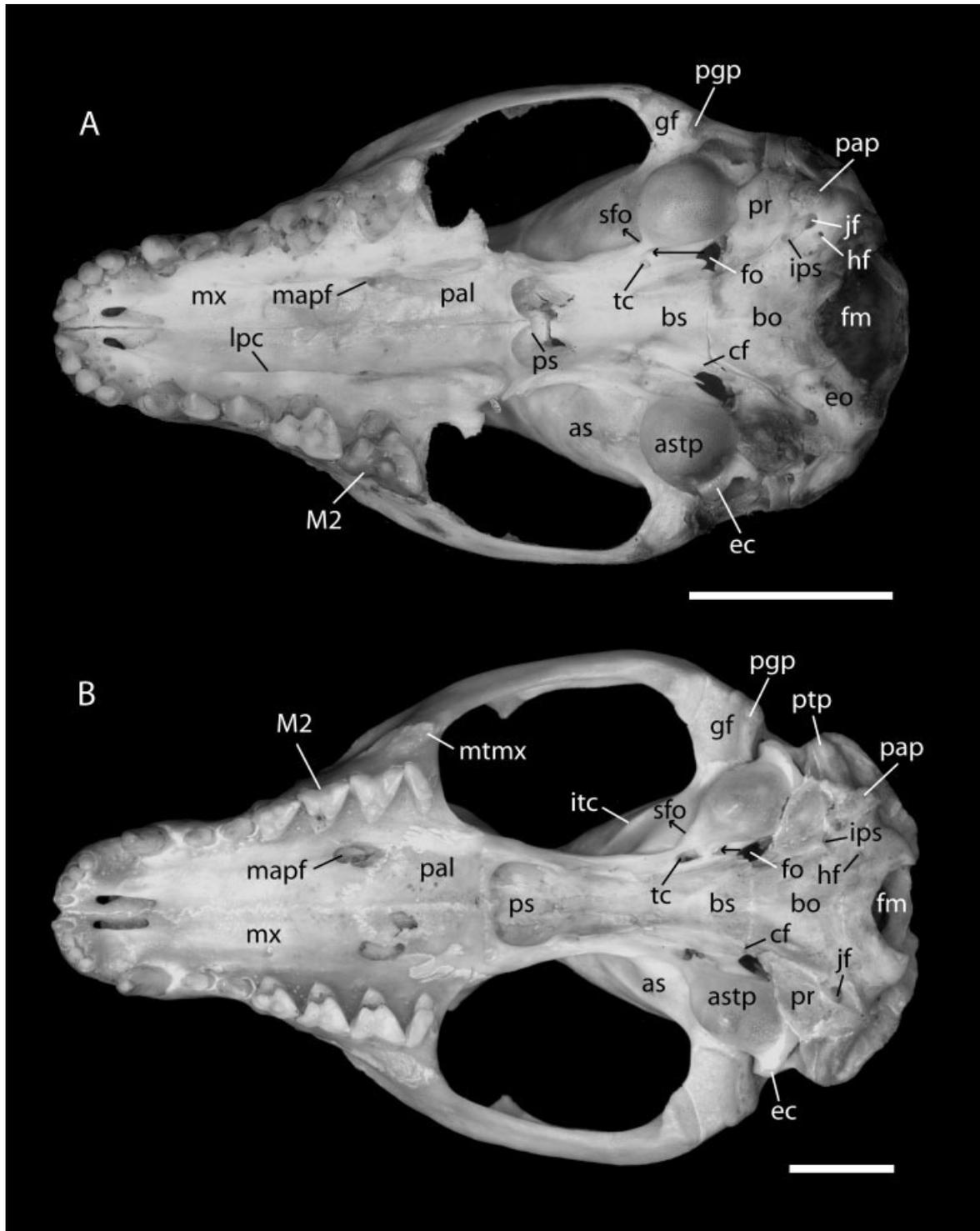


Fig. 5. Ventral view of the skull of young *Dasyurus albopunctatus* AMNH 151982 (A) and adult AMNH 157081 (B). as, alisphenoid; astp, alisphenoid tympanic process; bo, basioccipital; bs, basisphenoid; cf, carotid foramen; ec, ectotympanic; eo, exoccipital; fm, foramen magnum; fo, foramen ovale; gf, glenoid fossa; hf, hypoglossal foramen; ips, foramen for the inferior petrosal sinus; itc, infratemporal crest; jf, jugular foramen; lpc, lateral palatine crest; M2, second upper molar; mapf, major palatine foramen; mtmx, masseteric tuberosity of maxilla; mx, maxilla; pal, palatine; pap, paracondylar process; ppp, postglenoid process; pr, promontorium of the petrosal; ps, presphenoid; ptp, posttympanic process; sfo, secondary foramen ovale; tc, transverse canal. Arrows indicate the course of the mandibular division of the trigeminal nerve (V^3) between the primary and secondary foramen ovale. Scale bars = 10 mm.

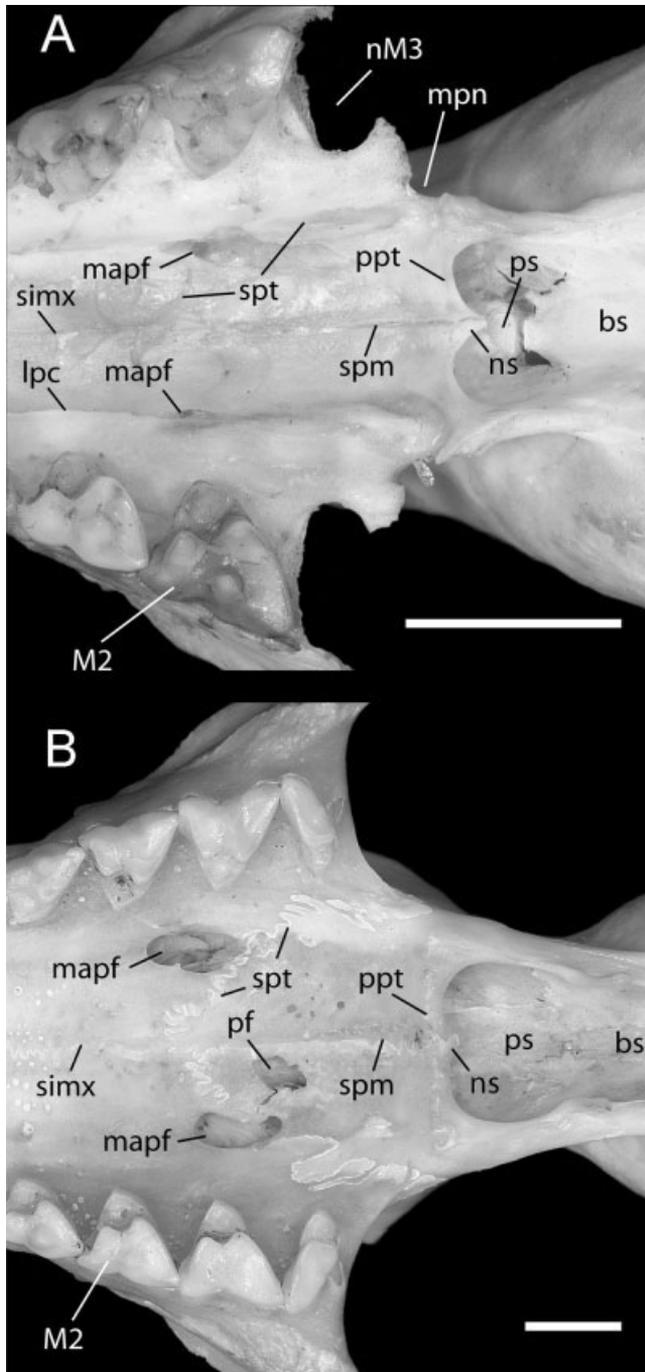


Fig. 6. Posterior portion of the palate of young *Dasyurus albopunctatus* AMNH 151982 (A) and adult AMNH 157081 (B). bs, basisphenoid; lpc, lateral palatine crest; mapf, major palatine foramen; mpn, minor palatine notch; nM3, notch for upper third molar; ns, nasal spine; pf, palatine fenestra; ppt, posterior palatine torus; ps, presphenoid; simx, sutura intermaxillaris; spm, sutura palatina mediana; spt, sutura palatina transversa. Scale bars = 5 mm.

males, but these appear to be due primarily to the increased size of males. Either females grow more slowly than males, or males prolong growth, or both.

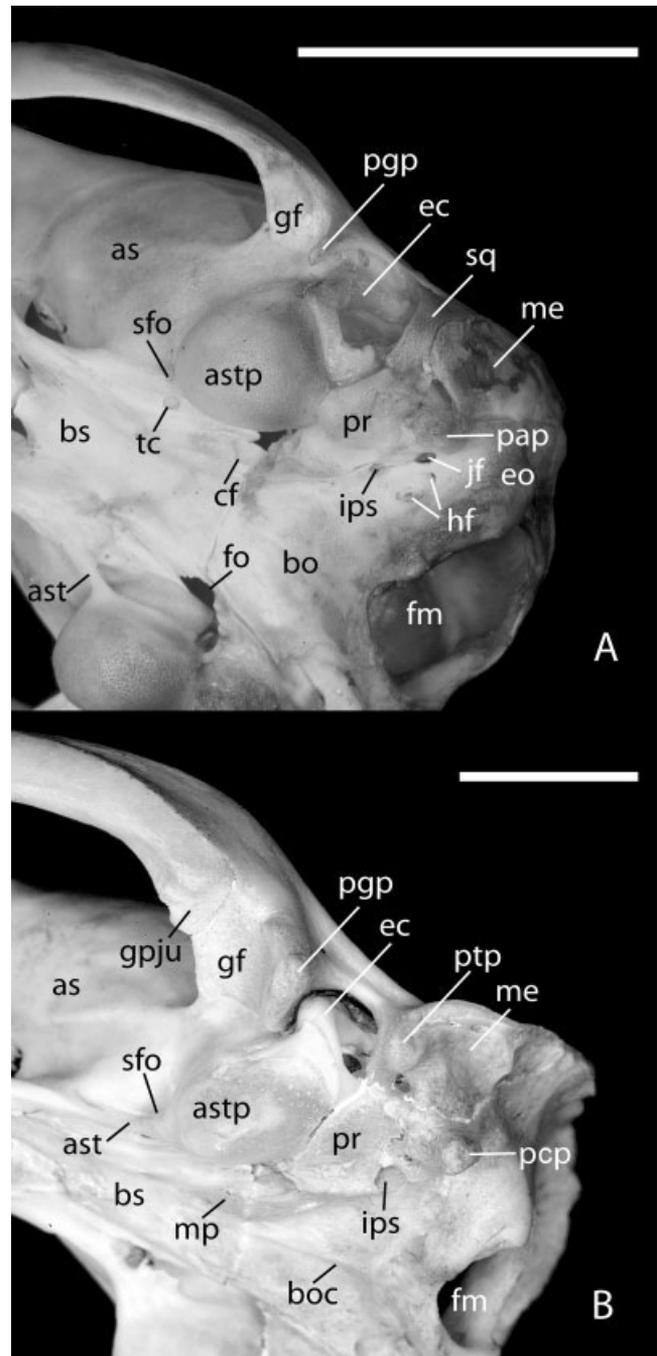


Fig. 7. Oblique (caudolateroventral) view of young *Dasyurus albopunctatus* AMNH 151982 (A) and adult AMNH 157081 (B). as, alisphenoid; ast, alisphenoid strut; astp, alisphenoid tympanic process; bo, basioccipital; boc, basioccipital crest; bs, basisphenoid; cf, carotid foramen; ec, ectotympanic; eo, exoccipital; fm, foramen magnum; fo, foramen ovale; gf, glenoid fossa; gpju, glenoid process of jugal; hf, hypoglossal foramen; ips, foramen for the inferior petrosal sinus; jf, jugular foramen; me, mastoid exposure; mp, muscular process; pap, paracondylar process; pgp, postglenoid process; pr, promontorium of petrosal; ptp, posttympanic process; sq, squamosal; tc, transverse canal. Scale bars = 10 mm.

TABLE 3. Results of the multivariate analysis of cranial allometry in *Dasyurus albopunctatus*

Variables	Expected allometry coefficient	Observed allometry coefficient	Observed departure	Untrimmed values				Trimmed values				Growth trend
				Resampled allometry coefficient	Bias	99% Confidence Interval	Growth trend	Resampled allometry coefficient	Bias	99% Confidence Interval	Growth trend	
Total length	0.267	0.261	-0.006	0.260	-0.001	0.241-0.279	=	0.244	-0.016	0.229-0.259	=	-
Length of nasals	0.267	0.291	0.024	0.298	0.006	0.247-0.349	=	0.273	-0.025	0.228-0.317	=	=
Height of muzzle	0.267	0.291	0.024	0.293	0.002	0.245-0.341	=	0.282	-0.012	0.244-0.319	=	=
Length of palate	0.267	0.223	-0.044	0.226	0.004	0.199-0.254	-	0.210	-0.017	0.188-0.231	-	-
Breadth of palate	0.267	0.236	-0.031	0.236	-0.001	-0.195-0.277	=	0.223	-0.013	0.190-0.256	=	-
Length of upper postcanine row	0.267	0.227	-0.040	0.222	-0.005	0.159-0.284	=	0.208	-0.014	0.154-0.262	=	-
Length of lower postcanine row	0.267	0.243	-0.024	0.236	-0.007	0.157-0.316	=	0.220	-0.016	0.181-0.259	=	-
Length of mandible	0.267	0.289	0.022	0.287	-0.002	0.256-0.318	=	0.270	-0.017	0.243-0.298	=	=
Height of mandible	0.267	0.413	0.146	0.409	-0.004	0.358-0.459	+	0.383	-0.026	0.342-0.424	+	+
Height of coronoid process	0.267	0.327	0.060	0.340	0.013	0.279-0.401	+	0.319	-0.021	0.274-0.365	+	+
Breadth of zygoma	0.267	0.312	0.045	0.308	-0.003	0.281-0.336	+	0.290	-0.019	0.267-0.313	+	(+)
Breadth of braincase	0.267	0.111	-0.156	0.104	-0.006	0.075-0.134	-	0.098	-0.006	0.076-0.120	-	-
Height of occipital plate	0.267	0.164	-0.103	0.165	0.001	0.127-0.203	-	0.156	-0.009	0.124-0.187	-	-
Length of orbit	0.267	0.220	-0.047	0.219	-0.001	0.153-0.285	=	0.200	-0.019	0.148-0.253	=	-

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 pseudovalue (see Materials and Methods). Allometry coefficient is the correspondent element of the first (unit) eigenvector per variable. The expected coefficient (0.267) is the value under isometry (equal for all variables). The observed coefficient is the value obtained with all specimens included ($n = 31$). The resampled coefficient is the first-order jackknife value. Bias is the difference between the resampled and observed coefficients. The jackknife 99% confidence interval is provided; allometric variables are those whose confidence interval 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, (+) positive allometric trend.

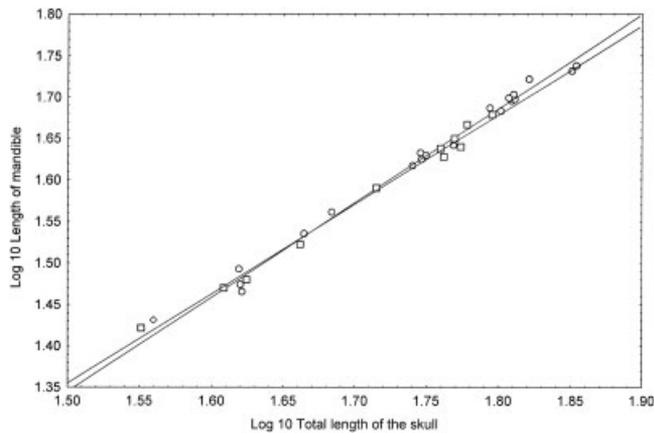


Fig. 8. Bivariate scatterplots of mandible length on condylo-basal length in males *Dasyurus albopunctatus* (circles) and females (squares). The diamond indicates a specimen of unknown sex.

Whatever the causes of the difference graphed in Figure 8, males clearly proceed further than females along a growth trajectory seemingly common to both sexes.

Comparative Growth

Allometric trends obtained in the different marsupials species sampled to date are compared in Table 4. The same trends are shared by all of them in three variables: the height of the mandible (positive allometry) and the breadth of the braincase and height of the occipital plate (both with negative allometry). These shared trends can be interpreted as present in the marsupial ancestor.

Two allometric trends are exclusively shared by *Dasyurus albopunctatus* and *Dromiciops gliroides*, the only other australidelphian studied using the

same methods to date. These are the isometry of the length of upper postcanine row (see below) and the isometry of the orbit (Table 4). Regarding the last trend, Giannini et al. (2004) reported the surprising finding that the orbit in *D. gliroides* scales isometrically with overall cranial growth—a feature in contrast not only with *Didelphis albiventris* and *Lutreolina crassicaudata*, but also with most vertebrates, in which the orbit typically is negatively allometric (Emerson and Bramble, 1993). In *D. albopunctatus* the orbit is similarly isometric when the allometry coefficient is calculated using untrimmed values (see above; Table 3), suggesting that this unusual feature may be common to other australidelphians as well.

Dasyurus albopunctatus departs from the scheme found in the other marsupials studied in a very significant way, insofar as the palatal length, palatal breadth, and zygomatic breadth show a markedly different allometric pattern (Table 4). The morpho-functional interpretation that we propose to explain these changes is as follows. In *D. albopunctatus* the space for the m. temporalis increases both by means of the negative allometry of the braincase (as in the other species compared) and the positive allometry of zygomatic breadth (isometric in the other species compared; see Fig. 4). Because of the last trend, the zygomatic arches of adults of *D. albopunctatus* are clearly more expanded laterally than in the other species studied so far. Regarding the other trends, the combined effect of negative allometry of palatal length (isometric in the other species compared) and isometry of the palatal breadth (negatively allometric in the other species compared) renders the palate short and broad in older animals, a morphology that visually characterizes all species in this genus (Fig. 5). These differences point to an emphasis on developing a strong bite, as they favor large temporal and masseteric muscles loading on a shortened tooth row

TABLE 4. Allometric comparison of *Dasyurus albopunctatus* (this study) with *Didelphis albiventris* (Abdala et al., 2001), *Lutreolina crassicaudata* (Flores et al., 2003), and *Dromiciops gliroides* (Giannini et al., 2004)

Variables	<i>Didelphis</i>	<i>Lutreolina</i>	<i>Dromiciops</i>	<i>Dasyurus</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	-	-	=	=

^aDifferent value depending on method used (see Flores et al., 2003). Symbols for isometry, negative allometry, and positive allometry, are =, -, and +, respectively. Parentheses indicate allometric trends. Underline indicate, similar allometry trends across species.

(in *Dasyurus* the canine is, compared to other marsupials, closer to the fulcrum). This is especially remarkable when considered together with the changes related to the dentition, cranial crests, and temporomandibular joint described above, and is likely connected with the carnivorous habits reported for quolls (Flannery, 1990; Menzies, 1991) as well as other dasyurids (e.g., Blackhall, 1980; Pellis and Nelson, 1984; Jones and Rose, 2001; Jones et al., 2001).

Finally, it is interesting to discuss the trends of the postcanine row lengths. Both upper and lower postcanine row lengths are isometric in *Dasyurus albopunctatus*. In the first case, the trend is shared with *Dromiciops gliroides*, while the isometry of the lower postcanine length departs from our previous studies. This measurement was found to be negatively allometric in *Didelphis albiventris* and *D. gliroides*, or is inconclusive (i.e., it produced different trends with different methods), as in *Lutreolina crassicaudata* (see Table 4). The length of the postcanine row is involved in the mutual adjustment of the lower and upper tooth rows during growth. Abdala et al. (2001) described a pattern in *D. albiventris* by which the upper tooth row has a faster growth rate than the lower toothrow, the latter always having one tooth more than the upper toothrow until all teeth emerge. This pattern was confirmed in *L. crassicaudata* (Flores et al., 2003). *Dasyurus albopunctatus* exhibits the same pattern of tooth emergence, but, by contrast, showed isometry of the length of upper and lower tooth rows. The postcanine series of *D. albopunctatus* show only two premolars, differing from the other marsupials studied so far, which display three premolars. This dissimilarity in premolar numbers (plus the presence of a long diastema between the first and second premolar in *D. albiventris*) is likely related to the different trends of *D. albopunctatus* for these variables in relation to didelphids. On the other hand, the isometry in the upper postcanines length of *D. gliroides* has apparently no connection with the number of premolars in the dentition.

CONCLUSIONS

Dasyurus albopunctatus exhibits some allometry trends already observed in three other species of marsupials (two didelphids and a microbiotheriid), but it also shares some trends uniquely with the only other australidelphian examined (the microbiotheriid *Dromiciops*), and it has a suite of trends not shared with any previously studied marsupials. We relate these allometry trends, together with the changes in qualitative traits and cranial sutures, with an overall strengthening of the skull and the development of a skull shape that favors a strong bite. As we are dealing with weaned individuals, those changes can be associated with the shift from milk suckling to an active feeding. Some of the

trends found in *Dasyurus albopunctatus* can be interpreted as a function of a distinctly carnivore feeding system in the adult.

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