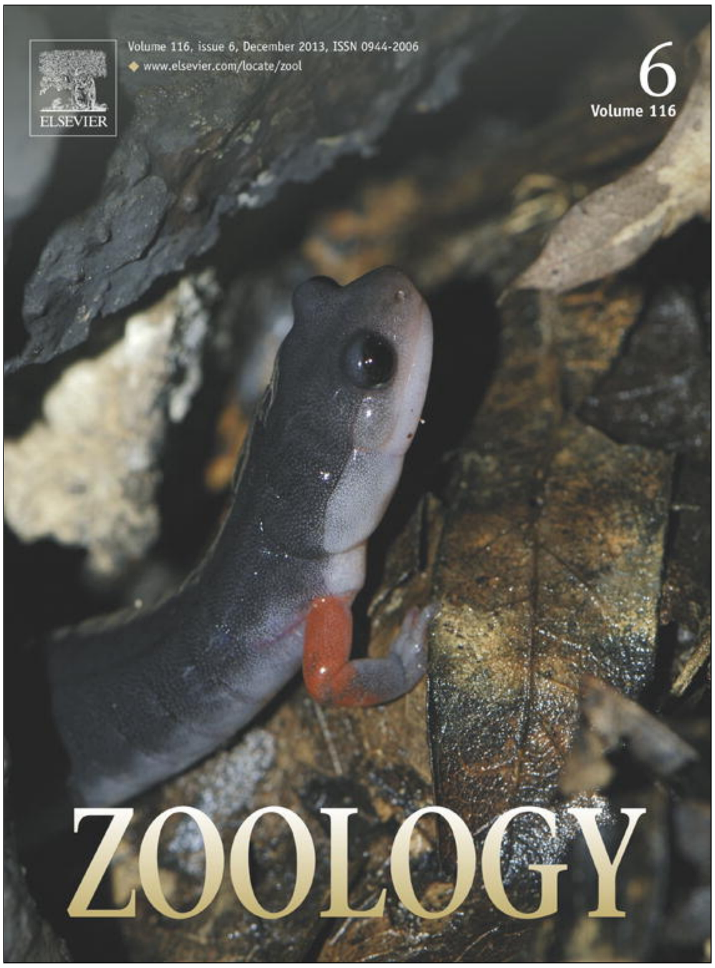
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Post-weaning cranial ontogeny in two bandicoots (Mammalia, Peramelomorphia, Peramelidae) and comparison with carnivorous marsupials

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ABSTRACT

The ontogeny of the skull has been studied in several marsupial groups such as didelphids, microbiotheriids, and dasyurids. Here, we describe and compare the post-weaning ontogeny of the skull in two species of bandicoots, *Echymipera kalubu* (Echymiperinae) and *Isoodon macrourus* (Peramelinae), analyzing specific allometric trends in both groups, describing common (and specific) patterns, and discussing them on functional and phylogenetic grounds. Growth patterns were analyzed both qualitatively and quantitatively, including bivariate and multivariate analyses of allometry. We also evaluated character transformation and phylogenetic signals of the allometric patterns in several groups of marsupials and some placentals. We identified morphological changes between juvenile and adult stages in both species of peramelids, many related to the development of the trophic apparatus. Notable differences were detected in the patterns of growth, suggesting divergences in ontogenetic trajectories between both species. Both bivariate and multivariate methods indicate that positive allometries in *E. kalubu* apply to longitudinal dimensions, whereas in *I. macrourus*, positive allometries are restricted to vertical dimensions of the skull. The comparison of the allometric trends of two bandicoots with previously studied taxa reveals that although peramelids exhibit a particularly short gestation period and divergent morphology compared to other marsupials, their pattern does not show any particular trend. Some allometric trends seem to be highly conserved among the species studied, showing weak phylogenetic signal. Marsupials in general do not show particular patterns of post-weaning skull growth compared with placentals.

1. Introduction

Bandicoots form an ancient clade considered among the most basal living marsupials from Australia and New Guinea (Meredith et al., 2008; Westerman et al., 2012). Although general features clearly indicate they are australidelphians, bandicoots exhibit a peculiar combination of traits which seem related to dasyurids, diprotodonts (Szalay, 1982, 1994), or American marsupials (Archer, 1976a,b). Bandicoots are syndactylous, like Diprotodontia, but their dentition is polyprotodont as in Dasyuromorpha and Ameridelphia (Nowak, 2005). Tarsal (Szalay, 1982) and sperm morphology (Hughes, 1965), as well as genetic evidence (e.g. Reteif et al., 1995; Asher et al., 2004; Baker et al., 2004; Beck, 2008; Meredith et al., 2008) indicate that bandicoots are basal australidelphians close to Dasyuromorpha. Bandicoots have a closer resemblance to another ancient group, the American caenolestids (Reteif et al., 1995; Krajewski et al., 1997; Palma and Spotorno, 1999), than to any other Australian marsupials (e.g., Asher et al., 2004), a fact already observed by Osgood (1921). Although the oldest fossil bandicoot came from the Late Oligocene of Australia (Travouillon et al., 2013), modern bandicoots are known only as far back as the Pliocene epoch, about 5 million years ago (Muirhead, 1999). One of the most important characters that define the group is the complex chorioallantoic placenta (Hughes et al., 1990; Tyndale-Biscoe, 2005), in which cells invade and fuse with the uterine wall, as in many placental mammals. This feature is quite likely functionally correlated with the rapid rate of development characteristic of peramelids (Gordon and Hulbert, 1989). Skull morphology and dentition in peramelids have been described in detail in taxonomic studies (e.g., Freedman and Joffe, 1967a,b; Freedman and Rightmire, 1971; Archer, 1976a; Dixon, 1981; Lyne and Mort, 1981; Flannery, 1990; Groves and Flannery, 1990; Aplin et al., 2010), and within a comparative framework of the basicranial anatomy (e.g., Archer, 1976b; Archer and Kirsch, 1977). In contrast, little is known about their skull development, as opposed to other marsupials and placentals recently studied in the context of allometry of growth (e.g.,

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Abdala et al., 2001; Flores et al., 2003, 2006, 2010; Giannini et al., 2004, 2010; Flores and Casinos, 2011; Segura and Prevosti, 2012; Tarnawski et al., 2013). The scarce ontogenetic data published for this group mostly deals with aging of specimens on the basis of tooth eruption (e.g., Kingsmill, 1962; Lyne, 1964, 1974; Lyne and Mort, 1981).

Here we report results of a comparative study of skull growth in two species of peramelids belonging to two different subfamilies, *Echymipera kalubu* (Echymiperinae) and *Isoodon macrourus* (Peramelinae), focusing on the functional framework of the splanchnocranium and neurocranium, as well as their interactions. This new information may shed light on the particulars of development in peramelids, and also provide data useful for a comparative framework in the context of the development of mammals with rapid growth. To this end, we integrated our data with the cranial ontogenetic patterns previously detected in both neotropical and australidelphian marsupials, as well as some placental representatives (Carnivores and Primates), thus providing a broader perspective on marsupial post-weaning skull ontogeny. Ontogenies may supply a great amount of phylogenetic information on marsupials even though their use is limited in comparison to placentals due to the early development of cranial structures (Lillegraven, 1975).

2. Materials and methods

2.1. The studied groups and species

Extant bandicoots are small to medium-sized animals widely distributed in Australia and New Guinea. They are the only syndactylous group of polyprotodontian marsupials (Lyne, 1990) comprising omnivorous species that eat insects, other invertebrates, underground fungal fruiting bodies, as well as grasses, seeds and plant roots (Gordon and Hulbert, 1989). As successful opportunists, they respond to favorable conditions with a rapid rate of reproduction (Lee and Cockburn, 1985; Gordon and Hulbert, 1989), exhibiting a short gestation period, rapid development of pouch young, minimal parental care, and early sexual maturity (Gordon, 1971; Hall, 1990). *Isoodon* and *Echymipera* belong to the two most speciose peramelid monophyletic groups: Peramelinae with seven species and Echymiperinae with nine species (e.g., Westerman et al., 1999, 2001; Cardillo et al., 2004; Groves, 2005; Meredith et al., 2008). The other clades (i.e., Thylacomyidae and Chaeropodidae; Westerman et al., 2012) remain largely unstudied to date, because good ontogenetic series can rarely be found in collections.

The gestation period of *I. macrourus* and *E. kalubu* is approximately 12.5 days. The development in the former species lasts ∼50 ± 7 days (Hall, 1990), whereas there is no information for *E. kalubu*. *I. macrourus* is weaned at an age of 2 months (Gemmell, 1982; Gemmell and Johnston, 1985; Hall, 1990) and the individual's first reproductive event is at 4 months old (Heinsohn, 1966). The same timing has also been suggested for other species in the group (e.g., *Isoodon obsoletus*: Stoddart and Braithwaite, 1979; *Perameles gunni*: Heinsohn, 1966; *Perameles nasuta*: Hughes, 1962; Lyne, 1971; Lyne and Hollis, 1979), which indicates that this particular breeding strategy is likely prevalent in the group.

2.2. Study specimens

We studied an ontogenetic series of 52 specimens of *E. kalubu* (29 males, 16 females and 7 specimens of unknown sex) and 58 specimens of *I. macrourus* (32 males, 21 females and 5 specimens of unknown sex) housed in the mammal collections of the American Museum of Natural History (AMNH) and the Smithsonian Institution (USNHM) (see Table S1 in the supplementary online Appendix). In our sample, 12 specimens of *E. kalubu* and 19 of *I. macrourus* were collected young before reaching the stage of full adult dentition. The smallest specimens of *E. kalubu* (AMNH 109733, male, condylo-incisive length of 37.11 mm) and *I. macrourus* (AMNH 160445, sex undetermined, condylo-incisive length of 35.96 mm) had the third lower molars (m3) erupted, the second upper molars (M2) erupting, and the small third lower (dp3) and upper (dP3) deciduous premolars present. The largest specimen of *E. kalubu* (AMNH 151877, male) measured 81.47 mm for condylo-incisive length, whereas the largest specimen of *I. macrourus* (USNHM 547635, male) measured 85.63 mm. Thus, in our samples the smallest individual was less than one-half of the maximum adult size for both species (46% for *E. kalubu* and 41% for *I. macrourus*). Larger specimens of both species exhibited molars with severe cusp wear. On the basis of known sequences of tooth emergence and wear (e.g., Kingsmill, 1962; Lyne, 1964, 1974; Lyne and Mort, 1981), our youngest specimens in both species were approximately 2 months old. Although adults of *I. macrourus* are larger than those of *E. kalubu* (see Smith et al., 2003), the smallest specimens in both samples were similar in size and dental formula.

2.3. Growth study

Following our previous studies on marsupials (Abdala et al., 2001; Flores et al., 2003, 2006, 2010; Giannini et al., 2004), we took two descriptive approaches. First, we compared qualitative features of the skull of young specimens with those of full adults within each species, and described observed differences using the anatomical terminology of Wible (2003). Second, we used 15 linear measurements (see Fig. 1) to estimate allometric growth in skulls. In both species, males tend to be larger than females of comparable age (Aplin et al., 2010), as shown by variables such as the condylo-incisive length measured in selected adults of our sample (*E. kalubu*: $t = 9.17$, d.f. = 20, $P < 0.01$; *I. macrourus*: $t = 6.8$, d.f. = 18, $P < 0.01$). However, both males and females clearly shared the same ontogenetic trajectory (non-significant slope and intercept differences in bivariate analyses of selected variables). Therefore, within each species we pooled the samples of males and females of all ages.

As in our previous reports, we used bivariate and multivariate analyses to estimate growth trends. In bivariate analyses, the scaling of any measurement can be affected by the choice of the independent variable (Smith, 1981; Wayne, 1986). Because our multivariate analyses indicated that the total length of the skull, or the condylo-incisive (= condylobasal) length (CIL) was isometric, it was taken as an indicator of size and used as independent variable in bivariate allometry. We used linear ($\log_{10}$) transformation of the power equation of growth for each variable (see Abdala et al., 2001 for details of this approach) and tested deviations from isometry by means of 2-tailed *t*-tests, after corroborating that the independent variable was normally distributed (Shapiro–Wilk test, *E. kalubu*: $w = 0.938$, $P = 0.44$; *I. macrourus*: $w = 0.966$, $P = 0.58$). Statistically significant deviations from isometry represent cases of "negative" allometry if $b_1 < 1.0$ and "positive" allometry if $b_1 > 1.0$. We used reduced major axis regression (RMA) (Abdala et al., 2001; Flores et al., 2003) and followed Warton et al. (2006) in using a likelihood ratio test for the common RMA slope, comparing it to a chi-squared distribution (Warton and Weber, 2002). If the species shared a common slope, we compared the significance of the common normalization constant (*y*-intercepts) using the Wald test (as described in Warton et al., 2006). All these regression coefficients, statistical parameters, and tests were performed using the SMATR package of R (Warton and Weber, 2002).

Multivariate coefficients of allometry were obtained from principal component analysis (PCA) based on a variance–covariance matrix of $\log_{10}$ transformed data (Jolicoeur, 1963). We tested the

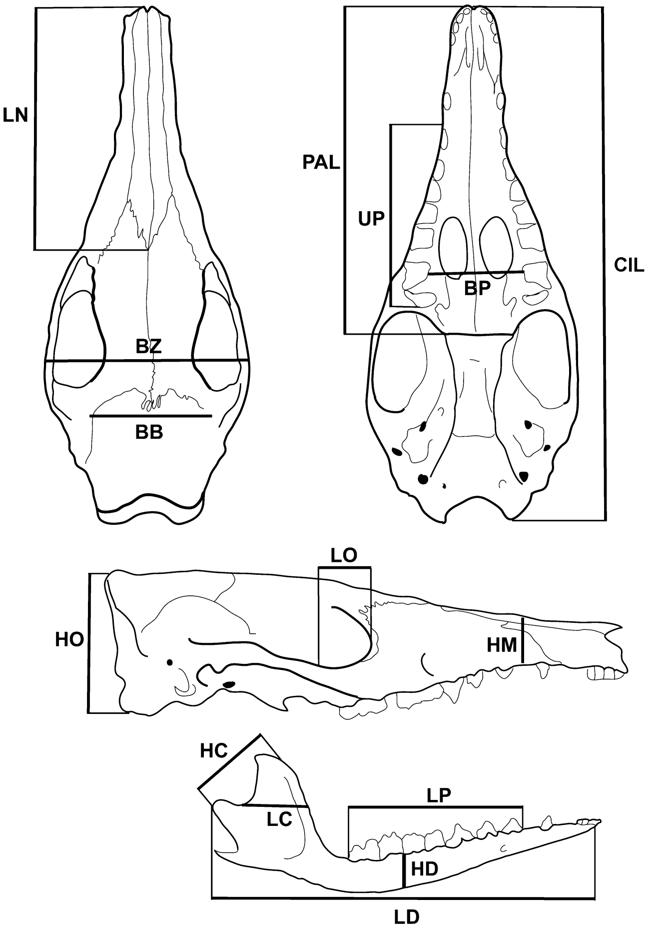

Fig. 1. Cranial measurements used in this study. *Abbreviations*: BB, breadth of braincase; BP, breadth of palate; BZ, zygomatic breadth; CIL, condylo-incisive length of the skull; HC, height of coronoid process; HD, height of dentary; HM, height of muzzle; HO, height of occipital plate; LC, length of coronoid process; LD, length of mandible; LN, length of nasals; LO, length of orbit; LP, length of lower post-canine row; PAL, length of palate; UP, length of upper post-canine row.

significance of multivariate coefficients of allometry with a resampling strategy using jackknife pseudovalues to generate confidence intervals (CIs) for the original coefficients (see Giannini et al., 2004 and Flores et al., 2006 for details of this method). Under isometry, an expected value for all multivariate coefficients of allometry, which depends only on the number of variables (p), is calculated as $1/p^{0.5}$ and so equals 0.258 for our set of 15 variables. Here we report untrimmed and trimmed calculations, but opting for the results with either lower average standard deviation or lower bias. Trimming the largest and smallest m pseudovalues (with $m = 1$) for each variable significantly decreased the standard deviations and allowed for more realistic allometric estimations.

For the bivariate analyses the computer program PAST (Hammer et al., 2001) was used. For the multivariate statistical analyses (PCA + jackknife resampling) the R-script of Giannini et al. (2010) was used and is available from the authors.

2.4. Comparative analysis

Taking into account our previous reports on allometric trends in different mammalian lineages, most of them obtained with the same quantitative methods, we integrated the results obtained for bandicoots with multivariate patterns obtained for carnivorous marsupials and placentals (e.g., Abdala et al., 2001; Flores et al., 2003, 2006, 2010; Giannini et al., 2004, 2010; Flores and Casinos, 2011; Segura and Prevosti, 2012). In this way, we searched for general patterns of skull growth in a broader sample of carnivorous marsupials and compared them with four placental out-groups. For *Didelphis albiventris* and *Lutreolina crassicaudata*, we re-analyzed our dataset which had exclusively been used in bivariate analyses (Abdala et al., 2001; Flores et al., 2003), now using multivariate analyses. For *Dromiciops gliroides* and the placentals studied previously (i.e., *Lycalopex culpaeus*, *Puma concolor, Cebus apella* and *Alouatta caraya*), we re-analyzed the available datasets using multivariate allometry analyses (Giannini et al., 2004, 2010; Flores and Casinos, 2011; Segura and Prevosti, 2012) but considering exactly the same 15 variables as in the present analyses, since the isometric value is affected by the number of variables considered.

With regard to a phylogenetic context, we mapped characters by transforming our multivariate coefficient of allometry (i.e., the confidence interval) to discrete character states of 0, 1, and 2, representing negative allometry, isometry, and positive allometry, respectively (see Wilson and Sánchez-Villagra, 2011). By mapping ontogenetic trends in a well-resolved tree including neotropical didelphids, *Dromiciops*, *Dasyurus*, both peramelids studied here (Horovitz and Sánchez-Villagra, 2003; Asher et al., 2004; Cardillo et al., 2004) and four placental out-groups, we could include phylogenetic and functional implications in the variation and maintenance of ontogenetic trends in natural groups. Although our sample includes few marsupial species, it is still possible to generate a phylogenetic background, because we cover most of the larger groups in the marsupial phylogeny (but excluding diprotodonts to date). We considered two phylogenetic hypotheses placing *Dromiciops* either as sister taxon to Dasyuromorphia and Diprotodontia (H1; Cardillo et al., 2004) or to Peramelomorphia and Diprotodontia (H2; e.g., Horovitz and Sánchez-Villagra, 2003; Asher et al., 2004). We defined 15 characters representing our multivariate allometric trends. Phylogenetic signal was obtained using random swapping of characters in terminal branches (Laurin, 2004). The distribution of character states (i.e., allometric trends) on the phylogenies was compared with the distribution on the 20,000 randomly generated trees. The number of evolutionary steps of each character of the randomly generated trees was also compared with the number of steps of that character in the phylogenies. We considered a character to have significant phylogenetic signal if the number of steps of at least 95% of the randomly generated trees was larger than that in the considered phylogeny. For phylogenetic signal calculation the R script of Prevosti et al. (2010) was used. For cladistic mapping and detecting phylogenetic signal we used the computer programs TNT v. 1.1 (Goloboff et al., 2008) and Mesquite v. 2.72 (Maddison and Maddison, 2009).

3. Results

3.1. Qualitative comparisons

The skull morphology of both species of bandicoots analyzed here exhibits an elongated rostrum, although this is more prominent in *E. kalubu*. There is no development of a sagittal crest in adult *E. kalubu*, but the lambdoid crests produce projections directed dorsally (Fig. 2). Modifications in the braincase of *I. macrourus* entail the development of a sagittal crest in adults, which is absent in juveniles (Fig. 3A and B). Remodeling of the temporal region in both species resulted in a nuchal crest overhanging the occiput which is not visible in dorsal view in either species (see Figs. 2A and 3A). Adults of both species have a postorbital constriction that enlarges latero-medially the space of the temporal fossa, but this opening is clearly more developed in *I. macrourus*.

In the occipital plate of juvenile *I. macrourus* the supraoccipital is forming the dorsal margin of the foramen magnum, whereas in adults the dorsal extension of the exoccipitals has displaced the

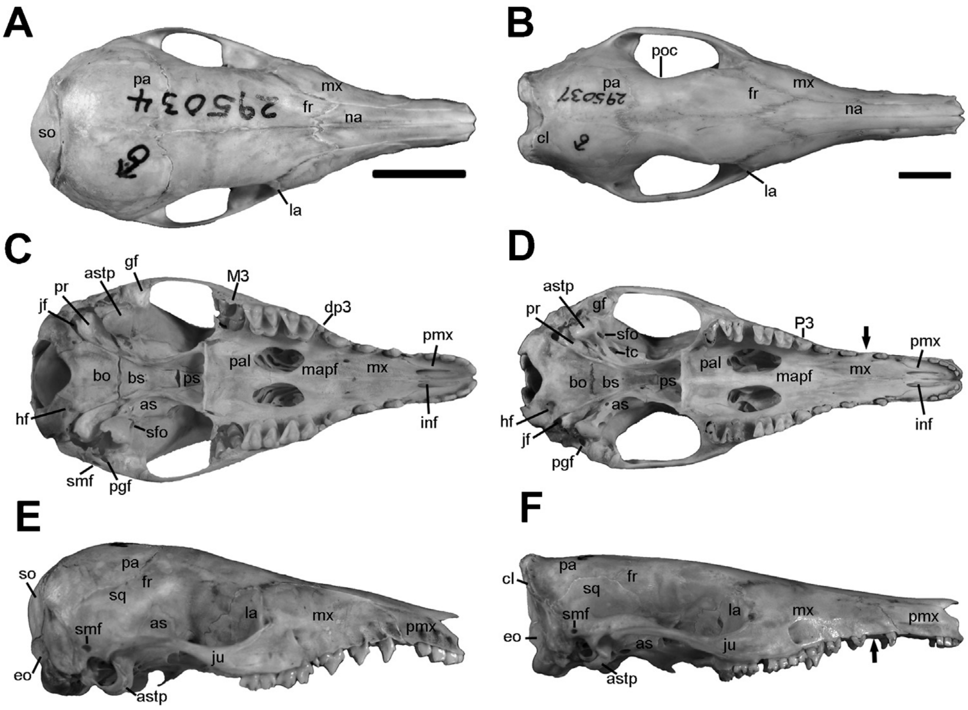

Fig. 2. Dorsal, ventral and lateral views (top to bottom) of *Echymipera kaluu* crania. (A, C, E) Juvenile (USNHM 295034); (B, D, F) adult (USNHM 295037). Abbreviations: as, alisphenoid; astp, alisphenoid tympanic process; bo, basioccipital; bs, basisphenoid; cl, lambdoid crest; dp3, deciduous third premolar; eo, exoccipital; fr, frontal; gf, glenoid facet; hf, hypoglossal foramen; inf, incisive foramen; jf, jugular foramen; ju, jugal;la, lacrimal; M3, third molar; mapf, major palatine foramen; mx, maxilla; na, nasal; P3, third premolar; pa, parietal; pal, palatine; pgf, postglenoid foramen; pmx, premaxilla; poc, postorbital constriction; pr, promontorium; ps, parasphenoid; sfo, secondary foramen ovale; smf, suprameatal foramen; so, supraoccipital; sq, squamosal; tc, transverse canal. Arrows indicate the largest diastemata in the adult. Scale bar = 10 mm.

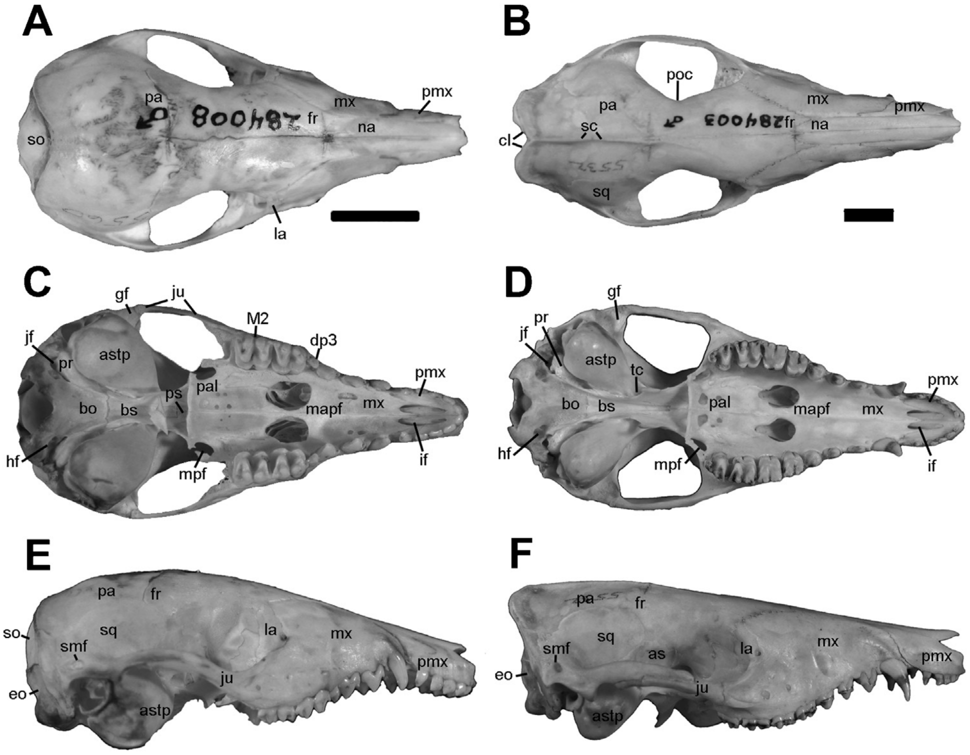

Fig. 3. Dorsal, ventral and lateral views (top to bottom) of *Isoodon macrourus* crania. (A, C, E) Juvenile (USNHM 284008); (B, D, F) adult (USNHM 284003). Abbreviations: as, alisphenoid; astp, alisphenoid tympanic process; bo, basioccipital; bs, basisphenoid; cl, lambdoid crest; dp3, deciduous third premolar; eo, exoccipital; fr, frontal; gf, glenoid facet; hf, hypoglossal foramen; if, incisive foramen; jf, jugular foramen; ju, jugal; la, lacrimal; M2, second molar; mapf, major palatine foramen; mpf, minor palatine foramen; mx, maxilla; na, nasal;pa, parietal; pal, palatine; pmx, premaxilla; poc, postorbital constriction; pr, promontorium; ps, parasphenoid; sc, sagittal crest; smf, suprameatal foramen; so, supraoccipital; sq, squamosal; tc, transverse canal. Scale bar = 10 mm.

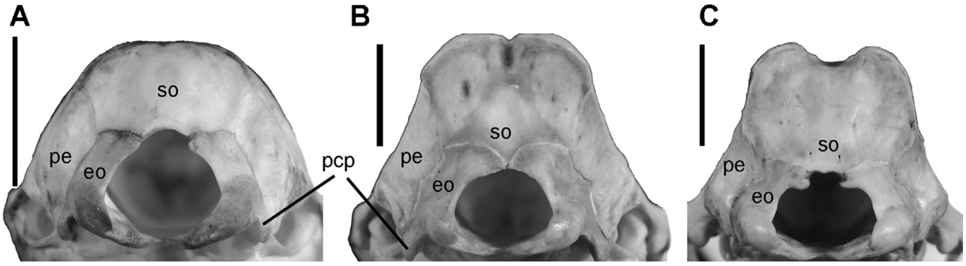

Fig. 4. Occipital plates of (A) a juvenile (USNHM 295034), (B) an adult (USNHM 295037) of *Isoodon macrourus*, and (C) an adult (USNHM 284003) of *Echymipera kalubu*. Abbreviations: eo, exoccipital; pcp, paracondylar process; pe, petrosal; so, supraoccipital. Scale bar = 10 mm.

supraoccipital from the foramen (Fig. 4A and B). In adult *E. kalubu* the dorsal portion of the exoccipitals sends projections that form a dorsal notch but this does not exclude the supraoccipital from the dorsal margin of the foramen magnum (Fig. 4C).

E. kalubu exhibits a proportionally longer snout than *I. macrourus*, a condition that is especially developed in the adult because of the appearance of a series of diastemata between the last incisor and the canine, and the canine and the first premolar (Fig. 2D and F). Several differences between juvenile and adult *E. kalubu* are linked to the lengthening of the snout and include: the position of the maxillo-incisive suture in lateral view, which is immediately rostral to the canine in the adult, and located midway between canine and the last incisor in juveniles; and the proportional lengthening of the major palatine and incisive foramina in the adult (Fig. 2C and D). The longitudinal extension of the snout is also perceived in the development of the nasals, which in adult *I. macrourus* show a long posterior projection forming a wedge between the frontals reaching the level of the anterior orbital margin. This projection is not observed in juveniles, in which the nasals end well anterior to the level of the anterior orbit. In *E. kalubu*, longitudinal growth of the lower jaw is enhanced because the tiny third deciduous premolar of the juvenile will be replaced by the largest permanent third premolar, implying a lengthening of the lower jaw approximately at the middle of the horizontal ramus (Fig. 5A and B). In addition, diastemata are visible between the last incisor and the canine, and between the canine and the first premolar, in adults.

Longitudinal growth of the snout and lower jaw is far less evident in *I. macrourus*. Diastemata in the upper and lower jaws are less conspicuous, there is no lengthening of the incisive foramen, and the major palatine foramen is clearly less developed than in *E. kalubu* (Figs. 2D and 3D). In contrast, the portion of the snout immediately anterior to the orbit is comparatively higher in adults of *I. macrourus*, a condition already present in juveniles (Fig. 3E and F).

The development of the canine teeth was also contrasting in these two species. In *E. kalubu* canine tooth size was comparable to that of the premolars in both juveniles and adults. In juvenile *I. macrourus* the canine teeth also were of similar size as the premolars, but in adults they were larger.

In relation to other neurocranial components, the large tympanic bullae of *I. macrourus* appeared even larger in the juvenile (Fig. 3C and E). An interesting difference between the two species is the fact that the fusion between the basioccipital and the exoccipital seems to take place earlier in *I. macrourus*; in juveniles with the second upper molar in eruption these bones are already fused. In contrast, a juvenile of *E. kalubu* with the third upper molar

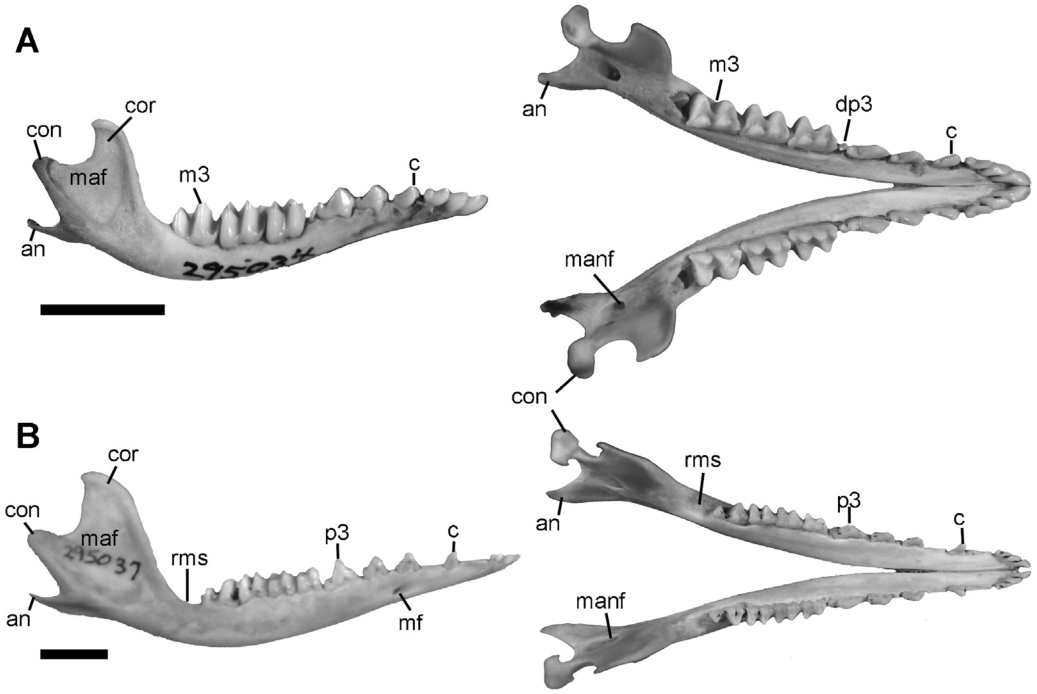

Fig. 5. Mandible in lateral (left) and dorsal (right) views of (A) a juvenile (USNHM 295034) and (B) an adult (USNHM 295037) of *Echymipera kalubu*. *Abbreviations*: an, angular process; c, canine; con, mandibular condyle; cor, coronoid process; dp3, deciduous third premolar; m3, third molar; maf, masseteric fossa; manf, mandibular foramen; mf, mental foramen; p3, third premolar; rms, retromolar space. Scale bar = 10 mm.

in eruption showed a clear suture between basioccipital and exoccipital.

3.2. *Cranial allometry in* E. kalubu

Bivariate analysis. All variables were strongly correlated with the total length of the skull, with $r^2 > 0.9$ in all but two variables, BB (breadth of braincase; $r^2 = 0.61$) and LO (length of orbit; $r^2 = 0.75$) (Table 1). HC (height of the coronoid process) and LO were the only variables that showed isometry with respect to the condylo-incisive length (CIL). Positive allometry was observed in five variables: LN (length of nasals), PAL (length of palate), LC (length of coronoid process) and LD (length of dentary) as well as HD (height of dentary). Eight variables scaled negatively, including variables from both the neurocranium and the splanchnocranium. BB exhibited the slowest growth rate ($b_{\mathrm{rma}} = 0.29$). The remaining variables with negative allometry, i.e., BZ (zygomatic breadth), BP (breadth of the palate), HM (muzzle height), and HC (height of the coronoid process), were related to tooth eruption (upper and lower tooth row) and other aspects of the trophic function.

Multivariate analysis. The first principal component explained 94.61% of the total variation. The multivariate approach showed more isometric variables than the bivariate analysis in *E. kalubu*, although the general trends were similar (Table 2). CIL and HC showed less departure from isometry (0.0011 and–0.0009, respectively), while BB exhibited the largest departure value (−0.19). Average estimated bias (using absolute jackknife values) across coefficients calculated from trimmed and untrimmed values were both small, favoring untrimmed over trimmed values (0.0005 average absolute bias against 0.002). Extreme pseudovalues slightly affected jackknife estimates, given that isometry was rejected in 11 variables using the untrimmed set as compared to12 in the trimmed set. Indeed, the only differences among multivariate (untrimmed) and bivariate approaches were limited to the isometric variables HM and HC.

3.3. *Cranial allometry in* I. macrourus

Bivariate analysis. All variables were strongly correlated with CIL, except for LO (length of the orbit), which was only moderately correlated ($r^2 = 0.5$; Table 1). Only 3 out of 14 variables were isometric: BZ, HM and UP (upper post-canine tooth row) (Table 1). Six variables were positively allometric: LN, PAL, LC, HC, LD, HD; and four variables were negatively allometric: BB, HO (height of the occipital plate), orbital length, and LP (length of the lower post-canine tooth row).

Multivariate analysis. The first principal component explained 92.68% of the total variation. The multivariate approach (Table 2) showed more isometric variables than the bivariate analysis, although, as observed in *E. kalubu*, the general trends were mostly similar in both analyses (Tables 1 and 2). CIL and PAL showed less departure from isometry (−0.006 and 0.001, respectively). BB (−0.14) and LC (0.15) exhibited the largest departure from isometry. Regarding untrimmed values, the only differences as compared to the bivariate results were the isometric values for LN, PAL and LP (in bivariate analyses, the first two variables were positively allometric and the third one was negatively allometric; cf. Tables 1 and 2).

3.4. *Comparative allometry of bivariate results in peramelids*

The likelihood ratio test indicates that although *E. kalubu* and *I. macrourus* shared 9 out of 15 trends in the bivariate analysis, only four variables (HM, PAL, LD and HD) exhibited statistically similar slope values (Table 3). In most cases, *I. macrourus* showed higher slope values, especially in variables related to the width and height

Table 1
Summary of bivariate regressions for skull elements of *Echymipera kalubu* and *Isoodon macrourus*, using total length of the skull as proxy of size (independent variable, see text for details).

Variable	Species	Range (mm)	r^2	b_{rma}	T_{iso}	P_{iso}	y-Intercept	Allometric trend
BZ	*E. kalubu*	17.32–33.82	0.97	0.74	−13.92	1.17E−18	0.09	–
	I. macrourus	17.03–42.81	0.96	0.98	−0.95	0.34	−0.29	=
LN	*E. kalubu*	17.21–44.54	0.99	1.16	12.87	2.50E−17	−0.57	+
	I. macrourus	17.56–45.37	0.99	1.10	6.18	8.29E−08	−0.46	+
HM	*E. kalubu*	4.31–8.83	0.92	0.92	−2.26	0.028	−0.83	–
	I. macrourus	4.3–10.38	0.87	1.03	0.50	0.62	−0.998	=
PAL	*E. kalubu*	22.08–50.37	0.99	1.03	2.92	0.005	−0.27	+
	I. macrourus	21.52–53.53	0.99	1.04	2.37	0.02	−0.28	+
BP	*E. kalubu*	14.67–22.72	0.89	0.48	−22.99	6.68E−28	0.42	–
	I. macrourus	14–25.02	0.92	0.67	−12.54	9.21E−18	0.09	–
UP	*E. kalubu*	13.35–29.45	0.97	0.87	−6.31	7.85E−08	−0.20	–
	I. macrourus	12.52–30.65	0.93	1.03	0.86	0.39	−0.49	=
LO	*E. kalubu*	4.31–12.92	0.75	1.16	1.88	0.066	−1.09	=
	I. macrourus	4.96–11.51	0.50	0.86	−1.78	0.08	−0.63	–
BB	*E. kalubu*	15.6–20.63	0.61	0.29	−27.03	4.20E−31	0.75	–
	I. macrourus	14.53–23.5	0.80	0.50	−16.67	3.66E−23	0.38	–
HO	*E. kalubu*	11.2–22.84	0.97	0.85	−7.57	8.58E−10	−0.27	–
	I. macrourus	10.89–24.17	0.97	0.93	−3.42	0.001	−0.42	–
LD	*E. kalubu*	27.1–65.91	0.99	1.10	7.53	1.01E−09	−0.28	+
	I. macrourus	26.56–65.97	0.99	1.10	6.47	2.84E−08	−0.29	+
HC	*E. kalubu*	7.2–18.24	0.94	0.96	−1.19	0.241	−0.59	=
	I. macrourus	6.93–25.62	0.94	1.29	6.83	7.22E−09	−1.10	+
LC	*E. kalubu*	2.07–7.97	0.92	1.42	7.41	1.51E−09	−1.83	+
	I. macrourus	2.17–8.66	0.94	1.66	11.64	1.86E−16	−2.26	+
HD	*E. kalubu*	2.76–7.32	0.93	1.26	5.59	9.87E−07	−1.56	+
	I. macrourus	2.12–8.14	0.89	1.33	5.62	6.56E−07	−1.641	+
LP	*E. kalubu*	14.99–29.24	0.96	0.83	−7.15	3.95E−09	−0.12	–
	I. macrourus	12.87–31.4	0.91	0.92	−2.24	0.03	−0.26	–

Abbreviations (variable acronyms) as in Fig. 1. Variables that show different trends for the two species are listed in bold script.
r^2, adjusted coefficient of correlation; b_{rma}, allometric coefficient in reduced major axis analysis; T_{iso}, 2-tailed Student's t-value under the assumption of isometry (expected allometric coefficient for isometry = 1; d.f. = 56); P_{iso}, P-value for T_{iso}.
=, isometry; +, positive allometry; –, negative allometry.

Table 2

Results of the multivariate analysis of cranial allometry in *Echymipera kalubu* ($n = 52$) and *Isoodon macrourus* ($n = 58$). The first three data columns show results using all specimens. The remaining columns show jackknife results calculated with untrimmed and trimmed ($m = 1$) sets of pseudovalues (see Section 2.3 for details). The allometric coefficient of a variable is the corresponding element of the first (unit) eigenvector per variable. The expected coefficient is the value under the assumption of isometry (0.258 for all variables). The observed coefficient is the value obtained with all specimens included. The resampled coefficient is the value generated by first-order jackknife resampling. Bias is the difference between the resampled and observed coefficients. The jackknifed 99% confidence interval (CI) is provided; allometric variables are those whose CIs exclude the expected value under the assumption of isometry (0.258).

					Untrimmed				Trimmed			
Variable	Species	Expected allometric coefficient	Observed allometric coefficient	Observed departure	Resampled allometric coefficient	Bias	99% CI	Growth trend	Resampled allometric coefficient	Bias	99%CI	Growth trend
CIL	*E. kalubu*	0.258	0.270	0.0121	0.27	−0.03959	0.255–0.282	=	0.271	−0.0006	0.261–0.281	+
	I. macrourus	0.258	0.251	−0.006	0.252	−7.00E−06	0.243–0.261	=	0.254	−0.001	0.248–0.260	=
BZ	*E. kalubu*	0.258	0.199	−0.0589	0.199	−0.000132	0.188–0.211	−	0.2	−0.0004	0.191–0.209	−
	I. macrourus	0.258	0.243	−0.015	0.242	0.0004	0.225–0.259	=	0.244	−0.0004	0.232–0.256	−
LN	*E. kalubu*	0.258	0.312	0.0542	0.312	0.09416	0.291–0.333	+	0.314	−0.001	0.299–0.329	+
	I. macrourus	0.258	0.274	0.016	0.274	−0.0002	0.255–0.293	=	0.276	−0.0009	0.262–0.289	+
HM	*E. kalubu*	0.258	0.239	−0.0189	0.237	0.0011	0.205–0.268	=	0.245	−0.0028	0.219–0.271	=
	I. macrourus	0.258	0.242	−0.016	0.239	0.001	0.199–0.279	=	0.241	0.0004	0.206–0.276	=
PAL	*E. kalubu*	0.258	0.278	0.0196	0.278	−0.00018	0.263–0.293	+	0.279	−0.0009	0.268–0.290	+
	I. macrourus	0.258	0.260	0.002	0.26	−0.0001	0.246–0.273	=	0.261	−0.0006	0.251–0.271	=
BP	*E. kalubu*	0.258	0.124	−0.1343	0.124	−0.05423	0.107–0.140	−	0.123	0.0003	0.109–0.137	−
	I. macrourus	0.258	0.164	−0.094	0.164	0.0001	0.148–0.179	−	0.164	0.0001	0.149–0.177	−
UP	*E. kalubu*	0.258	0.230	−0.0278	0.232	−0.00093	0.212–0.251	−	0.231	−0.0002	0.215–0.246	−
	I. macrourus	0.258	0.249	−0.009	0.251	−0.001	0.214–0.289	=	0.247	0.001	0.214–0.279	=
LO	*E. kalubu*	0.258	0.280	0.0224	0.281	−0.00047	0.211–0.352	=	0.267	0.0069	0.215–0.317	=
	I. macrourus	0.258	0.153	−0.104	0.155	−0.0007	0.105–0.204	−	0.146	0.004	0.103–0.189	−
BB	*E. kalubu*	0.258	0.062	−0.19585	0.063	−0.00056	0.042–0.084	−	0.06	0.0008	0.043–0.078	−
	I. macrourus	0.258	0.114	−0.144	0.114	5.30E−06	0.091–0.137	−	0.115	−0.0007	0.096–0.134	−
HO	*E. kalubu*	0.258	0.227	−0.0306	0.227	0.000299	0.210–0.243	−	0.232	−0.0025	0.220–0.245	−
	I. macrourus	0.258	0.233	−0.025	0.232	0.0001	0.219–0.246	−	0.235	−0.001	0.226–0.244	−
LD	*E. kalubu*	0.258	0.296	0.0382	0.296	−0.04324	0.284–0.308	+	0.297	−0.0005	0.289–0.307	+
	I. macrourus	0.258	0.275	0.017	0.275	0.0001	0.260–0.289	+	0.281	−0.003	0.273–0.289	+
HC	*E. kalubu*	0.258	0.255	−0.0028	0.257	−0.000986	0.229–0.285	=	0.248	0.0036	0.230–0.265	=
	I. macrourus	0.258	0.318	0.06	0.32	−0.001	0.288–0.352	+	0.31	0.004	0.291–0.329	+
LC	*E. kalubu*	0.258	0.375	0.1173	0.379	−0.002099	0.330–0.429	+	0.359	0.0079	0.330–0.389	+
	I. macrourus	0.258	0.409	0.151	0.409	3.10E-06	0.368–0.451	+	0.411	−0.001	0.388–0.435	+
HD	*E. kalubu*	0.258	0.334	0.0755	0.332	0.0008074	0.297–0.367	+	0.339	−0.0026	0.311–0.366	+
	I. macrourus	0.258	0.322	0.064	0.324	−0.001	0.264–0.384	+	0.307	0.007	0.276–0.338	+
LP	*E. kalubu*	0.258	0.220	−0.0385	0.22	−0.000257	0.191–0.249	−	0.229	−0.0048	0.213–0.245	−
	I. macrourus	0.258	0.221	−0.037	0.225	−0.001	0.188–0.262	=	0.215	0.003	0.189–0.241	−

Abbreviations (variable acronyms) as in Fig. 1. Variables that show different trends for the species (untrimmed) are listed in bold script.
=, isometry; +, positive allometry, −, negative allometry.

Table 3
Test for common slopes and common intercepts for the peramelid taxa *Echymipera kalubu* (E) and *Isoodon macrourus* (I).

Variable	Common slope			Common intercept		
	Lr_{b1}	P_{b1}	b_{1com}	$W_{(logb0)}$	$P_{(logb0)}$	$Log\ (b_0)_{com}$
BZ	45.0869	<0.001	I > E			
LN	9.7286	0.002	E > I			
HM	2.9851	0.084	0.958	19.98	<0.001	I > E
PAL	0.0978	0.754	1.032	16.22	<0.001	E > I
BP	26.9023	<0.001	I > E			
UP	15.0059	<0.001	I > E			
LO	6.1893	0.0128	E > I			
BB	22.2841	<0.001	I > E			
HO	7.5951	0.0058	I > E			
LD	0.0018	0.9659	1.096	36.05	<0.001	E > I
HC	32.3877	<0.001	I > E			
LC	8.1535	0.0043	I > E			
HD	0.8406	0.3592	1.293	46.19	<0.001	I > E
LP	4.0125	0.04516	I > E			

b_{1com}, common slope from reduced major axis analysis; $\log(b_0)_{com}$, common intercept from reduced major axis analysis; Lr, likelihood ratio (Warton et al., 2006); *w*, Wald statistic (Warton et al., 2006); P_{b1}, *P*-value of Lr parameter; $P_{(logb0)}$, *P*-value of W parameter.

of the skull (e.g., BZ, BP, HO). However, the orbital length seemed to have a higher growth rate in *E. kalubu* than in *I. macrourus*, as well as the nasal length, which was to be expected on the basis of the longer rostrum of *E. kalubu* (Figs. 2 and 3). For those few variables in which the slope values were not significantly different, the intercept values exhibited significant differences. Higher intercept values were found in *I. macrourus* in variables of height such as HM and HD, whereas the intercept values were significantly higher in *E. kalubu* in variables of length, such as PAL and LD, which is in agreement with the elongated aspect of the *E. kalubu* skull as compared to *I. macrourus*. This statistical comparison showed that the patterns of growth in both species are divergent in spite of shared trends of the ontogenetic trajectories.

3.5. *Comparison of ontogenetic patterns with other groups and character mapping*

Our comparison of patterns obtained with multivariate analyses (Table 4) indicates that no variable exhibited specific allometric trends for any group. Although peramelids exhibit a particular mode of rapid growth among marsupials, and also compared to mammals, this does not seem to have an obvious effect on peramelid ontogenetic patterns, or at least no effect detectable by the methods used in the present study. Peramelids did not show a unique pattern of allometric change. Five variables shared trends in all the marsupials sampled: BB, HO, BP, LC and HD (negative allometry for the first three characters and positive allometry for the latter two). Several marsupials shared positive allometry in HC, with the exception of *D. gliroides* and *E. kalubu* where it was isometric, and negative allomety in LO, except *C. philander*, *E. kalubu* and *D. gliroides*, where it was isometric. Variables related directly with biting and mastication, such as UP and LP, and HM also showed a moderate level of variation among groups, being isometric or negatively allometric in all cases studied. Characters with more variation in allometric growth were CIL, LP, LN, and ZB.

Our character mapping did not detect any specific patterns of change, although the trends of some characters were clearly adjusted to natural groups. For instance, isometry of CIL was recovered as a synapomorphy for Peramelidae in the hypothesis considering *D. gliroides* a sister group (H2), although the isometric condition was also detected in *L. crassicaudata* (Fig. 6A). If *D. gliroides* and dasyurids are sister groups (H1), then the negative allometry of CIL represents a synapomorphy for this group, with the isometric condition being plesiomorphic for marsupials (Fig. 6B). The same was observed for PAL, where isometry seems to be the plesiomorphic condition, whereas the negative allometry is mapped as another synapomorphy for the clade *D. gliroides*–*D. albopunctatus* (Fig. 6C).

Positive allometry of LD was the plesiomorphic condition in marsupials, whereas *D. gliroides* and *D. albopunctatus* showed isometry as a synapomorphy, a trend also presented in *C. philander* (Fig. 6D). The positive allometry of ZB was shared by the largest didelphids, *D. albiventris* and *L. crassicudata*, and also by the strongly carnivorous *D. albopunctatus* (Table 4). Our character optimization (Fig. 6E) indicates that the positive allometry of ZB is a plesiomorphic condition in Theria. The remaining variables exhibited few changes in marsupials. For splachnocranial variables, positive allometry was, in general, the plesiomorphic condition, except for HM (in which isometry was the plesiomorphic condition) and length of UP and LP (in which negative allometry was plesiomorphic).

3.6. *Test for phylogenetic signal*

Of the 15 characters used for multivariate analyses, three (CIL, PAL and LD) showed phylogenetic signal in the topology of the hypothesis that *Dromiciops* shares the same ancestor with *Dasyurus* (H1),while phylogenetic signal was detected for just one character (BZ) in the topology where *Dromiciops* and peramelids are sister groups (H2, Table 5). Four characters (HD, LP, UP, HC) had an invariant number of steps on all random trees and in both of the tested phylogenies, being therefore phylogenetically uninformative. Four characters (LC, HO, BB and BP) were also uninformative because they were invariant in their allometric conditions (Table 4).

4. Discussion

4.1. *Ontogenetic patterns of skull growth in bandicoots*

The evolution of modern bandicoots resulted in a relatively diverse group with a particular cranial morphology, whose most evident features are the long, pointed muzzles with small and relatively even-sized and pointed teeth (Gordon and Hulbert, 1989). Since bandicoots are morphologically distinctive among marsupials, especially in their postcranial morphology (e.g., Tate, 1948; Szalay, 1982; Gordon and Hulbert, 1989; Horovitz and Sánchez-Villagra, 2003), it is surprising that not many differences were found in the allometric skull patterns as compared to other species (Table 4). In general terms, allometric trends of *I. macrourus* and *E. kalubu* highlighted the predominance of the muzzle, a character also notable in American Caenolestidae. Significant differences in

Table 4
Ontogenetic trends in the skulls of marsupials and placentals studied with multivariate analysis. Marginally significant trends are listed in parentheses.

Species	Source	CIL	BZ	LN	PAL	UP	LP	LD	LC	HC	HO	BB	HD	LO	HM	BP
Marsupials																
Didelphis albiventris	Abdala et al. (2001)	(+)	(+)	+	(=)	–	–	+	+	+	–	–	+	–	–	–
Lutrelina crassicaudata	Flores et al. (2003)	=	+	–	–	–	–	+	+	+	–	–	+	–	=	–
Caluromys philander	Flores et al. (2010)	+	(=)	(=)	=	=	=	=	+	+	–	–	+	=	=	(–)
Dromiciops gliroides	Giannini et al. (2004)	–	–	–	–	=	–	=	+	=	–	–	+	(=)	–	–
Dasyurus albopunctatus	Flores et al. (2006)	–	+	=	–	–	(–)	=	+	+	–	–	+	–	=	(–)
Isoodon macrourus	This report	=	(=)	(=)	=	=	=	+	+	+	–	–	+	–	=	–
Echymipera kalubu	This report	=	–	+	+	–	–	+	+	=	–	–	+	=	=	–
Placentals																
Cebus apella	Flores and Casinos (2011)	(–)	+	+	–	–	–	+	+	+	–	–	+	–	–	–
Alouatta caraya	Flores and Casinos (2011)	=	–	+	=	–	–	+	+	+	–	–	+	–	=	–
Lycalopex culpaeus	Segura and Prevosti (2012)	=	+	+	–	(–)	=	+	+	+	–	–	+	–	(–)	–
Puma concolor	Giannini et al. (2010)	(+)	+	=	=	–	–	+	+	+	–	–	(–)	–	(=)	–

Abbreviations of variables as in Fig. 1.
=, isometry; –, negative allometry; +, positive allometry.

the slope and intercept values (Table 3) of the characters related with rostrum length are also clearly visible in qualitative terms (Figs. 2 and 3). The proportionally longer rostrum of *E. kalubu* (and the well-developed sagittal crests), as well as the higher rostrum of *I. macrourus* (already visible at an early age) are characters probably linked to differences in food selection, considering the different habitats where both species live. Tate (1948) suggested that the development of lambdoidal ridges at the back of the skull, as observed in adults of both species, is related to the bandicoots' 'pig-like habits' of rooting in the soil and vegetation. Different palate morphology in the adults of both species (Figs. 2 and 3) also reflects variations in rostrum development. The almost parallel position of the inner edge of the upper tooth row in adults of *I. macrourus* (Fig. 3D) is only shared by Caluromyinae among marsupials (Flores et al., 2010). Lower values of the allometric coefficients for BP in juveniles suggest that the posterior palate is proportionally wider and shorter in juveniles, reflecting the importance of the palate as a platform for the tongue for intraoral transport and swallowing of milk during suckling (German and Crompton, 1996; Abdala et al., 2001). Suckling is a key function during the early life of marsupials and determines several traits that are structural adaptations of the skull of neonates (Clark and Smith, 1993; Maier, 1993). Although the lactation phase is quite short in bandicoots (Lyne, 1964; Close, 1977), the early development of the palate guarantees this function. An important character observed only in peramelids among the sampled marsupials is the major palatine foramen, which is already well developed in juveniles. Because palatal vacuities originate through posterior gradual osseous resorption (Parker, 1886; Reig et al., 1987), the earlier occurrence of this event in peramelids as compared to other marsupial groups is indicative of a possible heterochronic process in this group, probably related to their rapid development and early weaning.

Most of the morphological features of the mandible, such as the well-defined curvature on the ventral margin of the horizontal ramus (= body; Fig. 5) and general positive trends shared by both species (Tables 1 and 2), such as the lower coefficient values for the height of the coronoid process and the height of the dentary in *E. kalubu* (Table 3), are indicative of a stronger mandible in *I. macrourus*. This condition, coupled with a more compact rostrum, suggests stronger bite forces in *I. macrourus*.

Taxonomic reviews of Peramelinae and Echymiperinae (e.g., Freedman and Joffe, 1967a,b; Freedman and Rightmire, 1971; Dixon, 1981) described the basicranial structure, although without considering ontogenetic changes. The huge tympanic bulla of *I. macrourus* (even comparatively larger in young specimens) shows an earlier fusion of the synchondrosis intraoccipitalis basilateralis (i.e., between basioccipital and exoccipital; see Fig. 3D). These differences are most likely the result of a history of living in arid and semi-arid habitats. Several mammals living in such landscapes also show an extreme development of the tympanic bulla (Archer, 1976b; Archer and Kirsch, 1977; Flores et al., 2000; Verzi, 2001; Alvarez, 2011), just like *I. macrourus*. Since the growth of the neurocranium and the splachnocranium are closely interrelated (e.g., Radinsky, 1968), the well-developed tympanic bulla in *I. macrourus* also affects the growth of the zygomatic breadth at the level of the temporo-mandibular joint. Different allometric trends in the

Table 5
Phylogenetic signal of allometric trends based on 20,000 permutations of two hypotheses of relationships. In H1 *Dromiciops* is sharing the same ancestor with *Dasyurus*, whereas in H2 it is sharing the same ancestor with peramelids. *P* indicates the probability of the found random trees being shorter than those of H1 or H2 (i.e. $p > 0.5$ means absence of pylogenetic signal).

Character	Steps H1	Permutation steps H1	*P* H1	Steps H2	Permutation steps H2	*P* H2
CIL	5	6	0.5564	6	6	1
BZ	5	4	1	4	5	0.3546
LN	6	4	1	6	4	1
PAL	5	6	0.8741	6	5	1
UP	3	3	1	3	3	1
LP	4	4	1	4	4	1
LD	2	3	0.2726	3	3	1
LC	–	–	–	–	–	–
HC	2	2	1	2	2	1
HO	–	–	–	–	–	–
BB	–	–	–	–	–	–
HD	1	1	1	1	1	1
LO	3	2	1	3	3	1
HM	4	2	1	4	3	1
BP	–	–	–	–	–	–

–, Indicates characters with an invariant allometric trend throughout our sample. Abbreviations of variables as in Fig. 1.

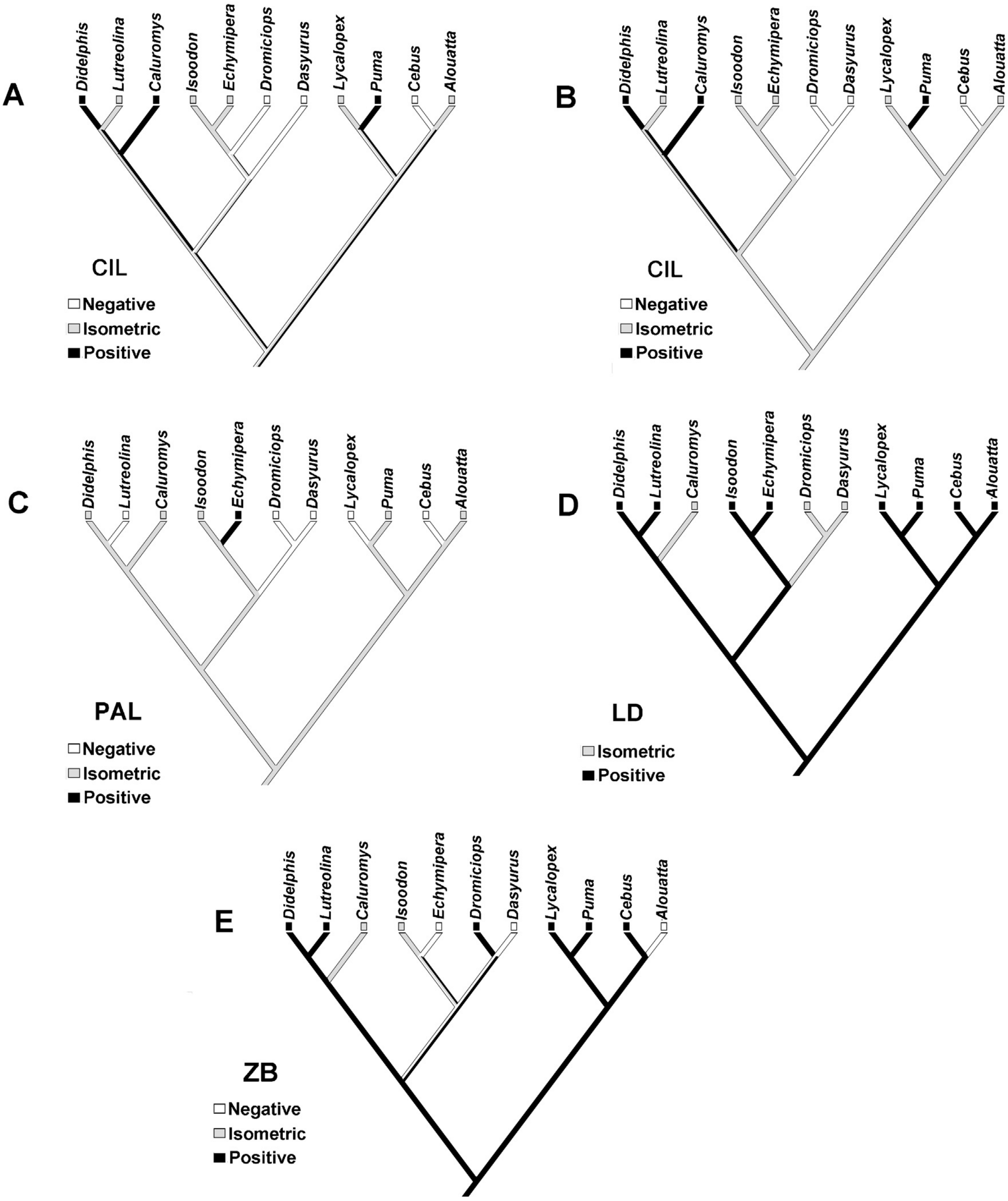

Fig. 6. Character mapping of some variables on the array of species considered. (A) Condylo-incisive length (CIL) under hypothesis H2; (B) condylo-incisive length under hypothesis H1; (C) length of palate (PAL) under hypothesis H1; (D) length of dentary (LD) under hypothesis H1; (E) zygomatic breadth (ZB) under hypothesis H1. See text for explanations.

zygomatic breadth (isometric in *I. macrourus* and negative in *E. kalubu*; Tables 1 and 2), in turn, directly affect the amount of space available for the temporal muscle, i.e. the space between the arch and the lateral wall of the braincase (fossa temporalis). Although the braincase of both species was, as expected, negatively allometric, the lower values detected for *E. kalubu* (Table 3) may compensate for the space generated by the negative allometry of the zygomatic breadth in this species, as corroborated by visual observation of adult skulls (Figs. 2 and 3).

The orbit is a neurocranial component that is expected to be negatively allometric (Emerson and Bramble, 1993). However, the isometric condition in *E. kalubu* indicates an accelerated growth as compared to *I. macrourus*, although the difference is not perceptible in adults, and there is no clear association between orbit size and life history. Although the trajectories of the height of the occipital plate exhibited similar slopes in both species, the statistically higher slope in *I. macrourus* and the statistically higher intercept in *E. kalubu* (Table 3) imply a transformation from a relatively high occipital plate in juvenile *E. kalubu* to a lower condition in adults, as compared to *I. macrourus*. Differences in the growth rates of neurocranial elements (orbit, occipital plate and braincase) between both species indicate a potentially high degree of variation in the postnatal development of sensory capsules in peramelids.

4.2. Comparison of allometric patterns and evolution of skull growth in carnivorous marsupials

The comparative study of ontogenetic trajectories is a way to detect and quantify a series of complex phenomena occurring during growth in an array of related species (Wilson and Sánchez-Villagra, 2011). The scarce phylogenetic signals in the present comparison (Table 5) suggest that skull growth is not strongly associated with phylogenetic relationships (although some shared trends were detected in some natural groups). Our comparison demonstrates that bandicoots do not exhibit a particular mode of growth, despite their rapid growth and basal position among australidelphians. Moreover, skull development observed in the marsupials studied to date exhibits variable patterns without any particular trends with respect to placental out-groups, and their strategies for organogenesis, integration, development and reproduction are also divergent (e.g., Clark and Smith, 1993; Smith, 1997; Shirai and Marroig, 2010; Goswami et al., 2012).

Even though condylo-incisive length is a character commonly considered an independent variable in bivariate approaches because it is an isometric proxy of size (see Janis, 1990 and Cassini et al., 2012 for ungulates; Abdala et al., 2001 and Flores et al., 2003 for didelphid marsupials; Flores and Casinos, 2011 for primates), it was not recovered as isometric for 6 out of 11 species compared in the present study (Table 4), indicating that it should be used with caution in bivariate approaches (e.g., Flores et al., 2010). In almost all vertebrates, accelerated differentiation of the central nervous system and sensory capsules produces embryos and neonates with large braincases, eyes, and auditory regions as compared to the trophic components of the skull (e.g., Emerson and Bramble, 1993; Maunz and German, 1996). In marsupials, virtually all neurogenesis occurs after birth and during lactation (i.e. during the pre-weaning period; Smith, 1997). While most neurocranial variables scale negatively in all marsupial species studied to date, the isometry of the orbit (which means that it grows faster than expected) in *D. gliroides*, *C. philander* and *E. kalubu* (Table 4) suggests that this condition may be relatively common among marsupials. However, and in agreement with the consistent negative allometry in almost all neurocranial variables found in marsupials and placentals (Table 4), the neurocranial region did not show any significant differences between groups in the morphospace distribution reported by Bennett and Goswami (2013).

The coordinated trends of the upper and lower post-canine rows are marked by the sequential eruption of discrete, size-invariant elements (teeth), involving the mutual adjustment of the lower and upper rows during growth. The pattern of tooth emergence in marsupials in general may require the upper tooth row to grow faster than the lower one, the latter always having one tooth in advance in relation to the upper tooth row until all teeth have emerged. This pattern has already been described for *Didelphis albiventris* (Tyndale-Biscoe and MacKenzie, 1976; Abdala et al., 2001), *Lutreolina crassicaudata* (Flores et al., 2003), *Caluromys* (Astúa de Moraes and Leiner, 2008; Flores et al., 2010), *Marmosops incanus* (Tribe, 1990), *D. gliroides* (Giannini et al., 2004), *Dasyurus albopunctatus* (Flores et al., 2006), and is reported here for the two studied bandicoots as well (see absolute values and intervals in Tables 1 and 2). Considering this sequence of tooth emergence, it is possible that such a relation of allometric trends between the upper and lower post-canine tooth rows is the plesiomorphic condition for marsupials. The lower variability in jaw morphology and post-canine dentition of carnivorous marsupials relative to placental carnivorans (Werdelin, 1987) may be associated to the dental developmental pattern of marsupials. In this group, molars erupt in the carnassial (i.e., the last) position, and the next erupting molar occupies the position of the previous element. In this way, all of the molars in marsupials occupy, at least for a brief time during growth, the position of the specialized carnassial teeth (Goswami et al., 2011). In contrast, only the last (fourth) upper premolar and the first lower molar of a placental carnivoran are specialized carnassials; therefore it has been argued that placental carnivorans can achieve greater dental and ecological diversity than their marsupial counterparts. Indeed, the allometric trends of the mandibular characters in marsupials (Table 4) demonstrate that they exhibit a low degree of variation, maintaining a relatively stable pattern of allometric growth, with weak phylogenetic signal (Table 5). However, Goswami et al. (2011) concluded that metatherian carnivores exhibit a morphological disparity which may exceed that of the more speciose eutherian carnivore radiations, refuting the hypothesis that developmental constraints have limited the morphological evolution of the marsupial skull, which is in agreement with Sánchez-Villagra (2013) about differences in diversity patterns between marsupials and placentals. A recent study (Bennett and Goswami, 2013) found that extant marsupials occupy a much smaller area of the morphospace than the placental taxa, supporting the hypothesis of developmental constraints limiting the evolution of the marsupial skull.

Although positive allometry of the zygomatic breadth was recognized as a plesiomorphic condition (Fig. 6B), it is clearly associated with feeding habits (irrespective of phylogenetic relationships), considering its moderate phylogenetic signal (Table 5). For instance, positive allometry was restricted to species with more carnivorous habits and a strong temporal musculature in marsupials, such as *D. albiventris*, *L. crassicaudata* and *D. albopunctatus* (Table 4). A more speciose sample might detect more phylogenetic signal in characters with functional demands like this, as Wilson and Sánchez-Villagra (2011) found some association between functional demands and phylogenetic relationships in turtles. The comparative study of Wroe and Milne (2007) in carnivores demonstrated that there were clade-specific constraints, but that different carnivore clades showed similar patterns of morphological variation associated with diet, and that skull shape, feeding behavior and bite force were significantly correlated (indeed more so in the sampled marsupials than in the placental carnivorans). Patterns observed in the growth of the palate suggest a high degree of variation (Fig. 6C and Table 4), but its breadth is highly conserved, exhibiting a negatively allometric trend in the entire group. Several authors have pointed out the functional demands on the palate during suckling in marsupials (see Section 4.1). Discovering the same trend for placentals indicates that functional constraints of the palate affect all mammal groups, independently of their reproductive or developmental strategies. In fact, Goswami et al. (2012) demonstrated a decrease in the integration of the oral region during the ontogeny of *Monodelphis domestica*, likely related to the early ossification in this species, and suggesting that a high integration during early postnatal ontogeny combined with functional constraints for suckling drive the low variance observed in this species and potentially in other marsupials as well.

5. Conclusions

The present study shows that wide-scale comparisons of growth data can provide important information that has rarely been assembled for marsupials. Our ontogenetic data on different marsupials allow an initial integrative view of the evolution and distribution of allometric patterns of skull ontogeny in marsupials. Our findings suggest that the evolution of several allometrically influenced characters maybe partially associated with phylogeny (Table 5). However, considering the relative positions of dasyurids and peramelids with respect to *D. gliroides* and Diprotodontia, it is important to take into consideration the ontogenetic data of several groups of Diprotodontia in order to find out if the synapomorphic trends shared between *D.gliroides* and *D. albopunctatus* (Fig. 6B and C) also include diprotodontians. As demonstrated by Gilbert et al. (2009) for papionin monkeys (primates) and by Wilson and Sánchez-Villagra (2011) for turtles, allometric data may be useful for revealing phylogenetic associations. However, it would be desirable to increase the sample, especially by including diprotodontians, more didelphids and long-nosed caenolestids, in order to reach more certainty with regard to phylogenetic implications and general growth trends in natural groups, as well as patterns of dispersion of ontogenetic trajectories in a multivariate morphospace (e.g., Wilson and Sánchez-Villagra, 2010; Wilson, 2013). Knowledge of the interspecific variations of rostral growth in living caenolestids may be important for exploring the morphological divergence between species of such ancient groups and the morphologically convergent peramelids.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.zool.2013.07.003.

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