

Ontogenetic trajectories of key morphofunctional cranial traits in South American subterranean ctenomyid rodents

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Ontogenetic allometries of craniomandibular and dental features linked to digging were analyzed in 5 species of the South American subterranean rodent *Ctenomys* (tuco-tucos). With the exception of upper incisor procumbency, variables showed high correlation with overall skull size. In particular, craniomandibular variables related to the production of bite forces at the incisors showed near-geometric similarity during postnatal growth and interspecific changes in early developmental stages resulting in different starting forms (lateral transposition). Such an interspecific pattern of change is similar to one previously reported to occur among living and extinct ctenomyid genera. These results suggest more evolutionary flexibility for changes in early ontogenetic stages and allow rejection of the hypothesis that interspecific shape differences in the skull of *Ctenomys* would be associated with differences in size alone. DOI: 10.1644/09-MAMM-A-411.1.

Key words: craniomandibular traits, ctenomyid rodents, ontogenetic allometries, subterranean habits

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The subterranean tuco-tucos of genus *Ctenomys* (Rodentia, Hystricognathi) are the single living representatives of Ctenomyidae, a family that differentiated during the late Miocene in southern South America. *Ctenomys* is represented in the living fauna by approximately 60 species (Woods and Kilpatrick 2005) resulting from cladogenetic events started in the late Pliocene or even earlier (Castillo et al. 2005; Verzi et al. 2010). The genus has been recognized as monophyletic (Cook and Lessa 1998; Lessa and Cook 1998; Verzi 2008) and assumed to have adaptive uniformity associated with its subterranean habit (Reig et al. 1990). All species of *Ctenomys* share morphological specializations for digging that set them apart from both the extinct ctenomyids and the genera of the sister family Octodontidae, which have fossorial to subterranean habits (Lessa et al. 2008; Verzi 2008; Verzi et al. 2010). As in other digging rodents, *Ctenomys* possesses cranial specializations that increase bite force at the incisors through larger masticatory muscles and more advantageous lever arms for these muscles that result in high mechanical moments on the mandibular joint (Hildebrand 1985; Lessa 1990; Stein 2000; Vassallo 1998). The distance between the mandibular condyle, which acts as fulcrum, and the tip of the incisors (i.e., the out-lever arm of masseteric adductor muscles) is shortened in comparison with other ctenomyid genera (Vassallo and Mora 2007; Verzi 2002). In addition, the lateral expansion of

the angular process of the mandible is greater to accommodate a larger mass of masseteric adductor muscles (Olivares et al. 2004; Vassallo and Mora 2007). Recent studies showed that subterranean rodents are capable of producing relatively high bite forces (Freeman and Lemen 2008), which is especially true for chisel-tooth-digging species (Van Daele et al. 2009).

Ctenomys is a claw and chisel-tooth-digging genus with a broad distribution from Perú to southernmost South America. Hence, particular species greatly differ in their habitat attributes, especially regarding soil hardness and obstacles to digging (i.e., roots and rocks). Whereas claw digging is the basic and general behavior of *Ctenomys*, evidence at hand shows that the degree of commitment to dento-excavation likely depends on soil attributes and can vary intra- and interspecifically (Camín et al. 1995; Vassallo 1998).

Beyond the accepted morphological and adaptive identity of *Ctenomys*, its species exhibit morphological variation in craniomandibular and dental traits assumed to be digging specializations, such as the ones mentioned above and incisor procumbency (Lessa 1993; Mora et al. 2003; Vassallo 1998;



Verzi and Olivares 2006). This variation has been detected through both multivariate and bivariate morphological analyses of adult individuals (Mora et al. 2003; Verzi and Olivares 2006). An examination of the ontogenetic trajectories of some of these traits has shown that changes in the maximum size reached by adults could represent an important source of the variation in shape detected between species (Vassallo and Mora 2007). Thus, the study of allometries—that is, size-related shape changes in ontogenetic trajectories—can contribute to understanding the origination of disparity (Atchley and Hall 1991; Emerson and Bramble 1993; Gerber et al. 2008; Klingenberg 1998).

Interspecific comparisons of the ontogenetic trajectories of traits provide information about possible changes in the dynamics of trait growth that result in morphological disparity. Following the proposal of Klingenberg (1998), allometric patterns representing evolutionary changes in ontogenetic trajectories include truncation or extension along a conserved trajectory (ontogenetic scaling), changes in early developmental stages that result in different starting forms (lateral transposition), and changes in the direction of trajectories. In the first 2 cases the ratio between growth rates of traits does not change during the ontogenetic period being studied; however, lateral transposition implies that dissociation between the growth rates of these traits has occurred in earlier stages of development. Changes in the direction of trajectories indicate dissociation between the growth rates of traits occurring within the analyzed stages.

Vassallo and Mora (2007) proposed that the variation in skull shape observed among *Ctenomys* species is explained by size, specifically, allometric growth of traits along an ancestral trajectory (ontogenetic scaling). We tested this hypothesis through the analysis of changes in postnatal ontogenetic trajectories of craniomandibular and dental characters linked to fossorial activities in 5 *Ctenomys* species. From among the digging specializations of the genus (Mora et al. 2003; Verzi and Olivares 2006), we selected variables assumed to reflect key traits linked to chisel-tooth digging. This analysis follows the previous study by Vassallo and Mora (2007) but is more comprehensive in terms of species and traits explored. Our sample comprises different clades: 3 of the 5 species examined, *Ctenomys australis* (sand-dune tuco-tuco), *Ctenomys mendocinus* (Mendoza tuco-tuco), and *Ctenomys porteousi* (Porteous' tuco-tuco), are part of a species group considered to have close phylogenetic relationships (*mendocinus* group—Massarini et al. 1991); *Ctenomys talarum* (Los Talas tuco-tuco) is more distantly related to the species of this group; and *Ctenomys magellanicus* (Magellanic tuco-tuco) belongs to another of the major clades recognized within the genus (Castillo et al. 2005; Slamovits et al. 2001). In addition, the sample variation in body size (90–900 g; see below) comprises much of the range of the genus (Mora et al. 2003). In this context we tested whether shape differences in *Ctenomys* result from overall size changes and discuss the morphofunctional and evolutionary significance of the variation among the ontogenetic trajectories analyzed.

MATERIALS AND METHODS

We studied postnatal ontogenetic series of 5 *Ctenomys* species (Appendix I): *C. australis* ($n = 56$), *C. magellanicus* ($n = 60$), *C. mendocinus* ($n = 58$), *C. porteousi* ($n = 48$), and *C. talarum* ($n = 65$). Although the species were chosen based on the availability of ontogenetic series in collections, the sample spans different clades and body sizes (Table 1). Given that the availability of pups with erupted deciduous P4 and M1–2 varied among the samples, the onset for trajectories was fixed at the smallest available individuals with erupted M3. To establish a criterion for relative age we considered basilar length, and each specimen was checked for condition of the sutures between basioccipital and exoccipital, supraoccipital and exoccipital, basioccipital and basisphenoid (Daly and Patton 1986; Lizarralde et al. 2001; Robertson and Shadle 1954; Samuels 2009), and basisphenoid and presphenoid and also for the presence of a fenestra at the junction of frontal or parietal bones, or both (Gardner and Anderson 2001). The basioccipital–exoccipital and supraoccipital–exoccipital sutures were visible only in the specimens with smallest basilar length. In contrast, the basioccipital–basisphenoid suture persisted in most individuals, even in the specimens with greatest basilar length that were indisputably adults. Likewise, some large-sized adult specimens showed a persistent fenestra of some type (Gardner and Anderson 2001). The basisphenoid–presphenoid suture was a good indicator of relative age because its fusion progressed as basilar length increased; thus, the presence of this suture was the criterion chosen to classify individuals as juveniles (Appendix I). Contrasting these results with data for reproductive status available for *C. mendocinus* (Rosi et al. 1992; M. I. Rosi, IADIZA-CONICET, Mendoza, Argentina, pers. comm.) showed that all the specimens classified as juveniles on the basis of the presence of basisphenoid–presphenoid suture were reproductively immature individuals, although at least some of them showed fusion of the basioccipital–exoccipital and supraoccipital–exoccipital sutures.

We measured 9 variables (Fig. 1). Craniomandibular variables were selected under the assumption that they are linked to the production of forces at the incisors according to the static equilibrium formula: $F_o = F_i \times L_i/L_o$, where F_o (out-force) is the force exerted at the tip of the incisors, F_i (in-force) is the force exerted by masseteric adductor muscles, and L_i and L_o are the in-lever and out-lever arms of these muscles, respectively (Lessa 1990; Stein 2000). The in-lever arm was estimated as $L_i = \sin \theta(ZI/2)$, where θ is the angle of masseter line of action with respect to the occlusal plane, estimated as 70° (Vassallo 2000), and ZI is the length of the zygomatic arch (Mora et al. 2003; Vassallo 2000). The out-lever arm (L_o) was measured as condyle–incisor distance, measured from the anterior tip of the condyle. Maximum mandibular width (J_w) was used as an estimator of the development of masseter muscles linked to the production of F_i (Olivares et al. 2004; Vassallo and Mora 2007). Dental variables included estimators of mechanical resistance and procumbency of the upper incisors. Procumbent incisors are assumed to be an adaptation

TABLE 1.—Body mass and basilar length of the samples of *Ctenomys* analyzed.

Species (n)	Body mass (g)		Basilar length (mm)	
	Total range	\bar{X} (range) in adults	Total range	\bar{X} (range) in adults
<i>C. australis</i> (56)	70–550	340 (215–550)	28.0–52.3	44.11 (39.7–52.3)
<i>C. magellanicus</i> (60)	110–432	293 (206–432)	30.7–52.4	45.09 (39.5–52.4)
<i>C. mendocinus</i> (58)	78–255	167 (90–255)	30.1–46.4	35.36 (31.8–40.6)
<i>C. porteousi</i> (48)	85–275	184 (120–275)	24.9–40.6	37.41 (32.8–46.4)
<i>C. talarum</i> (65)	44–165	120 (82–165)	24.6–37.8	32.76 (29.8–37.8)

to chisel-tooth digging in subterranean rodents (Lessa 1990). Mechanical resistance was estimated considering incisor cross section as an ellipse with major axis (I_w) represented by the transverse diameter of the incisor, and minor axis (I_d) represented by its anteroposterior diameter. The polar moment of inertia (J), calculated as $J = \pi(I_w/2)^3(I_d/2)^3/[(I_w/2)^2 + (I_d/2)^2]^2$, was used to estimate resistance to shearing stress, and the 2nd moment of area (I_o), calculated as $I_o = \pi/4[(I_w/2)(I_d/2)^3]$, to estimate resistance to bending stress (Irgens 2008). To measure upper-incisor procumbency (Proc) the angle formed between the chord of the exposed incisor and a line parallel to the occlusal plane of the upper molariforms (Thomas' angle) was measured on camera lucida drawings using a protractor (Reig et al. 1965) and later transformed into radians for the

analyses. Basilar length (Bl) was used as estimator of overall skull size because the previously used basicranial length (Radinsky 1985; Vassallo and Mora 2007) tracks the negatively allometric growth of the brain (Emerson and Bramble 1993) and its contribution to basilar length is compensated by the positive allometry of the rostrum. In addition, previous analyses of basilar length in *Ctenomys* have demonstrated a multivariate coefficient close to isometry (Mora et al. 2003:table 1). All linear measurements were taken using a digital caliper; Proc was measured using a Leica MS5 stereomicroscope (Leica Microsystems, Heerbrugg, Switzerland).

The relationship between each of these features (y) and overall size represented by Bl (x) was analyzed through the \log_{10} -transformed allometric equation $\log y = \log a + b \log x$, where $\log a$ is the y -intercept or elevation, and b is the slope of the line (allometric coefficient). Allometric equations were calculated using model II regressions (standardized major axis) given that both variables were considered as random and measured with error (Legendre and Legendre 1998). Departures from isometry were assessed by inspection of the 95% confidence intervals. Variations in elevation and slope were tested for evaluating evolutionary changes in allometric trajectories (Fig. 2). Differences between these parameters were assessed by heterogeneity tests. Common slope was tested by likelihood-ratio test (Warton et al. 2006). Where no significant heterogeneity in slope was found among species (i.e., when the direction of trajectories was conserved; $P_b > 0.05$), a Wald test was used to evaluate significant differences between intercepts of the allometries (i.e., looking for lateral transposition of ontogenies; $P_a < 0.05$) for each pairwise species comparison (Warton et al. 2006). These analyses were performed using the software SMATR 2.0 (Falster et al. 2006).

We assessed differences in Proc among adults of analyzed species through analysis of variance and Tukey's honestly significant difference test for pairwise comparisons with unequal n . Possible sexual dimorphism in the standardized variables was investigated in adults using a t -test. The only variables that differed significantly between males and females were J and I_o ($P < 0.05$); however, the growth trajectories for these variables did not differ between males and females in either slope or intercept. Consequently, both sexes were pooled for the allometric analyses. We used the statistical software PAST (Hammer et al. 2001) to perform these analyses after confirming the normality and homosce-

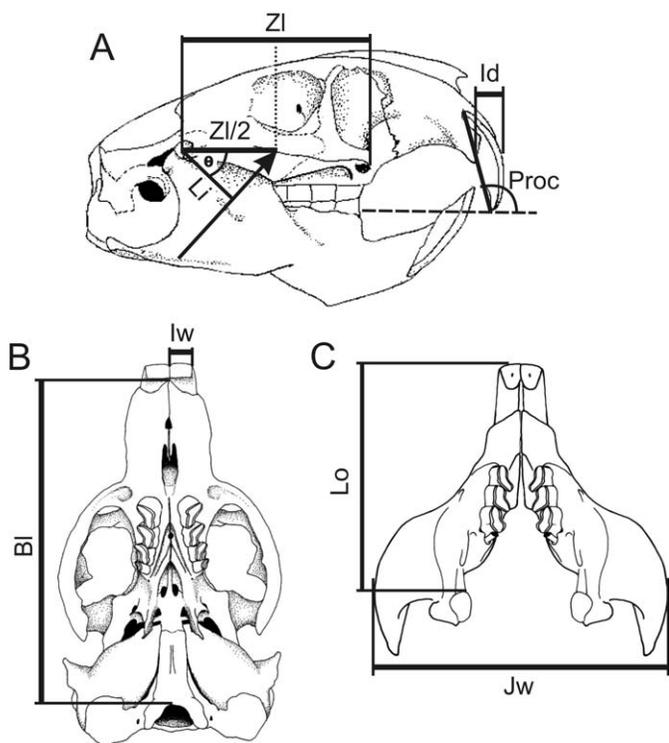


FIG. 1.—Skull, jaw, and dental measurements in *Ctenomys*: A) skull and jaw in lateral view, B) skull in ventral view, and C) jaw in dorsal view. Bl, basilar length; Id, upper incisor depth; Iw, upper incisor width; Jw, maximum jaw width; Lo, out-lever arm of masseters; Li, in-lever arm of masseters; Proc, procumbency of upper incisors; Zl, zygomatic length; θ , angle of masseter line of action with respect to occlusal plane (see the ‘‘Materials and Methods’’).

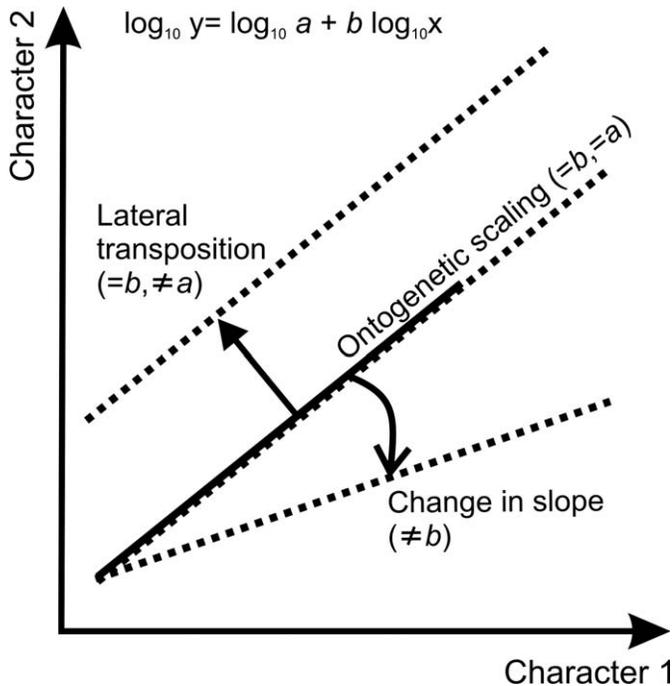


FIG. 2.—Bivariate plot showing allometric patterns representing evolutionary changes in ontogenetic trajectories. Solid line is an ancestral trajectory established for comparative purposes. Following Klingenberg (1998), ontogenetic scaling (conservation of ancestral trajectory with eventual truncation or extension) implies common slope (b) and elevation (a); lateral transposition (parallel change of the entire trajectory) implies common slope and different elevation; and change in slope represents change in the direction of trajectories.

lasticity of the data by the Shapiro–Wilk and Levene tests, respectively.

RESULTS

With the exception of Proc, all variables showed high correlation with size (Bl), with coefficients of determination ranging from 0.759 to 0.953 (Table 2; Fig. 3). In addition to the low correlation of Proc with skull size, we found significant differences among adults of analyzed species ($F_{4,189} = 18.396$, $P < 0.0001$). No significant differences ($P > 0.05$) in Proc were found between *C. magellanicus* and *C. talarum*, or between *C. australis*, *C. mendocinus*, and *C. porteousi*, but these 2 species groups differed significantly ($P < 0.005$).

The Lo was the only variable that showed isometric growth ($b = 1$) in all the species analyzed (Table 2). The Li of the masseteric muscles showed negative allometry in all species; the values of b for this variable were closest to isometry in *C. porteousi* and *C. mendocinus*. Concurrently, the Li:Lo ratio also showed negative allometry in all species (nonsignificant in *C. porteousi*, $P > 0.05$; results not shown). Jw exhibited isometric growth ($b = 1$) in *C. australis*, *C. mendocinus*, and *C. porteousi*; in *C. talarum* and *C. magellanicus* this variable showed slightly negative allometry, with maximum b values close to 1 (Table 2). J and I_0 of the upper incisor were

positively allometric (isometry: $b = 4$) in all species, with highest allometric coefficients in *C. australis* and *C. porteousi* (Table 2).

The cranial and mandibular variables showed highly conservative growth rates. The trajectories of each variable shared a common slope for all the species analyzed. Lateral transposition ($P_b > 0.05$; $P_a < 0.05$) occurred in all interspecific pairwise comparisons with the exception of *C. mendocinus* and *C. porteousi*, which exhibited both common slope and common elevation ($P_b > 0.05$; $P_a > 0.05$). Elevation for Jw was highest in *C. australis* and lowest in *C. magellanicus* (Fig. 3A). Likewise, Li showed highest elevation in *C. australis*, whereas lowest values occurred in *C. talarum* (Table 2; Fig. 3B). The variable Lo showed the most conservative growth pattern among the 5 species because only minor differences in elevation occurred between the different trajectories (Fig. 3C).

In contrast with the craniomandibular variables, the comparisons of trajectories of the dental traits showed changes in slope ($P_b < 0.05$; Table 2; Figs. 3D and 3E). In pairwise comparisons of J both *C. australis* and *C. porteousi* showed higher slope than *C. magellanicus*, *C. mendocinus*, and *C. talarum*. Lateral transposition occurred in the remaining interspecific comparisons. With respect to I_0 , *C. australis* showed higher slope than *C. mendocinus*, and *C. porteousi* showed a similar change with respect to *C. magellanicus*, *C. mendocinus*, and *C. talarum*. Ontogenetic scaling was present between *C. mendocinus* and *C. talarum*, and the remaining interspecific comparisons showed lateral transposition.

DISCUSSION

The masticatory morphology of different lineages and genera of ctenomyid rodents exhibits considerable disparity. Given that the masticatory mode of ctenomyids is essentially uniform (Verzi et al. 2004), such disparity is assumed to be linked to different degrees and strategies of fossoriality (Reig and Quintana 1992; Verzi 2008). *Ctenomys* differs from the fossil ctenomyids *Xenodontomys*, *Actenomys*, and *Praectenomys*, with presumably fossorial habits, in characters of the masticatory apparatus associated with digging (Fernández et al. 2000; Lessa et al. 2008; Quintana 1994; Verzi 2008). In a previous analysis of the scaling of mandibular width and condyle–incisor distance in ctenomyids, Vassallo and Mora (2007) found marked differences in elevation between the ontogenetic trajectories of *Ctenomys* and those of the fossorial genus *Actenomys*, suggesting intergeneric evolutionary changes in early developmental stages (lateral transposition). In that analysis *C. australis* and *C. talarum* showed conserved positively allometric trajectories. Accordingly, these authors suggested that shape changes in the skull of *Ctenomys* species would be associated with changes in size alone, while maintaining an ancestral trajectory (ontogenetic scaling).

Despite the differences in both number of species analyzed and type of analysis, our results partially support the proposal that the craniomandibular features we analyzed illustrate

TABLE 2.—Allometric parameters (log₁₀ craniomandibular and dental variables regressed on log₁₀ basilar length) for 5 species of *Ctenomys*, calculated from a standardized major axis regression model for each species: *b*, slope; *CI*, confidence interval (isometry in boldface type); log *a*, y-intercept. An asterisk denotes slope (*b**) and intercept values obtained when a common slope is fitted to the data. Abbreviations are as in the “Materials and Methods” (also see Fig. 1). Sample sizes were: *C. australis* (*n* = 56), *C. magellanicus* (*n* = 60), *C. mendocinus* (*n* = 58), *C. porteousi* (*n* = 48), and *C. talarum* (*n* = 65). NS, not significant.

Variables	Species	<i>P</i>	<i>b</i> (<i>CI</i>)	<i>b</i>	Log <i>a</i>	<i>r</i> ²
Jw	<i>C. australis</i>	<0.001	0.925 (0.853–1.003)	0.935	0.089*	0.912
	<i>C. magellanicus</i>	<0.001	0.873 (0.802–0.950)	0.935	0.021*	0.897
	<i>C. mendocinus</i>	<0.001	1.001 (0.909–1.102)	0.935	0.061*	0.871
	<i>C. porteousi</i>	<0.001	1.050 (0.932–1.183)	0.935	0.061*	0.837
	<i>C. talarum</i>	<0.001	0.906 (0.830–0.988)	0.935	0.047*	0.880
Li	<i>C. australis</i>	<0.001	0.757 (0.702–0.816)	0.769	–0.306*	0.924
	<i>C. magellanicus</i>	<0.001	0.774 (0.707–0.846)	0.769	–0.353*	0.884
	<i>C. mendocinus</i>	<0.001	0.814 (0.714–0.928)	0.769	–0.343*	0.759
	<i>C. porteousi</i>	<0.001	0.841 (0.751–0.942)	0.769	–0.341*	0.853
	<i>C. talarum</i>	<0.001	0.692 (0.618–0.775)	0.769	–0.373*	0.796
Lo	<i>C. australis</i>	<0.001	0.931 (0.863–1.005)	0.960	–0.053*	0.923
	<i>C. magellanicus</i>	<0.001	0.944 (0.872–1.022)	0.960	–0.044*	0.908
	<i>C. mendocinus</i>	<0.001	1.004 (0.940–1.072)	0.960	–0.070*	0.940
	<i>C. porteousi</i>	<0.001	0.912 (0.814–1.023)	0.960	–0.067*	0.851
	<i>C. talarum</i>	<0.001	0.968 (0.899–1.043)	0.960	–0.077*	0.913
J	<i>C. australis</i>	<0.001	5.286 (4.981–5.609)	—	–7.752	0.953
	<i>C. magellanicus</i>	<0.001	4.638 (4.189–5.136)	—	–6.836	0.849
	<i>C. mendocinus</i>	<0.001	4.482 (4.033–4.981)	—	–6.435	0.844
	<i>C. porteousi</i>	<0.001	5.646 (5.086–6.267)	—	–8.225	0.876
	<i>C. talarum</i>	<0.001	4.701 (4.283–5.161)	—	–6.732	0.862
I ₀	<i>C. australis</i>	<0.001	5.342 (5.020–5.684)	—	–8.167	0.948
	<i>C. magellanicus</i>	<0.001	4.871 (4.425–5.361)	—	–7.529	0.866
	<i>C. mendocinus</i>	<0.001	4.666 (4.196–5.189)	—	–7.021	0.842
	<i>C. porteousi</i>	<0.001	5.824 (5.227–6.490)	—	–8.812	0.866
	<i>C. talarum</i>	<0.001	4.891 (4.452–5.373)	—	–7.334	0.860
Proc	<i>C. australis</i>	<0.001	0.308 (0.255–0.372)	—	–0.275	0.516
	<i>C. magellanicus</i>	NS	0.453 (0.352–0.584)	—	–0.495	0.051
	<i>C. mendocinus</i>	<0.001	0.347 (0.274–0.440)	—	–0.298	0.206
	<i>C. porteousi</i>	0.023	0.414 (0.314–0.546)	—	–0.414	0.108
	<i>C. talarum</i>	0.002	0.495 (0.393–0.623)	—	–0.493	0.143

conserved growth rates (Vassallo and Mora 2007). Thus, the high frequency of common slopes among the ontogenetic trajectories suggests a tendency toward the conservation of an ancestral growth rate for the analyzed features of the masticatory apparatus. However, in contrast with previous results, lateral transposition was the most frequent change pattern; only *C. porteousi* and *C. mendocinus* showed markedly similar growth patterns, which could be due to their close phylogenetic relationship (Castillo et al. 2005; Massarini et al. 1991; Slamovits et al. 2001). In addition, because the craniomandibular variables were isometric or nearly isometric with respect to overall skull size, the assumption that size alone is responsible for shape changes is not supported.

Very few data about the digging behavior and performance of *Ctenomys* species are available, and thorough studies are necessary to improve our understanding of digging adaptations within the genus. Nevertheless, these results allow discussion of some morphofunctional patterns. The maintenance of near-geometric similarity throughout the growth of craniomandibular traits suggests that, within each species, few changes in relative bite force at the upper incisors are to be expected between juveniles and adults. Because the in-lever arm of the masseteric muscles showed slight negative allometric growth,

juveniles would be somewhat more efficient, in proportion, than adults of the same species to produce bite forces. This mechanical advantage would compensate the relatively less-developed musculature of pups and juveniles. In contrast to the growth of craniomandibular traits, that of the cross section of the upper incisors would make these teeth more adequate to resist shearing and bending stress in adults.

Differences in growth trajectories detected in pairwise species comparisons provide additional insights into patterns of morphofunctional variation. The trajectories for jaw width and in-lever arm of masseteric muscles showed markedly higher elevation in *C. australis* compared to the other species. This change in jaw width suggests that comparatively greater increase in masseteric muscle mass occurs during early developmental stages of *C. australis* (Vassallo and Mora 2007). That the out-lever arm of the adductor muscles showed the most conserved trajectories among all the species suggests that both juvenile and adult individuals of *C. australis* possess a more specialized morphology for generating forces at the incisors (Figs. 3A–C). However, *C. australis* exhibits the lowest values of procumbency (Fig. 3F), despite procumbent incisors being advantageous for biting into the substrate because of their more adequate angle of attack (Lessa 1990;

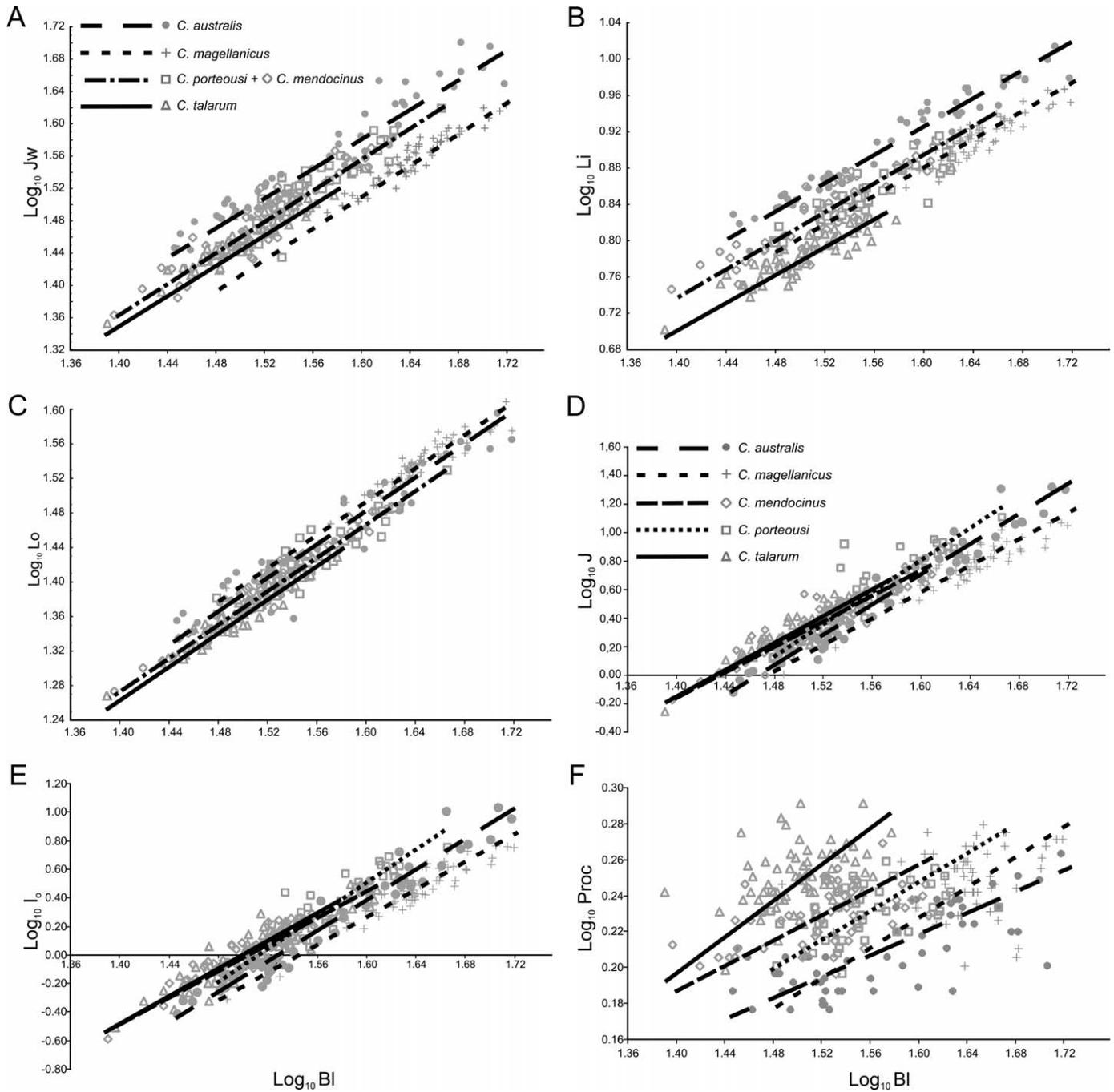


FIG. 3.—Allometric relationships (standardized major axis regressions) of \log_{10} -transformed craniomandibular and dental measurements versus basilar length for 5 species of *Ctenomys*. Parallel lines correspond to adjusted regression lines for common slope cases. References in A are the same for B and C; references in D are the same for E and F. Abbreviations are as in the ‘‘Materials and Methods’’ and Fig. 1.

Stein 2000; Verzi and Olivares 2006). In our sample *C. magellanicus*, the species with the proportionally narrowest jaw and short in-lever arm of the masseteric muscles throughout its ontogeny, showed comparatively more prominent incisors. Thus, zygomasseteric characters linked to force production are not correlated with an arrangement of the incisors especially favorable for chisel-tooth digging (Verzi and Olivares 2006). This supports the idea that the mode of

incisor use could be variable in burrowing rodents. *Ctenomys* is not exclusively a tooth-digger but rather a dual digger that makes considerable use of its forelimbs (De Santis et al. 1998; Dubost 1968; Stein 2000; Ubilla and Altuna 1990). In some cases the incisors might not be primary digging tools but are used to deal with challenges such as dense roots that are encountered during the construction of burrows (Stein 2000; Van Daele et al. 2009). Among the studied species, *C.*

TABLE 3.—Characteristics of habitats and soils occupied by the *Ctenomys* species analyzed.

Species	Habitat	Source
<i>C. australis</i>	Sand dune with grasses; very friable soils	Comparatore et al. (1992); Mora et al. (2006)
<i>C. magellanicus</i>	Patagonian steppe; medium soil	Luna et al. (2009)
<i>C. mendocinus</i>	Arid and semiarid environments in lowlands and mountainous regions; poorly developed sandy and gravelly to relatively compact soils	Rosi et al. (2005)
<i>C. porteousi</i>	Lowland grassland; medium soil	Luna et al. (2009)
<i>C. talarum</i>	Well-vegetated, grassy habitats; more or less sandy and friable to hard, clayey soils	Comparatore et al. (1992); Vassallo (1998)

australis is the one that occupies most friable soils (Table 3), and it frequently uses the incisors for cutting roots (Vassallo 1998).

Based on these results, *Ctenomys* encompasses a range of morphological and functional variation. Most of the changes that generate variation in the features examined here, especially in craniomandibular traits, are concentrated in early stages of development, prior to those represented in this study. This pattern is similar to the one detected in comparisons between *Ctenomys* and extinct ctenomyid genera with different digging strategies (Vassallo and Mora 2007; Verzi et al. 2010). This supports the hypothesis that more flexibility exists for early ontogenetic changes, with ancestral growth rates maintained later, rather than for other evolutionary changes in postnatal trajectories (Klingenberg 1998). Likewise, it suggests that the patterns of ontogenetic change underlying the generation of morphofunctional variation present some constancy at both intergeneric and interspecific levels in ctenomyids.

RESUMEN

Se analizaron alometrías ontogenéticas de rasgos craneomandibulares y dentarios vinculados con la excavación en 5 especies del roedor subterráneo sudamericano *Ctenomys* (tucu-tucos). A excepción de la procumbencia de los incisivos superiores, las variables mostraron alta correlación con el tamaño general del cráneo. En particular, las variables craneomandibulares, vinculadas con la producción de fuerzas de mordida en los incisivos, mostraron trayectorias cercanas a la isometría durante el crecimiento postnatal y cambios interespecíficos en estadios tempranos del desarrollo que resultan en diferentes formas iniciales (transposición lateral). Este patrón de cambio es similar al previamente detectado entre géneros vivientes y extintos de ctenómidos. Estos resultados sugieren mayor flexibilidad evolutiva para cambios en estadios ontogenéticos tempranos, y permiten rechazar la hipótesis de que diferencias interespecíficas en la forma del cráneo de *Ctenomys* están asociadas únicamente con diferencias de tamaño.

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- Ctenomys magellanicus* Bennett, 1835.—Río Grande, Tierra del Fuego Province, Argentina: MLP field numbers Ct 1, 2, 5–7, 17–19, 27, 29, 31, 32, 35–38, 40, 41, 44–46, 57–59, 72, 74; juveniles: MLP field numbers Ct 3, 16, 20, 30, 39, 42, 43, 71. San Sebastián, Tierra del Fuego Province, Argentina: MLP field numbers Ct 9, 10, 13, 15, 21–23, 33, 34, 47–49, 52, 54–56, 60, 62; juveniles: MLP field numbers Ct 8, 12, 14, 24, 50, 51, 53, 61.
- Ctenomys mendocinus philippi*, 1869.—Paramillos, Mendoza Province, Argentina: IADIZA-CM 02830, 02832, 02836–02838, 02981–02984, 02987, 02989, 06419, 06431, 06441, 06743, 06744; juveniles: IADIZA-CM 02842, 02844, 02851, 06404, 06411, 06412, 06416, 06418, 06436, 06449, 06454, 06458, 06734. Cacheuta, Mendoza Province, Argentina: IADIZA-CM 03407, 06475, 06609, 06612, 06615, 06621, 06622, 06626, 06627, 06630–06633, 06681, 06699, 06705; juveniles: IADIZA-CM 06459, 06461, 06471, 06472, 06623, 06624, 06628, 06646, 06648, 06659, 06708, 06714, 06739.
- Ctenomys porteousi* Thomas, 1916.—Bonifacio, Buenos Aires Province, Argentina: MMPMa 1337, 1340, 1342, 1343, 1347, 2288–2291, 2294, 2295, 2996–2998, 3191, 3194, 3195, 3213–3216, 3219–3224, 3305, 3309, 3310, 3312, 3414, 4213, 4215, I1392, I1406, I1407, I1412, I1413, I1543, I1550; juveniles: MMPMa 1338, 3196, 3197, 3198, I1537, I1539, I1542.
- Ctenomys talarum* Thomas, 1898.—Necochea, Buenos Aires Province, Argentina: LEMP N1, N5, N17, A(12), Ct(3), Ct(14)(19), Ct(15), Ct(16)(8), Ct(19), P87.2, P87.6, P87.7, P87.17, P87.20, P87.21, P87.44, 6D(2), 9D, 11P88, 102P88, 103P88, 111P88, 116P88, 118P88, 74i88, 77i88, 79i88, 80i88, 89i88, 92i88, 94i88, 51V88, 57V88, 59V88, 2FA88, 4FA88, 8FA88; MMPMa 4000–4003, 4006, 4030–4032, 4034, 4035, 4037, 4040–4044; juveniles: LEMP N1*, Ct(13)(20), Ct(16), P87.34, 5D(7), 8D, 121P88, 93i88, 54V88, 56V88; MMPMa 4036, 4039.

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APPENDIX I

Taxa and specimens examined. Institutional acronyms correspond to IADIZA-CM—Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina; LEMP—Laboratorio de Ecofisiología, Universidad Nacional de Mar del Plata, Argentina; MLP—Museo de La Plata, Argentina; and MMPMa—Museo de Ciencias Naturales “Lorenzo Scaglia,” Mar del Plata, Argentina.

Ctenomys australis Rusconi, 1934.—Necochea, Buenos Aires Province, Argentina: MLP 3.XI.95.5, 7.XI.95.1, 7.XI.95.1.2,