



## Craniodental ontogeny of the pacarana *Dinomys branickii* Peters 1873 (Rodentia, Hystricognathi, Caviomorpha, Dinomyidae)

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We investigate the cranial, mandibular, and dental ontogeny of the pacarana *Dinomys branickii*, the only extant species of the rodent family Dinomyidae. A bivariate allometric study (via reduced major axis), including 21 variables from the skull and 6 from the lower jaw on samples varying from 21 to 32 specimens, was produced. Results of the analyses indicate fast growth in the rostrum and palatal length but isometric growth in nasal width, rostral height, and length of the upper diastema. Positive allometry is also present in mandibular length, in retromolar length of the lower jaw, and, especially, in height of the articular process. Negative allometry is found in the length and width of the tympanic bulla, braincase width, width of the occipital condyles, and occipital height. We document for the 1st time the presence of a 3rd premolar (dP3), represented by a tiny, rooted element, and which is lost in early postnatal ontogeny. Replacement of dP4/dp4 occurs after eruption of M3/m3. The complete eruption of P4/p4 happens when M3/m3 are fully functional. Ontogenetic changes in the postnatal ontogeny of the skull of *D. branickii* are mostly related to the development of the occlusal system and action of associated muscles. This is evidenced by rapid growth of the facial region, a deepening and strengthening of the temporal and occipital regions and a widening of the posterior portion of the palate which is related to the eruption and replacement of molariform teeth. Some observed that craniomandibular trends in the ontogeny of *D. branickii* are reflected in the size of Ctenohystrica taxa, with small species of this lineage showing features similar to those of juveniles of *D. branickii* and large species resembling adults of the pacarana.

En este trabajo se presenta una investigación de la ontogenia craneana, mandibular y dentaria de la pacarana, *Dinomys branickii*, única especie existente de roedores de la familia Dinomyidae. Se realizó un estudio alométrico bivariado usando eje mayor reducido, de 21 medidas del cráneo y seis de la mandíbula en muestras representadas por 21 a 32 especímenes. El análisis indica un crecimiento rápido para la longitud del rostro y del paladar, e isométrico para el ancho de los nasales, la altura del rostro y la longitud del diastema superior. Alometría positiva está también representada en la longitud mandibular, longitud retromolar de la mandíbula, y especialmente en la altura del proceso articular. Alometría negativa caracteriza la longitud y ancho de la bula timpánica, el ancho de la caja craneana, el ancho de los cóndilos occipitales y la altura de la placa occipital. Se documenta por primera vez la presencia de un tercer premolar deciduo (dP3), un elemento pequeño con raíz que es perdido tempranamente en la ontogenia postnatal. El remplazo del dP4/dp4 se produce después de la erupción del M3/m3. La erupción completa del P4/p4 sucede cuando los M3/m3 son totalmente funcionales. Los cambios ontogenéticos en el desarrollo postnatal del cráneo de *D. branickii* están mayormente relacionados con el desarrollo del sistema oclusal y músculos asociados. Esto está evidenciado por un rápido crecimiento de la región facial, profundización y robustecimiento de las regiones temporal y occipital, así como por el ensanchamiento de la parte posterior del paladar que está relacionada con la erupción y remplazo de los molariformes. Algunos cambios ontogenéticos observados en las características del cráneo y mandíbula de *D. branickii* están reflejados en el tamaño de especies de Ctenohystrica: las especies pequeñas de este linaje muestran características similares a los juveniles de *D. branickii* y las especies más grandes se parecen, en los mismos caracteres, a adultos de la pacarana.

Key words: anatomy, bivariate analysis, *Dinomys branickii*, ontogeny, rodent, skull, South America

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Hystricognath caviomorphs are members of the oldest radiation of rodents in South America. The group is first recorded in the Middle-Late Eocene (Frailey and Campbell 2004; Vucetich et al. 2010; Antoine et al. 2012), had its maximum diversity in the Late Miocene, and now represents one of the most abundant groups of living mammals in South America (Mares and Ojeda 1982; Cione et al. 2000). There are 132 extant species, grouped in 12 families (Woods 1982; Wilson and Reeder 1993; Nedbal et al. 1996; McKenna and Bell 1997; Verzi 1994), including Erethizontidae (New World porcupines), Dasyproctidae (agoutis), Echimyidae (spine rats), and Dinomyidae (pacaranas), whose living representatives are restricted to the Brazilian zoogeographic subregion (Vucetich and Verzi 2002).

The family Dinomyidae has a single living species, *Dinomys branickii* Peters 1873 (the pacarana), but has a well-represented fossil record in South America, with more than 40 species (Mones 1986; Nasif 2009a, 2009b). They range from small forms, such as the Bolivian late Oligocene *Branisamys luribayensis* (Hoffstetter and Lavocat 1970), to gigantic, including *Telicomys* (Kraglievich 1926), *Eumegamys* (Kraglievich 1926), *Eumegamysops* (Kraglievich 1941), and *Josephoartigasia* (Mones 2007), all of them from the Miocene-Pliocene of Argentina, Venezuela, Brazil, and Uruguay (Pascual et al. 1967; Frailey 1986; Linares 2004; Rinderknecht and Blanco 2008). These forms represent the largest rodents known in that they may have reached weights up to 1,000 kg (Rinderknecht and Blanco 2008, but see Millien 2008). Dinomyids are an important and distinctive component in the Neotropical region, with an interesting evolutionary and biogeographical history, showing wide diversity and distribution of species in the past, an amazing range of body size, and an innovative craniomandibular design (Candela and Nasif 2006; Nasif 2009a, 2009b; Candela et al. 2013). Notwithstanding the importance of the group in the South American native fauna, the only living species remains poorly known in aspects ranging from natural history to anatomy and is today threatened with extinction (Walker 1975; Woods 1982; Santos 1984; Mones 1997; Wilson and Reeder 2005; Tirira et al. 2008; Osbahr and Azumendi 2009; Saavedra-Rodríguez et al. 2012).

Dinomyids are monophyletic, but their relationship with other caviomorphs is controversial. Based on neontological and paleontological evidence, dinomyids were considered to be closely related to several caviomorph families, including Dasyproctidae (Simpson 1980; Nedbal et al. 1996), Caviidae and Hydrochoeridae (Wood and Patterson 1959; Patterson and Wood 1982), Myocastoridae (Landry 1957), Heptaxodontidae (Ray 1964), Erethizontidae (Fields 1957; Ray 1958; Eisenberg 1974; Kleiman et al. 1979; Grand and Eisenberg 1982; Woods and Hermanson 1985), and Chinchillidae (Sánchez-Villagra et al. 2003; Huchon et al. 2007; MacPhee 2011; Kramarz et al. 2013), or as a family incertae sedis (Woods 1982; Verzi 1994). The most recent phylogenetic studies using molecular data indicate a close relationship between the Dinomyidae and Chinchillidae (Huchon and Douzery 2001; Honeycutt et al. 2003; Blanga-Kanfi et al. 2009; Upham and Patterson 2012; Voloch et al. 2013). However, a phylogenetic analysis

by the senior author, based on morphological characters, indicates a sister group relationships between Dinomyidae and Erethizontidae (Nasif 2009a, 2009b).

There are several publications on the osteology of the cranium and postcranium of *D. branickii* (Peters 1873a, 1873b; Anthony 1926; Ellerman 1940; Stehlin and Schaub 1951; Fields 1957; Ray 1958; Grand and Eisenberg 1982; White and Alberico 1992; Mones 1997; Krapovickas and Nasif 2011; MacPhee 2011; Hautier et al. 2012), but none of these consider ontogeny. The only previous studies dealing with ontogeny of dinomyids focused on dentition. Thus, Fields (1957) and Ray (1964) used evidence on dental replacement and occlusal variations in the molars of *D. branickii* to compare fossils of dinomyids and heptaxodontids (giant hutias). More recently, Candela and Nasif (2006) described an extinct dinomyid from the Miocene, represented by a well-preserved juvenile specimen where the 4th deciduous premolar is in the process of being replaced.

We present here the 1st exhaustive craniodontal ontogenetic study of *D. branickii*, which also represents the most detailed survey of the anatomy of the cranium, mandible, and dentition of members of the family Dinomyidae, and one of the few for caviomorph rodents. We present a qualitative approach in which we compare changes in the condition of key characters from juveniles to adults and we interpret the possible processes that influenced these changes. In addition, we present a quantitative analysis exploring the allometry of selected skull measurements.

Variation in the postnatal ontogeny of the mammalian skull is related mainly to differential ontogeny of the neurocranium and splanchnocranium which are subject to different growth trajectories, a consequence of different functional demands (Maunz and German 1996; Abdala et al. 2001). Growth of the splanchnocranium is linked to development of occlusal muscles and support of structures for breathing, whereas growth of the neurocranium is linked to development of the brain and sensory organs (Maunz and German 1996). We expect that most ontogenetic changes in the growth of the skull of *D. branickii* will be related to the early development of the brain and sensory organs and the late growth of the masticatory apparatus and related structures (e.g., masseteric and temporal musculature and dentition). Knowledge of ontogenetic variation in the single living species of the family Dinomyidae represents a valuable step to understand better the morphology of the fossil forms and provides additional elements to evaluate the evolutionary history of the Hystricognathi.

## MATERIALS AND METHODS

We evaluated 35 museum specimens deposited in collections from the United States, Brazil, Argentina, and Uruguay (Appendix I).

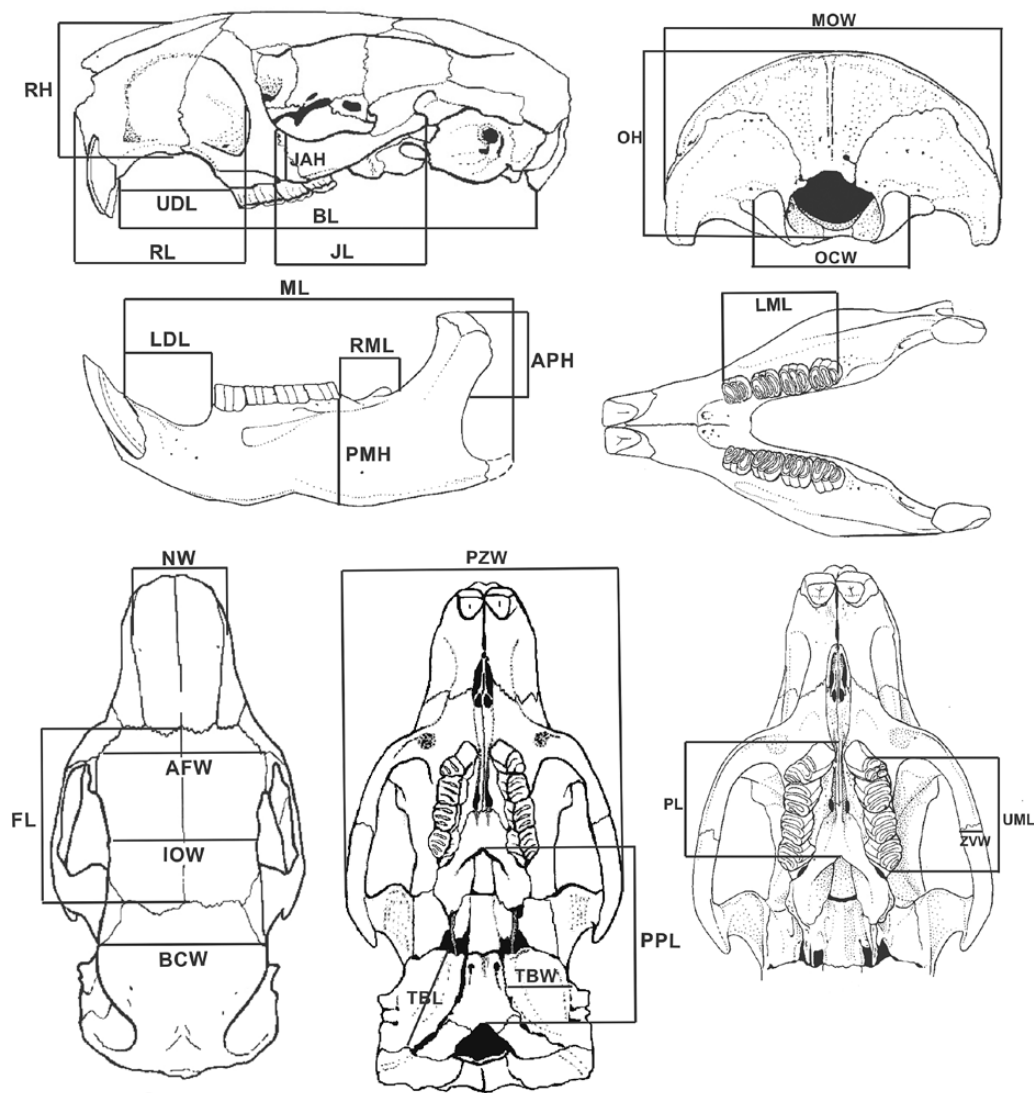
*Age sequence.*—Specimens were classified following the tooth-class system of Nelson and Shump (1978) with modifications. We identified the following classes: neonate I: dP4/dp4-M1/m1 with minimal wear; juvenile II: dP4/dp4-M2/m2 worn and M3/m3 at the beginning of its eruption; juvenile III: worn

out dP4 next to be replaced/dp4 replaced and p4 at the alveolar level, and M3/m3 with minimal wear; juvenile IV: recently emerged P4/p4 and M3/m3 continues with minimal wear; juvenile V: minimal wear on P4/p4 and further wear on M3/m3; subadult VI: functional P4/p4–M3/m3 less worn than in adults; adult VII: more wear in P4/p4–M3/m3 than in preceding stages (see Appendix II for assignation of specimens to age classes).

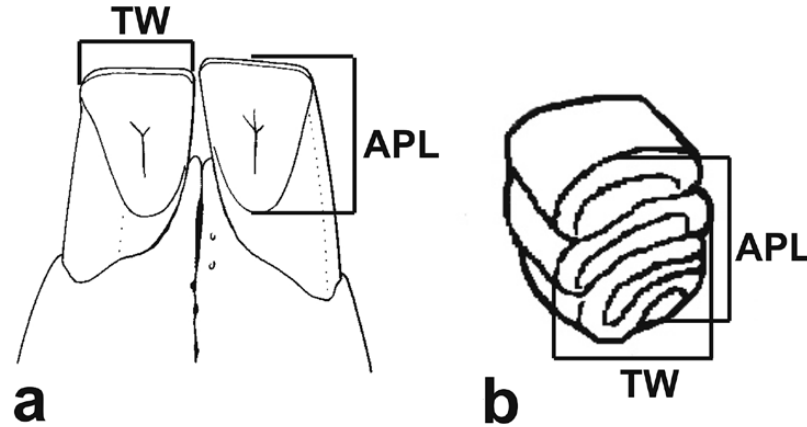
**Bivariate allometry.**—Measurements ( $n = 27$ ) were obtained (Fig. 1) for 31 specimens with skull lengths varying from 77.4 to 166.8 mm. Selecting of quantitative variables emphasized extremes landmarks rather than short dimensions (Voss 1988:361). In addition, extensive use of the same structure as a landmark for several variables was avoided. Bivariate analyses with log-transformed variables were performed comparing each measurement of the skull with the geometric mean of

all measurements of the sampled specimens (Coleman 2008; Tarnawski et al. 2014). Reduced major axis regression was used to obtain coefficients of allometry. We identified statistically significant positive and negative allometries (values greater or less than 1, respectively) and applied a Bonferroni correction before rejecting the hypothesis of isometry (see Table 4). We also performed  $t$ -tests with a subsample of 5 adult males and 6 adult females to assess the presence of sexual size dimorphism. Analyses were performed using software PAST 2.12 (Palaeontological Statistics—Hammer et al. 2001; Hammer and Harper 2006).

**Dental wear.**—Incisors, premolar, and molar occlusal surfaces (length and width) were measured (Fig. 2) with the aim of assessing variation in dental morphology and size during growth.



**Fig. 1.**—Cranial measurements of *Dinomys branickii* used in this study. Abbreviations: AFW, anterior frontal width; APH, articular process height; BCW, braincase width; BL, basal length; FL, frontal length; IOW, interorbital width; JAH, jugal anterior height; JL, jugal length; LDL, lower diastema length; LML, lower molar series length; ML, mandibular length; MOW, maximum occipital width; NW, nasal width; OCW, occipital condyles width; OH, occipital height; PL, palatal length; PMH, posterior mandibular height; PPL, postpalatal length; PZW, posterior zygomatic width; RH, rostral height; RL, rostral length; RML, mandible retromolar length; TBL, tympanic bulla length; TBW, tympanic bulla width; UDL, upper diastema length; UML, upper molar series length; ZVW, zygoma ventral width.



**Fig. 2.**—Dental measurements of *Dinomys branickii* used in this study, a) incisor and b) molar. Abbreviations: APL, anteroposterior length; TW, transverse width.

**Terminology.**—Anatomical nomenclature follows Abdala and Diaz (2000), Cherem and Ferigolo (2012), Hill (1935), Hoffstetter (1974), Moraes-Santos (1997), Popesko et al. (1992), Verzi (1994), Voss (1988), Wahlert and Souza (1988), and Woods (1984). Identification of foramina and muscle attachments follows Bugge (1985), Butler (1985), Cherem and Ferigolo (2012), Guthrie (1963), Hill (1935), Nasif (2009b), Novacek (1985), Patterson and Wood (1982), Voss (1988), Wahlert (1977; 1985a, 1985b), Woods (1972), and Woods and Howland (1979). For descriptions of molars, the following sources were used: Fields (1957), Mones (1982), and Ray (1964), and a recent proposal of molar occlusal homologies in dinomyids by Nasif (2009b). Dental abbreviations used are: I-i, incisor; dP-dp, deciduous premolar; M-m, molar, and P-p, premolar. Upper dentition is represented by upper case and lower dentition by lower case letters.

## RESULTS

### *Qualitative results*

**Skull.**—We present here cranial changes (summarized in Table 1) observed in *D. branickii* that represent notable qualitative differences between the skulls of juveniles and adults. The juvenile skull shows a semicircular outline, with convex parietals, forming a domed calvaria with the occipital region globular, whereas the adult skull outline shows a dorsal flattening, particularly in the parietal region but preserving a slight convexity in the nasofrontal region (Fig. 3). The posterior occipital portion is also flattened to a straight condition in lateral view.

In juvenile stages I–III, the maximum height of the skull is represented in the postzygomatic region, and the tympanic bulla is located below the level of the zygoma and of the dental series (Fig. 3). In adults, the prezygomatic region is higher and the ventral margin of the bulla is located at the same level as the zygoma. This reflects change in the angulation of the basicranium. As a byproduct of this modification in the basicranial angulation, the foramen magnum is oriented posteroventrally in juveniles and posteriorly in adults (Fig. 4).

The rostrum grows more in length than in width, resulting in longer and thinner nasals, especially in the posterior

portion (Fig. 5). In juveniles, nasals extend laterally in the rostrum, while in subadults and adults they are restricted to the roof of the rostrum. Lengthening of the nasals in the posterior end extends in front to the level of dP4 and the dorsal root of the anteorbital bridge in early juveniles of stage I (asterisk, Fig. 3a). The posterior margin of the nasal shows a progressive lengthening that extends to the level of dP4 in subsequent juvenile stages (asterisk, Fig. 3b) until it reaches the level of M1 in adults (asterisk, Fig. 3c). Lengthening of the nasals is also represented by the posterior shift of the nasal-frontal suture, which is located anteriorly to the premaxilla-frontal suture in juveniles, whereas they are positioned at the same level as the latter suture in adults (Fig. 5). The premaxilla-frontal suture is concave in juveniles and straight in adults.

The anteroventral and posterior portions of the crest delimiting the rostral masseteric fossa are poorly developed in juveniles (I–III) and, concomitantly, the fossa is less developed than in subadults and adults (IV–VII). The margins surrounding this fossa are rounded and slightly raised in juveniles and thicker and higher in adults, thus forming a more pronounced crest, especially in its dorsal part (Fig. 3). The maxillary fossa anterior to the dental series (area of superficial masseter muscle origin—Woods 1972) is slightly concave in juveniles and deeper in adults (VI–VII; Fig. 4b).

The anterior portion of the jugal increases approximately 3 times its dorsoventral height from the juvenile to the adult (see jugal anterior height in allometric analysis). In stages I–IV, this bone is extended more anteriorly, forming the posterior portion of the ventral root of the anteorbital bridge (Fig. 3a). In addition, juveniles feature a curved maxilla-jugal suture and an incipient paraorbital apophysis. In stages V–VII, the maxilla-jugal suture is straight, the paraorbital apophysis is well developed, extended anteroposteriorly, and with the dorsal margin smoothly rounded (Figs. 3b and 3c). The inferior jugal process is located anteriorly to the paraorbital fossa in juveniles (stages I–III), whereas they are located at the same level in adults.

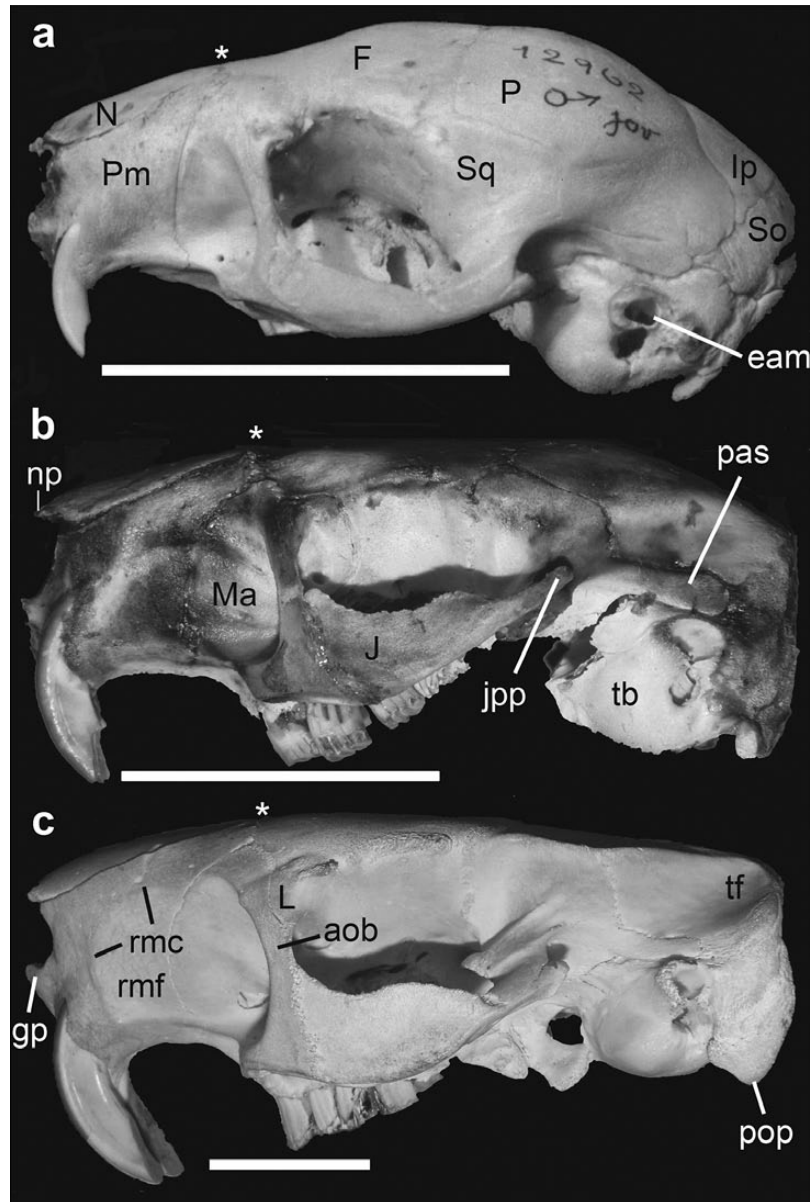
In the juvenile stage I, the interpremaxillary foramen is not shaped because the suture between the premaxillae is open, forming a continuous interpremaxillary sulcus (Fig. 4a). The

**Table 1.**—Morphological differences between smallest juveniles and largest adults of *Dinomys branickii*.

Characters	Figure	Juvenile	Adult
<b>Rostrum</b>			
1. Lateral extension of nasals	3 and 5	Extended laterodorsally in the snout	Only located on top of the rostrum
2. Maximum extension of nasals	3	Until the anterior level of the P4	Until the level of the P4 and M1
3. Level of cheek-teeth alveolar line	3	At zygomatic root level	Ventral to zygomatic root level
4. Premaxilla-frontal suture in dorsal view	5	Posterior to the nasal-frontal and curved	At same level to the nasal-frontal and straight
5. Anterior nasal process	3	Undeveloped	Developed
6. Interpremaxillary foramina	4	Not formed, open suture	Present
7. Accessory incisive foramina	4	Very small, in front of the premaxilla-maxilla suture	Large, immediately behind of the premaxilla-maxilla suture
8. Masseter crest	3	Shallow	Developed
<b>Orbital and zygomatic regions</b>			
1. Lacrimal and jugal extension on anteorbital bridge	3	Large	Short
2. Lacrimal sulcus	3	Open	Closed
3. Jugal apophysis	4	Small	Well developed
4. Maxillary fossa	3	Slightly concave	Deep
5. Maxilla-jugal suture	5	Curved	Straight
6. Squamosal in dorsal view	5	Not visible	Visible
7. Lacrimal, frontal-squamosal processes		Absent to incipient	Well developed
<b>Temporal and tympanic region</b>			
1. Temporal fossa	3 and 5	Shallow and short	Deep and elongated
2. Temporal crest	5	Incipient	Well developed
3. Margin of the external acoustic meatus	3	Continuous	Discontinuous
<b>Palatal region</b>			
1. Palatal crest	4	Low	High, reaching the alveolar level
2. Palatal sulcus	4	Deep	Very deep
3. Anterior palatine foramen	4	At level of dP4	Between M1-M2
4. Retromolar platform	4	Absent	Present
5. Posterior maxillary foramen	4	Absent	Present
6. Upper cheek-teeth series	4	Subparallel	Divergent
<b>Postfrontal region</b>			
1. Interparietal	5	Double in stage I	Merged since stage II–VII
2. Interparietal-supraoccipital suture	5	Present in stage I	Merged since stage II–VII
3. Supraoccipital	5 and 7	On the roof	Restricted at occipital plate
4. Postzygomatic constriction	5	Shallow	Deep
5. Parietal fossa in dorsal view	3	Absent	Present
<b>Basioccipital region</b>			
1. Basioccipital crest	4	Absent	Present
2. Basioccipital tubercles	4	Shallow	Well developed
<b>Occipital region</b>			
1. Supraoccipital-exoccipital suture	7	Visible	Totally merged
2. Nuchal and medial crests	7	Low	Well developed
3. Occipital fossa	7	Slightly concave	Very concave
4. Occipital tubercles	7	Absent	Conspicuous
4. Paracondylar process	7	Absent	Present
<b>Mandible</b>			
1. Masseteric crest origin	8	At level of dp4 or p4-m1	At level of m2-m3
2. Retromolar platform	9	Absent	Present
3. Anterior margin of symphysis	8	Below alveolar level of molariforms	At occlusal level of molariforms
4. Coronoid process	8 and 9	Developed in stage I	Reduced

interpremaxillary foramen is a long and narrow opening separated from the incisive foramina in juveniles of stage II to adults (Figs. 4b and 4c). In the maxilla, behind the incisive foramina, there is a pair of small oval accessory incisive foramina, delimited by a vomerian septum. These foramina are tiny and located at the level of the premaxilla-maxilla suture in juveniles of stage I, whereas they are larger and located immediately behind this suture in remaining ontogenetic stages.

The incisive foramina are included in the palatine fossa (palatine fissure—sensu Moraes-Santos 1997), which is a large gently concave sulcus that extends until the middle of the cheek-tooth series. This fossa becomes narrow and deep, ending in the palatine foramina. The palatine fossa has a progressive lengthening and an extreme narrowing during ontogeny, produced by the eruption of the definitive premolar (Fig. 4).



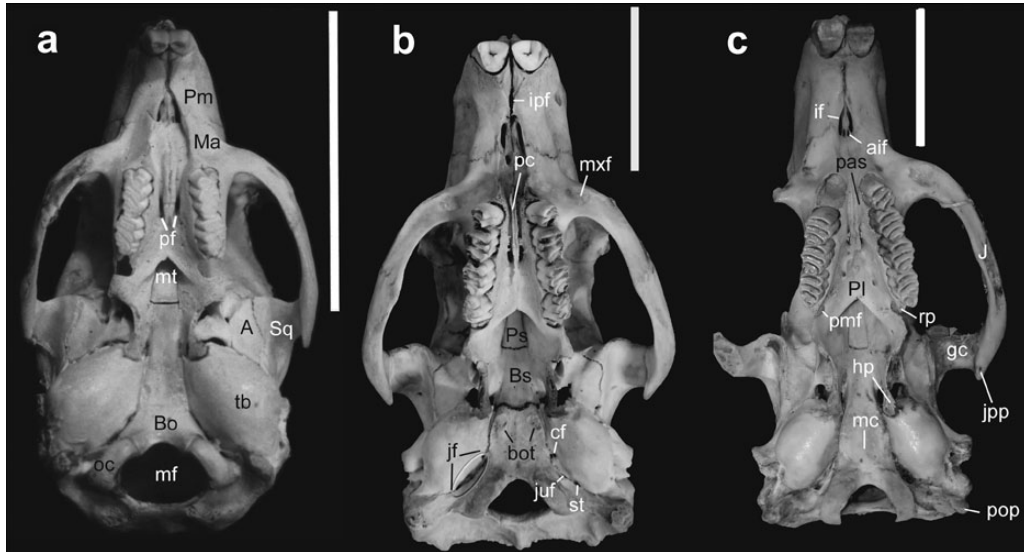
**Fig. 3.**—*Dinomys branickii*. Lateral view of the skull of a) MACN 12962 (BL: 75.0 mm); b) AMNH 100053 (BL: 87.79 mm); and c) AMNH 70354 (BL: 155.32 mm). Abbreviations: BL, basal length. AMNH, American Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia. aob, antorbital bridge; eam, external acoustic meatus; F, frontal; gp, gnathic process; Ip, interparietal; J, jugal; jpp, jugal posterior process; L, lacrimal; Ma, maxilla; N, nasal; np, nasal process; P, parietal; pas, posterior apophysis of the squamosal; Pm, premaxilla; pop, paroccipital process; rmc, rostral masseteric crest; rmf, rostral masseteric fossa; So, supraoccipital; Sq, squamosal; tb, tympanic bullae; tf, temporal fossa. Asterisk indicates nasal-frontal suture. Scale 4 cm.

There is a clear suture between maxillae along the palatal crest in all ontogenetic stages, but the crest changes from a low structure in juveniles to a tall structure in adults, where it reaches the alveolar level. The anterior palatine foramen has a posterior migration during growth, being located at the level of dP4 in stage I, whereas in specimens with the complete series of molars (stages V–VII), they are located between M1 and M2 (Figs. 4b and 4c).

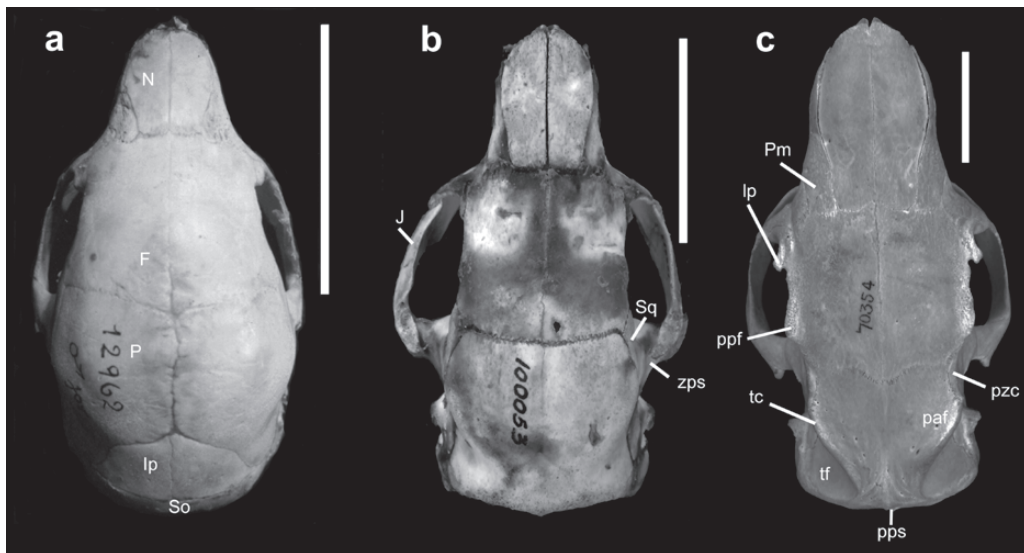
Changes observed in the palate are related to the gradual eruption of the cheek-teeth and enlargement and progressive posterior widening of the palate. Eruption of the cheek-teeth produces a posterior migration of the mesopterygoid fossa (and

lengthening of the palate), whose anterior margin is located at the posterior level of M1 in stage I, and at the level of the posterior portion of M3 in stage VII (Fig. 4). It is interesting to note that the palate continues growing in adulthood, as the position of the mesopterygoid fossa continues moving posteriorly even in adults. In addition, only subadults and adults (stages V–VII) develop a retromolar platform behind the last functional tooth and the posterior maxillary foramen located lingually at the level of the retromolar platform (Fig. 4c).

Upper molar series are subparallel in juveniles and posteriorly divergent in adults (Fig. 4). Dental eruption is related to the increase in width of the palate, especially in its posterior half



**Fig. 4.**—*Dinomys branickii*. Ventral view of the skull of a) MACN 12962 (BL: 75.0 mm); b) USNM 395160 (BL: 99.80 mm); and c) MACN 12961 (BL: 132.5 mm). Abbreviations: BL, basal length. MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; USNM, National Museum of Natural History, Smithsonian Institution. A, alisphenoid; aif, accessory incisive foramen; Bo, basioccipital; bot, basioccipital tubercle; Bs, basisphenoid; cf, carotid foramen; gc, glenoid cavity; if, incisive foramen; ipf, interpremaxillary foramen; hp, hamular process; J, jugal; jf, jugular fossa; juf, jugular foramen; jpp, jugal posterior process; Ma, maxilla; mc, medial crest of the basioccipital; mf, magnum foramen; mt, mesoptergoid fossa; mxf, maxillary fossa; pas, palatal sulcus; pc, palatine crest; pf, palatine foramen; Pl, palatine; Pm, premaxilla; pmf, posterior maxillary foramen; Ps, presphenoid; oc, occipital condyle; pop, paroccipital process; rp, retromolar platform; st, stapedia foramen; Sq, squamosal; tb, tympanic bullae. Scale 4 cm.



**Fig. 5.**—*Dinomys branickii*. Dorsal view of the skull of a) MACN 12962 (BL: 75.0 mm); b) AMNH 100053 (BL: 87.79 mm); and c) AMNH 70354 (BL: 155.32 mm). Abbreviations: BL, basal length. AMNH, American Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia. F, frontal; Ip, interparietal; J, jugal; lp, lacrimal process; N, nasal; P, parietal; paf, parietal fossa; Pm, premaxilla; ppf, posterior process of the frontal; pps, posterior process of the supraoccipital; pzc, postzygomatic constriction; So, supraoccipital; Sq, squamosal; tc, temporal crest; tf, temporal fossa; zps, zygomatic process of the squamosal. Scale 4 cm.

(at the level of M2 and M3). The width between dP4 and P4 is strongly reduced, with values varying from 6 mm in stage I to 2.49 mm in stage VII. The palatal posterior width in adults is practically twice that of juveniles.

Profound changes are represented in the temporal region of the skull. The temporal fossa is shallow and short, having its major extension at the level of the anterior portion of the bulla

in juveniles (stages I and II). This fossa in stage V is deeper and longer but does not reach the posterior margin of the skull. In stages VI–VII they are deep, elongated, and oblique dorsoventrally, reaching the posterior margin of the skull (Figs. 4 and 5). This change in orientation follows the development of the temporal crest, which is only represented by a short bulge in juveniles and becomes strong, forming a wide and sinuous

curve bordering the skull roof and reaching the occiput in adults (Fig. 5c).

The osseous bridge that differentiates the buccinomastatory foramina is only present in adults. The margin of the external acoustic meatus in the tympanic bullae is continuous until stage V, whereas in adults, it is interrupted posterodorsally (Verzi 1994). This change is related to ossification that is more intense in the anterior portion and so strengthens the bullar margin in adults (stage VII; Fig. 3c).

The basioccipital and basisphenoid are flat, broad, separated by a suture which is open until subadult stage V and closed but visible in the adult (VI–VII). The basioccipital is a progressively developing low medial crest that is manifest in adults (Fig. 4c). The parallel and elongated basioccipital fossae (described as muscle tubers by Popesko et al. 1992) are represented in juveniles as pits, and they become wider with high anterior and lateral margins in stages VI–VII.

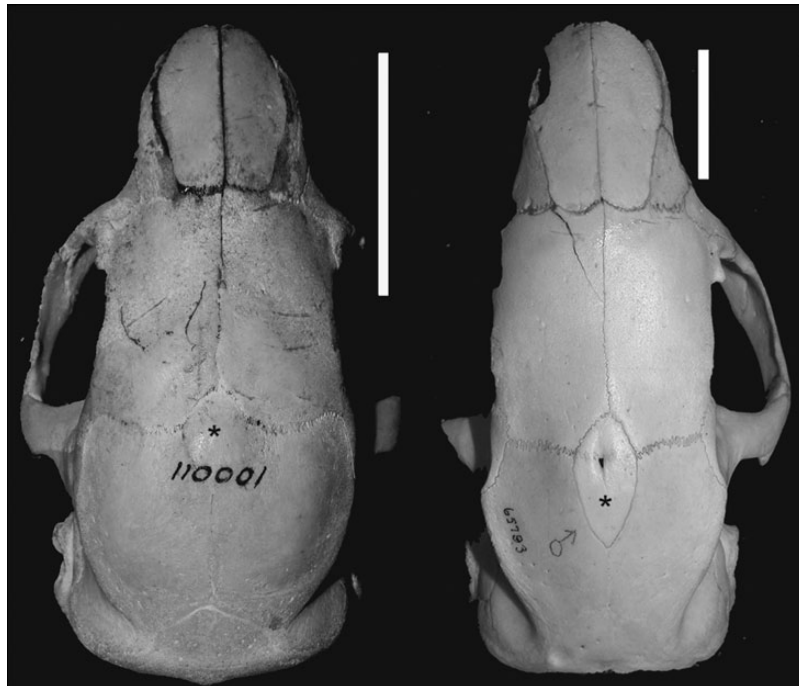
The contact between the basioccipital and the tympanic bulla is straight and less curved posteriorly in juveniles. The jugular fossa, located in the posterior half of this contact, extends until the posterior margin of the basioccipital and is wider and deeper in adults (Fig. 4). In the basioccipital-bullae contact, a narrow carotid channel is present anteriorly, and a wide jugular fossae posteriorly. The latter have 3 foramina, the carotid, stapedia, and jugular that are coalescent in juveniles and separated in adults (Fig. 4b).

The frontoparietal suture is highly variable and there is no obvious connection with ontogeny (i.e., several morphologies represented in similar stages). However, in adults, this suture frequently forms a small central concavity directed posteriorly (Fig. 5c). In spite of the small sample for this rare species,

there are 2 specimens showing a single bregmatic bone located between the frontal and parietals (Fig. 6). This abnormal bone is related to growth of the calvaria where the sagittal and coronal sutures meet. This bone also appears to be frequent in erethizontids and castorids (Schultz 1923).

In stage I, the suture between the parietal is patent and the interparietal is paired (Fig. 5a). Merging of the parietal and fusion of the interparietal occurs early during postnatal development. In stage I, sutures between parietal and surrounding bones are open (Fig. 5a). In stage II, the interparietal is a single bone also fused with the supraoccipital but with sutures remaining between this bone and the parietals. In stage III, prior to replacement of the 4th premolar, interparietal and parietals are fused (Fig. 5b). In subadults (V) and adults (VI–VII), the original margins of the interparietal are indicated by striations on the bone surface (Fig. 5c). This study confirms the existence of an interparietal in juvenile *D. branickii* (Mones 1997), and evidence in Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) 12962 indicates that this element originated as a paired bone (Fig. 5a).

During ontogeny, the combination of delayed braincase growth, gradual deepening of the temporal fossae, and widening of the occipital plate produces changes in the postzygomatic constriction (Fig. 5c) that are merely suggested in juveniles from stages I–IV, distinct in juveniles from stage V and conspicuous in subadults and adults (stages VI–VII). Concomitant with these changes, there is gradual development of temporal ridges and of a pair of shallow parietal fossae evident only in the adults. These fossae support the origin of the upper part of the temporalis muscle and are located in the middle third of the dorsal surface of the parietal (Fig. 5c).



**Fig. 6.**—*Dinomys branickii*. Bregmatic bone (indicated by an asterisk) in juvenile (AMNH 100011) and adult (FMNH 65793). Scale 4 cm. Abbreviations: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History.



In juveniles of stage I, the supraoccipital is a wide belt, visible in dorsal view, which contacts the interparietal anteriorly (Fig. 5a). With growth of the temporoparietal area, the supraoccipital is restricted to the occipital plate of the skull in stages V–VII (Fig. 7).

Profound modifications occur in the occipital region during growth, due to strengthening of bones, fusion across sutures, and the development of processes, ridges, and fossae. This is a response to mechanical stress imposed by the cervical muscles to support the heavy head that continues growing during maturity. Supraoccipitals and exoccipitals are well differentiated by open sutures until the subadult stage (V), but in adults, they form 1 element (Fig. 7). This plate in adults features strong nuchal crests and an additional nuchal crest on the occipital plate, in the area of fusion between supraoccipital and exoccipitals (Fig. 7b). The median occipital crest is incipient in the youngest specimens; in stage IV, it is more clearly developed as a crest and in the next stages, the conspicuous crest reaches the dorsal margin of the foramen magnum (Fig. 7c).

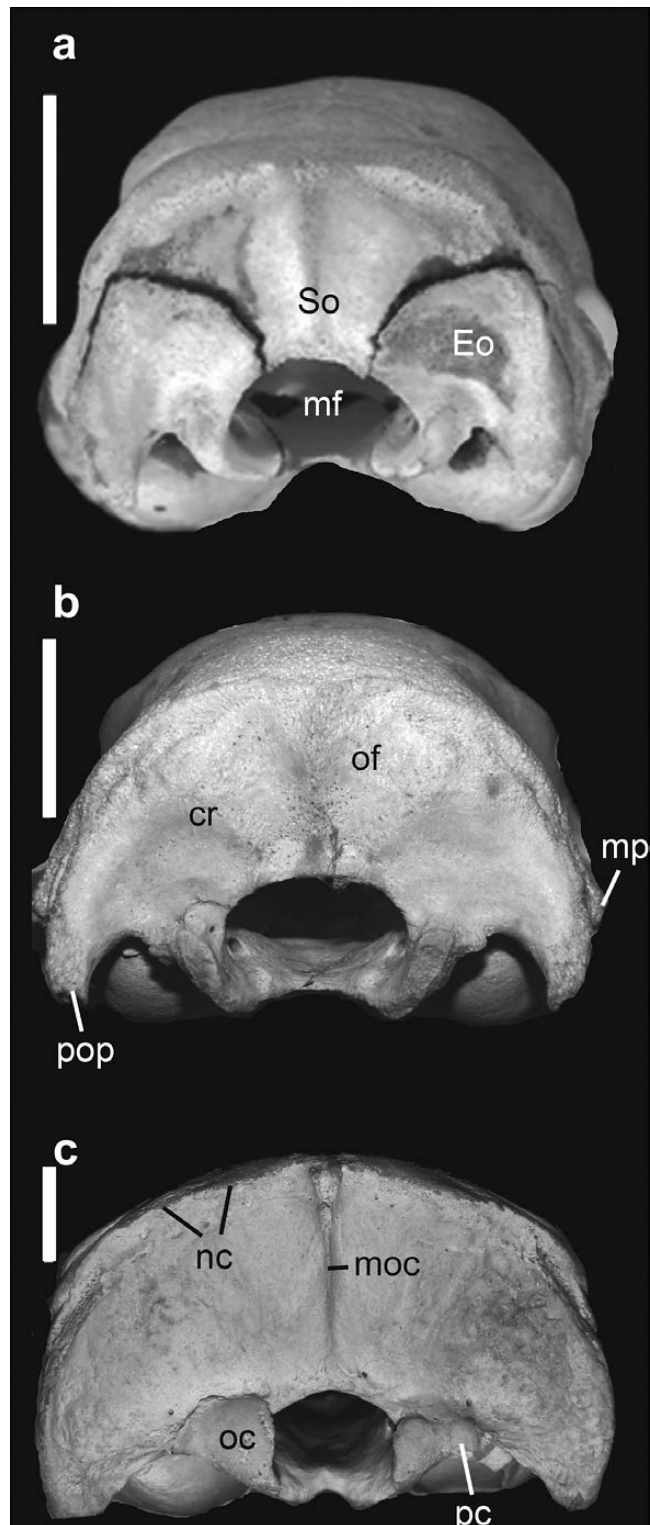
The suture between exoccipitals and basioccipital is open in juveniles and becomes fused in stage IV, whereas there is a crest formed in this area in adults (Fig. 4). The development of the paracondyles or accessory occipital condyles (only known in dinomyids among mammals) is late: they are weak in stage V and well developed only in adults of stages VI–VII (Fig. 7). The progression in the growth of the condyles and paracondyles is accompanied with the development of a shallow fossa located on the dorsal margin of these structures.

There is a gradual and synchronized development of the posterior process of the lacrimal, the postorbital process of the frontal, and the posterior process of the supraoccipital. This development is absent or outlined in stage I, slightly marked in stage V, and well developed in adults of stages VI–VII (Fig. 5c).

A feature of the dinomyids that distinguishes them from other caviomorphs is that most cranial sutures are obvious in all ontogenetic stages (Nasif 2009b). In the ontogeny of *D. branickii*, complete sutural fusion is restricted to the 2 components of paired bones, including interparietal, parietal, and exoccipital, and to the supraoccipital-exoccipitals—all elements that form the braincase (Fig. 5c). The interfrontal suture is variable and can be differentiated or partially fused in adults (see Figs. 5 and 6). Basisphenoid-basioccipital and basisphenoid-presphenoid sutures close belatedly without complete fusion (Fig. 4).

In the juvenile stages (I–IV), the exits of the sphenoplatine and ethmoid foramina are nearby and drain to a wide longitudinal slit situated at the contact between the interorbital portions of the frontal and maxilla (Fig. 3a). In adults, this gap is partially closed, and the remains of the slit connect the sphenoplatine with the ethmoidal foramina. The sphenoplatine foramen is always below the lacrimal foramen but at the level of M1 in stage I, between M1 and M2 in stage V, and at the level of M2 in adults of stages VI–VII.

**Mandible.**—Changes that occur in the mandible during ontogeny are related mainly to lengthening and strengthening of the body, and a trend to a more vertical orientation of the symphyseal region. The lengthening of the mandible is evident



**Fig. 7.**—*Dinomys branickii*. Occipital view of the skull of a) AMNH 100011 (BL: 77.52 mm); b) USNM 300797 (BL: 99.80 mm); and c) AMNH 70354 (BL: 155.32 mm). Abbreviations: BL, basal length. AMNH, American Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution. cr, second crest of the occiput; Eo, exoccipital; mf, magnum foramen; moc, median occipital crest; mp, mastoid process; nc, nuchal crest; oc, occipital condyle; of, occipital fossa; pc, paracondyle process; pop, paroccipital process; So, supraoccipital. Scale 2 cm.

in the posterior displacement of particular structures. Thus, the origin of the masseteric crest in subadults (I–V) is at the level of the contact between p4-m1, whereas it is located at the level of m1-m2 in adults, where it reaches its maximum labial expansion (Fig. 8). Also, the horizontal ramus becomes shallow, the ascending ramus slender, and the angular process more posteriorly directed in adults (Fig. 8).

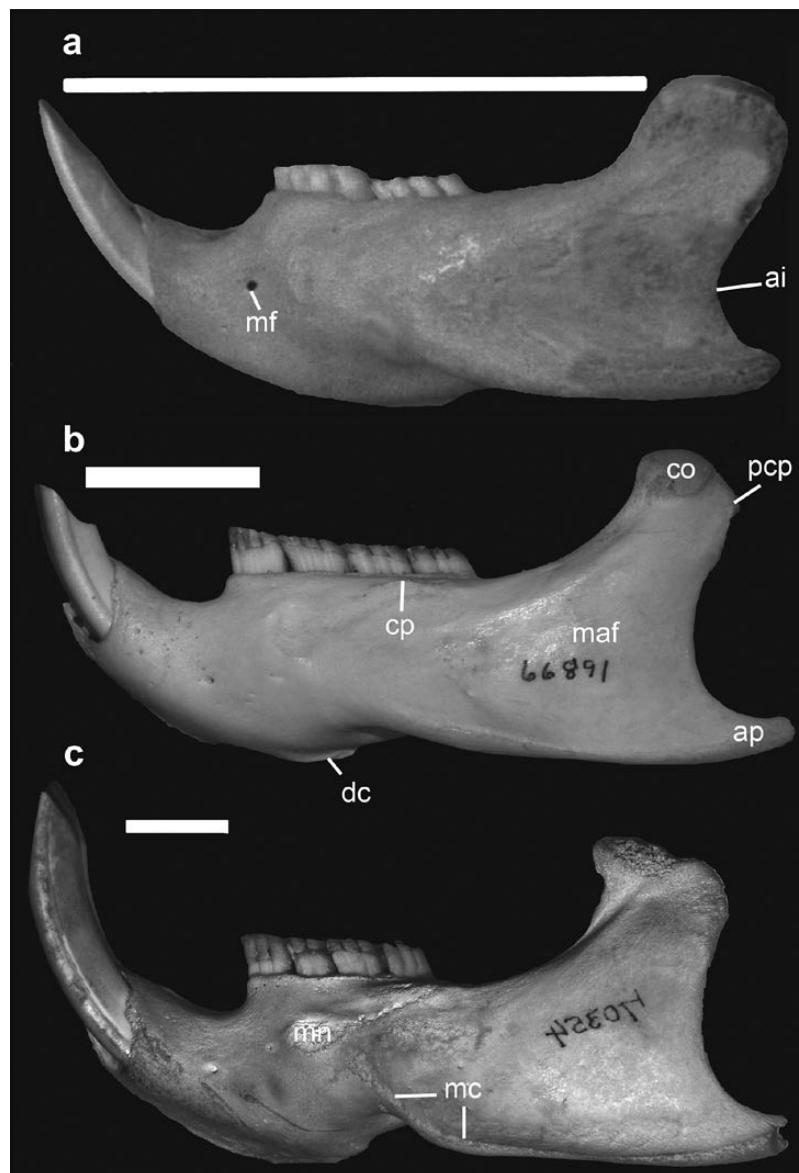
In stage I, the anterior margin of the mandibular symphysis is below the alveolar level of molariform teeth and the diastema is slightly concave, whereas in stages V–VII, the anterior margin of the symphysis is higher, almost reaching the occlusal level of molariforms and shows a deeply concave diastema (Fig. 8). This results in more vertically oriented incisors in adults.

The articular process becomes higher and gradually strengthened towards adulthood (Fig. 8). The angular process grows in

thickness and has a marked posterior extension: in stage I, the posterior end of the process is aligned with the rear margin of the postcondyloid process, and in stage VI, it extends far behind the posterior margin of the postcondyloid process (Fig. 8).

There is a gradual increase in hystricognathy of the mandible (Hautier et al. 2011) and deepening of the masseteric fossa. It is shallow in stage I and concave in stages V–VII (Fig. 8). The digastric crest, for insertion of the digastricus muscle (Woods 1972; Woods and Howland 1979), is low and short in stages I–IV, extending only to the level of the p4-m1, whereas in stage VII, it reaches the level of m2-m3.

The coronoid process is an incipient structure that has a slight gradual reduction during ontogeny. In stage I, it has its maximum development as a process that tapers to a point (Fig. 9), in stages II–IV, it is represented as a low prominence and in



**Fig. 8.**—*Dinomys branickii*. Lateral view of the lower jaw of a) MACN 12962 (ML: 60.61 mm); b) FMNH 66891 (ML: 115.41 mm); and c) AMNH 70354 (ML: 155.32 mm) (flipped horizontally). Abbreviations: ML, mandibular length. AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia. ai, angular incisure; ap, angular process; cp, coronoid process; co, mandibular condyle; dc, digastric crest; maf, masseteric fossa; mc, masseteric crest; mf, mental foramen; mn, masseteric notch; pcp, postcondyloid process. Scale 2 cm.



**Fig. 9.**—*Dinomys branickii*. Juvenile FMNH 147996 skull and mandible. Abbreviations: FMNH, Field Museum of Natural History. cp, coronoid process; dP3, deciduous 3rd premolar; dP4 and dp4, deciduous 4th premolars; M1 and m1, 1st molars. Scale 2 cm.

stages VI and VII, after premolar replacement, the process is a low crest extended parallel to the alveolar margin, at the level of the last molar.

The masseteric notch (scar of the infraorbital part of the medial masseter tendon—sensu Woods and Howland 1979) is more circular, with diffuse margins and located at the level of dp4/p4 in juveniles; in subadults and adults, it is lenticular, placed at the level of p4-m1 and with its dorsal edge continued by a groove extending behind m3. The posterior portion of the diastema is curved and rises gradually in juveniles and more abruptly in adults. The articular condyle is elliptic and slightly convex in juveniles, whereas in adults, it is very convex, with distinct medial and lateral facets (Fig. 8). The postcondyloid process is wide and more robust in subadults and adults.

**Dentition.**—Modifications in the dentition during the ontogeny of *Dinomys* are mostly related to growth of the incisors, eruption of cheek-teeth, replacement of the 4th premolar and growth, and wear of the cheek-teeth.

Incisors have subcylindrical and subcircular sections only in the youngest specimens (stage I) and a flatter and triangular section in the remaining stages. From stages II–VII, the incisor grows continuously in all dimensions, even after eruption of the entire permanent cheek-tooth series (Tables 2 and 3).

Incisor growth involves elongation and widening of the tooth. The 1st process is defined by a more posterior position of the base in relation to the cheek-tooth series (Ray 1964). Thus, the base of the upper incisor is at the level of dP4, P4 in juveniles (stages I–V), between P4-M1 in subadults (stage VI), and at the level of M1 in adults. Incisor growth is more marked in the jaw, where the base of the tooth is always at or behind the last cheek-tooth: at the level of m1 in stage I, behind m2 in stage II, at the level of m3, below the alveolar level, in

stage V, and behind m3, at the alveolar level, in stages VI–VII. During growth the lower incisor tends to become vertical in its anterior half.

In the occlusal portion of the incisors, the anteroposterior length (APL) and the transverse width (TW; Fig. 2) are similar in younger specimens from stage I. The APL of upper incisors increases more than 3 times (77%) and the TW more than 2 times (59%) from juveniles to adults (Table 2). In lower incisors, the increase of these measurements is similar: 79% for APL and 59% for TW (Table 3). Growth of incisors continues during the entire life of an individual, but growth of incisors in adults with a complete series of cheek-teeth, particularly in stages VI and VII, is markedly slower.

The cheek-teeth of *Dinomys* are euhyposodont (sensu Mones 1982), with open bases during ontogeny (except for deciduous teeth, see below). *Dinomys* has 2 upper deciduous premolars (dP3 and dP4) and 1 lower (dp4). The eruption sequence is dP3-dP4-M1/dp4-m1, in stage I, followed by the eruption of M2/m2 in stage II, M3/m3 in stage III, and, finally, P4/p4 in stage IV. Deciduous P4 erupts slightly earlier than M1. This is inferred by the higher position of the former which is close to the occlusal line, whereas M1 is lightly above the alveolar line. The same condition is represented in dp4 and m1 (Fig. 9). Tooth dP3 is present only at a very early stage of postnatal development (Field Museum of Natural History [FMNH] 147996, stage I; Fig. 9). It is a tiny, rooted, non-molariform tooth, located in front of dP4, showing an elongated smooth crown lacking distinct cusps (Fig. 9). This tooth is inserted in a subtriangular alveolus, with a bilobed lingual outline, indicating the putative presence of 2 roots. It is clear that this tooth is a remnant of a nonfunctional element that is shed in a very early postnatal stage when dP4 and M1 are erupting and show

**Table 2.**—Upper dentition dimensions (mm) of specimens of *Dinomys branickii*. Abbreviations: APL, anteroposterior length; TW, transverse width. AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; OMNH, Sam Noble Oklahoma Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution.

Specimen	Age stage	Upper dentition											
		Incisor		dP4		P4		M1		M2		M3	
		APL	TW	APL	TW	APL	TW	APL	TW	APL	TW	APL	TW
FMNH 147996	I	2.3	2.1	5.0	3.0			4.1	2.5				
MACN 12962	I	3.0	2.7	7.0	3.6			6.0	3.6				
AMNH 100011	II	5.5	5.1	5.4	4.2			6.1	4.6	5.2	4.3		
AMNH 100053	II	6.3	5.1	5.2	4.6			5.5	5.1	5.2	4.1		
FMNH 34412	II	7.0	5.0	7.3	5.2					8.0	5.0		
AMNH 46551	III	7.2	6.2	6.7	5.2			8.0	5.8	7.9	5.5	5.7	4.1
FMNH 34405	III	7.3	6.2	6.6	4.6			8.0	6.3	8.4	5.8	6.5	4.1
FMNH 70811	IV	7.0	5.3	4.0	3.5			8.4	5.0	7.8	5.2	5.0	3.6
USNM 559409	V	7.0	6.0			5.0	5.0	8.0	6.5	8.0	6.0	8.0	6.0
AMNH 183828	V	8.0	7.0			4.5	4.0	7.0	6.0	7.0	6.0	8.0	7.0
USNM 395453	V	9.0	7.0			6.8	5.4					8.0	7.5
OMNH 7904	VI	9.5	6.5			7.0	6.4	7.0	6.4	6.4	6.3	7.0	5.5
FMNH 34413	VI					7.4	6.3	8.3	6.0	8.3	6.0	5.0	4.0
FMNH 66891	VI	8.0	6.9			6.0	4.1	7.2	6.0	7.0	6.0	7.0	5.2
FMNH 34410	VI	10.0	8.5			7.5	6.0	8.2	6.4	8.0	6.0	8.0	5.0
USNM 359454	VI	11.0	9.0			9.0	7.0	8.0	7.0	8.5	7.0	9.0	8.6
AMNH 70354	VII	13.4	11.5			7.6	7.7					9.5	8.6
MACN 12961	VII	10.0	7.4			7.0	6.3	7.0	7.0	8.7	6.6	9.6	6.5
FMNH 34409	VII	10.0	8.0			8.6	7.0	9.0	7.0	9.0	7.0	10.0	6.0
FMNH 34404	VII	10.0	8.0			7.6	6.6	8.0	7.0	7.0	6.0	9.0	6.0
FMNH 24232	VII	10.0	8.5			8.0	7.5	8.0	7.5	8.5	7.5	10.0	7.0
FMNH 65793	VII	10.0	8.5			8.6	6.5	8.0	7.5	9.0	7.0	8.4	6.0
MNHN 3796	VIIIs					8.0	6.0	8.5	6.4	7.0	6.0	8.4	6.2
FMNH 160021	VIIIs	10.0	8.0			6.2	6.0	8.0	7.5	8.0	8.0	9.0	7.5

**Table 3.**—Lower dentition dimensions (mm) of specimens of *Dinomys branickii*. Abbreviations: APL, anteroposterior length; TW, transverse width; AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; OMNH, Sam Noble Oklahoma Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution.

Specimen	Age stage	Lower dentition											
		Incisor		dp4		p4		m1		m2		m3	
		APL	TW	APL	TW	APL	TW	APL	TW	APL	TW	APL	TW
FMNH 147996	I	2.1	2.1	4.4	2.1			5.0	4.0				
MACN 12962	I	5.5	2.5	6.2	3.4			6.0	4.0				
AMNH 100011	II	5.5	5.0	6.0	3.3			6.0	4.1	5.2	3.1		
AMNH 100053	II	6.0	5.0	5.4	4.0			5.6	5.0	6.7	4.7		
FMNH 34412	II												
AMNH 46551	III	8.6	6.5					7.4	5.8	8.3	5.3	6.8	4.5
FMNH 34405	III	7.5	5.3					6.7	4.5	7.8	4.8	5.3	4.0
FMNH 70811	IV	8.4	6.0	3.5	3.0			7.2	5.1	8.6	4.7	6.6	4.1
USNM 559409	V	10.0	7.0			5.0	4.0	8.0	6.0	8.0	6.0	8.5	5.0
AMNH 183828	V	10.0	6.5			5.8	4.5	6.0	6.0	7.0	5.5	7.0	5.5
USNM 395453	V	8.2	6.0			6.4	4.8	6.0	6.0	6.5	5.6	7.6	5.3
OMNH 7904	VI	10.0	6.0			6.5	5.0	6.5	6.0	6.5	6.0	7.3	6.0
FMNH 34413	VI												
FMNH 66891	VI	9.3	6.7			6.3	4.0	7.7	5.6	8.0	6.0	7.3	5.0
FMNH 34410	VI												
USNM 359454	VI												
AMNH 70354	VII	10.0	9.0			9.0	6.0	6.0	7.0	8.0	6.5	7.0	6.0
MACN 12961	VII	12.4	7.4			6.4	5.6	7.0	6.0	8.6	7.4	8.4	6.8
FMNH 34409	VII												
FMNH 34404	VII												
FMNH 24232	VII												
FMNH 65793	VII	10.3	7.3			7.0	5.0	6.6	6.0	7.6	6.4	8.0	5.5
MNHN 3796	VIIIs												
FMNH 160021	VIIIs	10.2	8.0			10.0	7.0	8.2	8.2	8.0	8.3	9.0	6.3

incipient wear (MACN 12962, stage I; Fig. 4a). Remaining deciduous premolars are retained from stages I to III. American Museum of Natural History (AMNH) 46551 shows variation in the replacement timing of the upper and lower premolars in that p4 is at the alveolar level, while dP4 has not yet been replaced.

Ontogenetic changes in the occlusal morphology of cheek-teeth are represented by variation in the number of structures of the tooth. These will influence the morphology of the occlusal surface (Figs. 10 and 11) and include partial or complete fusion of lophs/lophids and variation in length and width of the crown.

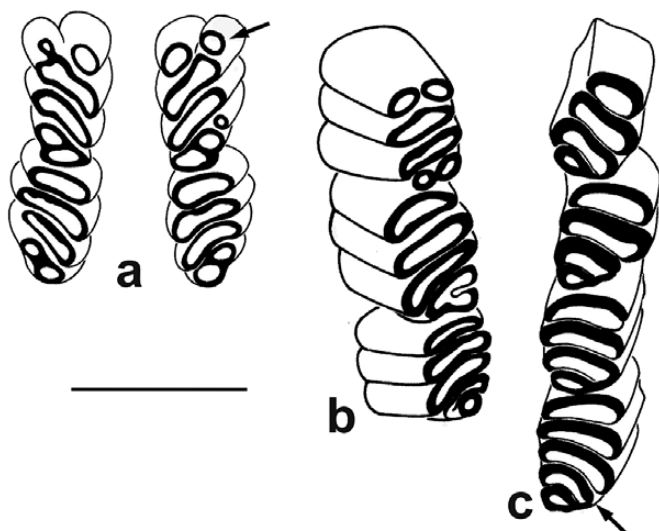
In their early development, the molars are formed by laminar structures composed of cylindrical subunits of dentine and enamel (Figs. 10 and 11), with an open base. These structures fuse rapidly and with subsequent wear in stage I they acquire the tetralophodont (= tetralaminar) occlusal pattern with parallel and slightly oblique lophs/lophids. M3 has a tiny posterior 5th loph until stage VI (e.g., National Museum of Natural History, Smithsonian Institution [USNM] 359454), which may persist (e.g., FMNH 34409) or disappear with more wear in adults (e.g., FMNH 160021).

The following ontogenetic trends in the dentition of *Dinomys* are apparent (see Figs. 10 and 11): 1) worn deciduous premolars have more structures (complete laminae subdivided to 7 in upper and 6 in lower) in stage I, but they become tetralophodont in stage III by fusion of subunits; definitive premolars are tetralophodonts from the moment they reach the occlusal level (stages IV–V); 2) fusion of 2 last lophs lingually (Fig. 10c) and 2 anterior lophids labially (Fig. 11c), producing a tetralophodont pattern (Nasif 2009a) in euhypsodont deciduous premolars of stage IV, and in permanent molariforms when they reach the

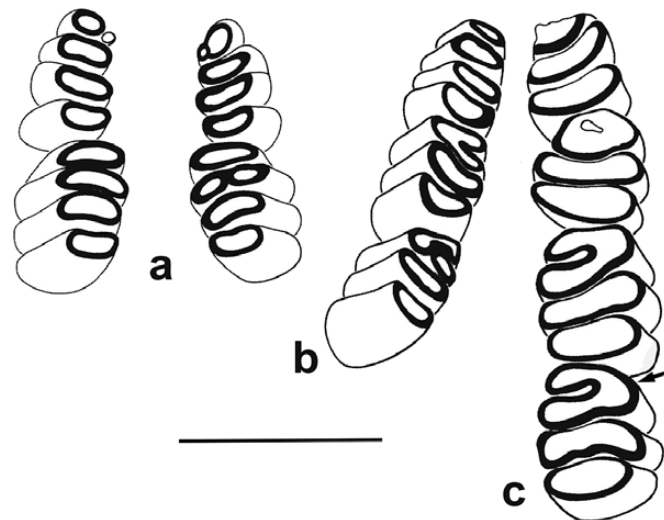
occlusal surface; this pattern persists until the oldest age (stage VII); 3) supernumerary structures, more frequently represented in the mesial and distal portion of the tooth, are present in definitive molars when the tooth has little wear; when molariforms are very worn, these supernumerary structures remain only in P4/p4 and M3; 4) prior to replacement, dP4 has an oval outline of the crown in stage I and a rectangular outline in stage III, having its anteroposterior axis aligned with that of the tooth row; 5) P4 with little wear (stage V) is subcircular in outline (Fig. 10b) and becomes rectangular with increased wear (stage VI), with its anteroposterior axis oriented obliquely in relation to the axis of the tooth row (Fig. 10c); and 6) M1 and M2 can have up to 5 structures during stages I and II and acquire a tetralophodont pattern after the eruption of the last molar; in adults with much wear in their teeth, M1/m1 become trilophodont and M3 can vary between tetra- or pentalophodont.

Variation in the dimensions of cheek-tooth occlusal surface during ontogeny includes: 1) dP4 and dp4 become longer and wider until stage II and both dimensions become reduced up to nearly half before replacement in stage V and 2) length and width of P4, p4, and molars increase to almost twice their size during development from juveniles to adults and continue growing until old age (Tables 2 and 3).

*Bivariate allometry.*—Table 4 shows the allometric coefficient obtained for each measurement. The fit of the variables to the linear model, as expressed by  $R^2$  (coefficient of determination) and varies from 0.63 to 0.97, with 12 measurements having values above 0.89. Seven variables display positive allometry, 5 are negatively allometric, and 15 measurements are isometric. The highest coefficient of allometry is represented by the



**Fig. 10.**—*Dinomys branickii*. Upper cheek-teeth showing occlusal ontogenetic variations, a) dP4-M1 of right and left series of juvenile, stage I (MACN 12962); b) dP4-M2 of left series of juvenile, stage II (AMNH 100011); c) right series of adult, stage VII (MNHN 3796). The arrow in a) indicates the cylindrical structures in juvenile teeth, and in c) the fused pattern of the 2 last lophs. Scale 1 cm. Abbreviations: AMNH, American Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; MNHN, Museo Nacional de Historia Natural.



**Fig. 11.**—*Dinomys branickii*. Lower cheek-teeth showing occlusal ontogenetic variations, a) dp4-m1 of right and left series of juvenile, stage I (MACN 12962); b) dp4-m2 of left series of juvenile, stage II (AMNH 100011); c) right series of adult, stage VII (MACN 12961). The arrow in c) indicates the fused pattern of the 2 first lophs. Scale 1 cm. Abbreviations: AMNH, American Museum of Natural History; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia.

**Table 4.**—Bivariate analysis of *Dinomys branickii*. Results of allometric coefficients ( $b_1$ ) by reduced major axis (RMA) method. See Fig. 1 for variables acronyms. “+” indicates positive allometry, “-” indicates negative allometry and “=” is isometry. Independent variable is the geometric mean of all the measurements of the specimens. Bonferroni-corrected value for rejecting the null hypothesis of isometry is  $0.05/27 = 0.0018$ .

Variable	<i>N</i>	$b_1$ (RMA)	$P(a = 1)$	$R^2$	Trend
Basal length (BL)	32	1.14	0.06	0.88	=
Rostrum length (RL)	31	1.19	0.0014	0.94	+
Palatal length (PL)	32	1.28	0.0007	0.90	+
Post palatal length (PPL)	32	0.96	0.63	0.79	=
Frontal length (FL)	30	1.4	1.6E-06	0.94	+
Upper diastema length (UDL)	32	1.14	0.05	0.88	=
Jugal length (JL)	29	1.04	0.47	0.93	=
Tympanic bulla length (TBL)	31	0.48	6.2E-10	0.77	-
Nasal width (NW)	30	0.95	0.42	0.90	=
Braincase width (BCW)	31	0.71	0.0007	0.68	-
Interorbital width (IOW)	28	0.86	0.01	0.91	=
Anterior frontal width (AFW)	28	0.99	0.88	0.87	=
Posterior zygomatic width (PZW)	32	0.99	0.87	0.97	=
Zygoma ventral width (ZVW)	31	1.29	0.03	0.73	=
Tympanic bulla width (TBW)	32	0.58	1.4E-07	0.65	-
Maximum occipital width (MOW)	30	0.93	0.1	0.94	=
Occipital condyles width (OCW)	31	0.63	9.8E-06	0.63	-
Rostral height (RH)	30	1.06	0.23	0.93	=
Jugal anterior height (JAH)	30	1.74	0.0006	0.81	+
Occipital height (OH)	30	0.84	1.2E-06	0.97	-
Upper molar length (UML)	29	1.16	0.04	0.89	=
Mandibular length (ML)	24	1.19	2.4E-04	0.97	+
Lower diastema length (LDL)	26	1.25	0.07	0.74	=
Retromolar length (RML)	22	1.81	2.9E-04	0.79	+
Posterior mandibular height (PMH)	25	1.19	0.01	0.92	=
Articular process height (APH)	21	2.03	2.8E-06	0.88	+
Lower molar length (LML)	20	1.24	0.023	0.89	=

articular process height (2.03), whereas the smallest is the tympanic bulla length (0.48).

Considering the quantitative growth analyses in *D. branickii*, several of the measurements representing splanchnocranium lengths are allometrically positive (Table 4). These include rostrum, palatal, mandibular, and retromolar (highly allometric) lengths. Two heights also related to the splanchnocranium are positive: jugal anterior and articular process height (highly allometric). Negative allometries are represented in neurocranial variables such as tympanic bulla length and width, braincase width (BCW), occipital height, and the width across the occipital condyles.

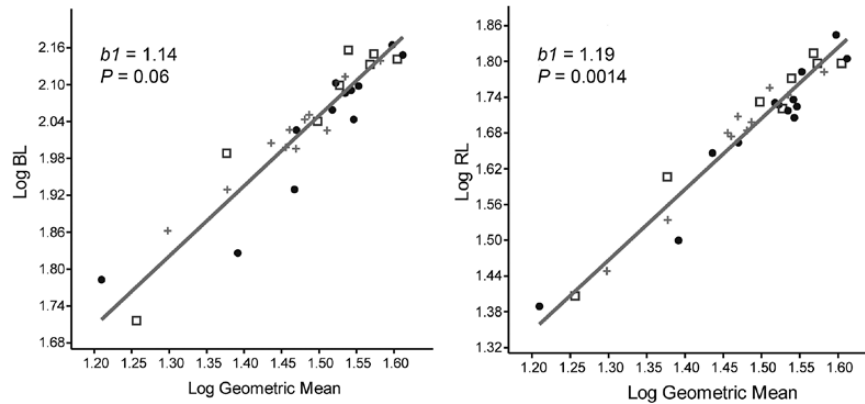
Four variables more likely to reflect sexual size dimorphism were chosen to implement *t*-tests (basal length [BL], BCW, posterior zygomatic width [PZW], and rostral length). Only BL and PZW show significant size dimorphism ( $P = 0.015$  and  $0.009$ , respectively). Inspection of bivariate plots for those variables does not show systematic trends in the distribution of sexed specimens with adult males and females being located above and below the regression line (Fig. 12). The reduced sample of sexed specimens (6 females and 5 males) hampered allometric analyses discriminated by sex. Examination of adults of different sexes, however, did not reveal sexual shape dimorphism. Sexual differences in BL between the larger sexed specimens is 4%, confirming the small difference (8%) previously reported by Allen (1942).

## DISCUSSION

*Craniomandibular ontogeny.*—There are 2 main processes recognized during ontogeny of the skull and mandible of *D. branickii*: elongation and strengthening. Elongation is evidenced by an increase in total skull length, represented by a range of 90 mm between the extremes of our sample (Fig. 3). Correlated with this elongation are changes in skull morphology, variation in extension and bone morphology, and variation in location and form of cranial foramina. Strengthening is evinced by suture closing and the development of structures (e.g., fossae, crests, and processes; Figs. 3–8; Table 1). These 2 processes are related mainly to powerful occlusion in adults (i.e., expansion of masseter and temporalis muscles) and with the development of cervical musculature for the support of the adult skull.

Our data suggest that skull growth continues during adulthood as shown by differences between adults of stage VI (e.g., MACN 12961) and old adults of stage VII (e.g., Museo Nacional de Historia Natural [MNH] 3796, FMNH 160021). Differences in skull length between these ages vary between 18% and 20%. This condition is also evident in the mandible lengths of adults and old adults, although the differences are smaller than in the skull (approximately 10.5–14%).

Mones (1997) noted that fusion of bones with loss of sutures in *Dinomys* occurs late, even after sexual maturity, but our observations indicate that the majority of the sutures remain distinct



**Fig. 12.**—Bivariate plots of logarithm of the BL, on the left, and of the RL, on the right, against the logarithm of the geometric mean.  $b_1$  is the allometric coefficient, crosses are females, squares are males, and dots are unknown sex. Abbreviations: BL, basal length; RL, rostral length.

in adults and only the occipital elements fuse fully (Fig. 7). Thus, supraoccipitals and exoccipitals are differentiated by open sutures until the subadult stage (V), but in adults, these bones are completely fused, forming 1 element. This adult occipital plate features strong lambdoid crests and a ventral nuchal crest in the area of fusion between the occipital bones (Fig. 7). These crests represent the insertion of occipitoscapular and cleidocephalic muscles (Woods 1972; Popesco et al. 1992) that become increasingly important in adulthood, as is also suggested by the fusion of cervical vertebrae (Mones 1997). In juveniles, the interparietal is represented by 2 elements that fuse quickly and attach to the supraoccipital. Rodents show some variation in the original number of interparietals, varying between 1 and 4 original elements (Koyabu et al. 2012). In Hystricognathi, Hoffstetter (1974:512) noted that the interparietal is often retained as an independent element and that this trait is plesiomorphic for the group (see also Wilson and Sánchez-Villagra 2009).

Our results show that the few fused bones in the skull of *Dinomys* (interpalatine, interparietal, exoccipito-supraoccipital, and exoccipito-basioccipital) are also fused in other Hystricognathi (Wilson and Sánchez-Villagra 2009) and, in a wider context, in most therians (Rager et al. 2014). However, the fusion of frontal-frontal, frontal-parietal, and frontal-nasal reported for Euarchontoglires (Rager et al. 2014) is poorly represented in Hystricognathi (Wilson and Sánchez-Villagra 2009) and absent in *Dinomys*. The large proportion of unfused bones in *Dinomys* is comparable with that reported for the Cavimorpha *Hydrochoerus hydrochaeris* and *Dasyprocta fuliginosa* and is a condition perhaps linked to large (> 100 mm) skulls (Wilson and Sánchez-Villagra 2009). The sutures between the basioccipital-basisphenoid and basisphenoid-presphenoid in adults *Dinomys* are usually open, but there is some variation, with cases of fusion.

Morphological changes in the skull of *D. branickii* are interpreted as being related to a strong but gradual growth of skull length (the skull enlarges more than 2-fold in our sample). This is accompanied by a straightening of the postzygomatic region (particularly represented in the cranial vault, see Fig. 3) and perhaps in a change in angulation between the prechordal and postchordal cranial base during ontogeny (Lieberman et al. 2008).

Skull allometry shows growth in the rostrum that is faster (as conveyed by the nasal length and, partially, by palatal length) than that of the postpalatal region. This trend shows clear differentiation between juveniles (stage II) and subadults (stage VI). The progressive posterior movement of the orbits in the ontogeny of *D. branickii* (Figs. 3 and 5) is a consequence of the fast growth of the rostrum. In Ctenohystrica, small species have the orbits located more anteriorly than larger ones (Hautier et al. 2012). Strong positive allometry is present in the anterior jugal height. Rapid development of the anterior jugal (in the form of a zygomatic plate) is a trend also recognized in the skull of *Agouti paca* (Nelson and Shump 1978). This trend is related to increased importance of the masseter superficialis and lateralis profundus that originate from the ventral surface of the anterior margin of the zygoma (Woods 1972).

Palate length shows faster growth, and the postcanine series changes from a subparallel orientation in juveniles to an anteriorly convergent condition in adults (Fig. 4). This change in orientation mirrors the condition reported in Ctenohystrica, with small species featuring subparallel postcanine rows, and larger species with anteriorly convergent rows (Hautier et al. 2012). This suggests that orientation of the postcanine series is correlated with size.

Variables associated with the braincase show negative allometry (i.e., length and width of tympanic bullae, BCW, and occipital height). Rapid differentiation of the central nervous system and sensory capsules, relative to components of the feeding apparatus, produce embryos and neonates with large braincases, eyes and otic regions, and a concomitant negative allometry for neurocranial components (Massoia and Fornes 1969; Emerson and Bramble 1993; Gay and Best 1996; Abdala et al. 2001).

In stages IV–VII, there is remarkable development of the crest and temporal fossa (Fig. 5). These cranial structures continue their development in adults. Even with a paucity of studies on cranial myology in *D. branickii*, our ontogenetic data permits some functional hypotheses. For example, the large size of the temporal fossa and crests in the skull of fossil dinomyids is usually linked to gigantic species (Kraglievich 1926; Pascual et al. 1967; Blanco et al. 2011). However, smaller living pacarana

also show a well-developed temporal fossa and strong temporal crests. The development of crest and temporal fossa in adults of *Dinomys* is linked with the expansion of the temporalis muscle for an increased occlusal pressure (Hautier et al. 2012). It is interesting to highlight the interplay of BCW negative allometry and isometry of PZW in the expansion of the temporal fossa. Growth of the temporal fossa is more dependent on the negative allometry of a neurocranial component, a fact that was also recognized in the cranial ontogeny of didelphid marsupials (Abdala et al. 2001; Flores et al. 2003; Giannini et al. 2004; Flores et al. 2010).

An open carotid foramen is present in adult living New World porcupines and in extinct hystricomorphs (Lavocat and Parent 1985), indicating a functional internal carotid system (Bugge 1985:376). A similar condition is documented here for juvenile and adult of *D. branickii* and is also known in fossil dinomyids (Nasif 2009b; MacPhee 2011). This new evidence shows that a functional arterial circulation system is more widespread in living hystricognathids than previously thought.

Overall changes in the morphology of the horizontal and ascending rami and angular process during ontogeny of *D. branickii* are also reflected in Ctenohystrica. Juveniles of *D. branickii* and small species of Ctenohystrica have deep horizontal and robust ascending rami, and a short angular process (Hautier et al. 2012; Fig. 8). The coronoid process of *Dinomys* is reduced (Peters 1873a; Patterson and Wood 1982; Mones 1997; Blanco et al. 2011) and features maximum reduction in living caviomorphs (Nasif 2009a, 2009b). This process is developed in a very early postnatal stage (Fig. 9) and becomes reduced early during ontogeny to form a tiny projection from the horizontal ramus in adults. In stages I–IV, the process provides an effective surface for attachment of the main and orbital parts of the temporalis. After replacement of the 4th premolar in stages IV–VII, the main insertion of the temporalis is more likely to occur on the retromolar platform or the flat dorsal surface of the posterior portion of the mandible, as mentioned by Woods (1972) for *Myocastor*. Phylogenetic studies of dinomyids suggest there is a trend towards reduction of the coronoid process: well developed in basal protohypsodontid Potamarchinae and reduced in the medium to large euhypsodontid Eumegamyinae, that include the pacarana (Nasif 2009b). Therefore, the ontogenetic trend towards a reduction of the coronoid process in the ontogeny of the pacarana is also reflected in the phylogeny of the dinomyids.

*Dental ontogeny.*—A dP3 represented in very early postnatal stages of *D. branickii* (Nasif and Abdala 2014) is described here for the 1st time (Fig. 9). A deciduous upper 3rd premolar (dP3) is present in late Oligocene *Branisamys*, the earliest member of the Family Dinomyidae (Patterson and Wood 1982; Nasif 2009b). In both cases, dP3 is a tiny, rooted, non-molariform tooth located in front and very close to dP4. The dP3 is shed and not replaced and its alveolus becomes ossified. Shedding of dP3 in *Branisamys* occurred in an advanced stage of development, before or during the replacement of dP4 (Hoffstetter and Lavocat 1970:173, figure B.I.), whereas

*Dinomys* sheds this tooth in a very early postnatal stage where dP4 and M1 are erupting and show incipient occlusal wear. There are different rodent groups with a dP3 not replaced by a definitive tooth (Hartenberger 1985). Among the caviomorphs, dP3 has been documented in *Cachiyacuy* from the middle Eocene, the dasyproctid *Incamys* from the late Oligocene, the Miocene putative octodontoid *Protadelphomys*, and the early Miocene erethizontids *Parasteiromys* and *Steiromys* (Patterson and Wood 1982; Candela 1999; Vucetich et al. 2010; Antoine et al. 2012). The presence of dP3 in these taxa may be related to a mechanism that explains oral pathologies: rudimentary tooth primordia loci that were present in the ancestor can be “rescued” from their suppression, revitalize, and have an autonomous development (Peterkova et al. 2014).

*Dinomys* is one of the few living caviomorphs that replaces its 4th premolar during ontogeny (Fields 1957; Ray 1964; Hartenberger 1985; Nasif 2009b) and this plesiomorphy in the hystricognathid rodents (Hartenberger 1985) is widespread in Dinomyidae. This is the case for several protohypsodontid dinomyid taxa, including *Olenopsis*, *Potamarchus*, *Paranamys* (Fields 1957; Candela and Nasif 2006; Nasif 2009b), and some euhypsodonts, including undescribed taxa from northwestern Argentina (Nasif 2009b).

After examining specimen AMNH 46551, Ray (1964) indicated that M3 and m3 of *Dinomys* become functional earlier than P4 and p4. Timing of the eruption of these elements is validated by our extended sample. In addition, an X-ray of the juvenile MACN 12962 shows the base of dP4 and dp4 is open initially. This characteristic differs from the deciduous teeth of protohypsodonts such as *Elasmodontomys obliquus*, in which dp4 has roots from a very young stage (Ray 1964:112). We infer that the open base of dP4/dp4 is kept until stage II, and possibly later (stage III), during eruption of M3/m3. Afterward dP4 and dp4 become pinched at the base with the crown showing an indistinct pattern of loph/lophids and the fusion of flexes/flexids.

Our data show some trends in dental ontogeny of *Dinomys*: 1) there is a reduction in the number of structures, due mainly to the merging of contiguous smaller subunits in both deciduous and permanent teeth, as well as by loss due to wear of the last loph and first lophid (Figs. 10c and 11c); 2) there is antero-posterior shortening, particularly in upper teeth, and transverse widening of deciduous teeth (Tables 2 and 3); 3) there is a gradual increase in TW, and, most notably, in the APL of M3 and m3, until the well-advanced adult stage VII (e.g., FMNH 34409, FMNH 24232, and FMNH 160021). Consistent with the last 2 trends, Fields (1957:354) noted a difference in tooth size between juveniles and adults of *Dinomys* suggesting the tooth may grow in diameter during eruption: “in the teeth of *Dinomys*, which are entirely rootless, the process of diametric growth is possible, as the enamel organ supplies new enamel to the base of the column throughout at least part of the life of the individual.”

The alveolus of P4 is shifted anteriorly and erupts obliquely, forming an angle with respect to the main axis of M1 (Fig. 10). A similar situation occurs in fossil dinomyids (Nasif 2009b)



and other hystricognaths such as *Elasmodontomys* (Ray 1964). This forward displacement of P4 alveoli is related to the growth of the incisor and the position of its base, as indicated by Ray (1964:120). In young stages, the base of the upper incisor is located at the level of dP4 (as is observed in an X-ray of MACN 12962), leaving a short space between dP4 and M1. The shift of P4 is a consequence of growth in the base of the incisor and produces an enlargement of the space between P4 and M1 in which the larger base of the incisor would be located.

The change of orientation of P4 is reinforced in adults (Fig. 4c) where this element has an anteromedial to posterolateral orientation, oblique to the axis of the rest of the cheek-tooth series. As a consequence, there is a divergence of M1 relative to P4 in subadults and adults and a labially displaced occlusal surface of P4 in relation to those of the molars. This change of orientation results in the distal margin of P4 having restricted contact with the mesial margin of M1 (Fig. 10c). This condition is different in juveniles, where dP4 is aligned with the anteroposterior axis of M1-M3, and the contact involves almost all faces of dP4 and M1 (Fig. 10b).

Moreover, teeth of the younger specimens of *D. branickii* (FMNH 147996 and MACN 12962) have tooth wear that may indicate the lactation period is very short and solid food involving chewing is processed at an early age. This may be linked to a more effective survival strategy in juveniles. Alternatively, worn teeth may be the consequence of a propalinal movement of the mandible, that is manifested very early in ontogeny and produces wear on the occlusal surface due to contact between teeth, but not necessarily involving food mastication, as was reported in *Myocastor coypus* (Sone et al. 2008). In this regard, according to Rensberger (1973:516), cheek-teeth in many mammalian groups possibly achieve an optimum operating efficiency only after moderate wear has occurred.

*General remarks.*—Our extensive data on the morphological variation during the cranial ontogeny of *D. branickii* shows several important changes that shape the feeding apparatus. Several variables connected with this system show positive allometry. With regard to the dentition, the upper molar series are subparallel in juveniles and posteriorly divergent in adults. The dental eruption is indeed responsible for the increase in width of the posterior half of the palate at the level of M2 and M3. In contrast, the distance of the anterior margins of dP4 and P4 remain mostly constant during the ontogeny, but this width is reduced in relation to the remaining variables of the growing skulls (Fig. 4). The proportionally wide anterior palate in early juveniles may be related to the suckling process, as the level of pressure in the anterior mouth is dependent on an effective “tongue to palate” and “tongue to teat” seals (Thexton et al. 1998; German et al. 2006; Campbell-Malone et al. 2011:285, figure 1). Also, contact between tongue and palate is important for the posterior push of the milk in the oral cavity (Thexton et al. 1998:332, figure 1; German et al. 2006). It is interesting that subparallel check-teeth series with wide palatal platforms is a common condition in small-sized Ctenohystrica (Hautier et al. 2012), perhaps implying an important liquid component in the diet of small species of the group. The proximity of the

check-teeth series in adults will optimize the action of the dentition during the propalinal phase of mandibular movement.

Ontogenetic changes in the postnatal ontogeny of the skull of *D. branickii* are mostly related to the development of the occlusal system and action of the associated muscles (masseters and temporalis). This is evidenced by rapid growth of the facial region, a deepening and strengthening of the temporal and occipital regions and a widening of the posterior portion of the palate in relation to the eruption and replacement of molariform teeth. The evidence obtained in this study supports the view that *D. branickii* is one of the few living taxa showing a dP3 which is shed and not replaced. The dP4/dp4 are replaced after the M3/m3 have erupted and features some wear. The complete eruption of P4/p4 occurs only when M3/m3 are fully operational.

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## APPENDIX I

### SPECIMENS EXAMINED.—

The specimens of *Dinomys branickii* included in this research were stored in the following collections: in United States, at American Museum of Natural History (AMNH), New York; Field Museum of Natural History (FMNH), Chicago, Illinois; National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C.; and Sam Noble Oklahoma Museum of Natural History, Norman (OMNH); in Argentina, at Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires; and in Uruguay, Museo Nacional de Historia Natural (MNHN), Departamento de Mamíferos, Montevideo.

List of specimens examined: AMNH 46551 (Pichincha, Ecuador; female), AMNH 70354 (zoo), AMNH 98636 (Peru), AMNH 100011 (zoo; female), AMNH 100053 (zoo; female), AMNH 183828 (zoo; male), AMNH 185372 (zoo), FMNH 24232 (Rio Chinchao, Hacienda Buena Vista, Peru; male), FMNH 24233 (Pozuzo, Pasco, Peru; male), FMNH 24234 (Pozuzo, Pasco Peru; male), FMNH 34404 (Rio Chinchao, Hacienda Buena Vista, Peru; male), FMNH 34405 (Rio Chinchao, Hacienda Buena Vista, Peru), FMNH 34409 (Rio Chinchao, Hacienda Buena Vista, Peru), FMNH 34410 (Rio Chinchao, Hacienda Buena Vista, Peru), FMNH 34411

(Pozuzo, Pasco, Peru), FMNH 34412 (Pozuzo, Pasco, Peru), FMNH 34413 (Pozuzo, Pasco, Peru), FMNH 34414 (Pozuzo, Pasco, Peru), FMNH 34702 (Pozuzo, Pasco, Peru; female), FMNH 65793 (Chanchamayo, Peru; male), FMNH 66891 (Marcapata, Cuzco, Peru; female), FMNH 70810 (Valdivia, Antioquia, Colombia; male), FMNH 70811 (Valdivia, Antioquia, Colombia; female), FMNH 147996 (zoo), FMNH 160021 (zoo), USNM 259454 (Rio Chinchao, Hacienda San Antonio, Peru; female), USNM 300797 (zoo; male), USNM 395160 (female), USNM 395453 (female), USNM 559409 (Rio Manu, Madre de Dios, Peru), OMNH 7409 (zoo, Bolivia; female), MACN 12961 (Bolivia; female), MACN 12962 (Bolivia; male), MNHN 3795 (Acre, Brazil), MNHN 3796 (Acre, Brazil). In addition, some specimens were studied by examining photographs. We also supplemented our data with published morphological accounts (Peters 1873b; Ellerman 1940; Mones 1997; Moraes-Santos et al. 1998).

## APPENDIX II

### SPECIMENS AGE CLASSES ASSIGNED.—

The specimens of *Dinomys branickii* included in this research were assigned in the following age classes: neonate I (FMNH 147996, MACN 12962); juvenile II (AMNH 100011, AMNH 100053, FMNH 34412, USNM 300797); juvenile III (Museum of Zoology, University of Michigan UMMZH 395160; observed at <http://animaldiversity.ummz.umich.edu>, accessed 16-1-2014; AMNH 46551, FMNH 34405, FMNH 34413); juvenile IV (FMNH 70811, USNM 559409); juvenile V (USNM 395453, AMNH 183828); subadult VI (OMNH 7904, USNM 259454, FMNH 34410, FMNH 66891); adult VII (AMNH 70354, MACN 12961, MNHN 3796, FMNH 34409, FMNH 34404, FMNH 24232, FMNH 65793, FMNH 160021). Specimens MNHN 3796 and FMNH 160021 are considered in stage VII, but they show a higher degree of wear in their cheek-teeth, particularly in m1 and therefore are old adults.