



# SKULL GEOMETRIC MORPHOMETRICS AND PALEOECOLOGY OF SANTACRUCIAN (LATE EARLY MIOCENE; PATAGONIA) NATIVE UNGULATES (ASTRAPHOTHERIA, LITOPTERNA, AND NOTOUNGULATA)

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**Abstract.** Three orders of South American extinct native ungulates are recorded from the Santa Cruz Formation along the Atlantic coast of Patagonia: Notoungulata (*Adinotherium* Ameghino, *Nesodon* Owen, *Interatherium* Ameghino, *Protypotherium* Ameghino, *Hegetotherium* Ameghino, and *Pachyrukhos* Ameghino), Litopterna (*Theosodon* Ameghino, *Anisolophus* Burmeister, *Tetramerorhinus* Ameghino, *Diadiaphorus* Ameghino, and *Thoatherium* Ameghino), and Astrapotheria (*Astrapotherium* Burmeister). An ecomorphological study based on geometric morphometrics of the masticatory apparatus was performed. The reference sample included 618 extant specimens of the orders Artiodactyla, Perissodactyla, Hyracoidea, and Diprotodontia. Thirty six cranial and 27 mandibular three-dimensional landmarks were digitized. Allometric scaling, principal component analyses, and phylogenetic generalized estimating equations on the cranium and mandible were performed. Analyses of cranial shape show strong phylogenetic constraints, whereas the mandibular analyses show a functional pattern related to habitat/diet and hypsodonty. The extant brachyodont ungulates from closed habitats show a more elongated and narrower mandibular symphysis with a lower mandibular corpus, than hypsodont, open habitat species. The latter have short symphyses with a high, curved mandibular corpus. This morphological pattern was also present among Santacrucian ungulates, allowing characterization of notoungulates mainly as open habitats dwellers, with some taxa foraging on grass (*Protypotherium*, *Interatherium*), and others on grass and leaves (*Hegetotherium*, *Pachyrukhos*, and *Adinotherium*), depending on the availability. *Nesodon* may have dwelled in mixed habitats and had a mixed feeding behavior, while small proterotheriids (*Anisolophus* and *Thoatherium*) may have fed predominantly on dicotyledonous plants. The remaining litopterns (*Tetramerorhinus*, *Diadiaphorus*, and *Theosodon*) and *Astrapotherium* may have foraged in closed habitats and fed on dicotyledonous plants.

**Keywords.** Ecomorphology. Masticatory apparatus. Skull allometry. Habitat. Diet. Paleobiology.

**Resumen.** MORFOMETRÍA GEOMÉTRICA CRÁNEO-MANDIBULAR Y PALEOECOLOGÍA DE LOS UNGULADOS NATIVOS (ASTRAPHOTHERIA, LITOPTERNA y NOTOUNGULATA) SANTACRUCENCES (MIOCENO TEMPRANO TARDÍO; PATAGONIA). En la Formación Santa Cruz a lo largo de la costa atlántica patagónica se registran tres órdenes de ungulados nativos sudamericanos: Notoungulata (*Adinotherium* Ameghino, *Nesodon* Owen, *Interatherium* Ameghino, *Protypotherium* Ameghino, *Hegetotherium* Ameghino y *Pachyrukhos* Ameghino), Litopterna (*Theosodon* Ameghino, *Anisolophus* Burmeister, *Tetramerorhinus* Ameghino, *Diadiaphorus* Ameghino y *Thoatherium* Ameghino) y Astrapotheria (*Astrapotherium* Burmeister). Se realizaron estudios ecomorfológicos mediante morfometría geométrica del aparato masticatorio. Se incluyeron 618 especímenes actuales de los órdenes Artiodactyla, Perissodactyla, Hyracoidea y Diprotodontia como marco de referencia. Se utilizaron 36 *landmarks* tridimensionales craneanos y 27 mandibulares. Se realizaron análisis alométricos, componentes principales y ecuaciones de estimación generalizada con control filogenético de cráneo y mandíbula. Los análisis craneanos estuvieron más condicionados por la filogenia, mientras que la mandíbula muestra un patrón funcional complejo entre hábitat/dieta e hipsodancia. Los ungulados actuales de ambientes cerrados y braquiodontes poseen mandíbulas con la sínfisis alargada y estrecha y cuerpo mandibular más bajo que las especies de ambientes abiertos e hipsodontes, las cuales poseen mandíbulas con la sínfisis corta y cuerpo mandibular alto y curvado. Este patrón morfológico se repite entre los ungulados santacrucenses, permitiendo ubicar a los Notoungulata principalmente en ambientes abiertos. Algunos taxones forrajearían en pasturas (*Protypotherium*, *Interatherium*), otros lo harían en pasturas o hierbas (*Hegetotherium*, *Pachyrukhos* y *Adinotherium*), dependiendo de la disponibilidad. *Nesodon* habitaría ambientes mixtos y tendría dieta mixta, mientras que los proterotéridos pequeños (*Anisolophus* y *Thoatherium*) se alimentarían predominantemente de dicotiledóneas. Los Litopterna restantes (*Tetramerorhinus*, *Diadiaphorus* y *Theosodon*) y *Astrapotherium* forrajearían en ambientes cerrados, alimentándose sobre dicotiledóneas.

**Palabras clave.** Ecomorfología. Aparato masticatorio. Alometría cráneo-mandibular. Hábitat. Dieta. Paleobiología.

SOUTH American native ungulates include several extinct lineages that evolved within the context of South American Cenozoic geographic isolation (Bond, 1999). They are part

of the "first faunal stratum" of Simpson (1950) or the Early South American Phase of Goin *et al.* (2012) and are composed of some endemic families of the Order Condylarthra,

and the representatives of the orders Astrapotheria, Litopterna, Notoungulata, Pyrotheria, and Xenungulata (Patterson and Pascual, 1968; Simpson, 1980; Bond *et al.*, 1995). Although they were all once united in a single taxon, Meridiungulata, originally founded on the idea that pre-Interchange South American ungulates were monophyletic (McKenna, 1975), the phylogenetic relationships among these groups and with other Eutherian clades remain unclear (see Casini *et al.*, 2012a and references therein). Their paleobiology has generally been interpreted through gross comparisons of cranial and postcranial morphology with extant ungulates of the clades Artiodactyla and Perissodactyla, even though some members resemble hyraxes, caviomorph rodents, and rabbits (Ameghino, 1889, 1898, 1907; Sinclair, 1909; Scott, 1937a; Croft, 1999; Bond *et al.*, 2001; Reguero *et al.*, 2007). The ecological significance of these varied morphologies in controlled geographic, chronologic, and stratigraphic contexts has not been fully evaluated. The goal of this work is to

contribute to this major issue by studying a set of reasonably complete and contemporaneous specimens of South American native ungulates.

Notoungulata, Litopterna, and Astrapotheria are among the most abundant mammals of the late early Miocene Santacrucian Age (Fig. 1), an interval best documented from the Santa Cruz Formation in Southern Patagonia, east of the Andes (Fig. 2). This formation, particularly the outcrops on or near the Atlantic coast of the Santa Cruz Province (~18–16 Ma; Fleagle *et al.*, 2012; Perkins *et al.*, 2012), provides a large number of well preserved and articulated specimens that make an excellent sample for paleoecological analyses.

Casini *et al.* (2012a) provided an updated description of the diversity of Santacrucian ungulates of the coastal Santa Cruz Formation. The notoungulates, with seven genera, account for most of the taxonomic and morphological diversity (Toxodontia: *Adinotherium* Ameghino, 1887a [Fig. 1.1], *Nesodon* Owen, 1846, and *Homalodotherium* Flower, 1873;



**Figure 1.** Representatives of each family of Santacrucian ungulate skulls, left side (except where indicated)/ *Cráneos y mandíbulas de los representantes de cada familia de los ungulados santacrucenses, lado izquierdo (salvo indicados)*. **1, *Adinotherium***, MPM-PV 3667 (cranium/ cráneo), MPM-PV 3666 (mandible right side; reversed/ *mandible lado derecho; imagen reflejada*); **2, *Interatherium***, MPM-PV 3471 (right side of the cranium reversed/ *cráneo lado derecho; imagen reflejada*); **3, *Hegetotherium***, MPM-PV 3526 (cranium right side; reversed/ *cráneo lado derecho; imagen reflejada*), MPM-PV 4316 (mandible/ *mandíbula*); **4, *Theosodon***, MACN-A 9269–88 (right side; reversed/ *lado derecho; imagen reflejada*); **5, *Diadiaphorus***, MPM-PV 3397; **6, *Astrapotherium***, AMNH 9278 (mandible right side; reversed/ *mandíbula lado derecho; imagen reflejada*). Scale bar/ *escala*= 10 cm (except for 2 and 3 in wich it is 5 cm/ *excepto para 2 y 3 para las cuales es 5 cm*).

Tyotheria: *Interatherium* Ameghino, 1887b [Fig. 1.2], *Protyotherium* Ameghino, 1887b, *Hegetotherium* Ameghino, 1887a [Fig. 1.3], and *Pachyrhokos* Ameghino, 1885). They are followed by the litopterns, which are represented by five genera: the macraucheniid *Theosodon* Ameghino, 1887a (Fig. 1.4) and the protheroheriids *Anisolophus* Burmeister, 1885, *Diadiaphorus* Ameghino, 1887a (Fig. 1.5), *Tetramerorhinus* Ameghino, 1894, and *Thoatherium* Ameghino, 1887a. The astrapotheres are represented by one genus (*Astrapotherium*, Burmeister, 1879; Fig. 1.6). Body size estimates for these ungulates range from ~1.3 kg to ~1000 kg depending on the methodology used (Scarano *et al.* 2011; Cassini *et al.*, 2012b; Elissamburu, 2012).

In a baseline paleoecological study of the mammalian fauna of the coastal Santa Cruz Formation, Vizcaíno *et al.* (2010) suggested that the coexistence of so many different ungulate lineages implies marked vegetation resource partitioning. Recent work by Cassini *et al.* (2011, 2012a) generated inferences about habitat and feeding preferences in Santacrucian astrapotheres, notoungulates, and litopterns using classic morphometrics and novel computer techniques of knowledge discovery. The results suggest that all Santacrucian notoungulates have morphologies characteristic of 'open habitat' extant ungulates in agreement with classical ideas (Scott, 1937a; Patterson and Pascual, 1968; Tauber, 1996; Madden, 1997). Specifically, the Toxodontia exhibits morphological patterns characteristic of living mixed-feeders and grazers, and the Tyotheria shows exaggerated traits of specialized grazing ungulates (but see Townsend and Croft, 2008). In contrast, the Litopterna and Astrapotheria exhibit morphologies that indicate they inhabited closed habitats and were mainly browsers (Cifelli and Guerrero, 1997; Soria, 2001; Cassini *et al.*, 2012a).

The present contribution complements the aforementioned articles by studying the masticatory apparatus of the coastal Santacrucian ungulate assemblage through a geometric morphometric analysis of the skull in an ecomorphological framework. Ecomorphology characterizes communities by identifying patterns that link morphological and ecological traits and their interactions, that are also independent of the taxonomic composition ("taxon-free") and the time period studied (Mendoza *et al.*, 2005). Inspired by the pioneering work by Janis (1990), this study includes a broad sample of extant mammalian herbivores (artiodactyls, perissodactyls, macropodids, and hyraxes) to infer habitat and feeding behavior of the Santacrucian ungulates. In doing so, 3D landmarks and modern geometric morphometric analy-

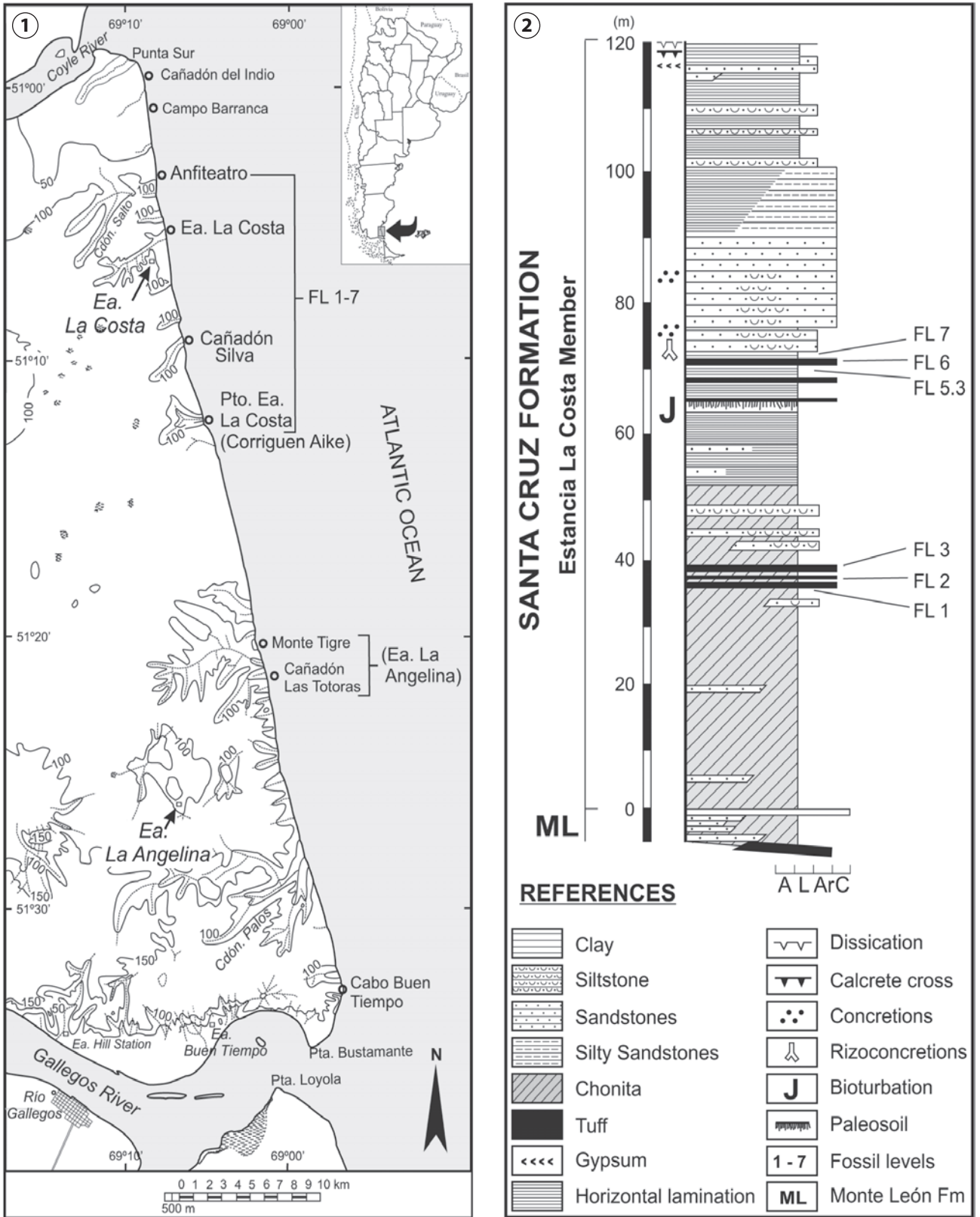
ses of size, allometric scaling, cranial and mandibular shape variation are used within a controlled phylogenetical framework. Phylogenetically controlled tests were performed in order to detect ecologically relevant traits on the extant reference sample, which may be masked by common ancestry (Garland Jr *et al.*, 2005; Paradis, 2006). These ecologically relevant traits were then evaluated in Santacrucian ungulates in order to infer characteristics of their paleobiology.

### **Summarized geological context**

The Santa Cruz Formation extends through much of southern Patagonia, Argentina. It crops out east of the South Patagonian Cordillera (Cordillera Patagónica Austral) from Lago Buenos Aires south to the Río Turbio area, and from southern extra-Andean Patagonia east to the Atlantic coast between Golfo de San Jorge and northern Tierra del Fuego (Vizcaíno *et al.*, 2012 and references therein). The formation encompasses a relatively broad temporal span (about 19–14 Ma in the Andean foothills, and 18–16 Ma in the Atlantic coastal plain; Fleagle *et al.*, 2012; Perkins *et al.*, 2012). The best specimens for ecomorphological studies come from the exposures of the Santa Cruz Formation in the Atlantic coastal area of Santa Cruz Province, Austral Patagonia, between the Coyle and Gallegos rivers (Fig. 2). Tauber (1997) and Matheos and Raigemborn (2012) provided the stratigraphic framework and described the sedimentary environments of the geological section in the area. According to them, the sedimentary sequence consists mainly of fine and tuffaceous sediments in the lower section (Estancia La Costa Member) and coarser and siliciclastic sediments towards the top (Estancia La Angelina Member). The lower member in particular bears a rich mammalian association of Santacrucian Age that is distributed in some 20 fossiliferous levels (FL), differentially exposed in the localities (Tauber, 1997; Krapovickas *et al.*, 2008; Matheos and Raigemborn, 2012) (Fig. 2). Based on tephrostratigraphic correlations, Perkins *et al.* (2012) proposed that several of Tauber's (1997) lower fossiliferous levels (FL 1–7) can be considered pencontemporaneous.

## **MATERIALS AND METHODS**

**Institutional abbreviations.** AMNH, American Museum of Natural History, New York, USA; MACN-A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ameghino Collection, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MPM-PV, Museo Regional Provincial Padre M. Jesús Molina, Río Gallegos, Argentina; YPM-VPPU, Yale Peabody Museum, Vertebrate Paleontol-



**Figure 2. 1,** Map showing the localities of the Santa Cruz Formation considered in this study/ *Mapa mostrando las localidades de la Formación Santa Cruz consideradas en este estudio* (modified from/ *modificado de* Kay et al., 2008, 2012). **2,** Stratigraphic column of the Estancia La Costa Member of the Santa Cruz Formation/ *Columna estratigráfica del Miembro Estancia La Costa de la Formación Santa Cruz* (modified from/ *modificado de* Vizcaino et al., 2010).

ogy Princeton University Collection, New Haven, USA.

**Index and morphological abbreviations.** **AIC**, Akaike information criterion; **bm**, body mass; **cs**, centroid size; **CVA**, Canonical Variate Analysis; **GAM**, Generalized Additive Models; **GEE**, Generalized Estimating Equations; **GLM**, Generalized Linear Models; **GPA**, Generalized Procrustes Analysis; **HI**, hypsodonty index; **PCA**, Principal Component Analysis; **SPR**, Symmetric Procrustes Rotation.

**Specimens.** Two subsamples of Santacrucian ungulates were chosen for analysis based on their morphological integrity (*i.e.*, with little to no apparent deformation), as well as landmark availability. The cranial subsample included 16 toxodontids and 21 tytopheres (Notoungulata), seven proterotheriids and one macraucheniid (Litopterna), and two astrapotheres (Astrapotheria) (see Appendix 1 for taxon list). The mandibular subsample included ten toxodontids and 14 tytopheres (Notoungulata), five proterotheriids and three macraucheniiids (Litopterna), and three astrapotheres (Astrapotheria) (see Appendix 1). The reference sample of extant ungulates consisted of 505 specimens belonging to 162 species (141 Artiodactyla, 16 Perissodactyla, and 5 Hyracoidea; supplementary material 1), with all families and subfamilies represented. Only adult specimens with the third molar erupted and in occlusion were included, and animals that had led captive lives were avoided as much as possible. Additionally, for cranial analyses landmark configuration of 113 Macropodidae (13 species) from Milne and O’Higgins (2002) were included.

**Landmark data.** The 3D landmark coordinates were acquired with a Microscribe G2L digitizer (Immersion Corporation, San José, CA, USA). The landmarks are defined in Tables 1 and 2 and shown in Figure 3. Both lateral sides and midline landmarks were included and comprise 36 cranial and 27 mandibular landmarks of type I (anatomic), II (mathematic), and III (semilandmarks) (see also Milne and O’Higgins, 2002; Cassini and Vizcaíno, 2012).

On the mandible, semilandmarks were placed over the caudal border of the mandibular angle along the masseteric scar (L20 to 22; Tab. 2 and Fig. 3.3), the rostral and caudal border of coronoid process (L8 to 11 and 13 to 14; Tab. 2 and Fig. 3.3), and the ventral margin of mandibular corpus (L24 to 27; Tab. 2 and Fig. 3.3). Initially, more semilandmarks were taken to characterize the curves, then they were resampled, reduced in number, and equispaced using “resample” software of NYCEP (Reddy *et al.*, 2007).

**Ecomorphological analyses.** The ecomorphological analytical procedures evaluate the relationships of craniomandibu-

lar morphology with the ecological aspects of extant ungulates. The procedure followed here is a hierarchical analysis that first identifies the correlation between cranio-mandibular morphology and habitat type, and then correlates the morphology with feeding behavior within each habitat category. This contrasts with the approach of Spencer (1995),

**TABLE 1 - Cranial landmarks, names and definitions used in the present study (see also Cassini *et al.*, 2012b)/Nombres y definiciones de los landmarks craneanos utilizados en este estudio (ver también Cassini *et al.*, 2012b).**

Number	Name	Definition of landmark
1 & 22	Stephanion	Sutura coronalis at the intersection with the linea temporalis
2 & 23		Sutura frontolacimalis at the margo orbitalis
3 & 24	Dacryon	Sutura zygomaticolacimalis at the margo orbitalis
4 & 25		Anterior point of the processus zygomaticus of the os temporale
5 & 26		Sutura zygomaticotemporal on the margo dorsal of the arcus zygomaticus
6 & 27		Superior root of the zygoma (on the temporal bone)
7 & 28		Sutura zygomaticotemporal on the margo ventrale of the arcus zygomaticus
8 & 29		Antermost origin of musculus masseter/Lowest point of the ‘masseteric process’
9 & 30		Distal margo alveolare of the last molar
10 & 31		Mesial margo alveolare of first functional premolar
11 & 32		Foramen infraorbitale
12 & 33		Sutura maxilloinsiciva at the margo intralveolaris
13 & 34		Distal margo alveolare of the lateralmost incisor or horny pad scar
14 & 35		Sutura nasoinsiciva at the margin of the nasal aperture
15 & 36		os nasale, frontale and maxilla junction
16	Lambda	Sutura occipitoparietalis
17	Bregma	Sutura coronalis in the midline
18	Nasion	Sutura frontonasalis on the sagittal plane
19	Rhinion	Rostral edge of the os nasale on the sutura internasalis
20	Nasospinale	Sutura interincisiva on the mid-sagittal plane of nasal aperture
21	Prosthion	Sutura interincisiva on the margo alveolaris

who evaluated habitat preference within dietary categories.

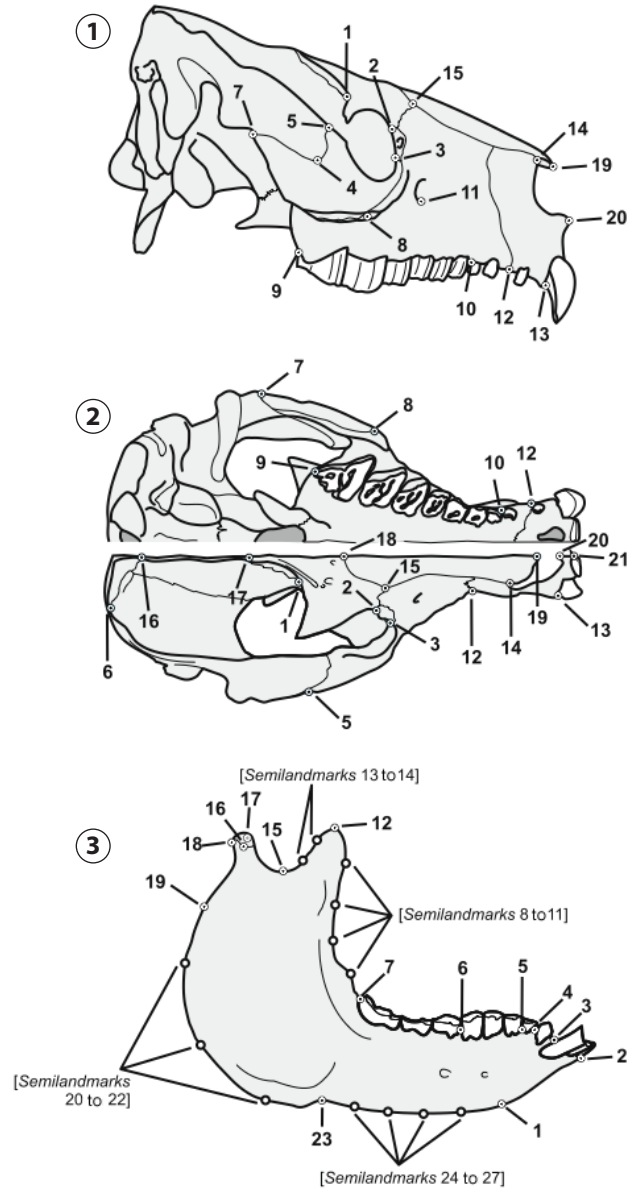
The habitat types were classified following Mendoza *et al.* (2005): (1) open habitat, characterized by treeless or scarcely wooded savannahs, grasslands, dry deserts or semi-arid steppes; (2) mixed habitat, characterized by ecotone, wooded savannahs, bushlands, and open forests and including species dwelling in both open and closed habitat without preference; and (3) closed habitat, characterized by closed woodlands and riverine, deciduous or evergreen forests.

The extant species were divided into five broad dietary

categories (Mendoza and Palmqvist, 2006, 2008): (1) grazers, feeding mainly on grasses; (2) mixed feeders, including those species in which grass and leaves are consumed based on their availability; (3) browsers, feeding predominantly on dicotyledonous plants; (4) frugivores, feeding predominantly on fruits and other non-fibrous soft material; (5) omnivores, eating vegetation, fungus, and occasionally animal tissues. For a discussion of the dietary terminology see Bargo and Vizcaíno (2008).

**TABLE 2 - Mandibular landmarks, names and definitions used in the present study/ Nombres y definiciones de los landmarks mandibulares utilizados en este estudio.**

Number	Name	Definition of landmark
1	Gnathion	Caudo-ventral margin of the mandibular symphysis on the midline
2	Infradentale	Alveoli dentalis of i1 in the midline
3		Distal margin of alveoli dentalis of the last lower incisor.
4		Distal margin of alveoli dentalis of the lower canine.
5		Mesial margin of the alveoli dentale of the first functional premolar
6		Margo interalveolaris between last premolar and first molar
7		Distal margin of the alveoli dentale of the last molar
8-11	semilandmarks	Over the ascending process of ramus mandibulae and processus coronoideus.
12	Coronion	The most superior point on the processus coronoideus
13-14	semilandmarks	over caudal margin of processus coronoideus.
15	Mandibular notch	The most inferior point on the incisura mandibulae
16	Condylion lateral	Most medial margin of mandibular condyle
17	Condylion medial	Most lateral margin of mandibular condyle
18		caudal margin mandibular condyle
19		Most dorsal-caudal rugosity from musculus masseter insertion
20- 22	semilandmarks	over caudal-ventral margin of angulus mandibulae.
23		Most anterior roughness from musculus masseter insertion
24-27	semilandmarks	over ventral margin of corpus mandibulae.



**Figure 3.** Landmark configuration on *Adinotherium* cranium (1, 2) and mandible (3)/ Configuración de landmarks sobre el cráneo (1, 2) y mandíbula (3) de *Adinotherium*. Definitions in Tables 1 and 2/ Definiciones en Tablas 1 y 2. The landmarks are shown on the right side and midline/ Los landmarks están representados sobre el lado derecho y la línea media (modified from/ modificado de Cassini *et al.*, 2012b).

The ecomorphological analyses were carried out in a morphogeometric framework (Dryden and Mardia, 1998) and separately for the cranial and mandibular subsamples. The data were analyzed using Morphologika 2.5 (<http://www.york.ac.uk/res/fmc/resources/software.htm>) (O'Higgins, 1999, 2000a, b) and MorphoJ (Klingenberg, 2011) which supports the use of three dimensional data. Additional analyses and graphics were made using R statistical package (R Development Core Team, 2012).

In order to remove the spatial variation that does not correspond to form, the landmark configurations were superimposed, using rotation, translation and reflection transformations, using GPA (Rohlf, 1990). The cs of each landmark configuration was stored to evaluate the relationship of shape relative to HI and size. For HI regressions, when the residuals were not randomly distributed (see results), it was necessary to use smoothing models from the GAM family (see Zuur *et al.*, 2009). To verify that the difference between tangent space and shape space was minimal, interspecimen tangent distances were regressed on Procrustes distances (Frost *et al.*, 2003). The resultant correlation and root mean square error in parentheses of the cranium sample, 0.9999 (0.0014), and the mandible sample, 0.9999 (0.00076), indicated that these two spaces were nearly identical.

**Allometry.** In geometric morphometric analyses, shape and size are decomposed and cs is used as a proxy for size (Goodall, 1991; Dryden and Mardia, 1998). While differences in geometric scale were removed during the GPA, the allometric components of shape were not. In the absence of allometry, cs does not correlate with shape (Bookstein, 1986; Kendall, 1986). Hood (2000) concluded that cs is a geometric measure of size that follows the same mathematical behavior as body mass. In addition, other authors (Frost *et al.*, 2003; Ercoli and Prevosti, 2011; Meloro and O'Higgins, 2012; Cassini *et al.*, 2012b) found that cs is highly correlated with and an excellent variable to predict bm. In order to evaluate allometric shape variation, the landmark coordinates of aligned specimens were regressed on log10-transformed cs using MorphoJ software.

**Multivariate shape variation.** The landmark configurations were projected from the Kendall curve to the tangent Euclidean space (Bookstein, 1996), which allows exploration of shape variation using multivariate analyses (*e.g.*, PCA and CVA). In this study, visualization of shape change was accomplished by adding the product of the eigenvalue and the score in the evaluated pc (Kent, 1994) to the Cartesian coordinates of consensus shape using the software Morphologika 2.5. Morphospaces were defined in relation

to the taxonomic and ecological distribution of the extant sample allowing evaluating patterns of shape change. The paleoautoecological inferences for fossil specimens were based on their distribution in the defined morphospaces. When ecological patterns were found (see results) CVA was used in MorphoJ to find the shape features that best distinguish ecologic groups.

In both morphometric analyses (PCA and allometric regressions), the results produce vectors in shape space. In order to compare those vectors (*i.e.*, to examine the similarity between an allometric regression vector and the PCA), an angular comparison to compare vector directions was made using MorphoJ software. Additionally, to compare the similarities of two ordinations (PC scores) with slightly different orientation and scaling, a Procrustes rotation from Vegan package in R was used. Procrustes rotation uses uniform scaling (expansion or contraction) and rotation to minimize the squared differences between two ordinations. The significance was assessed by permutation test.

In order to analyze putative phylogenetic biases in the distribution of the sample of extant mammals, a variance decomposition test was performed. This test was proposed by Ollier *et al.* (2006) to evaluate the phylogenetic dependence of a given trait and whether it is concentrated in one or more particular nodes of a tree that includes the taxa under study. A tree representing the phylogenetic relationships of the extant mammals of the sample was built (supplementary material 2), based on phylogenetic hypotheses available in the literature (Cardillo *et al.*, 2004; Hernández Fernández and Vrba, 2005; Price *et al.*, 2005; Bininda-Emonds *et al.*, 2007; Mona *et al.*, 2007; Duarte *et al.*, 2008; Steiner and Ryder, 2011). Following Ollier *et al.* (2006), four statistical tests were applied here to evaluate the differences between the observed and the simulated decomposition distributions. In addition, associations of morphological and ecological traits, taking in account the phylogenetic relationships, were analyzed by means of GEE for the extant ungulate taxa. It uses a GLM approach incorporating the phylogenetic relatedness among species as a correlation matrix in the model (Morgan, 2009; Fraser and Theodor, 2011a). The advantage of using GEE in relation to other comparative methods is that the response variable can follow non-normal distributions, the independent variables can be continuous or categorical, and the model can include additive, interactive and nested effects among the predictors (see Paradis and Claude, 2002 for a detailed description and evaluation of the method). The GEE analyses were run using the APE package in R (Paradis *et al.*, 2004).

**RESULTS**

**Cranial analyses**

There was a significant correlation between Procrustes distances and the phylogenetic distances (at species level;  $r = 0.665 \pm 0.0088$  95% CI;  $p < 0.0001$ ). This correlation is higher when macropodids were removed ( $r = 0.7492947 \pm 0.007673$  95% CI;  $p < 0.0001$ ).

The log-transformed cs values are not phylogenetically independent in the whole sample (Tab. 3) or in most orders (Artiodactyla and Perissodactyla) or families (Macropodidae, Bovidae, Cervidae, and Suidae). There is no significant size difference among habitat categories (except in the total sam-

ple, artiodactyls, and cervids subsets) even after taking into account the phylogenetic relationships (Tab. 3). In contrast, there is significant difference in log-transformed cs among dietary categories (Tab. 4). In the whole sample, as well as among artiodactyls and bovids, the grazers were larger than members of other feeding groups and browsers seem to be larger than frugivores (Tab. 4), despite some differences between non-phylogenetic and phylogenetically controlled tests. **Allometry.** Table 5 shows the regression results of shape versus log10-transformed cs. With some exceptions (*i.e.*, Hippotraginae, Muntiacini, Tragulidae, Rhinocerotidae, and Hegetotheriidae), cs and shape showed a significant relation-

**TABLE 3 - Phylogenetic signal on size (log-transformed centroid size) and differences between habitat categories and diet/ Señal filogenética en el tamaño (logaritmo del tamaño del centroide) y diferencias entre las categorías de hábitat y dieta.**

<b>Taxon</b>	<b>Habitat</b>	<b>GLM F - d.f.(gp, res)</b>	<b>Tukey</b>	<b>GEE F - d.f.(gp, phy-res)</b>	<b>M. Comp.</b>
Total	O;M;C	5.58 ** (2, 49)	O>C	18.48 *** (2, 13.36)	M > O > C
Macropodidae	O;M;C	4.01 (2, 10)		4.76 (2, 7.97)	
Procavidae	O;C	0.25 (1, 3)		0.25 (1, 2.96)	
Artiodactyla	O;M;C	4.32 * (2, 115)	M>C	17.52 *** (2, 19.88)	M > O = C
Bovidae	O;M;C	1.39 (2, 65)		4.91 (2, 23.78)	
Alcelaphinae	O;M	0.94 (1, 4)		0.86 (1, 2.52)	
Antilopinae	O;M	0.57 (1, 10)		0.2 (1, 5.26)	
Bovinae	O;M;C	0.3 (2, 9)		4.33 (2, 2.55)	
Caprinae	O;M	0.53 (1, 18)		0.02 (1, 8.94)	
Cephalophinae	C	Na			
Hippotraginae	O;M	1.08 (1, 4)		0.43 (1, 1.71)	
Reduncinae	O;M	0.0004 (1, 5)		0.49 (1, 2.04)	
Cervidae	O;M;C	3.35 (2, 20)		12.37 ** (2, 6.01)	O = M > C
Capreolinae	O;M;C	0.93 (2, 10)		4.35 (2, 2.6)	
Odocoileini	O;M;C	3.62 (2, 8)		9.69 (2, 2.65)	
Cervinae	O;M;C	2.88 (2, 7)		4.19 (2, 2.75)	
Cervini	O;M;C	0.26 (2, 4)		0.91 (2, 1.64)	
Suiformes	O;C	2.79 (1, 9)		2.77 (1, 3.16)	
Suidae	O;C	2.62 (1, 6)		2.36 (1, 3.46)	
Tayassuidae	C	Na			
Perissodactyla	O;M;C	0.97 (2, 13)		5.63 (2, 2.03)	
Equidae	O	Na			
Rhinocerotidae	O;C	Na			
Tapiridae	M;C	0.07 (1, 2)		3.65 (1, 0.52)	

**GLM**, generalized linear model/ modelo lineal generalizado; **GEE**, generalized estimating equation/ ecuación de estimación generalizada; **d.f.**, degrees of freedom/ grados de libertad (**gp**, groups/ grupos; **phy**, phylogeny/ filogenia; **phy-res**, phylogenetic corrected of residual/ residuos corregidos por la filogenia; **res**, residual/ residuos); **Tukey**, Honestly Significant Difference test/ Prueba de la Diferencia Significativa Honesta de Tukey; **M. Comp.**, multiple comparisons/ comparaciones múltiples; **na.**, analysis not applicable/ análisis no aplicable. **Habitat categories/** Categorías de Hábitat: **O**, open/ abierto; **M**, mixed/ mixto; **C**, closed/ cerrado. \* Significant at 0.05 level/ significativo al nivel de 0.05; \*\* significant at 0.01 level/ significativo al nivel de 0.01; \*\*\* significant at 0.001 level/ significativo al nivel de 0.001.



ship. The allometric scaling of the overall cranial shape variation was low in the total sample (-18%), in most Bovidae subfamilies, Equidae, and Procaviidae. Artiodactyl families (except hippopotamids and giraffids), tapirs, macropodids, and Santacrucian ungulates have a large allometric component (range approx. 30% to 45%). Only among the hippos and giraffes (both represented by two species with very different body mass and, consequently, cs) was shape variation mostly explained by size (>65%) (Tab. 5).

A shared pattern of allometry is common among all regressions. Small forms were characterized by a narrow muzzle, short rostrum, broad palate, more anteriorly positioned orbits, large temporal fossa, and laterally expanded zygomatic arch (Fig. 4.1). In contrast, large forms showed wide muzzle, long rostrum, narrow palate, lateralized and more posteriorly located orbits, small temporal fossa, and a medially compressed zygomatic arch (Fig. 4). These features also parallel the fact that in the extant species, most browsers

**TABLE 4 - Differences in size (log-transformed centroid size) between diet categories/ Diferencias de tamaño (logaritmo del tamaño del centroide) entre las distintas categorías de dieta.**

Taxon	Diet categories	GLM F - d.f.(gp, res)	Tukey	GEE F - d.f.(gp, phy-res)	M. Comp.
Total	G;M;B;F;O	8.71 *** (2, 147)	G>M=B=F†	69.13 *** (4, 11.36)	G>M>B>F; O=(M,B,F)
Macropodidae	G;M;B	3.83 (2, 10)		4.21 (2, 7.97)	
Procaviidae	G;M;B	1.59 (2, 2)		3.17 (2, 1.96)	
Artiodactyla	G;M;B;F;O	8.46 *** (4, 113)	G>M=B=F†	61.84 *** (4, 17.88)	G>M=B>F; O=(M,B,F)
Bovidae	G;M;B;F	9.68 *** (3, 64)	G > M > B; G > F	12.52 *** (3, 22.78)	G>M=B‡
Alcelaphinae	G;M	0.94 (1, 4)		0.86 (1, 2.52)	
Antilopinae	M;B	1.53 (1, 10)		0.34 (1, 5.26)	
Bovinae	G;M;B	4.89 * (2, 9)	G>B	11.73 (2, 2.55)	
Caprinae	G;M	0.1 (1, 18)		8.44 * (1, 8.94)	G>M
Cephalophinae	M;F	241.81 ** (1, 2)	F>M	216.53 * (1, 1.53)	F>M
Hippotraginae	G;M	4.04 (1, 4)		2.71 (1, 1.71)	
Reduncinae	G;B	2.05 (1, 5)		1.23 (1, 2.04)	
Cervidae	G;M;B;F;O	1.29 (4, 18)		12.58 * (4, 4.01)	B > F
Capreolinae	M;B;F	1 (2, 10)		5.21 (2, 2.6)	
Odocoileini	M;B;F	1.11 (2, 8)		5.99 (2, 2.65)	
Cervinae	G;M;O	1.97 (2, 7)		1.05 (2, 2.75)	
Cervini	G;M	0.6 (1, 5)		0.05 (2, 1.64)	
Suiformes	G;M;O	3.81 (2, 8)		7.74 (2, 2.16)	
Suidae	G;M;O	4.48 (2, 5)		8.8 (2, 2.46)	
Tayassuidae	O	na			
Perissodactyla	G;M;B	0.96 (2, 13)		4.99 (2, 2.03)	
Equidae	G	na			
Rhinocerotidae	G;M;B	na			
Tapiridae	M;B	0.03 (1, 2)		2.36 (1, 0.52)	

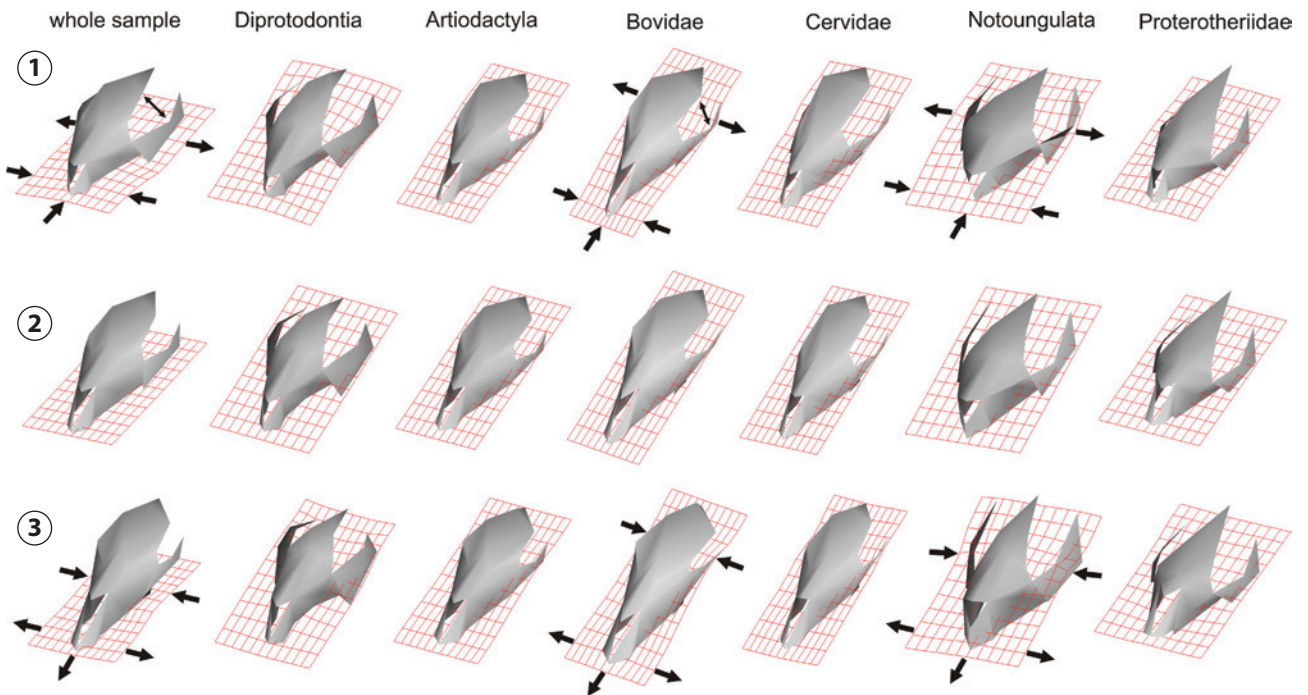
**d.f.**, degrees of freedom/ grados de libertad; **(gp, groups/ grupos, phy: phylogeny/ filogenia, phy-res, phylogenetic corrected of residual/ residuos corregidos por la filogenia; res, residual/ residuos); GLM: generalized linear model/ modelo lineal generalizado; GEE, generalized estimating equation/ ecuación de estimación generalizada; Tukey, Honestly Significant Difference test/ Prueba de la Diferencia Significativa Honesta de Tukey; M. Comp., multiple comparisons/ comparaciones múltiples; na., analysis not applicable/ análisis no aplicable. Diet categories/ Categorías de Dieta: G, grazer/ pastador; M, mixed feeders/ intermedios; B, browser/ ramoneador; F, frugivore/ frugívoro; O, omnivore/ omnívoro. Significant at 0.05 level/ significativo al nivel de 0.05; \*\* significant at 0.01 level/ significativo al nivel de 0.01; \*\*\* significant at 0.001 level/ significativo al nivel de 0.001; † Omnivores did not differ from others diets categories/Los omnívoros no difieren de las otras categorías de dieta; ‡ Frugívoros did not differ from others diets categories/Los frugívoros no difieren de las otras categorías de dieta.**

and frugivores are small while most grazers are large (Tab. 4). In addition, the differences among small and large taxa remained significant after controlling for phylogenetic autocorrelation, principally in artiodactyls and bovids. Figure 4 shows that in Santacrucian ungulates, as in macropods, differences in the temporal fossa are less evident.

**Multivariate shape variation.** The PCA of tangent space coordinates for the total sample resulted in the first seven PCs accounting for nearly 80% of the total variation (Tab. 6). PC1 explained ~33% of the total variance and together with PC2 accounted for most of the 50% cumulative variance. Only PC1 correlates negatively with log-transformed cs ( $R^2 = 0.47$ ;  $F(1, 660) = 586.95$ ;  $p < 0.0001$  after 10000 rounds of permutation test) and with a vector angle of  $21.632^\circ$  (note that MorphoJ inverts the angle vectors above  $90^\circ$ , so it corresponds to  $158.368^\circ$ ) with the log-transformed cs regression ( $p < 0.0001$ ). Although PC3 and PC4 show a significant relationship with log-transformed cs ( $p < 0.0001$  after 10000 rounds of permutation test) the coefficient of determination  $R^2$  (or variance explained) was always lower than 0.1. None of the seven PCs were clearly correlated with habitat or diet categories, but the first two components show well-defined taxonomic zones. These results do not change even if the analysis is repeated using subsets of the total refer-

ence sample for each category separately (*i.e.*, open, mixed, or closed habitat). Although some rotations between the shape vectors are significant, the high Procrustes correlation indicates high congruence between these multivariate spaces (Tab. 6). The orthonormal decomposition of variance indicates that the first seven PCs are shaped by phylogenetic history because four test statistics (R2Max, SkR2k, Dmax, and SCE) reveal a significant departure from H0 (Tab. 6) with no prevalence of a particular node (further details in supplementary material 3 and 4).

As for the total sample, the first seven PCs of the Santacrucian ungulates assemblage account for almost 80% of the cumulative variance. PC1 explains ~29% of the total variance and together with PC2 accounts for almost 45% of the cumulative variance. Although the first seven PCs account for almost 80% of the cumulative variance, from the fourth onwards they explain less than 10% of the total variance. The shape changes implied by the first and second eigenvectors are visualized in Figure 5 (supplementary material 5.1). Negative values of PC1 are characterized by a high and narrow skull with enlarged temporal fossa and an orbit close to the tooth row, whereas positive values are associated with a low and broad skull with orbits on the dorsal edge of the calvaria. On PC2, the shape changes on negative values include an ex-



**Figure 4.** Thin plate spline gridlines of cranial shape vs log10-transformed centroid size regressions/ *Grillas de deformación de las regresiones de la forma del cráneo vs el logaritmo decimal del tamaño del centroide*: (1) small forms/ *formas pequeñas*, (2) consensus/ *consenso*, (3) large forms/ *formas grandes*. The arrows indicate the principal shape change directions/ *Las flechas indican las principales direcciones de cambios en la forma*.

panded and vaulted frontal bone, retracted nares and slender zygomatic arch, whereas on positive values indicate a strong and laterally expanded zygomatic arch and temporal fossa. In the morphospace depicted by PC1 and PC2, the Santacrucian ungulates occupy four distinct regions. The hegetotheriids are grouped in the positive quadrant, the nesodontines in the second quadrant (negative PC1; positive PC2), the litopterns plus astrapotheres in the third quadrant (negative PC1 and PC2), and the intertheriids in the fourth quadrant.

Shape variation related to lithostatic deformation was investigated in all PCs irrespective of their low explained variance. Only PC7 showed evidence of deformation that accounts for nearly 3% of the total variance. The principal signs of deformation were a lateral compression of the zygomatic arch and an orbit unaligned to the sagittal plane, breaking the bilateral asymmetry (see supplementary material 5.2).

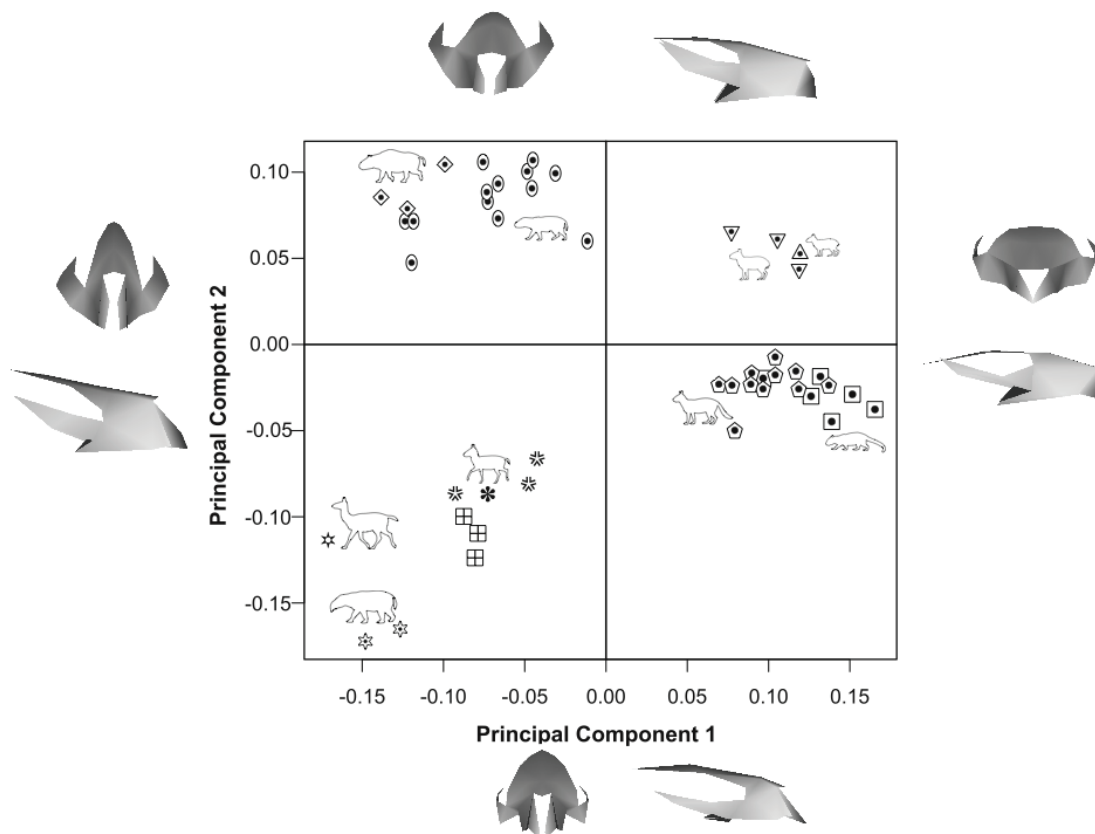
Only PC1 correlates significantly and negatively with

log-transformed cs ( $R^2 = 0.86$ ;  $F(1, 45) = 275.39$ ;  $p < 0.0001$ ) and with a vector angle of  $66.956^\circ$  (note that MorphoJ inverts the angle vectors above  $90^\circ$ , so it will correspond to  $113.044^\circ$ ) with the log-transformed cs regression of Santacrucian shape coordinates ( $p = 0.00342$ ).

**Mandible analyses**

The Procrustes distances for configurations of extant species shows a significant correlation ( $r = 0.782 \pm 0.007$  95% CI;  $p < 0.0001$ ) with the phylogenetic distances.

**Allometry.** The regressions of shape vs log10-transformed bm were significant in the total sample and in those based upon orders and some families (Table 7). The allometric scaling of the overall mandibular shape variation was very low in the total sample ( $-7\%$ ) as well as in artiodactyls ( $-2.5\%$ ). The tylopods, perissodactyls, and Santacrucian ungulates (Notoungulata and Litopterna) have a large allometric component (range approx. 30% to 45%), only surpassed by hippopotamids and



**Figure 5.** Cranial PCA of Santacrucian ungulate specimens/ *Análisis de Componentes Principales del cráneo considerando sólo los especímenes de ungulados santacrucenses.* Taxa are distributed in the morphospace defined by the two first PCs/ *Distribución de los taxa sobre el morfoespacio de los dos primeros componentes.* Shape (frontal and lateral norm) of extreme negative and positive values of each component/ *Formas del extremo negativo y positivo (en vista frontal y lateral) de cada componente.* Reference/ *Símbolos:* Astrapotheria: ✱✱, *Astrapotherium*; Litopterna: ▣, *Diadiaphorus*; ✱, *Tetramerorhinus*; ✱, *Thoatherium*; ✱, *Theosodon*; Notoungulata: ▣, *Interatherium*; ◇, *Nesodon*; ○, *Protypotherium*; ○, *Adinotherium*; ▽, *Hegetotherium*; △, *Pachyrukhos*.

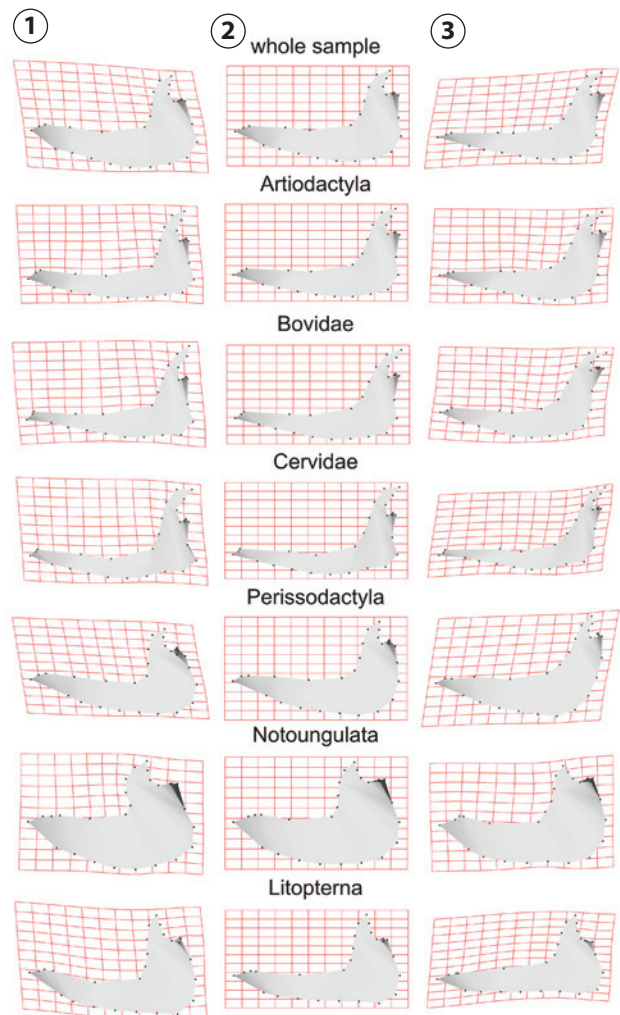
**TABLE 5 - Regressions of cranial shape vs log10-transformed centroid size/ Regresiones de la forma del cráneo vs el logaritmo decimal del tamaño del centroide.**

Taxon	Total SS	Resd. SS	% Pred.	p-value
Total sample	22.11	18.16	17.87%	< 0.001
Macropodidae	0.89	0.62	30.09%	< 0.001
Procaviidae	0.12	0.10	17.09%	< 0.001
Artiodactyla	10.07	9.32	7.39%	< 0.001
Bovidae	2.80	2.41	13.84%	< 0.001
Alcelaphinae	0.12	0.10	16.46%	0.006
Antilopinae	0.28	0.25	12.81%	0.014
Bovinae	0.34	0.30	12.19%	0.005
Caprinae	0.58	0.53	9.49%	< 0.001
Cephalophinae	0.04	0.04	21.21%	0.001
Hippotraginae	0.05	0.04	15.51%	ns
Reduncinae	0.06	0.05	15.80%	< 0.001
Cervidae	0.76	0.51	32.97%	< 0.001
Capreolinae	0.57	0.35	38.30%	< 0.001
Odocoileini	0.41	0.26	35.94%	< 0.001
Cervinae	0.17	0.11	35.19%	< 0.001
Cervini	0.11	0.08	29.79%	< 0.001
Muntiacini	0.02	0.01	25.58%	ns
Camelidae	0.29	0.18	36.69%	< 0.001
Giraffidae	0.05	0.01	76.68%	0.0003
Tragulidae	0.04	0.03	31.01%	ns
Hippopotamidae	0.09	0.03	66.62%	0.002
Suiformes	1.00	0.72	28.42%	< 0.001
Suidae	0.40	0.26	36.10%	< 0.001
Tayassuidae	0.25	0.20	22.87%	< 0.001
Perissodactyla	1.75	1.05	40.01%	< 0.001
Equidae	0.05	0.04	17.33%	< 0.001
Rhinocerotidae	0.05	0.03	35.31%	ns
Tapiridae	0.12	0.09	27.66%	0.009
Santacrucian	1.39	1.01	27.18%	< 0.001
Litopterna	0.15	0.09	38.85%	0.004
Proterotheriidae	0.05	0.03	40.22%	0.01
Notoungulata	0.91	0.56	38.51%	< 0.001
Hegetotheriidae	0.03	0.02	44.42%	ns
Interatheriidae	0.27	0.22	19.80%	< 0.0001
Nesodontinae	0.15	0.10	31.09%	0.002

**Total SS**, total squared sums of shape coordinates/ suma total de cuadrados de las coordenadas de forma; **Resd. SS**, squared sums of shape coordinates not explained by size or due to error (residual)/ suma de cuadrados de los residuos de las coordenadas de forma no explicadas por el tamaño; **% Pred.**, percent of shape variance explained by size (equivalent to R2)/ porcentaje de la varianza de forma explicada por el tamaño (equivalente a R2); **p-value**, probability of independence between variables after 10000 rounds of permutation test/ probabilidad de independencia entre las variables después de 10000 repeticiones de la prueba de permutación; **ns**, not significant/ no significativa.

giraffids (> 55%). A similar pattern of allometry is shared at the order level: small forms are characterized by an acute angle between the mandibular corpus and the ramus, whereas larger forms are characterized by an obtuse angle. The thickness of the mandibular corpus and the length of the diastema between incisors and premolars also vary with size. Another remarkable feature implies a more developed masseteric fossa in small forms and a posteriorly curved coronoid process on large forms (see Fig. 6). These shape changes were also represented on PC1 of the total sample (see below), which varies in the same directions as habitat preferences and diets, with small forms being closed habitat browsers or frugivores and large forms being open habitat grazers (see Tab. 3 and 4).

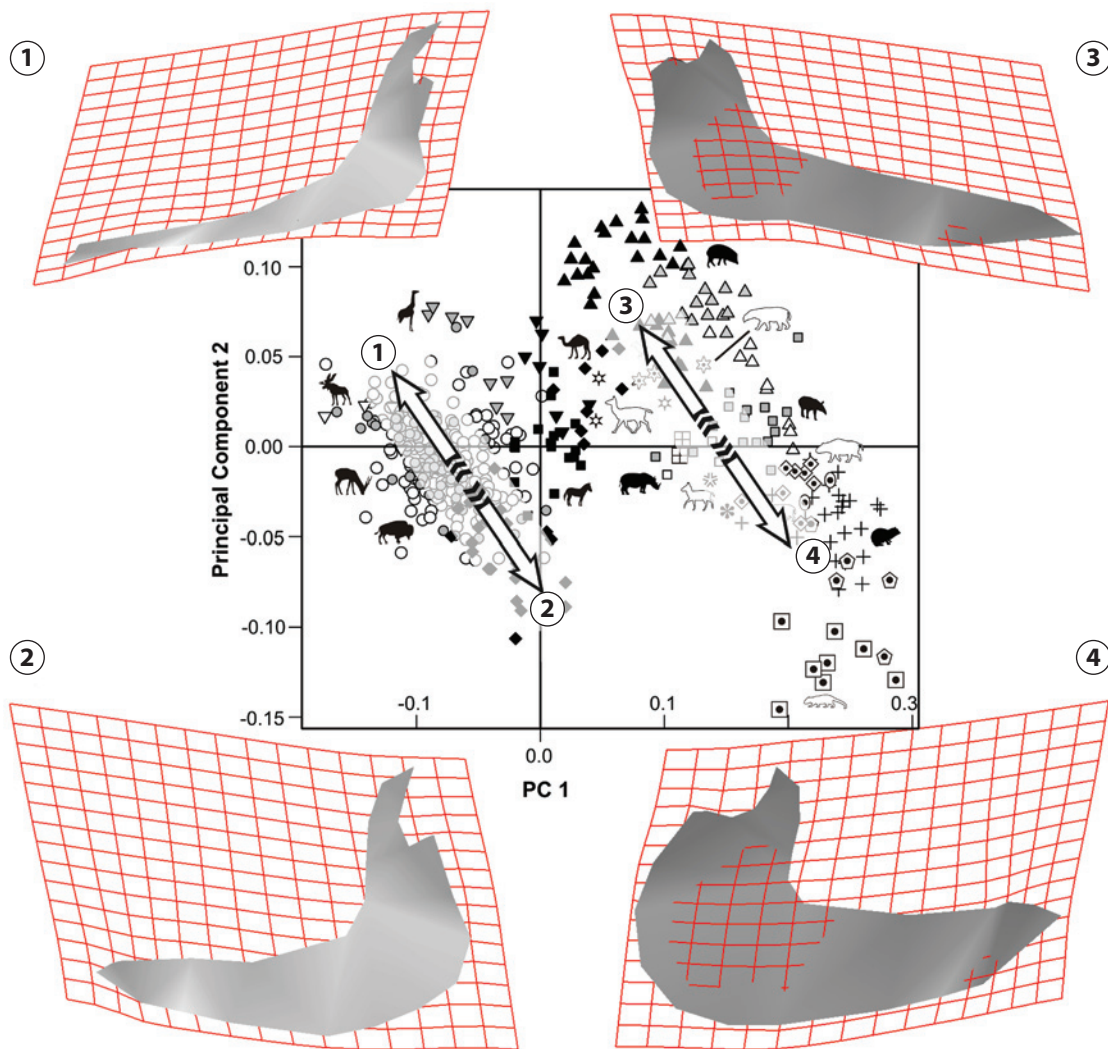
**Multivariate shape variation.** The PCA of tangent space



**Figure 6.** Thin plate spline gridlines of mandibular shape vs log10-transformed centroid size regressions/ Grillas de deformación de las regresiones de la forma de la mandíbula vs el logaritmo decimal del tamaño del centroide: (1) small forms/ formas pequeñas, (2) consensus/ consenso, (3) large forms/ formas grandes.

coordinates of the total sample resulted in six PCs that account for nearly 85% of the total variation (Tab. 8). PC1 explained ~56% of the total variance and together with PC2 accounted for most of the 66% cumulative variance. The shape changes implied by the first eigenvector (PC1) were similar to the allometric scaling (Fig. 7; see also supplementary material 6). Associated with this configuration was the change in shape of the mandibular symphysis, being slender and elongated rostrocaudally (on the negative end) to short and laterally expanded in association with the presence of a hypertrophied canine or incisor (on the positive end). Toward the negative end were mainly bovines, while tragulids,

camels, rhinoceroses, tapirs, hippos, suines and hyraxes lay towards the positive side. Consequently, taxa with lower values of PC1 are the forms with less developed canines (e.g., *Catagonus* Ameghino, 1904) and those with higher values are forms with much hypertrophied canines (e.g., *Babyrousa* Perry, 1811). PC2 represents shape changes mainly varying from a short and deep mandible with a curved corpus on the negative end to a long, low and straight mandible on positive side. The symphysis varies from short, narrow, and vertically oriented for negative values, to large, broad, and horizontally oriented on the positive side. Width and height of the coronoid process are also represented on PC2.



**Figure 7.** Thin plate spline gridlines on mandibular PCA taking the two first PC of the whole sample/ *Grillas de deformación en el morfoespacio de los dos primeros componentes del PCA de mandíbula para muestra completa*: (1) to/ hacia *Litocranius* (2) to/ hacia *Vicugna* (3) to/ hacia *Hylochoerus*, (4) to/ hacia *Procavia*. Reference extant mammals/ *Símbolos mamíferos actuales*: +, Hyracoidea; ■, Equidae; □, Tapiridae; □, Rhinocerotidae; △, Hippopotamidae; ▲, Suidae; △, Tayassuidae; ▽, Tragulidae; ▽, Antilocapridae; ▽, Giraffidae; ◆, Camelidae; ○, Bovidae; ○, Cervidae. Santacrucian ungulates/ *ungulados Santacrucenses*: Astrapotheria: ⚡, *Astrapotherium*; Litopterna: +, *Anisolophus*; ⊞, *Diadiaphorus*; ✱, *Tetramerorhinus*; ✱, *Thoatherium*; ☆, *Theosodon*, Notoungulata: □, *Interatherium*; ◆, *Nesodon*; ⊕, *Protypotherium*; ⊕, *Adinotherium*; ▽, *Hegetotherium*.

In the morphospace depicted by the first and second components, extant taxa are distributed in two clouds with similar shape gradient. The left cloud includes bovids, cervids and South American camelids. At the left upper margin are the closed habitat browsers such as *Litocranius* Kohl, 1886 (Alcelaphini; Bovidae) with a gracile mandible, while *Vicugna* Lesson, 1842 (Camelidae, mixed feeder) is located at the opposite end with a more robust mandible and more developed masseteric fossa (supplementary material 7). In the right cloud, *Hylochoerus* Thomas, 1904 (Suidae, omnivorous) lies on the upper left and *Procavia* Storr, 1780 (Procaviidae, grazer) on the bottom right (Fig. 8). These two components were the most morphologically informative allowing the identification of trend shapes among diet-habitat category complexes.

Santacrucian ungulates are arranged similarly, close to the right cloud, with *Theosodon* in the top and *Interatherium* in the bottom (Fig. 7; supplementary material 8). Among notoungulates, the interatheriids are placed close to *Procavia* (open habitat grazers) and the nesodontines are close to *Heterohyrax* Gray, 1868 (Procaviidae) and *Hippopotamus* Linnaeus, 1758, while *Pachyrhinos* lies close to *Astrapotherium*, far from remaining notoungulates, surrounded by *Camelus*

Linnaeus, 1758 (Tylopoda; intermediate diet), *Phacochoerus* Cuvier, 1826 (Suidae; grazer), and *Babyrousa* (Suidae; omnivore). Among Litopterna, *Theosodon* is close to *Hyemoschus* Gray, 1845 (Tragulidae; browser) while proterotheriids are near rhinoceroses.

Although all PCs (except PC4) show significant regressions with log-transformed cs (p<0.001 after 10000 rounds of permutation test) the determination coefficient R<sup>2</sup> (or variance explained) was always lower than 0.1.

The regression of the centroid at the species level of PC-scores with the HI (taken from Janis, 1988) was significant for PC2 and PC3 and correlates negatively (Fig. 8.1). However, only the first relationship has a determination coefficient R<sup>2</sup> higher than 0.3 (AIC= -468.365; ΔAIC= 1.495). As consequence, about 35% of the shape change in PC2 is explained by the HI. Among Santacrucian ungulates, only the interatheriids deviate from the relationship between PC2 and HI (i.e., they have higher negative values of PC2 than expected by their HI). Using GAM, a better fit was obtained (pseudoR<sup>2</sup>= 0.4951; AIC= -496.861; ΔAIC= 0). In addition, the latter has an Akaike weight of 0.68 (vs. 0.32 for the linear model), which indicates it has 68% chance of being the best of both. However, the *Interatherium* specimens were still

**TABLE 6 - Principal component analysis of the skull for the total sample, angular comparisons and Procrustes Correlation with habitat subsets of extant sample (open, mixed, and close)/ Análisis de componentes principales del cráneo de la muestra completa, comparaciones angulares y de correlación de Procrustes de los subconjuntos por categoría de hábitat de la muestra de actuales (abierto, mixto y cerrado).**

PC	Eigenvalues	% Var.	R2Max	SKR2k	Dmax	SCE	Open habitat	Mixed habitat	Closed habitat
PC1	0.0109756	32.814	0.088	54.802	0.328	7.643	16.24°	21.12°	<b>85.73°*</b>
PC2	0.0061654	18.433	0.156	61.179	0.324	5.700	33.30°	34.84°	<b>80.54°*</b>
PC3	0.0031932	9.547	0.106	60.383	0.288	5.043	64.33°	61.95°	41.63°
PC4	0.0025942	7.756	0.064	71.493	0.160	1.641	58.85°	43.01°	37.99°
PC5	0.0017382	5.197	<b>0.050*</b>	69.631	0.204	2.600	<b>82.40°*</b>	57.04°	63.05°
PC6	0.0011637	3.479	0.142	54.735	0.346	7.743	65.61°	<b>81.62°*</b>	<b>75.62°*</b>
PC7	0.0010645	3.183	0.100	66.662	0.208	2.943	<b>74.64°*</b>	<b>74.54°*</b>	<b>87.49°*</b>
C. Var. %		80.41					84.06%	89.99%	87.27%
Proc. Corr							0.9773	0.9777	0.9679

**PC**, principal components/ componentes principales; **% Var.**, percent of variance explained by each PC/ porcentaje de varianza explicada por cada PC; **C.Var. %**, Cumulative variance percent/ porcentaje de varianza explicada; **R2Max**, Orthonormal max squared coefficients/ Coeficientes ortonormales cuadrados máximo; **SKR2k**, variance distribution of orthonormal squared coefficients/ distribución de la varianza de los coeficientes ortonormales cuadrados, **Dmax**, max cumulative orthogram/ ortograma acumulado máximo; **SCE**, average local variation of the orthogram/ variación local promedio del ortograma. Values in last three columns correspond to angles between vectors in shape space from PCs (first to seventh) of total sample vs. the same PC of each habitat/ Los valores de las últimas tres columnas corresponden a los ángulos entre los vectores del espacio de forma de los PCs (primero a séptimo) de la muestra total vs. los mismos PC de cada habitat. **Proc. Corr**, Procrustes correlation in a symmetric Procrustes rotation indicates the congruence of the two ordinations (whole sample vs habitat subsets) using the seven first PCs/ Correlación de Procrustes en una rotación de Procrustes simétrica indica la congruencia de ambos ordenamientos (muestra completa vs subconjuntos de hábitats) usando los primeros siete PCs. All tests (Orthonormal variance decomposition, angular comparisons and Procrustes correlations) were significant at 0.05 level except those tagged by and asterisk and bold faced/ Todos las pruebas (Descomposición ortonormal de la varianza, comparación angular y de Correlación de Procrustes) resultaron significativas con un alfa de 0.05 con excepción de aquellas señalados por un asterisco y en negritas.

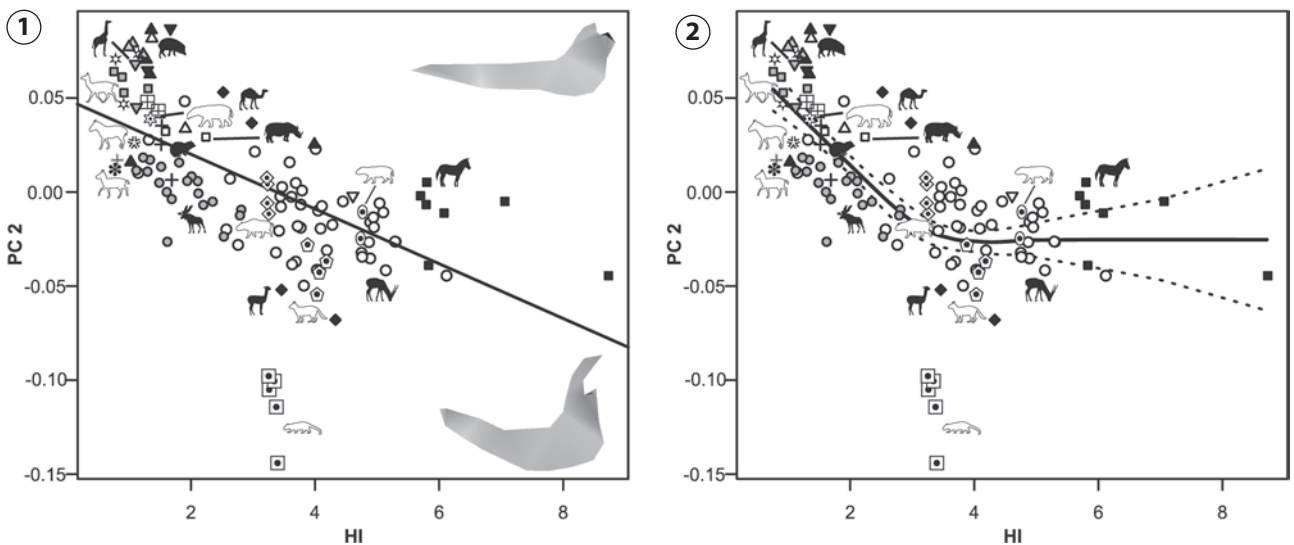
outliers. When fossil specimens are omitted the  $R^2$  of linear model increases to  $-0.43$  ( $AIC = -428.737$ ;  $\Delta AIC = 18.55$ ) and the GAM model a pseudo $R^2 = 0.5433$  ( $AIC = -447.309$ ;  $\Delta AIC = 0$ ). Between these two models the Akaike weight of GAM model was  $\sim 0.9999$  (*i.e.*, 99.99% chance of being the best model). In addition, linear regression residuals are not randomly distributed, indicating that is not the best model. Clearly, both GAMs are the appropriated model, without residual patterns, and showed more negative quasi-linear relationships up to  $HI < 4$  and asymptotic to approximately  $-0.04$  on PC2 for  $HI > 4$  (Fig. 8.2).

The CVA of habitat categories supports the shape gradient given by PC1 and PC2. Two canonical variate axes were obtained; the first accounts for  $\sim 86\%$  of variance and shows separation between the open and close habitat extant ungulates. The Procrustes distances among groups are significant between open and closed habitats ( $p = 0.105$ ;  $p\text{-value} < 0.001$ ) and mixed and closed habitats ( $p = 0.101$ ;  $p\text{-value} < 0.001$ ). When diet categories were evaluated, four canonical variate axes were obtained. The first accounts of  $\sim 61\%$  of the variance and differentiates the omnivores from other categories. The second explains  $\sim 21\%$  of the variance and shows a cline from grazers to intermediate feeders to browsers plus frugivores. The shape variation parallels the shape gradient given by PC1 and PC2 (supplementary material 9).

The PCA of tangent space coordinates of Santacrucian

ungulates resulted in the six PCs accounting for nearly 85% of the total variation. PC1 explained  $\sim 45\%$  of the total variance, and PC2 and PC3 of about 15% and 10%, respectively. These three PCs account for most of the 70% cumulative variance. The shape changes associated to the first eigenvector (PC1) are shown in Figure 9. The main shape variation is from a straight mandibular corpus on the negative end to a curved mandibular corpus on the positive end. Another remarkable feature is the position of the condyle, which is high on negative values and low (close to the occlusal plane) on the positive side. These condyle positions are correlated with an m3 farther and closer from the pivot, respectively. The PC2 represents shape changes mainly associated with lateral expansion of the symphysis on negative values and narrowed on positive values. The alveoli of incisors are above the occlusal plane and the masseteric fossa is deep and well defined on negative values (Fig. 9). On the positive side, the alveoli of incisors are below the occlusal plane and the masseteric fossa is less developed. Width and height of the coronoid process are also represented on PC2. Among the notoungulates all tyotheres, except for *Pachyrukhos*, are on the positive sides of PC1 and PC2. *Pachyrukhos* is located on the negative side of PC1, with a value very close to zero on PC2. The nesodontines *Adinotherium* and *Nesodon* are close to zero on PC1 but have very negative values on PC2.

Among Litopterna, proterotheriids are arranged almost



**Figure 8.** Regressions of hypsodonty index (HI) and second PC/ *Regresión del índice de Hipsodondia (HI) contra el segundo componente principal*: (1) linear model/ *modelo lineal*, (2) generalized additive model/ *modelo aditivo generalizado* (GAM). Reference extant mammals/ *Símbolos mamíferos actuales*: +, Hyracoidea; ■, Equidae; □, Tapiridae; □, Rhinocerotidae; △, Hippopotamidae; ▲, Suidae; △, Tayassuidae; ▽, Tragulidae; ▽, Antilocapridae; ▽, Giraffidae; ◆, Camelidae; ○, Bovidae; ○, Cervidae. Santacrucian ungulates/ *ungulados Santacruceses*: Astrapotheria: ☆, *Astrapotherium*; Litopterna: +, *Anisolophus*; □, *Diadiaphorus*; ☆, *Tetramerorhinus*; \* *Thoatherium*; ☆, *Theosodon*, Notoungulata: □, *Interatherium*; ◆, *Nesodon*; ○, *Protypotherium*; ○, *Adinotherium*; ▽, *Hegetotherium*.

**TABLE 7. Regression of mandibular shape vs log10-transformed centroid size/ Regresión de la forma de la mandíbula vs el logaritmo del tamaño del centroide.**

Taxon	Total SS	Resd. SS	% Pred.	p-value
Total sample	10.46	9.74	6.86%	< 0.001
Procaviidae	0.10	0.09	5.45%	ns
Artiodactyla	5.38	5.24	2.47%	< 0.001
Bovidae	0.96	0.87	9.59%	< 0.001
Alcelaphinae	0.04	0.03	23.82%	< 0.001
Antilopinae	0.10	0.08	11.08%	0.028
Bovinae	0.14	0.12	11.59%	ns
Caprinae	0.28	0.25	11.68%	< 0.001
Cephalophinae	0.04	0.03	15.42%	ns
Hippotraginae	0.03	0.03	11.67%	ns
Reduncinae	0.05	0.04	11.00%	ns
Cervidae	0.39	0.33	17.07%	< 0.001
Capreolinae	0.26	0.20	25.71%	< 0.001
Odocoileini	0.17	0.11	33.36%	< 0.001
Cervinae	0.12	0.10	11.93%	< 0.001
Cervini	0.06	0.05	26.02%	< 0.001
Muntiacini	0.05	0.04	5.13%	ns
Camelidae	0.25	0.14	42.86%	< 0.001
Giraffidae	0.02	0.01	70.73%	0.006
Tragulidae	0.01	0.01	14.53%	ns
Hippopotamidae	0.08	0.03	58.31%	0.001
Suiformes	0.53	0.38	27.06%	< 0.001
Suidae	0.17	0.15	11.99%	< 0.001
Tayassuidae	0.22	0.18	18.32%	< 0.001
Perissodactyla	0.63	0.40	36.29%	< 0.001
Equidae	0.06	0.05	19.10%	0.001
Rhinocerotidae	0.02	0.01	71.02%	ns
Tapiridae	0.07	0.07	5.06%	ns
Santacrucian	0.62	0.48	23.77%	< 0.001
Litopterna	0.07	0.04	42.74%	0.018
Protheroheriidae	0.02	0.02	24.59%	ns
Notoungulata	0.31	0.21	33.59%	< 0.001
Hegetoheriidae				
Interatheriidae	0.12	0.10	11.60%	ns
Nesodontinae	0.04	0.03	15.00%	ns

**Total SS**, total squared sums of shape coordinates/ suma total de cuadrados de las coordenadas de forma; **Resd. SS**, squared sums of shape coordinates not explained by size/ suma de cuadrados de los residuos de las coordenadas de forma no explicadas por el tamaño; **% Pred.**, percent of shape variance explained by size (equivalent to R<sup>2</sup>)/ porcentaje de la varianza de forma explicada por el tamaño (equivalente a R<sup>2</sup>); **p-value**, probability of independence between variables after 10000 rounds of permutation test/ probabilidad de independencia entre las variables después de 10000 repeticiones de la prueba de permutación; **ns**, not significant/ no significativa.

parallel to PC1. In contrast, *Theosodon* specimens are arranged in the upper left side of the second quadrant. Considering the set of all the Litopterna, Astrapotheria, and Nesodontinae, there is an oblique cloud of points from *Theosodon* at the upper left to *Nesodon* in the lower right (Fig. 9). On this line, the transformation goes from a slender jaw in *Theosodon* to a more robust jaw in *Nesodon* (Fig. 9). The shape variation associated with this diagonal point cloud is close similar to that described for the whole sample.

## DISCUSSION

Phylogenetic signal was found in almost all the morphogeometric analyses performed here. Similar results were recorded in previous studies focused on other mammalian groups (Bogdanowicz *et al.*, 2005; Cardini and Elton, 2008; Barčiová, 2009). Unlike classical morphometrics, the results obtained here indicate a significant correlation between Procrustes and phylogenetic distances. Furthermore, PC scores retain phylogenetic information with no prevalence of particular node (see below).

Size is one of the most important aspects of biology because it is highly correlated with various aspects of life (Brown and West, 2000). Centroid size shows a consistent relationship with body mass (Hood, 2000; Ercoli and Prevosti, 2011; Meloro and O’Higgins, 2012; Cassini *et al.*, 2012b). The results here demonstrate that size and shape are constrained by the phylogenetic history, even when evaluated at different levels of the taxonomic hierarchy. A different opinion was suggested by Smith *et al.* (2004), who concluded that the evolutionary diversification of size in terrestrial mammals over space and time cannot be explained solely by phylogeny.

Particularly among ungulates, several authors have found a link between food and habitat choice with body size (Hofmann, 1989; Pérez-Barbería and Gordon, 2001; Pérez-Barbería *et al.*, 2001). The results obtained here for the whole sample indicate that after removing the effects of phylogenetic autocorrelation, ungulate taxa of mixed and open habitats tend to be larger than those dwelling in closed habitats. However, these relationships disappear when the analysis is repeated at the order and family levels, except for artiodactyls and cervids. Grazers also tend to be larger than browsers and frugivores in the whole sample as well as in the artiodactyl and bovid subsamples. These results agree with the conclusions of Bro-Jørgensen (2008) on bovines and Jarman’s (1974) idea that a browsing diet was associated with small body size. The shape variation difference



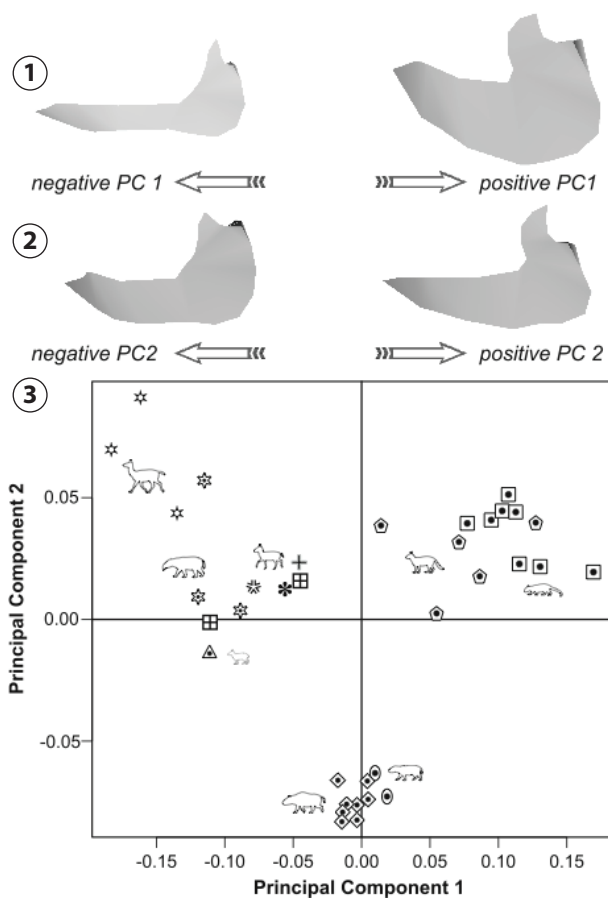
between large open habitat grazers and small closed habitat browsers can be partially explained by allometric scaling, but explains a low proportion of the total variance. Given that bovids are the most diverse and abundant group among artiodactyls and that they account for most of diversity in our sample, they may have biased the results of the whole sample. As found in extant ungulates, habitat and diet are correlated (Pérez-Barbería *et al.*, 2001). The habitat trend could be modeled by the correspondence between grazing and dwelling in open and mixed habitats. Therefore, it should be expected that among Santacrucian ungulates, the small typotheres and proterotheriids were closed habitat browsers, *Adinotherium* and macraucheniids mixed feeders, and the large *Nesodon* and *Astrapotherium* open habitat grazers. However, this scheme fits only partially with other recent ecomorphologic and biomechanic feeding characterizations of the same assemblage (Cassini and Vizcaíno, 2012; Cassini *et al.*, 2011, 2012a). The cranial PCA helped to identify the variation in shape due to lithostatic load deformation. The main effects are the loss of bilateral symmetry, the flattening of the zygomatic arch and shear lateral compression (supplementary material 5.2). The effect of lithostatic load deformation is more evident in morphogeometric than in classical morphometric methods. However, shape variation due to deformation was found in PC7, which accounts only 3% of the total variation. Therefore, the deformation recorded after the selection of the specimens does not affect the results of the analyses that included the skull shape.

The PCA of the cranium does not allow a clear interpretation of the morphological patterns related to diet or environment type. As indicated by the angular and Procrustes rotation analyses, the separate analyses of the different habitat subsets (close, mixed, and open) resulted in a clear rotated sub-morphospace from the whole sample, which does not reflect a pattern of morphological change related to diet. Even more, the orthonormal variance decomposition analysis reveals that the cranial morphospaces reflect phylogenetic patterns. Several studies have reported that morphogeometrical cranial data retain phylogenetic information, and it was possible to reconstruct phylogenetic relationships consistent with molecular hypothesis (Polly, 2003; Bogdanowicz *et al.*, 2005; Caumul and Polly, 2005; Cardini and Elton, 2008; Barčiová, 2009; González-José *et al.*, 2008).

The Santacrucian ungulates occupy a cranial morphospace distant from extant cattle, deer, and horses (supplementary material 3) and closer to macropodids, hyraxes, ceratomorpha, and camels, with which they share a large tempora-

lis fossa and relatively short rostrum. These groupings partly match the classical works that proposed analogies of the Santacrucian ungulates with extant forms: *e.g.*, the interatheriids *Interatherium* and *Protypotherium* with hyraxes (Ameghino, 1898; Sinclair, 1909); the macraucheniid *Theosodon* with American camelids (Scott, 1910, 1937a) and *Astrapotherium* with tapirs (Scott, 1928, 1937b).

The cranial shape variation of Santacrucian ungulates allows recognizing two basic size related models. The smaller forms (*i.e.*, typotheres) are characterized by a low skull with the craniomandibular joint close to the occlusal plane and the orbit on the dorsal margin of the skull, whereas the larger forms (*i.e.*, nesodontines, litopterns, and astrapotheres) are characterized



**Figure 9.** Mandibular PCA of Santacrucian ungulate specimens/ PCA de la mandíbula de los especímenes de ungulados santacrucenses. (1) shape (lateral norm) of extreme negative and positive first component/ Formas del extremo negativo y positivo (vista lateral) del primer componente; (2) shape (lateral norm) of extreme negative and positive second component/ Formas del extremo negativo y positivo (vista lateral) del segundo componente; (3) Taxa are distributed in the morphospace defined by the two first PCs/ Distribución de los taxones en el morfoespacio definido por los dos primeros componentes. Referencia/ Símbolos: Astrapotheria: ☆, *Astrapotherium*; Litopterna: +, *Anisolophus*; □, *Diadiaphorus*; ✱, *Tetramerorhinus*; ✱, *Thoatherium*; ☆, *Theosodon*; Notoungulata: □, *Interatherium*; ◇, *Nesodon*; ○, *Protypotherium*; ○, *Adinotherium*; △, *Pachyrukhos*.

by high, laterally compressed skull with ventrally displaced orbits. Except for some similarities with macropods and hyraxes, the shape associated with the small tyotheres is more similar to caviomorph rodents and leporids than to artiodactyls and/or perissodactyls ungulates (Cassini *et al.*, 2011). Litopterns and *Astrapotherium* also show retraction of the nares. Among litopterns, the proterotheriid *Diadiaphorus* shows greater retraction of the nares than *Tetramerorhinus*, while *Astrapotherium* has the largest retraction of the nares among Santacrucian ungulates (supplementary material 10). The retraction of the nares is related to shape changes in other regions of the skull, such as deeper frontal fossa, the craniomandibular joint closer to the occlusal plane of the teeth, elevation of mesial rim of M3 alveolus, and caudal projection of sagittal and nuchal crests. The retraction of the nares has been associated with the presence of a proboscis as in the tapir (Witmer *et al.*, 1999), the saiga antelope (Clifford and Witmer, 2004a), and dik-diks (*Madoqua Ogilby*, 1836) (Frey and Hofmann, 1997) and has been proposed for *Astrapotherium* (Riggs, 1935). However, not all ungulates that have retracted nares have a proboscis (Clifford and Witmer, 2004b); for example, the long snout of moose (*Alces Gray*, 1821) has a moderated nasal retraction but an exaggerated extension of the premaxilla. Although the shape change in the morphospaces of the Santacrucian ungulates could be consistent with the presence of a proboscis or another muzzle specialization, a reconstruction of the soft tissues of the rostrum is needed to properly test this hypothesis.

In this contribution, mandible landmark configurations also showed significant phylogenetic signal but, unlike the cranium, the mandibular PCA was ecologically informative and permitting identifying shape gradients among diet-habitat category complexes. The orthonormal variance decomposition analyses indicate that not all PCs shared the same phylogenetic signal. In addition, after controlling for phylogenetic autocorrelation, the mandibular PC-scores retain ecological information. Results were similar between the PCA and CVA analyses. Vizcaíno and Bargo (1998), and Bargo and Vizcaíno (2008) also suggested that the mandible reflects masticatory function better than the cranium, which has experienced different selective pressures. In this context, Caumul and Polly (2005), and Cardini and Elton (2008) found that the cranium (especially the braincase) and the teeth are the best predictors of phylogenetic relationships, while the jaws show mixed effects.

The shape variation of the mandible explained by allometric scaling was lower than in the cranial analyses, but the transformations were shared by the first eigenvector of the PCA analysis. The variance explained in the first component (55%) is much higher than in the analysis of the skull, in which PC1 and PC2 together account for only 45% of the total variance. This indicates that the transformation of shape in PC1, given by a very slender jaw on the negative side and a more robust jaw towards positive values, is the most evident pattern. The taxa with slender

**TABLE 8 - Principal component analysis of the mandible for the total sample. Phylogenetic signal and phylogenetically controlled test by habitat and diet categories/ Análisis de componentes principales de la mandíbula de la muestra completa. Pruebas de señal filogenética y de diferencias entre categorías de hábitat y dieta con control filogenético.**

PC	Eigenvalues	% Var.	R2Max	SkR2k	Dmax	SCE	GEE Habitat	GEE Diet
PC1	0.0127	56.6	0.162	56.357	0.210	2.892	8.932	23.036
PC2	0.0020	9.02	0.129	55.236	0.255	3.336	75.375	91.585
PC3	0.00175	7.78	<b>0.066 *</b>	58.014	0.212	2.535	52.741	29.408
PC4	0.00127	5.66	0.134 *	76.618 *	0.118 *	0.449 *	2.132 *	60.117
PC5	0.000805	3.58	0.118	51.950	0.311	4.484	97.071	118.677
PC6	0.000565	2.51	<b>0.132 *</b>	61.171	<b>0.20 *2</b>	1.962	<b>3.209 *</b>	67.407

**PC**, principal components/ componentes principales; **% Var.**, percent of variance explained by each PC/ porcentaje de varianza explicada por cada PC; **R2Max**, Ortonormal max squared coefficients/ Coeficientes ortonormales cuadrados máximo; **SkR2k**, variance distribution of ortonormal squared coefficients/ distribución de la varianza de los coeficientes ortonormales cuadrados; **Dmax**, max cumulative orthogram/ ortograma acumulado máximo; **SCE**, average local variation of the orthogram/ variación local promedio del ortograma; **GEE Habitat**, Generalized Estimating Equations F-test for habitat categories with (2, 17.66) degrees of freedom/ pruebas F de ecuaciones de estimación generalizadas por categorías de hábitat con (2, 17.66) grados de libertad; **GEE Diet**, Generalized Estimating Equations F-test for Diet categories with (4, 15.66) degrees of freedom/ pruebas F de ecuaciones de estimación generalizadas por categorías de dieta con (4, 15.66) grados de libertad.

All tests (ortonormal variance decomposition, and GEE F-test) were significant at 0.05 level except those tagged by and asterisk and bold faced/ Todos las pruebas (Descomposición ortonormal de la varianza, y pruebas F de GEE) resultaron significativas con un alfa de 0.05 con excepción de aquellas señalados por un asterisco y en negritas.

jaws have incisiform canines (bovids), while herbivorous taxa with well-developed canines or hypertrophied incisors (hippos, hyraxes, notoungulates) have more robust jaws like the omnivores (Suidae). This pattern was also described by De Esteban-Trivigno (2011), who analyzed bidimensional mandible shape of three broad diet categories (omnivores, insectivores, and herbivores) in a broad taxonomic sample (*i.e.*, artiodactyls, perissodactyls, carnivores, and xenarthrans). Here, a more complex morphology was found that involves a laterally expanded and horizontally directed symphysis, which is also related to the hypsodonty index within these two broad morphologies (slender and robust jawed taxa). For example, among taxa with slender mandible, the brachydont species have more elongated and narrow symphysis and low mandibular corpus, like the huemul (*Hippocamelus* Leuckart, 1816), a closed habitat browser, in accordance with the observations of Fraser and Theodor (2011b) for ruminants. At the opposite end of this spectrum, hypsodont species have a short symphysis and high and curved mandibular corpus, like the vicuña (*Vicugna*), a mixed feeder in open habitats (Fig. 7). The same morphological pattern is repeated on the robust mandible forms. The brachydont species of closed habitats are represented mainly by omnivores like the peccary (*Pecari* Reichenbach, 1835). The open habitat species are mainly grazing forms like the hippo (*Hippopotamus*) and the hyrax (*Procavia*). This pattern suggests an association “gradient” between mandibular shape and foraging, from dense to more open habitats. Vrba (1980) postulated that the most hypsodont forms have deep jaws to provide more space to accommodate high crowned teeth. This is also shown in our GAM of PC2 with HI (Fig. 8). Santacrucian ungulates are oriented in a similar pattern but are grouped with existing forms that have hypertrophied canines. Many of the Santacrucian forms have hypertrophied tusk-like teeth, as the canines in *Astrapotherium* and the lateral incisors in the nesodontines *Nesodon* and *Adinotherium*. In proterotheriids tusks are either more (*Diadiaphorus*) or less (*Thoatherium*) developed according to body size. These parallelisms between forms with gracile and more robust mandibles (“omnivore-like” mandible *sensu* De Esteban-Trivigno, 2011) allow to test some recently postulated ecomorphological hypotheses on the Santacrucian ungulates (Townsend and Croft, 2008; Cassini *et al.*, 2011, 2012a, b, c). Among Notoungulata, tyotheres were classified as grazers and selective feeders, based on their body mass. In this study, the interatheriids, particularly *Protyotherium*, show convergences with the

grazing hyrax *Procavia* while *Interatherium* exaggerates the traits associated with an open habitat hypsodont mandible (Fig. 7 and 8), pointed out through a classical morphological approach by Cassini *et al.* (2011). In the opposite morphological type, hegetotheriids (rodent-like tyotheres) have a mixed feeder camelid-like mandibular shape, and as Cassini and Vizcaíno (2012) stated, *Pachyrhokos* has the typical herbivore biomechanical configuration (*i.e.*, a masticatory system with predominance of the masseter over the temporalis). Concerning *Hegetotherium*, McCoy and Norris (2012) postulated that its skull characters match those of mammalian woodpeckers, which feed by boring through wood to reveal grubs. The results obtained here cannot refute either support this hypothesis. Among toxodontids, Townsend and Croft (2008) proposed that *Nesodon* and *Adinotherium* were leaf browsers, but later Cassini *et al.* (2011) suggested a mixed and grazer feeding behavior for these taxa, respectively. Both taxa plot within interatheriids and litopterns. In this study, both toxodontids could be characterized as mixed feeders, with *Nesodon* in mixed habitats and *Adinotherium* in more open habitats. The latter result is consistent with the proposal of Cassini *et al.* (2012b).

Among litopterns, proterotheriids were likely browsers in closed habitats. The shape gradients on the mandibular analyses and the cranial shape change associated with retracted nares and muzzle specialization in cranial landmarks (supplementary material 10) suggest that the smaller forms *Thoatherium* and *Anisolophus* browsed in more mixed habitats. Based on postcranial indices, Cassini *et al.* (2012a) stated that *Thoatherium* was the most gracile and would have had better capabilities for fast locomotor activities, like running, than other proterotheriids (see also Soria, 2001). This is in accordance with the idea of being a mixed habitat dweller.

The macraucheniid *Theosodon* would have inhabited mainly closed habitats and had more browsing habits. In fact, it had the most closed-habitat browser-like mandible shape and, following Cassini and Vizcaíno (2012), the most biomechanically gracile mandible among the Santacrucian ungulate assemblage.

*Astrapotherium* had a peculiar morphology among the Santacrucian ungulates. It shows morphological traits consistent with the presence of a proboscis or another muzzle specialization and a mandibular configuration associated to well-developed tusks. It has been considered inhabitant of riparian or meadow habitats who fed upon vegetation

with a high water content (Riggs, 1935; Scott, 1937b). Although Cassini *et al.* (2012b) pointed out that given its large body size *Astrapotherium* would be expected to be a grass bulk feeder, Cassini *et al.* (2012a) and Cassini and Vizcaíno (2012) characterized *Astrapotherium* as a browser or mixed feeder in closed habitats. Both cranial and mandibular results suggest that it was a browser in closed habitats and a selective feeder.

### ***Integrated paleoecology of Santacrucian ungulates***

The Santacrucian flora is characterized by the presence of herbaceous components (chlorioid, panicoid, danthonioid, pooid, and festucoid grasses) and arboreal elements (Araucariaceae, Lauraceae, Arecaceae, Nothofagaceae, Myrtaceae, Cunoniaceae, and Fabaceae) showing a mixture of habitats (Brea *et al.*, 2012). The coexistence of many herbivores in a living assemblage implies partitioning of vegetation as a food source (Hirst, 1975). In this context, the interpretations of the paleobiology of the native ungulates of the Santa Cruz Formation proposed in this study, together with the recent studies, support the hypothesis of Vizcaíno *et al.* (2010, p. 517): “the coexistence of many ungulates from different lineages implies marked vegetation resource partitioning that can be deduced from the interpretation of craniodental morphology”. The environments and dietary preferences of the Santacrucian ungulate assemblage includes grazers in open habitats (*Protypotherium*), browsers and mixed feeders foraging in mixed habitats (*Thoatherium* and Nesodontinae, respectively), and browsers in closed environments (large Proterotheriidae, Astrapotheria).

Although the Santa Cruz Formation spans between 19 and 14 Ma (Fleagle *et al.*, 2012; Perkins *et al.*, 2012), all the genera (except *Pachyrhukhos*) considered in this study have been recorded in a constrained set of localities (FL 1–7; Fig. 2) of the lower part of the Santa Cruz Formation in the Atlantic coast, representing a very narrow temporal window (-17.4 to 17.5 Ma; Fleagle *et al.*, 2012; Perkins *et al.*, 2012), which permits paleoecological integration. Due to its limited geographic and temporal range, Kay *et al.* (2012) considered the fauna recorded in FL 1–7 analogous to a single modern fauna developed in a forested area (similar to those existing today in the Patagonian Andes and the piedmont) that coexisted with grasslands and permanent and temporary water bodies. The habitat and dietary interpretations presented here together with other biological traits indicate that the Santacrucian ungulates would have fitted well with the environmental reconstruction proposed by Kay *et al.* (2012).

## **CONCLUSIONS**

Niche partitioning among the Santacrucian ungulates was based on the differential use of open, mixed, and closed areas, as well as in the differentiation of dietary resources mainly reflected in two biological attributes: (1) body size, and (2) form and function of the craniodental traits.

The open habitat ungulates include small forms feeding predominantly on grass (*Protypotherium*, *Interatherium*: Typotheria, Interatheriidae), and small forms (*Hegetotherium* and *Pachyrhukhos*: Typotheria, Hegetotheriidae) and medium size forms (*Adinotherium*: Toxodontia) feeding on grass and leaves depending on their availability. The mixed habitat ungulates include medium size forms feeding predominantly on dicotyledoneous plants (*Anisolophus* and *Thoatherium*: Litopterna, Proterotheriidae) and large forms feeding on grass and leaves, depending on their availability (*Nesodon*: Toxodontia). The closed habitat ungulates include medium size forms (*Tetramerorhinus* and *Diadiaphorus*: Litopterna, Proterotheriidae) and large size forms (*Theosodon*: Litopterna, Macraucheniiidae and *Astrapotherium*: Astrapotheria) all feeding predominantly on dicotyledoneous plants.

Santacrucian ungulates are morphologically distant from extant herbivorous equids and bovids. They shared more morphological similarities with hyraxes, macropods, ceratomorphans (tapirs and rhinos), llamas, and suids. The mandible reflects masticatory function better than the skull, although they all show a robust suid-like shape, which is due to putative constraints on overall shape because of the well-developed canines or incisors.

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**Appendix I.** List of Santacrucian ungulate skulls examined in this work including taxonomic identifications and collection numbers.

**Notoungulata.** Toxodontia (Toxodontidae): *Adinotherium* AMNH 9141, 9571, 9532; MACN-SC 4355; MACN-A 923, 926, 5346; MLP 12-5, 84-III-9-10; MPM-PV 3476, 3666, 3667; YPM-VPPU 15118, 15382. *Nesodon* AMNH 9192, 9510. MACN-A 775, 5145; MLP 12-250; YPM-VPPU 15000, 15252, 15256, 15260, 15336, 15492. Typotheria, Interatheriidae: *Interatherium* AMNH 9299, 9483; MPM-PV 3469, 3471, 3527, 3528; YPM-VPPU

-1502, 15043, 15100, 15296, 15300, 15554. *Protypotherium* AMNH 9226, 9260, 9286, 9482, 9534, 9565; MPM-PV 3470, 3959; MACN-A 3882; YPM-VPPU 15189, 15195, 15650, 15665, 15828. Hegetotheriidae: *Hegetotherium* AMNH 9159; MPM-PV 3526; YPM-VPPU 15542. *Pachyrhinos* AMNH 9219, 9283.

**Litopterna.** Proterotheriidae: *Anisolophus* YPM-VPPU 15996. *Diadiaphorus* AMNH 9196, 9270, 9291; MPM-PV 3397; MACN-A 9200-9208. *Tetramerorhinus* MACN-A 5971, 8666, 8970-71. *Thoatherium* AMNH 9245; YPM-VPPU 15719. Macrauchiidae: *Theosodon* MACN-A 2487-90, 9297; YPM-VPPU 15164.

**Astrapotheria.** Astrapotheriidae: *Astrapotherium* AMNH 9278; YPM-VPPU 15142, 15332, 15261.

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