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The armadillos (Mammalia, Xenarthra, Dasypodidae) of the Santa Cruz Formation (early–middle Miocene): An approach to their paleobiology

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Abstract

The Santacrucian (early–middle Miocene) fauna is exceptional in its richness (over 70 species recorded in 21 stratigraphic levels). In this contribution we attempt a preliminary paleobiological characterization of the armadillos (Dasypodidae and Peltephilidae). Santacrucian Dasypodidae includes the genera *Prozaedyus* Ameghino, *Proeutatus* Ameghino, *Stenotatus* Ameghino, and *Stegotherium* Ameghino. The Peltephilidae include the genus *Peltephilus* Ameghino and others undergoing systematic revision. Body masses and locomotory habits are inferred from the sizes of the proximal and middle shaft dimensions of the limb bones from allometric equations and indices previously modeled in living dasypodids. Masticatory and dietary interpretations are based on the jaw mechanics, the analysis of the temporomandibular joint and mandibular symphysis, and the shape, arrangement and wear patterns of teeth. The body mass averages are 15.28 kg for *Proeutatus*, 3.72 kg for *Stenotatus*, 1.12 kg for *Prozaedyus*, 11.47 for *Stegotherium*, and 11.07 kg for *Peltephilus*. The diversity in limb bone proportions is not so marked as in the living species; forelimb indices reflect proportions similar to those of the living dasypodines and euphractines, all of whom are relatively good diggers. None of the Santacrucian taxa reach the degree of cursoriality of *Tolypeutes* Illiger, the extreme fossoriality of *Priodontes* F. Cuvier, or the subterranean habits of *Chlamyphorus* Harlan. Within a potentially generalized omnivory, some specializations can be easily detected within the Santacrucian armadillos: herbivory in *Proeutatus* and *Peltephilus*, and myrmecophagy in *Stegotherium*. This could help to explain the potential coexistence of so many genera in a single area, diminishing the degree of competition for resources.

Keywords: Xenarthra; Armadillos; Santa Cruz Formation; Miocene; Paleobiology

1. Introduction

The Santa Cruz Formation (early–middle Miocene) along the Atlantic coast of southernmost continental Patagonia, Argentina, between the rivers Coyle and Gallegos, bears a fauna exceptional in its richness (over 70 species from 23 stratigraphic levels have

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been recorded in this region, Tauber, 1997a,b, 1999) that document an assemblage very different from the any other living mammalian community. These localities are situated at about 52° South latitude, barely 100 km from the Magallanes Strait (Fig. 1). The fieldwork performed by members of our group confirms Hatcher's impressions of more than 100 years ago: especially at the site of Corriguen Aike (Puesto Estancia La Costa), this is the richest assemblage of pre-Pleistocene mammalian skulls and articulated skeletons (Fig. 2) known in the continent (Hatcher, 1903).

A British sea captain Bartholomew Sulivan collected the first fossils coming from the region, and sent them to Charles Darwin (Brinkman, 2003). Larger scale collecting of Santacrucian fossils began in the late 19th Century through the efforts of Carlos Ameghino (collections in Museo de La Plata and Museo Argentino de Ciencias Naturales of Buenos Aires) and, later, John Bell Hatcher (collections at the Yale Peabody Museum–formerly at Princeton University–and American Museum of Natural History). Subsequently, a number of other expeditions of limited duration were undertaken with collections residing in the Field Museum, Chicago (Riggs collection) and University of Kansas Museum (H. T. Martin collection). For a review of this history refer to Marshall (1976) and Simpson (1984). From the late 1980s, Tauber (1997a,b) surveyed the geology of the Santa Cruz Formation south of Coy Inlet, reidentified the most productive fossil sites and levels and made important collections (mostly housed at the University of Córdoba, Argentina). Other researchers (e.g. Fleagle) made extensive collections of Santa Cruz Formation mammals further north in Santa Cruz Province but did not collect south of Coy Inlet.

The above features offer an unusual window for reconstructing the community structure of a South American mammalian community using an ecomorphological approach, of the sort attempted by R. Kay and R. H. Madden at La Venta (middle Miocene, Colombia; Kay and Madden, 1997a,b) based on precise or detailed functional analysis in a well defined phylogenetic framework. This is one of the major objectives of an

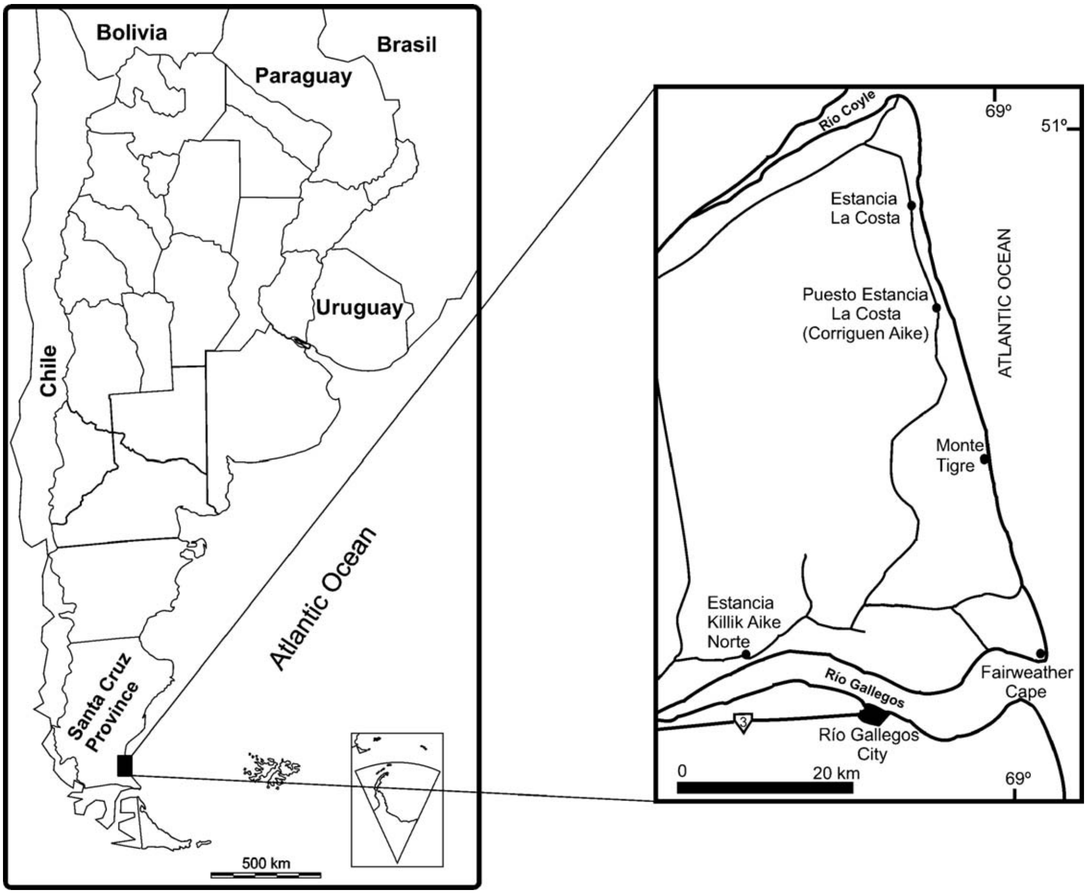

Fig. 1. Geographic location of the area of study in the coast of Santa Cruz Province, Argentina.

Fig. 2. An almost complete specimen of *Prozaedyus* sp. collected in Corriguen Aike during the 2005 field season.

ongoing program of field collecting that begun in 2002, with precise stratigraphic and geographic control. As a first step in a plan to examine the autecology of the fauna as a whole, we attempt a preliminary paleobiological characterization of the armadillos, one of the most common elements of that fauna. Following the classificatory scheme of McKenna and Bell (1997), armadillos comprise the typical armadillos (Dasypodidae), including about 25 species of fossil and living armadillos (Wetzel, 1985), and the horned peltephilines (Peltephilidae). Within Dasypodidae, McKenna and Bell include Dasypodinae (Dasypodini and Stegotheriini), Euphractinae (Euphractini, Eutatini, Utaetini and Chlamyphorini) and Tolypeutinae (Tolypeutini and Priodontini).

The Santacrucian armadillos include the dasypodid genera *Prozaedyus* Ameghino (Euphractinae, Euphractini), *Proeutatus* Ameghino and *Stenotatus* Ameghino (Euphractinae, Eutatini) and *Stegotherium* Ameghino (Dasypodinae, Stegotheriini), and the Peltephilidae *Peltephilus* Ameghino. Although these genera are well established and accepted taxa, there are the others such as *Paraeutatus* Scott (Eutatini), *Anantiosodon* Ameghino and *Peltecoelus* (Moreno and Mercerat) (Peltephilidae), of which an approximate total of 17 species have been described (see Scillato-Yané, 1980), but are in need of adequate systematic revisions (some of them were described only from scutes and others are lost).

Most living armadillos are specialized diggers and their limbs are well designed for that activity, including big claws and large tuberosities for strong muscular insertions, and long lever arms for the line of action of the principal muscles. The masticatory apparatus of the armadillos is very peculiar and its adaptive interpretation presents an interesting challenge due to their strong phylogenetic constraints (Vizcaíno and De Iuliis, 2003). The dentition, as among all other xenarthrans, is greatly simplified. Armadillos (except for the peculiar living *Priodontes maximus* Kerr) usually have nine or ten rather small teeth in each jaw quadrant. Enamel is absent in the adult and all extant (except *Dasypus* species) and possibly all extinct xenarthrans lack deciduous teeth. The cuspal patterns present in other mammals are also absent. The teeth, composed of osteodentine, are always hypselodont. They may be lobate, but are usually simple and separated by short diastemata. These peculiarities of the dentition must have imposed severe functional and biomechanical constraints as lineages adapted to different diets. Although living armadillos are mainly carnivorous or omnivorous (see Redford, 1985), the fossils developed a variety of dietary habits, including herbivory (see Vizcaíno et al., 2004 and references therein).

In recent years there have been an increasing number of morphofunctional and biomechanical studies of armadillos and other xenarthrans that provide the basis for understanding armadillo paleobiology (for a compilation see Bargo, 2003 and references therein). Many of these studies have provided new insights on long accepted hypotheses, and generated conclusions on the assessment of bite forces and, hence, dietary preferences. Paleoenvironmental data (geology, paleoclimatology and paleovegetation) are now better documented and provide a paleoecological context.

2. Geologic background

The Santa Cruz Formation is developed over much of the south of Patagonian Argentina both in surface exposures (along the Atlantic coast and in adjacent estuaries) (Bown and Fleagle, 1993; Tauber, 1997a) and in drill logs (Malumián, 1999). Coastal Santa Cruz rocks are a sequence of superimposed mudstones of volcanoclastic origin containing immature paleosols laid down on a coastal plain with sand bodies (with some pebbles) representing river channels. Some relatively unaltered tuffs also occur (Bown and Fleagle, 1993). A description of typical coastal Santa Cruz lithology at Monte León and Monte Observación, north of Río Coyle, is presented by Bown and Fleagle (1993).

The lithology of the coastal Santa Cruz Formation south of Río Coyle and north of Río Gallegos (at Estancia La Costa, Puesto Estancia La Costa (Corriguen Aike), Monte Tigre and other coastal sites) is slightly more complicated than that at Monte Observación. Tauber (1997a, 1999) recognizes two members, a lower very fossiliferous Estancia La Costa Member, with predominance of pyroclastic deposits, claystones and mudstones, and an upper Estancia Angelina Member, with very few fossils, chiefly composed of claystones, mudstones and sandstones (Fig. 3). The author also recognized 19 fossiliferous levels containing vertebrate remains that allowed proposing a biostratigraphic scheme, recognizing preliminary two Interval Biozones. The lithology and fossil content of the Estancia La Costa Member is most similar to that of the Santacrucian rocks at Monte Observación (Tauber, 1997a,b). Recently, Tauber has extended his geologic observations to the important site of Killik Aike Norte along the estuary of Río Gallegos, which is believed also to represent the lower Estancia La Costa Member (Tauber et al., 2004a).

At Monte Observación and Monte León, several $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ dates and a short magnetostratigraphic section provide a basis of determining the age of the Santa Cruz Formation. Santa Cruz Formation dates range between 16.42 Ma and 16.18 Ma from three levels in the lower one-third of the fossiliferous levels at Monte Observación and between 16.56 Ma and 16.28 Ma at Monte León. The dates are not wholly concordant but permit the assignment of bulk of the coastal Santacrucian faunas to a late early Miocene. Fleagle et al. (1995) report a magnetostratigraphy of Santa Cruz rocks that begins with a reversed interval, followed by a normal and a reversed interval at the top, consistent with a relatively short temporal interval obtained from the radiometric dates.

The beds below and above the Santa Cruz Formation are consistent with a late early Miocene age. The nearshore marine Monte León Formation underlies the Santa Cruz Formation. It has surface exposure at Monte León and in subsurface drill cores north and south of Río Coyle (Bown and Fleagle, 1993; Malumián, 1999). The Monte León Formation may be conformable and regressional with respect to the coastal Santa Cruz Formation (Bown and Fleagle, 1993; Malumián, 1999). An ash in the Monte León Formation yielded a date of 19.33 Ma (Fleagle et al., 1995). This is consistent with an early Miocene age of the molluscan assemblage from that formation (del Río, 2004). Southward towards Cabo Buen Tiempo at the mouth of the estuary of Río Gallegos, the Santa Cruz Formation is capped by the marine Fairweather Formation of Pliocene age.

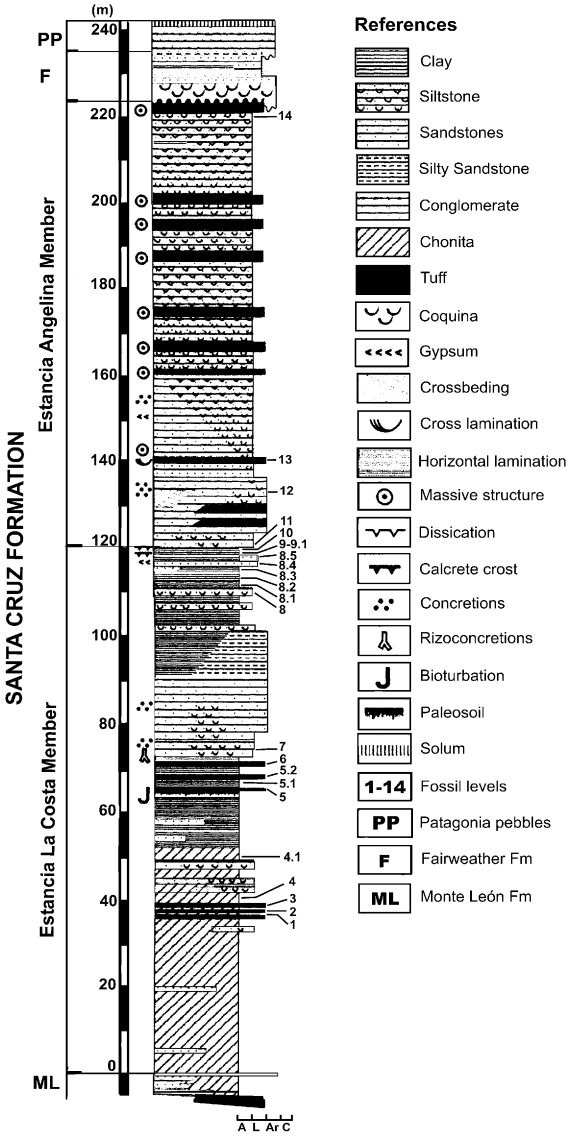

Fig. 3. Stratigraphic column of the Santa Cruz Formation (modified from Tauber, 1997a, 1999).

3. Material and methods

3.1. Acronyms

FMNH — Field Museum of Natural History, Chicago, USA
MACN — Museo Argentino de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina
MLP — Museo de La Plata, La Plata, Argentina
MPM-PV — Museo Regional Provincial Padre Manuel Jesús Molina, Rio Gallegos, Argentina
YPM — Yale Peabody Museum, New Haven, Connecticut, USA.

3.2. Materials

FMNH P 13197. *Proeutatus oenophorus*. Santa Cruz Formation. La Angelina Ranch (12 miles N of Cape Fairweather), Santa Cruz, Argentina.

MACN A-1063 *Proeutatus* sp. Santa Cruz Formation. Santa Cruz, Argentina. C. Ameghino.

MACN A-7958/59. *Anantiosodon nanus* Type. Santa Cruz Formation. La Cueva, Santa Cruz, Argentina. C. Ameghino.

MACN A-7910/40. *Peltephilus ferox*. Santa Cruz, Argentina. C. Ameghino.

MLP 69-IX-8-11. *Proeutatus* sp. Santacrucian, Santa Cruz, Argentina.

MLP 69-IX-5-1. *Stenotatus* sp. Santacrucian. Santa Cruz, Argentina.

MPM-PV 3506. *Prozaedyus* sp. Santa Cruz Formation. Corriguen Aike, Santa Cruz, Argentina.

YPM PU 15214. *Proeutatus robustus*. Type. Santa Cruz Formation (Miocene). 10 miles S. of Coy Inlet Santa Cruz, Argentina. J.B. Hatcher, Princeton University Expedition (1896).

YPM PU 15389. *P. robustus*. Santa Cruz Formation (Miocene). Cape Fairweather Santa Cruz, Argentina. J.B. Hatcher, Princeton University Expedition (1896).

YPM PU 15957. *P. robustus*. Santa Cruz Formation (Miocene). 10 miles S of Coy Inlet Santa Cruz, Argentina. O.A. Peterson.

YPM PU 15613. *Proeutatus lagena*. Santa Cruz Formation (Miocene). Near Coy Inlet Santa Cruz, Argentina. O. Peterson, Princeton University Expedition (1896).

YPM PU 15863. *Stenotatus patagonicus*. Santa Cruz Formation (Miocene). Killik Aike, Santa Cruz, Argentina. J.B. Hatcher, Princeton University Expedition (1896).

YPM PU 15579. *Prozaedyus exilis*. Santa Cruz Formation (Miocene). Killik Aike, Santa Cruz, Argentina. J.B. Hatcher, Princeton University Expedition (1896).

YPM PU 15604. *Prozaedyus* sp. Santa Cruz Formation (Miocene). Coy Inlet Santa Cruz, Argentina. J.B. Hatcher and O. Peterson, Princeton University Expedition (1896).

YPM PU 15566. *Stegotherium tessellatum*. Santa Cruz Formation (Miocene). Coy Inlet Santa Cruz, Argentina. J.B. Hatcher, Princeton University Expedition (1896).

YPM PU 15390. *Peltephilus strepens*. Santa Cruz Formation (Miocene). 10 miles S. of Coy Inlet Santa Cruz, Argentina. J.B. Hatcher, Princeton University Expedition (1896).

4. Methods

4.1. Body mass and locomotion

Body masses were estimated based on adult interspecific allometric equations from long bones of living dasypodids (Fariña and Vizcaíno, 1997) (Table 1).

Locomotory habits were characterized based on the morphology and proportions of the bones of the proximal and middle segments of the limbs taking the measurements and calculating the indices defined and used previously by Vizcaíno and Milne (2002) and Vizcaíno et al. (2003). The following measurements were used to calculate the indices: humeral length (HL); proximal humeral length (PH) is the distance from the distal end of the deltoid tuberosity to the proximal end of the humerus; ulnar length (UL); olecranon length (OL) is the distance measured along the long axis of the ulna, from the center of the trochlear notch to the tip of the olecranon process; functional femoral length (FL); proximal femoral length (PF) is the distance from the distal end of the third trochanter to the proximal point of the femoral head; leg length (LL);

Table 1
Allometric equations used for body mass estimations from Fariña and Vizcaíno (1997)

Measurement	Equation
Humeral length (HL)	Log mass = (log HL − 1.5865)/0.3155
Humeral anteroposterior diameter (HD)	Log mass = (log HD − 0.6314)/0.4195
Ulnar length (UL)	Log mass = (log UL − 1.6313)/0.3089
Ulnar anteroposterior diameter (UD)	Log mass = (log UD − 0.7037)/0.374
Femoral length (FL)	Log mass = (log FL − 1.6886)/0.391
Femoral anteroposterior diameter (FD)	Log mass = (log FD − 0.7146)/0.3795
Leg length (LL)	Log mass = (log LL − 1.636)/0.3134

mid-leg width (LW); and the anteroposterior diameters, measured at diaphyseal midshaft (FD, HD and UD) for femur, humerus and ulna respectively. For a description of each measurement see Vizcaíno and Milne (2002) and Vizcaíno et al. (2003).

The calculated indices were the Shoulder Moment Index (SMI); Brachial Index (BI); Index of Fossorial Ability (IFA); Hip Moment Index (HMI); Leg Robusticity Index (LRI); Crural Index (CI); and Intermembral Index (IMI). For a description of the measurement involved in the calculation of each index and their individual functional interpretation see Vizcaíno and Milne (2002) and Vizcaíno et al. (2003).

Principal components analyses applied to the indices were conducted using GenStat (GenStat Release 4.21 Lawes Agricultural Trust—Rothamsted Experimental Station). These analyses were carried out to explore further how the Santacrucian armadillos fit the patterns of structure and function already observed in the limbs of living armadillos by Vizcaíno and Milne (2002).

4.2. Mastication and diet

Masticatory and dietary interpretations were summarized previously using several methods (see Vizcaíno et al., 2004 for a review), principally a geometric model of jaw mechanics. The mandible is viewed as a lever, with its fulcrum at the temporomandibular joint, an input (muscular) force generated by the masticatory musculature, and an output (masticatory) force exerted by the teeth on food. The moment arms of the temporalis and masseter muscles are estimated so that the effective power of each muscle and the corresponding bite force may be estimated. For a complete explanation see Vizcaíno et al. (1998).

Occlusal patterns and mandibular movements were determined through analysis of the craniomandibular joint (including manipulation), the shape and arrangement of teeth (including occlusal wear patterns), and symphysis.

5. Results

5.1. Body size and limb proportions

Measurements of the humerus, ulna, femur and tibia-fibula of the different specimens are provided in Table 2, while Table 3 presents body mass estimations of the specimens obtained using allometric equations from living armadillos (Fariña and Vizcaíno, 1997). The body mass averages for each taxon are 15.28 kg for *Proeutatus*, 3.72 kg for *Stenotatus*, 1.12 kg for *Prozaedyus*, 11.47 kg for *Stegotherium*, and 11.07 kg for *Peltephilus*. The tiny *Anantiosodon nanus* was excluded from every analysis because it is known only for a single, very small femur (body mass average 1.69) and no indices can be calculated. *Peltephilus strepens* (body mass average 6.45) was also excluded from the analyses because it is a very young specimen and the influence of ontogenetic allometry cannot be evaluated. Table 4 shows the indices calculated for 12 specimens belonging to five genera. Only 1 specimen (*Prozaedyus*) is complete enough to provide measurements to calculate all the indices. Table 5 summarizes the indices of the five Santacrucian genera in comparison with those of living armadillos (Vizcaíno and Milne,

Table 2
Limb bone measurements (in mm)

Specimens	Humerus			Ulna			Femur			Tibia	
	HL	PH	HD	UL	OL	UD	FL	PF	FD	LL	LW
Proeutatus sp. MACN A-1063	94.3	44.6	13.7	–	–	–	–	–	–	–	–
Proeutatus sp. MLP 69-IX-8-11	98.5	49.0	15.6	–	–	–	–	–	–	–	–
P. robustus YPM PU 15957	–	–	–	95.5	42.0	–	–	–	–	–	–
P. robustus YPM PU 15214	94.3	52.0	15.9	101	43.5	15.6	–	–	–	–	–
P. robustus YPM PU 15389	–	–	–	–	–	–	110.6	52.7	14.5	83.8	31.5
P. lagena YPM PU 15613	–	–	–	–	–	–	91.6	45.8	12.5	–	–
P. oenophorus FMNH P 13197	93.6	50.1	14.9	–	–	–	109.3	52.6	16.5	100.4	40.1
Stenotatus sp. MLP 69-IX-5-11	–	–	–	–	–	–	–	32.4	8.7	–	–
S. patagonicus YPM PU 15863	54.0	28.7	8.6	60.0	23.0	8.1	–	34.2	–	–	–
Prozaedyus exilis YPM PU 15579	38.0	20.0	6.1	41.4	14.8	5.7	39.0	15.0	4.7	37.0	11.8
Prozaedyus sp. YPM PU 15604	40.0	19.6	6.4	–	–	–	–	–	–	–	–
Stegotherium tessellatum YPM PU 15566	82.5	44.0	13.3	–	–	–	106.0	56.5	11.5	103.0	31.0
Anantiosodon nanus MACN A-7958/59	–	–	–	–	–	–	58.5	23.7	6.5	–	–
Peltephilus ferox MACN A-7910/40	91.0	47.3	10.7	94.4	40.3	13.7	–	–	–	–	–
P. strepens YPM PU 15390	–	–	10.7	87.1	33.0	13.3	81.0	37.6	9.8	–	–

Table 3
Body mass estimations (in kg) using allometric equations of living armadillos (Fariña and Vizcaíno, 1997)

Specimens	Humerus				Ulna				Femur				Tibia	
	HL	Mass	HD	Mass	UL	Mass	UD	Mass	FL	Mass	FD	Mass	LL	Mass
Proeutatus sp. MACN A-1063	94.3	16.97	13.7	16.0	–	–	–	–	–	–	–	–	–	–
Proeutatus sp. MLP 69-IX-8-11	98.5	19.49	15.6	21.82	–	–	–	–	–	–	–	–	–	–
P. robustus YPM PU 15957	–	–	–	–	95.5	13.45	–	–	–	–	–	–	–	–
P. robustus YPM PU 15214	94.3	16.97	15.9	22.84	101.0	16.13	15.6	20.34	–	–	–	–	–	–
P. robustus YPM PU 15389	–	–	–	–	–	–	–	–	110.6	8.1	14.5	15.04	83.8	8.25
P. lagena YPM PU 15613	–	–	–	–	–	–	–	–	91.6	4.99	12.5	10.17	–	–
P. oenophorus FMNH P 13197	93.6	16.57	14.9	19.56	–	–	–	–	109.3	7.85	16.5	21.14	100.4	14.68
Stenotatus sp. MLP 69-IX-5-11	–	–	–	–	–	–	–	–	–	–	8.7	3.91	–	–
S. patagonicus YPM PU 15863	54.0	2.90	8.6	5.28	60.0	2.98	8.1	3.53	–	–	–	–	–	–
Prozaedyus exilis YPM PU 15579	38.0	0.95	–	–	41.4	0.89	–	–	39.0	0.56	–	–	37.0	0.60
Prozaedyus sp. YPM PU 15604	40.0	1.12	6.4	2.61	–	–	–	–	–	–	–	–	–	–
Stegotherium tessellatum YPM PU 15566	82.5	11.11	13.3	14.92	–	–	–	–	106.0	7.26	11.5	8.17	103.0	15.9
Anantiosodon nanus MACN A-7958/59	–	–	–	–	–	–	–	–	58.5	1.58	6.5	1.81	–	–
Peltephilus ferox MACN A-7910/40	91.0	15.16	10.7	8.88	94.4	12.95	13.7	7.30	–	–	–	–	–	–
P. strepens YPM PU 15390	–	–	10.7	8.87	87.1	9.97	13.3	13.28	81.0	3.65	9.8	5.36	–	–

2002). IFA, SMI, HMI and LRI of *Proeutatus* and SMI of *Prozaedyus* represent mean values; all the remaining indices correspond to single specimens. In order to include the remaining genera in the multivariate analysis we have filled in missing data with the averages for each index.

In the forelimb, the highest IFA among Santacrucian taxa is showed by *Proeutatus*, followed by *Peltephilus*, *Prozaedyus* and *Stenotatus*; we do not have actual data for *Stegotherium*. In *Proeutatus*, and *Peltephilus*, the IFA is higher than those of *Tolypeutes matacus*, dasypodines, and euphractines, but lower than priodontines and *Chlamyphorus truncatus*. *Prozaedyus* is close to the average for the euphractines and within the range of dasypodines. In *Stenotatus* the value is within the upper maximum range of *T. matacus*, and lower than the rest of the living forms. Also in the forelimb, SMI of the five Santacrucian genera are within the range of euphractines and dasypodines. The BI could be calculated for *Proeutatus*, *Stenotatus*, *Prozaedyus* and *Peltephilus*. The first three have values within the range of euphractines and dasypodines, while *Peltephilus* has a lower value between the priodontines and *C. truncatus*.

In the hind limb, the HMI values of *Proeutatus*, *Stegotherium* and *Peltephilus* are lower than dasypodines, falling within the range of *T. matacus*, euphractines and priodontines. *Prozaedyus* shows the lowest HMI, close to the lower minimum range of *C. truncatus*. The LRI and CI could be estimated for *Proeutatus*, *Prozaedyus*, and *Stegotherium*. *Proeutatus* has a higher LRI than dasypodines and euphractines and within the

Table 4
Indices calculated from each specimen[a]

Specimens	IFA	SMI	BI	HMI	LRI	CI	IMI
Proeutatus sp. MACN A-1063	–	47.29	–	–	–	–	–
Proeutatus sp. MLP 69-IX-8-11	–	49.74	–	–	–	–	–
P. robustus YPM PU 15957	78.50	–	–	–	–	–	–
P. robustus YPM PU 15214	75.65	55.14	61.0	–	–	–	–
P. robustus YPM PU 15389	–	–	–	47.65	37.59	75.77	–
P. lagena YPM PU 15613	–	–	–	50.0	–	–	–
P. oenophorus FMNH P 13197	–	53.52	–	48.12	39.94	91.77	–
S. patagonicus YPM PU 15863	62.16	53.14	68.51	–	–	–	–
Prozaedyus exilis YPM PU 15579	69.67	52.63	64.21	38.46	31.89	94.87	82.10
Prozaedyus sp. YPM PU 15604	–	49.0	–	–	–	–	–
Stegotherium tessellatum YPM PU 15566	–	53.33	–	53.3	30.1	97.17	–
Peltephilus ferox MACN A-7910/40	74.49	51.97	59.45	–	–	–	–

[a] IFA: index of fossorial ability. SMI: shoulder moment index. BI: brachial index. HMI: hip moment index. LRI: leg robusticity index. CI: crural index. IMI: intermembral index. Indices are described in the text or mentioned in the references.

Table 5
Indices of the Santacrucian genera, in comparison with living armadillos (from Vizcaíno and Milne, 2002), including the code used for interpreting the plots and the means replacing missing data (*)

Taxa	Code	IFA	SMI	BI	HMI	LRI	CI	IMI
Proeutatus	Pro	77.08	50.73	61.0	48.59	38.77	83.77	75.62*
Stenotatus	Ste	62.16	53.14	68.51	47.6*	32.68*	92.37*	75.62*
Prozaedyus	Prz	69.67	50.82	64.21	38.46	31.89	94.87	82.10
Stegotherium	Stg	76.46*	53.33	65.28*	53.3	30.1	97.17	75.62*
Peltephilus	Pel	74.49	51.97	59.45	47.6*	32.68*	92.37*	75.62*
T. matacus	To	58.02 ± 9.16	58.78 ± 1.28	80.17 ± 5.30	46.05 ± 4.11	18.91 ± 6.85	101.5 ± 4.48	68.29 ± 2.32
Dasypodini	Da	66.85 ± 3.11	48.44 ± 1.56	69.29 ± 3.32	54.49 ± 1.52	36.75 ± 0.76	81.93 ± 2.33	70.93 ± 2.33
Euphractini	Eu	69.44 ± 3.61	56.07 ± 0.74	63.21 ± 1.00	50.40 ± 1.06	36.48 ± 1.74	85.48 ± 3.58	84.71 ± 1.91
Priodontini	Pr	92.86 ± 6.04	68.67 ± 3.86	55.92 ± 1.98	51.08 ± ± 6.51	42.35 ± 7.59	81.22 ± 4.01	77.11 ± 9.63
C. truncatus	Ch	112.68 ± 5.99	77.40 ± 0.44	61.54 ± 5.41	42.24 ± ± 4.62	22.13 ± 1.44	105.02 ± 4.20	70.60 ± 0.78

The abbreviations of the indices are the same as in Table 4.

lower range of priodontines; the other two have lower values than dasypodines, euphractines and priodontines, but higher than *T. matacus* and *C. truncatus*. *Prozaedyus*, and *Stegotherium* have higher CI than dasypodines, euphractines and priodontines, but lower than *T. matacus* and *C. truncatus*. *Proeutatus* falls within the range of dasypodines, euphractines and priodontines. The IMI is known only for *Prozaedyus* and is within the range of euphractines and priodontines.

Fig. 4 include plots of the first two principal components resulting from analyses of the data of Santacrucian genera plus the species or tribe means from Vizcaíno and Milne (2002). Data for all indices are available only for *Prozaedyus*, and the resulting plot is very similar to that of the extant armadillos (Fig. 4A). The digging ability (forelimb power) is represented on PC1; the larger species have lower scores on PC2 ($r = -0.76$), reflecting their lower third trochanters are positioned lower on the diaphysis (HMI correlation with body size $r = 0.62$) and more robust leg bones (LRI $r = 0.77$). This analysis indicates that *Prozaedyus* is about as fossorial as *Euphractus*, and more cursorial (or perhaps just smaller than *Dasypus* or *Euphractus*). In order to include the remaining genera in the analysis we have filled in missing data with the averages for each index (Table 5). In this plot (Fig. 4B) the fossil species show artificially low variation due to the use of mean values to replace missing data. However, PC1 still relates to digging ability and PC2 is still correlated with size (correlation of body mass with PC2 = 0.63, with LRI = 0.71, and with HMI = 0.56). Even with the caveats imposed by the missing data, these results mirror the analysis of the indices individually suggesting that all the Santacrucian genera had limb proportions similar to the digging living armadillos, i.e. euphractines and dasypodines. The fact that the forelimb proportions better reflects digging ability (Vizcaíno and Fariña, 1997; Vizcaíno and Milne, 2002) and that we have data for all forelimb indices for *Stenotatus* and *Peltephilus* makes us confident in our hypotheses about these taxa. *Stenotatus* appears to be as good a digger as the dasypodines, probably more cursorial than *Prozaedyus*. *Peltephilus* appears to be a better digger than euphractines, but not as powerful as the priodontines. The same applies to *Proeutatus* and *Stegotherium*, although with a lower degree of confidence.

5.2. Mastication

Vizcaíno and Bargo (1998) analysed the masticatory apparatus of some eutatines including the Santacrucian *Proeutatus* and *Stenotatus* to test the hypothesis of herbivory. The general shape of the mandible and teeth of *Proeutatus*, as well as other eutatines, resembles that of some ungulates. The mandibular condyle is elevated above the tooth row to improve the mechanical advantage of the masseter muscle. The concave to flat morphology of the condyle allows considerable lateral and anteroposterior mandibular movements. The unfused symphysis may be related to transverse chewing movements, produced by the pterygoid muscles, as in artiodactyls as interpreted by Greaves (1978). The teeth of eutatines are better adapted for cutting or shearing than those of living armadillos. They display flat-grinding surfaces in the posterior two thirds of the tooth row. The outer and the inner hard dentine layers, elevated above the level of softer medial dentine, are almost parallel to the long axis of the tooth, which implies a strong lateral component in mastication. The outer layer forms ridges that may have been important in slicing up food.

Vizcaíno and Bargo (1998) note that the masticatory apparatus of *Stenotatus* suggests that it could not bite as

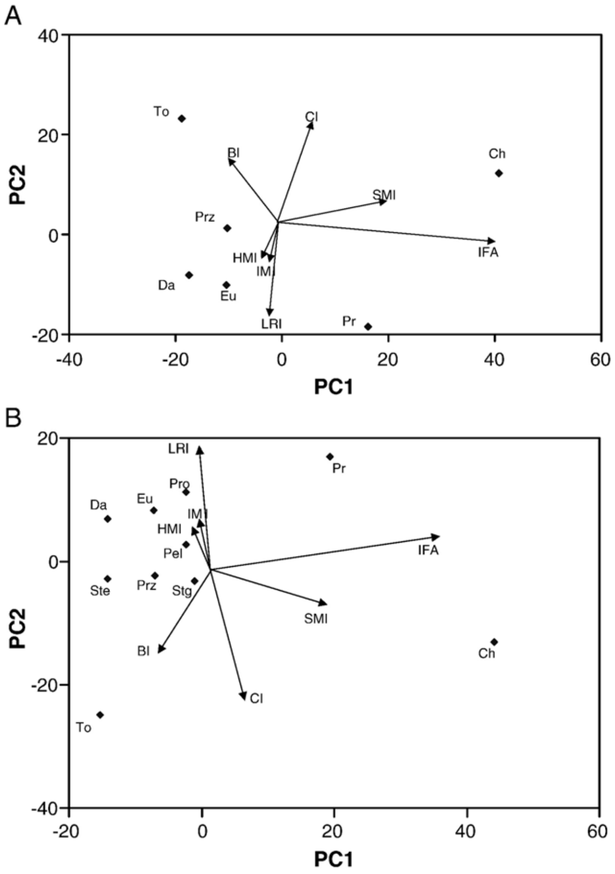

Fig. 4. (A) Bivariate plot of the first and second axes of a Principal Components analysis of armadillo limb structure. Included are extant armadillos and the Santacrucian *Prozaedyus*. PC1 accounts for 63.7% of the variance; PC2 accounts for an added 27.5% of variation. (B) Bivariate plot of the first and second axes of a Principal Components analysis of armadillo limb structure. Included are extant armadillos and all the other Santacrucian taxa mentioned in the text, a result achieved by substituting mean values for missing values. PC1 accounts for 62.2% of the variance; PC2 accounts for an added 25.7% of variation.

powerfully as *Proeutatus* and euphractines of similar size like the hairy armadillo *Chaetophractus villosus* (body mass around 4 kg) (Vizcaíno and Fariña, 1994). The relatively weak masticatory apparatus of *Stenotatus*, and the elongation of the palate and the rostrum suggest some specialization toward insectivory. The teeth are more euphractine-like, i.e. chisel-shaped and the different layers of dentine are not very evident. Thus, it may have been an omnivore, morphologically and ecologically intermediate between living euphractines and the living long-nosed armadillo *Dasypus* in the dietary classification proposed by Redford (1985: Table 1).

There is no published biomechanical analysis of the masticatory apparatus of *Prozaedyus* species as compared with the previous taxa. A preliminary morphofunctional evaluation by Vizcaíno and Fariña (1994) identifies a remarkable resemblance between *Prozaedyus* and the living euphractine *Zaedyus pichiy* Ameghino, although the rostrum of *Prozaedyus* is more elongate, and the coronoid process of the mandible is more slender, the symphysis shorter, the masseteric fossa deeper, and the angular process more hook-like. Moreover, the teeth are comparatively smaller. The similarity of *Prozaedyus* with the living species indicates a grossly similar diet, i.e. omnivorous with preference for rotten flesh and larvae and cocoons of ants and/or termites. Vizcaíno and Fariña (1994) pointed out that the differences mentioned above suggest a higher degree of insectivory.

The skull of *S. tessellatum* Ameghino resembles that of the living dasypodines of the genus *Dasypus*, although there are marked differences in many respects. The rostrum is more elongate in the region of the nasals, premaxilla, and anterior portion of the maxilla, while more posteriorly, the area containing the minute teeth is shortened. Analysis of both the craniomandibular joint and muscular attachment sites of *S. tessella-*

tum (Vizcaíno, 1994, 1997) indicates that jaw movements were primarily oriented anteroposteriorly (Vizcaíno, 1994). The glenoid cavity is a narrow, elongate, longitudinal groove and the mandibular condyle is very low, sessile, longitudinal and scroll-shaped (Scott, 1903–1904). The descending process of the zygomatic arch and the elongation of the masseteric fossa on one side and the pterygoid and the angular process of the mandible on the other are spatially distributed in such a way as to emphasize the anteroposterior component of line of contraction of the masseter and pterygoid muscles (Vizcaíno, 1994). The great reduction in number and size of the teeth and the extreme elongation of the rostrum (though differently than in the living analogues *Dasypus* Linnaeus and *Priodontes* F. Cuvier) clearly suggest a myrmecophagous diet (Scott, 1913; Patterson and Pascual, 1968; Scillato-Yané, 1982; Vizcaíno, 1994, 1997).

Finally, the peltephilines comprise a group of armadillos traditionally regarded as specialized cursorial carnivores (Ameghino, 1910; Winge, 1941; Hoffstetter, 1958; Scillato-Yané, 1977). However, a reanalysis by Vizcaíno and Fariña (1997) of the available evidence, including a morphofunctional study suggests a quite different view of this group; thus, a longer summary is provided here. Material assumed to be peltephiline coprolites (Ameghino, 1910) are in fact reidentified as seeds belonging to angiosperms. In their biomechanical analyses, Vizcaíno and Fariña (1997) conclude that the peculiar morphology makes peltephilines poorly designed to be strictly carnivorous. In peltephilines the main masticatory force must have been exerted in the anterior part of the jaw, as evidenced by the larger anterior teeth that, however, seem too weak to resist strong bending because they are rather flat and triangular in cross section (see Biknevicius and Van Valkenburgh, 1996). The strongly fused mandibular symphysis might be interpreted as a reinforcement of the jaw anterior region, which has to withstand the larger forces and resisting lateral bending moments at the symphysis exerted by the inferred large pull of the masseters during strong lateral movements. The convex-shaped, backwards-directed condyle allowed the mandible to rotate, acting as a pivot when the pterygoids and the anterior part of the contralateral masseter complex contracted. The moment arms of the bite points along the tooth row are high (even higher than those of *Euphractus*) compared to jaw lengths as a consequence of the shortness of the tooth row. However, the ratios of the muscle to bite points are moderate due to the low moment arm of the masseter. Vizcaíno and Fariña (1997) postulate that a compromise is reached in regard to the tooth row length between a stronger bite and a larger gape, the latter presumably related to a rather large size of food items. The temporomandibular joint is situated at the same level as the tooth rows. The anterior teeth are higher than the posterior ones, so the occlusion must have taken place as a rearward succession. By manipulating the jaw, a strong lateral component of the jaw movement becomes apparent while propalinal movements are hardly possible.

All this body of evidence suggests that peltephilines must have performed their main masticatory effort with the front teeth, which implies a poor mechanical advantage in biting, as the output force has a longer lever arm. This could be partially compensated through the enlarged masticatory muscles. On the basis of these studies, Vizcaíno and Fariña (1997) suggest that peltephilines fed on soft, plant material of underground origin (roots or tubers) although scavenging habits cannot be excluded as a possibility for peltephiline diet, since it is a commonplace in armadillos biology (Redford, 1985).

6. Discussion

Size, locomotion and feeding are fundamental features needed for a biological characterization of any animal. The influence of body size on animal's life history is reflected in virtually all life traits such as metabolism, limb bone dimensions and biomechanics of locomotion, population density and home range, behavior, and susceptibility to extinction (see Fariña et al., 1998 and references therein). Studies of the locomotion and mastication allow assessment of the movements and activities that the animal was well designed to perform. In regard to locomotion, their habits can be assessed, and the mammals can be classified as runners, diggers, tree dwellers, etc. The masticatory models address the diet the animals were best fitted to process. These approaches are among the most relevant data for the interpretation of the main aspects of the biology of a fossil mammal (paleoautoecology) and its classification in a paleoecological framework (paleosinecology) (Bargo, 2003). There have been several paleoecological approaches to the study of Cenozoic South American faunas that have taken one of more of these three features as starting points (Kay and Madden, 1997a,b; Fariña, 1996; Tauber, 1999; Croft, 2001).

Tauber (1999) performed a paleoecological study of the armadillos and other vertebrates of the Santa Cruz Formation based on the presence/absence in the different levels and inferred habits. His method was to infer these behavioral aspects on the basis of phylogenetic affinities with living taxa, and on that basis provided a discussion on the value of the armadillos as indicators of climatic conditions. Beyond the fact that Tauber (1999) questioned previous interpretations by Vizcaíno (1994) based on an erroneous review of the literature (see Vizcaíno, 2001), he accepted that *S. tessellatum* would have tolerated well-defined seasonal changes. He also mentioned that *P. lagena* and *Proeutatus* cf. *deleo*, recorded in the lowest levels of the Santa Cruz Formation in the area of study, were slightly larger than *P. oenophorus* from the upper levels, suggesting less favourable conditions for these upper levels. So far, the comparison of body mass estimations of *P. lagena* and *P. oenophorus* provided in our analysis, based on measurements of the femur of a single specimen, indicates a larger body size for *P. oenophorus*. Additionally, the body sizes of living armadillos (SFV, personal observations) suggest that at least the euphractine *C. villosus* from Southernmost Patagonia, and hence inhabiting "less favourable conditions" (colder and desertic), should be larger than specimens from the Pampean region (central Argentina). Thus, Tauber's hypothesis remains to be tested pending more reliable information.

Our results indicate that the Santacrucian armadillos possessed body masses between those of the most common and diverse armadillos. None of the Santacrucian taxa reached the extremes recorded today with the 85 g of tiny *C. truncatus* and the 50 kg for the giant armadillo *P. maximus*. The Miocene *Prozaedyus* is slightly smaller than the small euphractines, the Patagonian pichy *Zaedyus pichyi* (1 to 2 kg) and the screaming hairy armadillo *Chaetophractus vellerosus* (around 1 kg). *Stenotatus* is closely comparable to the common long-nosed armadillo *Dasypus novemcinctus*. *Peltephilus* was one of the largest of the Santacrucian armadillos, being the average equivalent to the size of the second largest living armadillo, the greater long-nosed armadillo, *Dasypus kappleri* (8.5 to 10.5 kg). *Stegotherium* and *Proeutatus* are somewhat larger than the latter living species.

As mentioned above, living armadillos are primarily specialized diggers and their limbs are well designed for that activity. Vizcaíno et al. (1999) divided their fossorial habits into three categories: (1) species that are mostly cursorial (Jenkins, 1971; Stein and Casinos, 1997) and non-digging; (2) species that often dig, but for which digging plays no essential part in their alimentary strategy; and, (3) species that are burrowers or that feed on termites or ants. In the first category are the tolypeutines, the second includes the euphractines and dasypodines, and the third the priodontines and chlamyphorines. These categories have been shown to be correlated with limb proportions (Vizcaíno and Milne, 2002) and this permits the evaluation of locomotion in fossil armadillos (Vizcaíno et al., 2003). The Santacrucian armadillos have a more restricted range of locomotor adaptations than seen in living armadillos; all appear to be relatively good diggers. The forelimb indices reflect proportions similar to those of the living dasypodines and euphractines (Category 2 of Vizcaíno et al., 1999). Only in *Proeutatus* (IFA) and *Peltephilus* (IFA, BI), do some values begin to approach the values seen in the more specialized digging priodontines and *C. truncatus*. This result is important because *Peltephilus* has previously been proposed as having cursorial habits (Hoffstetter, 1958; Scillato-Yané, 1977). In *Stenotatus* some values (IFA) fall within the range of *T. matacus*, which would indicate a lesser degree of specialization for digging. Unfortunately the forelimb of *Stegotherium* is not well known so IFA and BI cannot be calculated, but the SMI is very much as in the others. The structure of the hind limbs is more difficult to interpret. While HMIs are similar to living armadillos, *Proeutatus*, *Prozaedyus*, and *Stegotherium* have higher CIs than the living dasypodines, euphractines and priodontines, but lower than *T. matacus* and *C. truncatus* suggesting a relative extension of the distal part of the hind limb and some degree of cursoriality. The high LRI of *Proeutatus* would suggest body weight was transferred more to the hind limb, perhaps liberating the forelimb from this function during the locomotion in a similar way to that seen in *P. maximus*. Summing up, although there is some diversity in limb bone proportions in Santacrucian armadillos, the range is far less than in the living species. None of the Santacrucian taxa attained the degree of cursoriality of *Tolypeutes*, the fossoriality of *Priodontes*, or the subterranean habits of *Chlamyphorus*. In the multivariate analysis, the second principal component (Fig. 4A and B) reflects body mass and in both cases there are positive loadings for LRI, HMI and IMI, and negative loadings for CI (and BI). The indices most strongly correlated with body size are LRI, HMI and CI. Thus it seems that features of the hind limbs are most strongly related to body size while features of the forelimbs are related to digging ability. The leg robusticity index has a clear relationship with body size, as the larger species have more robust bones, and it is also clear that smaller animals are more adapted for speed (BI and CI) but the explanation of the relationship of HMI is less clear. In the larger species the third trochanter is placed more distally along the shaft of the femur and this may provide more leverage for the gluteus maximus and tensor fascia lata muscles that attach there.

The geographic provenance of the materials and the work by Tauber (1997a) suggest that there were between five (*Prozaedyus*, *Proeutatus*, *Stenotatus*, *Stegotherium* and *Peltephilus*) and eight (including *Paraeutatus*, *Anantiosodon* and *Peltecoelus*) genera, and up to 17 species, of armadillos that potentially coexisted in the upper levels (5 to 10, Tauber, 1997a) of the Estancia La Costa Member of Santa Cruz Formation in the area of the present coast of Southern Patagonia between 50° and 52° South. Although not all the taxa have been recorded in any single level recognized by Tauber (1997a,b), at this stage of the knowledge we followed the criterion that the absence of those present either below or above one level is an artifact of the record. Intensive field studies currently under way (Tauber et al. 2004a,b) would provide more precise evidence of the coexistence of these animals in a single level.

Except for *Paraeutatus*, *Anantiosodon* and *Peltecoelus* that have been not studied yet, we have established that the Santacrucian armadillos were very homogeneous in their body sizes and locomotor adaptations, similar to the living armadillos included in the second category of Vizcaíno et al. (1999). Therefore we would rule out body size and locomotor specialization as a basis for the very high alpha diversity of Santacrucian armadillos. The most likely basis for the much observed richness of Santacrucian armadillos seems to be their greater range of dietary adaptations.

Given the relatively limited geographic range of the Santacrucian specimens that provide the basis for our estimate of species richness, it would appear that the list of armadillos from the Santacrucian would more closely approximate alpha (local) rather than gamma (regional) richness. For example, an analysis of the distribution of the living armadillos (Wetzel, 1985) reflects that the largest gamma diversity (richness) today is present in a more or less restricted region east of the Andes in central South America, between 12° and 32° of latitude. The area coincides greatly with the Chaqueña Province of the biogeographic division of the Neotropical Region (Fig. 5) proposed by Cabrera and Willink (1980). Depending on the accuracy of the distribution maps, marginal areas of the Amazonia, Yungas, Cerrado, Paranense, Puneña, Monte and Espinal Provinces are also involved. The first four belong to the Amazonic Domain of the proposed division that is characterized by a dense vegetational cover and abundant and diverse flora and fauna developed in a warm and humid climate and limited seasonality in rainfall. The last three, together with the Chaqueña Province belong to the Chaqueño Domain, with predominant xerophytic vegetation in a continental climate with low to moderate rainfalls and cool winters and hot summers. In this province, 7 genera and 11 species of armadillos belonging to the five tribes recognized by Wetzel (1985) are recorded. They represent the complete range of size and digging capacities of living armadillos, including the cursorial tolypeutines, and the digging euphractines, dasypodines and priodontines, and the subterranean chlamyphorines.

The differences in feeding styles could be the best clue to understand niche partitioning among the Santacrucian armadillos. All living armadillos consume a considerable amount of animal material (see Redford, 1985, and references therein). Redford (1985: 429) noted that living armadillos “show a range of trophic specialization from the generalized carnivore–omnivore through the generalist insectivore to the specialist insectivore.” In the above-mentioned Chaqueña Province all the categories of feeding styles are present (Redford, 1985). They include carnivore–omnivores (euphractines), generalist (terrestrial) insectivores (dasypodines), generalist (fossorial) insectivores (chlamyphorines), and ant and/or termites specialists (tolypeutines and priodontines). Many Santacrucian armadillos were generalized carnivore–omnivores like their living counterparts. *Prozaedyus* is comparable with the small living euphractines *Z. pichiy* and *C. vellerosus*. While *Stenotatus* must have been an omnivore with some specialization toward insectivory, intermediate between living euphractines and the living long-nosed armadillo *Dasypus*, *Stegotherium* represents the highest morphological adaptation to strict myrmecophagy in armadillos. Competition for ants or termites as food resources with other strict myrmecophages like the Vermilingua present in the Santa Cruz Formation is improbable because the later must have been at least semi-arboreal like the living *Tamandua* (Vizcaíno et al. in progress).

Some other dietary specializations not present in living armadillos can be easily detected within the Santacrucian armadillos. Herbivory especially must have been better developed than today. Although it retains many typical armadillo features and omnivory cannot be discounted, *Proeutatus* shows clear adaptations in that direction. *Peltephilus* also departs from the typical armadillo architecture in ways suggesting an important specialization for feeding on plant material of underground origin. Thus the dietary range of Santacrucian armadillos certainly surpasses that of living armadillos and might explain the potential coexistence of so many genera in a single area, diminishing the degree of competition for the resource.

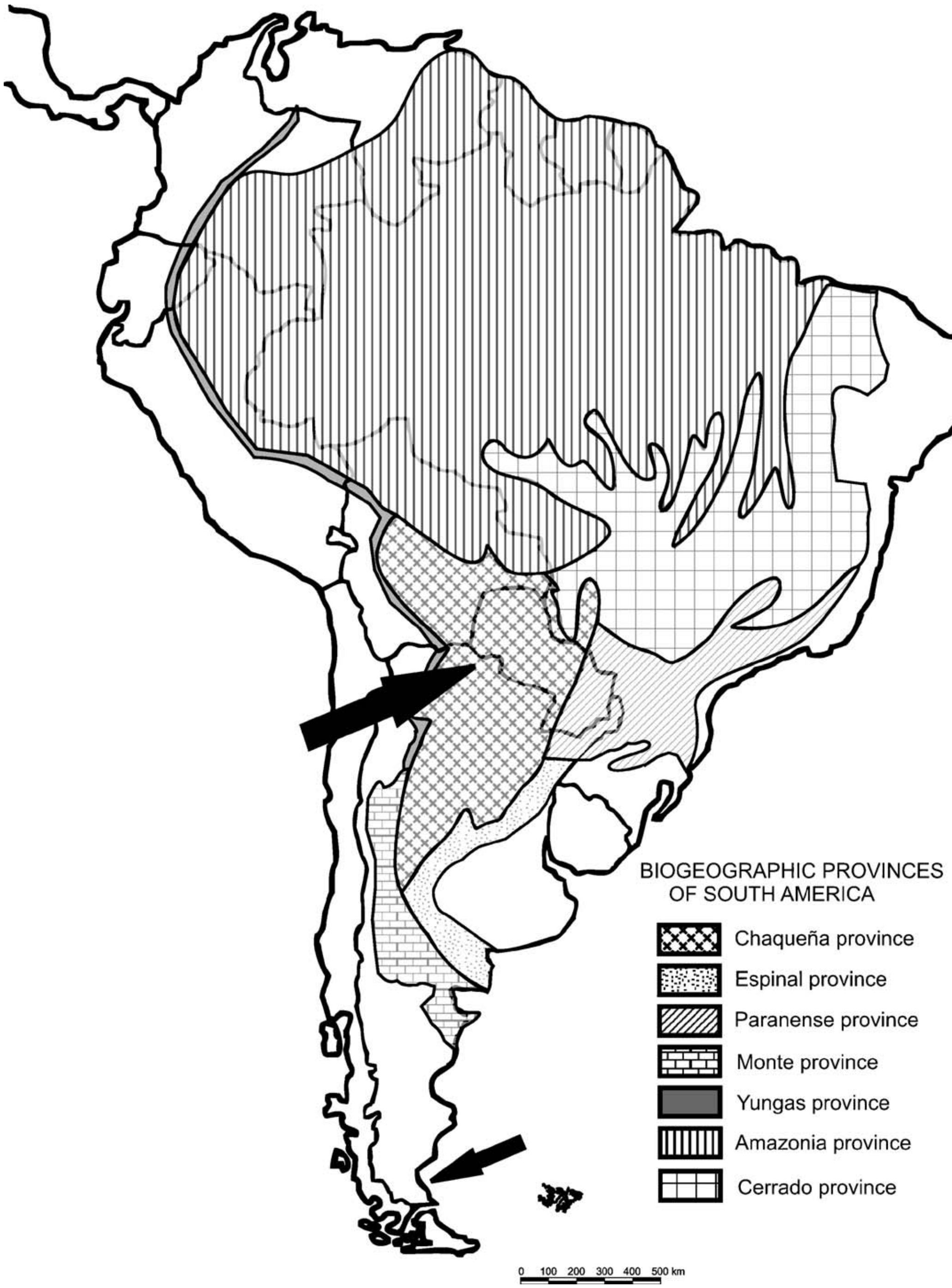

Fig. 5. Some Biogeographic Provinces of South America following Cabrera and Willink (1980). For simplicity, only those Provinces mentioned in the text were included. The large arrow indicates the Chaqueña Province where the largest diversity of the living armadillo species is recorded. The small arrow indicates the area where the fossil armadillos were recorded.

If the metabolic requirements and other related biologic parameters such as population density were comparable to those of the living faunas, the diversity recorded is consistent with the environmental interpretation of Tauber (1997a,b) of open vegetation in relatively dry conditions with marked seasonality for the upper levels (Estancia La Costa and Estancia La Angelina members).

7. Summary

(a) At least five genera of armadillos were sympatric in the Santa Cruz Formation.
(b) They all fall in the range of body size of medium sized living armadillos.
(c) Despite some variation in limb proportions, all of them were good diggers, and none of them reached the degree of fossoriality found in some specialized living forms.
(d) The degree of variation of the masticatory apparatus exceeds that in the living species denoting a broader range of specializations (herbivory and strict myrmecophagy).
(e) This diversification of feeding styles suggests strong niche partitioning.
(f) The high taxonomic diversity is similar to that recorded today in the Chaqueña Biogeographic Province.
(g) This diversity supports the environmental interpretation of open vegetation in relatively dry conditions.

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