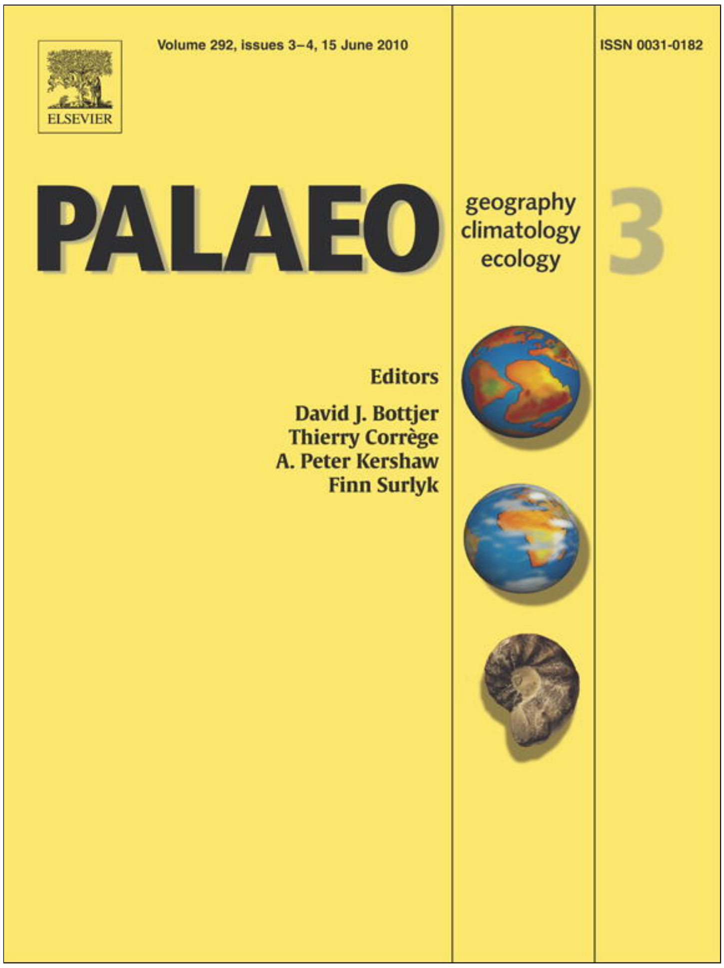

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A baseline paleoecological study for the Santa Cruz Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina

Sergio F. Vizcaíno [a,b,*], M. Susana Bargo [a,b], Richard F. Kay [c], Richard A. Fariña [d], Mariana Di Giacomo [d], Jonathan M.G. Perry [e], Francisco J. Prevosti [f], Néstor Toledo [a,b], Guillermo H. Cassini [a], Juan C. Fernicola [g]

[a] *División Paleontología de Vertebrados, Museo de La Plata, Paseo del bosque s/n, B1900FWA, La Plata, Argentina*
[b] *CONICET-CIC, Argentina*
[c] *Department of Evolutionary Anthropology, Duke University, Box 90383, Durham, NC 27705, USA*
[d] *Sección Paleontología, Facultad de Ciencias, Universidad de al República, Iguá 4225, 11400 Montevideo, Uruguay*
[e] *Department of Anatomy, Midwestern University, 555 31st St., Downers Grove, IL, 60515, USA*
[f] *División Mastozoología , Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina*
[g] *División Paleontología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina*

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ABSTRACT

Coastal exposures of the Santa Cruz Formation (late–early Miocene, southern Patagonia, Argentina) between the Coyle and Gallegos rivers have been a fertile ground for recovery of Miocene vertebrates for more than 100 years. The formation contains an exceptionally rich mammal fauna, which documents a vertebrate assemblage very different from any living community, even at the ordinal level. Intensive fieldwork performed since 2003 (nearly 1200 specimens have been collected, including marsupials, xenarthrans, notoungulates, litopterns astrapotheres, rodents, and primates) document this assertion. The goal of this study is to attempt to reconstruct the trophic structure of the Santacrucian mammalian community with precise stratigraphic control. Particularly, we evaluate the depauperate carnivoran paleoguild and identify new working hypotheses about this community. A database has been built from about 390 specimens from two localities: Campo Barranca (CB) and Puesto Estancia La Costa (PLC). All species have been classified as herbivore or carnivore, their body masses estimated, and the following parameters estimated: population density, on-crop biomass, metabolic rates, and the primary and secondary productivity. According to our results, this model predicts an imbalance in both CB and PLC faunas which can be seen by comparing the secondary productivity of the ecosystem and the energetic requirements of the carnivores in it. While in CB, the difference between carnivores and herbivores is six-fold, in PLC this difference is smaller, the secondary productivity is still around three times that of the carnivore to herbivore ratio seen today. If both localities are combined, the difference rises to around four-fold in favour of secondary productivity. Finally, several working hypotheses about the Santacrucian mammalian community and the main lineages of herbivores and carnivores are offered.

1. Introduction

1.1. Background

The Santa Cruz Formation (late–early Miocene) cropping out on the Atlantic coast of southernmost continental Patagonia, Argentina, between the rivers Coyle and Gallegos, bears an exceptionally rich fauna that documents an assemblage very different from any living mammalian community. These localities are situated at about 52 degrees South latitude, barely 100 km from the Strait of Magellan (Fig. 1). Many collections of fossil vertebrates were made in this region in the nineteenth century beginning with the efforts of the Ameghino brothers in 1891–1892 and later by J. B. Hatcher's group (see Marshall, 1976). Extensive anatomical descriptions and illustrations of these fossils are available in the Reports of the Princeton University Expeditions to Patagonia edited by W.B. Scott between 1900 and 1932 (see Scott, 1903–1905, 1910, 1912, 1928, and Sinclair, 1906, 1909).

Few further systematic efforts to collect here were made before the work of A. Tauber. This author (Tauber, 1997a,b) surveyed the geology of the Santa Cruz Formation south of Coy Inlet, reidentified the most

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* Corresponding author. División Paleontología de Vertebrados, Museo de La Plata, Paseo del bosque s/n, B1900FWA, La Plata, Argentina. Tel.: +54 221 425 9161x129, 38; fax: +54 221 425 7527.

E-mail addresses: vizcaino@fcnym.unlp.edu.ar (S.F. Vizcaíno), msbargo@fcnym.unlp.edu.ar (M.S. Bargo), richard.kay@duke.edu (R.F. Kay), faria@fcien.edu.uy (R.A. Fariña), maru.digi@gmail.com (M. Di Giacomo), jperry@midwestern.edu (J.M.G. Perry), protocyon@hotmail.com (F.J. Prevosti), ntoledo@fcnym.unlp.edu.ar (N. Toledo), gcassini@fcnym.unlp.edu.ar (G.H. Cassini), jctano@macn.gov.ar (J.C. Fernicola).

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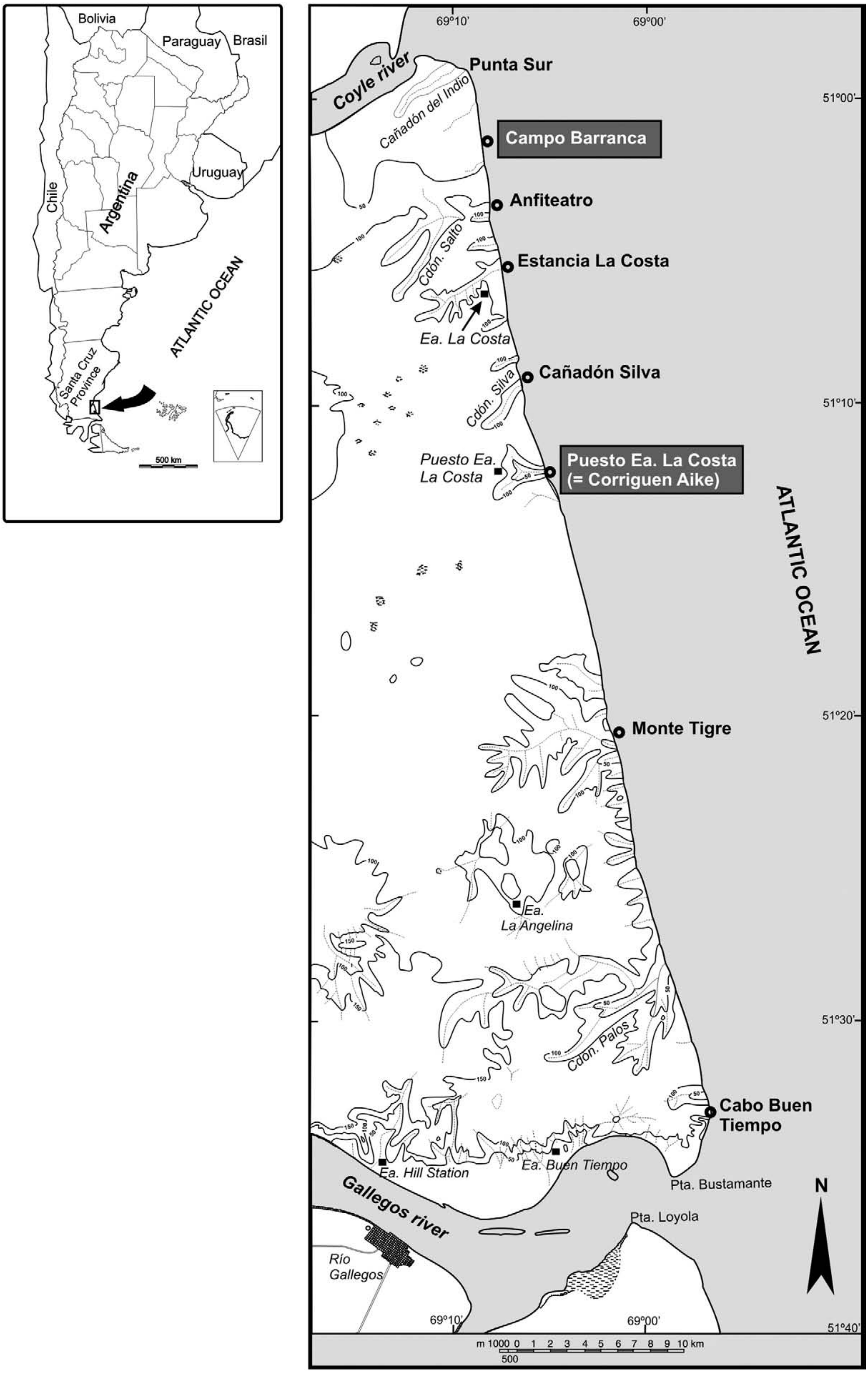
Bolivia
Paraguay
Brasil
Uruguay
Chile
Argentina
ATLANTIC OCEAN
Santa Cruz Province
500 km
69º10'
69º00'
51º00'
51º10'
51º20'
51º30'
51º40'
Coyle river
Punta Sur
Cañadón del Indio
Campo Barranca
Anfiteatro
Cdón. Salto
Estancia La Costa
Ea. La Costa
Cañadón Silva
Cdón. Silva
Puesto Ea. La Costa
Puesto Ea. La Costa (= Corriguen Aike)
ATLANTIC OCEAN
Monte Tigre
Ea. La Angelina
Cdón. Palos
Cabo Buen Tiempo
Ea. Hill Station
Ea. Buen Tiempo
Pta. Bustamante
Gallegos river
Pta. Loyola
Río Gallegos
N
50
100
150
m 1000 0 1 2 3 4 5 6 7 8 9 10 km
500

productive fossil sites and levels, and made important collections (mostly housed at the Museo de Paleontología, National University of Córdoba, Argentina). Tauber recorded about 60–70 species from 27 fossiliferous levels (FLs) in this region and identified two Biozones: the *Protypotherium attenuatum* Zone and the *Protypotherium australe* Zone (Tauber, 1997a,b, 1999; Krapovickas et al., 2008; see below, Geological Framework). Other researchers (e.g. Bown and Fleagle, 1993) made extensive collections of Santa Cruz Formation mammals farther north in Santa Cruz Province but did not collect south of Coy Inlet.

Since 2003, intensive fieldwork performed by our team, in the costal localities between the Gallegos and Coyle rivers, has confirmed Hatcher's impressions of more than 100 years ago, especially at the site of Corriguen Aike (Puesto Estancia La Costa, Tauber, 1997a,b): this is the richest assemblage of pre-Pleistocene mammalian skulls and articulated skeletons (Fig. 2) known on the continent (Hatcher, 1903). At present, nearly 1200 specimens have been collected by our group. Marsupials, including marsupials, xenarthrans, several South American ungulate lineages (notoungulates, litopterns and astrapotheres), rodents, and primates constitute the main mammalian taxa present. Among birds, the phorusrhacoids are worth noting.

Some work has been undertaken in the past to reconstruct aspects of the paleoecology of the Santa Cruz Formation based on the composition of the mammalian remains. In a landmark paper, Pascual and Ortiz-Jaureguizar (1990) examined faunal change among South American Cenozoic mammals based on the percentages of herbivorous species with different crown heights. As chronologic units they used South American Land Mammal Ages. They include the Deseadan, Colhuehuapian and Santacrucian mammal faunas collectively as the "Patagonian faunistic cycle," and recognize two subcycles within it — Deseadan and Pansantacrucian. The latter, encompasses the Colhuehuapian and the Santacrucian Land Mammal Ages, representing an interval of about 4 million years from ~20 ma to about 16 Ma. From low-crowned and rooted to high crowned, rootless and ever-growing cheek teeth, they recognize four categories: brachydont, mesodont, protohypsodont and euhypsodont. According to their analysis, by the beginning of the Patagonian Faunistic Cycle (late Oligocene) many families of mammals had evolved protohypsodont and euhypsodont cheek teeth, a phenomenon they attribute to the increase in the number of grazing species coevolving with the spread of grasslands at middle Patagonian latitudes. Further changes are noted between the Deseadan and Pansantacrucian subcycles: brachydont genera decreased from 15% to 6%, mesodont taxa increased from 31% to 48%, protohypsodont forms decline slightly from 31% to 23% and euhypsodont taxa remain at 23%. These changes are attributed to a shifting balance of grassland and woodland habitats provided by a "park savanna." Such analyses, while broadly useful, lack the kind of stratigraphic and chronologic precision so valuable for an understanding of ecological conditions at a single place and within a narrow range of time.

The Santa Cruz Formation offers a unique window for reconstructing the structure of a South American mammalian palaeocommunity with precise stratigraphic and geographic control. To date, just one analysis of Santacrucian faunas has been published that is more narrowly restricted in its scope. Croft (2001) used cenogram analysis (a plot of vertebrate body sizes within a community; Valverde, 1964) to interpret palaeoenvironmental conditions for some of the best-known South American fossil mammal assemblages from the Eocene to the Pleistocene. These were then compared to more traditional interpretations (based on herbivore craniodental and postcranial adaptations) to judge congruence between the different methods of palaeoenvironmental reconstruction. Croft (2001) included two faunas from the early to middle Miocene Santacrucian Age: Tauber (1997a) *Protypotherium attenuatum* and *Protypotherium australe* Biozones. He found them to be very similar, suggesting that no environmental characteristics distinguish them. Although usually interpreted as a "mixed" habitat due to the presence of at least one arboreal primate (*Homunculus*) in addition to many (supposed) savanna-adapted mammals, the cenogram statistics suggest the area was wetter and less open than previously thought (e. g., Pascual and Ortiz-Jaureguizar, 1990). The lack of differentiation between the two faunas is notable because it contrasts with the suggestion of Tauber (1997b, 1999) (based on various lines of faunal evidence) that the climate had become less humid and more "open," that is with fewer trees, during this interval. If anything, the analysis of Croft (2001) suggests slightly greater rainfall in the upper (*P. australe*) zone as indicated by the slope of the medium-sized mammals. Another observation of the study of Croft (2001), was the "depauperate nature of the carnivore palaeoguild in South America" prior to the Great American Biotic interchanges (Croft, 2001: 283), with only one and two mammalian predators in the *P. attenuatum* and *P. australe* zones respectively.

Fariña (1996) provided a different approach to analyzing mammalian palaeocommunity structure using a general ecological relationship between population density and body size (Damuth, 1981, 1987, 1991). Since body size has long been known to be related to basal metabolic rate (Kleiber, 1932; McNab, 1980, Peters, 1983), Fariña (1996) assessed the abundance of herbivorous and carnivorous mammals larger than 10 kg listed for the Luján Local Fauna in Tonni et al. (1985). The same method was used to examine the palaeoecological characteristics of an important mid-Pliocene faunal turnover dated at ca. 3.3 Ma (Vizcaíno et al., 2004). Although this approach rests on rather general approximations, it provides a tool to compare different extinct faunas to generate or identify working hypothesis to be tested using more specific methods.

The goal of this contribution is to evaluate one aspect of the study of Croft (2001): his hypothesis of the depauperate carnivore paleoguild for some Santacrucian faunas, and identify new working hypotheses about the Santacrucian mammalian community to be tested using an ecomorphological approach, of the sort used by R. F. Kay and R. H. Madden on the La Venta fauna (middle Miocene, Colombia; Kay and Madden, 1997a,b) based on precise or detailed functional analysis in a well defined phylogenetic framework.

1.2. Geologic framework

The Santa Cruz Formation occurs in southern Patagonian Argentina 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 volcanoclastic mudstones containing immature paleosols laid down on a coastal plain incised by channel sand bodies containing some pebbles. Some relatively unaltered tuffs also occur (Bown and Fleagle, 1993). Bown and Fleagle describe typical coastal Santa Cruz lithology from Monte León and Monte Observación, north of Coyle River.

The stratigraphy of the coastal Santa Cruz Formation south of Coyle river and north of Gallegos river (at Campo Barranca, Anfiteatro, Estancia La Costa, Puesto Estancia La Costa [Corriguen Aike], and Monte Tigre and other coastal sites; Fig. 1) is slightly more complicated than that at Monte Observación. Tauber (1997a) recognized two members: a lower very fossiliferous Estancia La Costa Member, with predominance of pyroclastic deposits, claystones and mudstones, and a fossil-poor upper Estancia Angelina Member, chiefly

Fig. 1. Geographic location of the coastal localities of the Santa Cruz Formation at Santa Cruz Province, Argentina. Highlighted in gray boxes are the localities considered in this study. Modified from Kay et al., 2008.

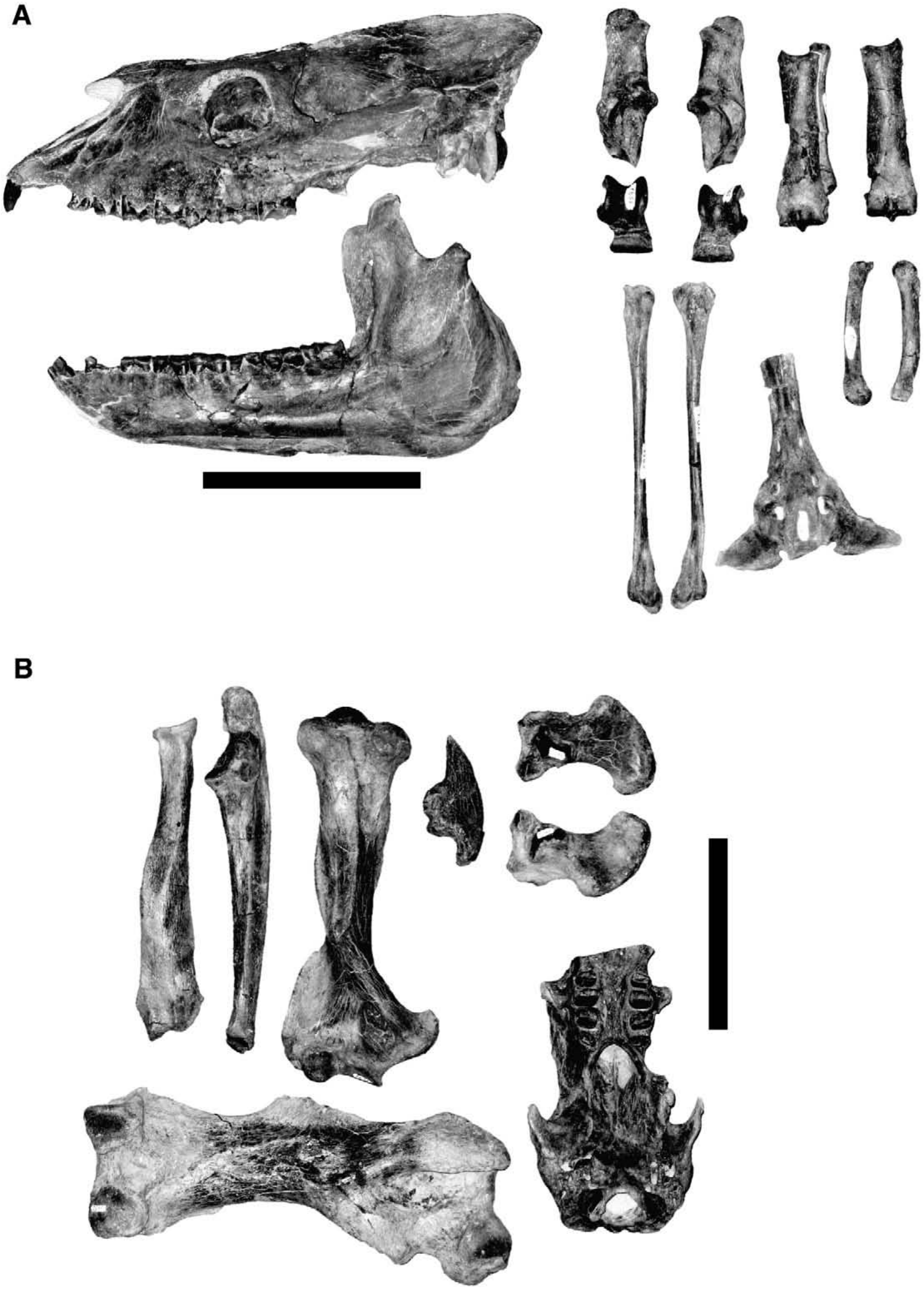

Fig. 2. Specimens collected by our team during 2007 and 2008 field seasons in Campo Barranca and housed at the Museo Regional Provincial "Padre M. J. Molina" (MPM-PV), Río Gallegos, Santa Cruz Province. A. Skull, mandible and part of the associated skeleton of the litoptern *Diadiaphorus majusculus* (MPM-PV 3397). B. Skull and part of the associated skeleton of the megalonychid sloth *Eucholaeops* sp. (MPM-PV 3651).

composed of claystones, mudstones and sandstones (Fig. 3). He also identified 22 fossiliferous levels, which have increased now to 27 (see Krapovickas et al., 2008): 23 of these fossil levels occur in the lower, Estancia La Costa Member, which he grouped into two biozones mentioned above and four FL in the upper Estancia Angelina Member. The Estancia La Costa Member is more similar to the Santacrucian rocks at Monte Observación than is the Estancia Angelina Member (Tauber, 1997a). Recently, Tauber has included the important site of Killik Aike Norte, along the estuary of Río Gallegos, in the lower Estancia La Costa Member (Tauber et al., 2004).

At Monte Observación and Monte León, several ^{40}Ar/^{39}Ar dates and a short magnetostratigraphic section bear upon the age of the Santa Cruz Formation. Dates from three levels in the lower one-third of the Santa Cruz fossiliferous beds at Monte Observación, range

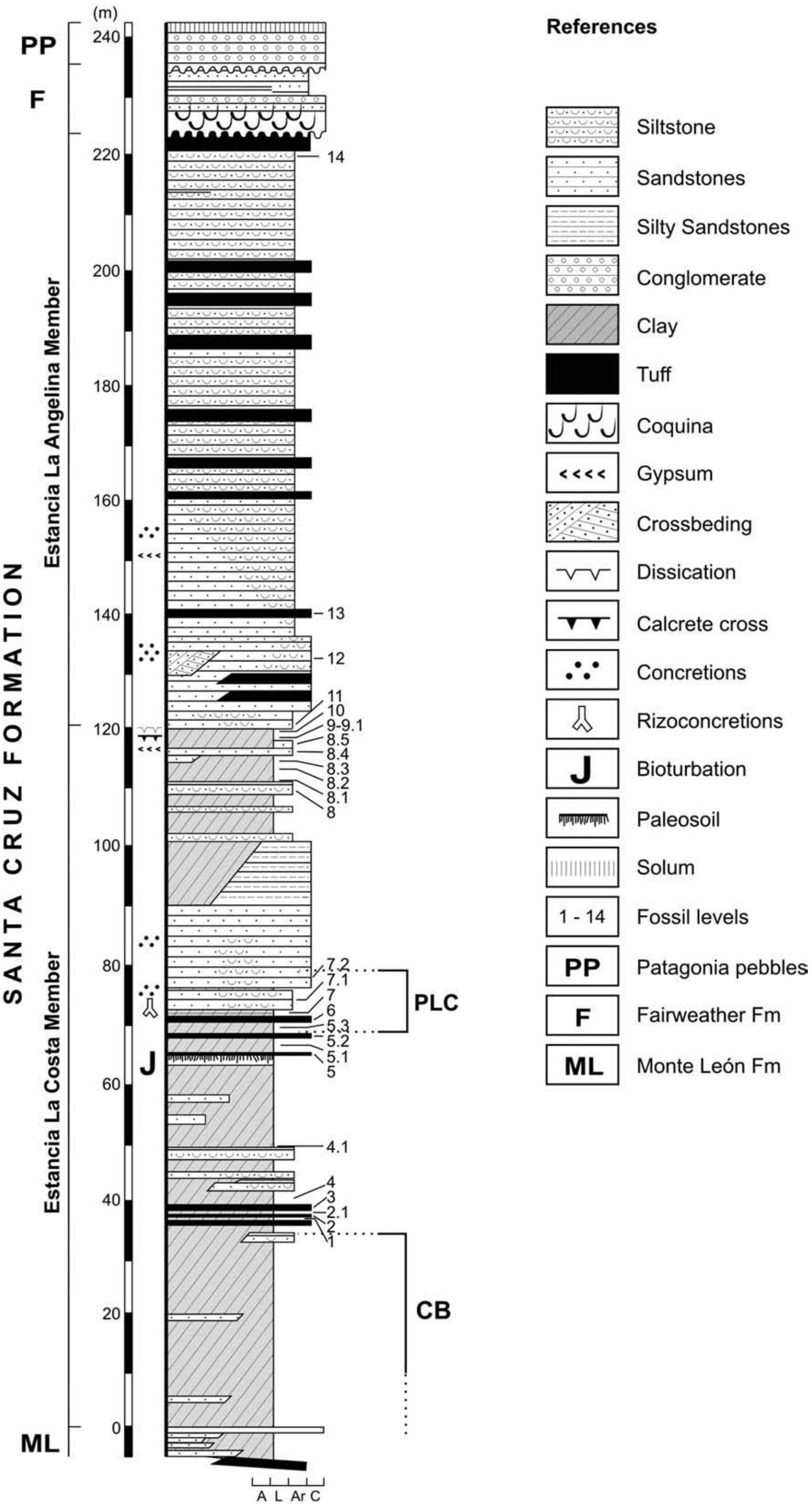

Fig. 3. Stratigraphic column of the Santa Cruz Formation.
Modified from Vizcaíno et al., 2006b, and Krapovickas et al., 2008.

between 16.42 Ma and 16.18 Ma and between 16.56 Ma and 16.28 Ma at Monte León. The dates are not wholly concordant but permit the assignment of the bulk of the coastal Santacrucian faunas to the late–early Miocene (Fleagle et al., 1995). These authors also report a magnetostratigraphic framework of Santa Cruz rocks that begins with a reversed interval, followed by a normal then a reversed interval at the top. This is in accordance with the 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 near-shore marine

Monte León Formation underlies the Santa Cruz Formation. It has surface exposure at Monte León and is present in drill cores north and south of Río Coyle. 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 yields a date of 19.33 Ma (Fleagle et al., 1995). The latter date is consistent with an early Miocene age of the molluscan assemblage from that formation (del Río, 2004). Southward, the Santa Cruz Formation is capped by the Pliocene Fairweather Formation.

For this study, we focus on the two localities that we sampled most exhaustively. Both are in the intertidal zone, and belong to the Estancia La Costa Member.

Campo Barranca (CB) is at approximately W 69º 09′ longitude, between S 51º 00′ and S 51º, 02′ latitude (Fig. 1), that is 2 km south of Punta Sur, at the mouth of the Coyle River, and 6 km north of the entrance to the beach at Estancia La Costa (ELC) (Kay et al., 2008: Fig. 2B). The area of exposure of this locality is approximately 4 km north–south and 250 m east–west. It is bounded to the north by cross-bedded channel sandstones that yield only a few broken fossil vertebrates. Because of the cover to the west by beach silt and to the east by the sea, the temporally bounding rock units cannot be observed. The Campo Barranca fossil level (i.e. the platform exposed during low tide; Fig. 4A) is composed of greenish silty clay. In places, the clay is finely laminated — some layers have ripple marks and others are carbon-rich. Elsewhere, it is bioturbated, preserving calcified root casts, and has poorly defined bedding.

Puesto Estancia La Costa (PLC; Corriguen Aike of the older literature, see Marshall (1976) and Tauber (1991) for a discussion of the names of this locality) is at approximately S 51º 12′ latitude and W 69º 04′ longitude, about 12 km south of the Estancia La Costa locality. The area of exposure of this locality is approximately 3 km north–south

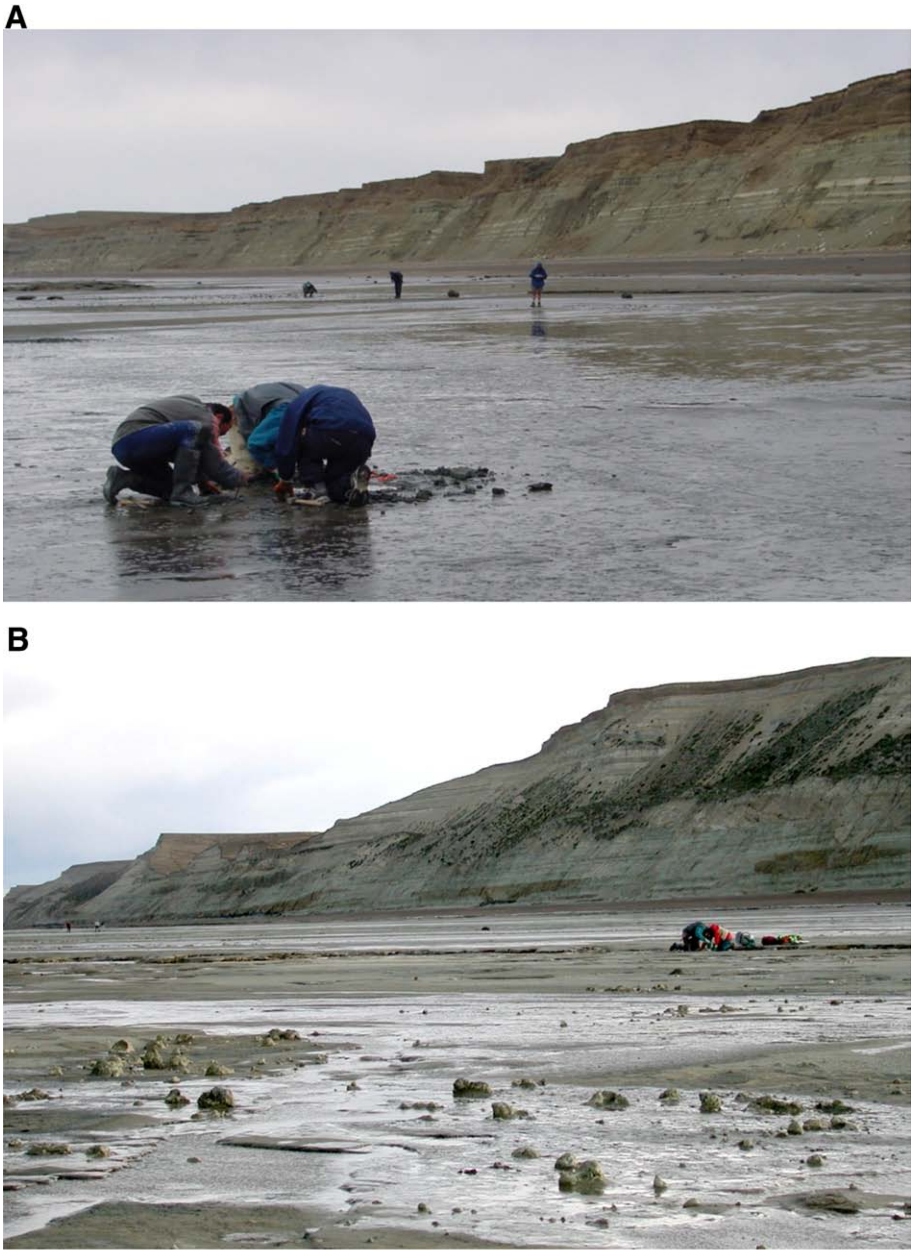

Fig. 4. Panoramic views of the outcrops of the Santa Cruz Formation during low tide at the localities studied, in both cases as seen from the North. A. Campo Barranca. B. Puesto Estancia La Costa.

and 300–400 m east–west, depending on the amplitude of the low tide (Fig. 4B). In this locality, Tauber (1997a) identified two main fossiliferous levels: FL 6 composed by tuffaceous silty sands, and FL 7, composed by greenish silty clays. More recently, Tauber et al. (2004) identified new levels: FL 5.3 (subjacent to FL 6), composed by greenish silty clays with carbonatic concretions, which probably became evident in the last decade — a consequence of the vanished of part of the FL 6 due to sea erosion, and FL 7.1 and 7.2 superjacent to FL 7 (Fig. 3) (see also Krapovickas et al., 2008: Fig. 1).

2. Materials and methods

2.1. Faunal information

On average, a team of eight people collected fossils for 15 to 20 days over seven field seasons. Virtually all identifiable specimens were collected independently of size and taxonomic interest. While half of the crew worked recovering medium to large size articulated specimens, the other half prospected and collected small specimens, usually more valuable for stratigraphic correlation. As a consequence, the sample studied is a reliable, accurate representation of the taxonomic richness of the faunas that inhabited the area during the time of sediment deposition at both localities. A database was built by compiling identifications resulting from about 390 specimens studied by us and collected in both localities (CB and PLC). We did not include museum specimens in our database, because in most cases their exact provenance along the coast is not certain. Necessary stratigraphic information has been available only since the work of Tauber (1997a). Even for the classic locality Corriguen Aike, which is generally accepted to be the Puesto Estancia La Costa locality of Tauber (1997a), we cannot be certain that the specimens collected 100 years ago come from the same rocks we are sampling today. This uncertainty is partly due to the strong erosion produced by the ocean.

In many cases, a taxonomic decision at the species level could not be made formally. Therefore, we made tentative identifications following the advice of the specialists on the number of morphotypes that can be recognized with confidence. Thus, this project has promoted the systematic revision of most of the groups.

Each species was classified as herbivore or carnivore based on the literature. Body masses were estimated using different methods: from previous published estimates, using regression equations generated from modern relatives, from geometric similarity with a phylogenetically close relative (of known mass for living ones or with an appropriate estimate for fossil ones), or using gross anatomical similarity with living analogues. For carnivorous marsupials, estimates were obtained by application of equations in Van Valkenburgh (1990) and Gordon (2003). For the herbivores, estimates for xenarthrans were taken from Vizcaíno et al. (2006a), Vizcaíno et al. (2006b) and Bargo et al. (2009); for ungulates from our own estimates using an average of equations in Janis (1990); those for rodents were taken from Croft (2000); those for Primates were taken from Smith and Jungers (1997). For phorusrhacoid birds, masses were estimated applying equations from Campbell and Marcus (1992).

2.2. Palaeoecology

Those species whose body mass estimates were less than 10 kg were not considered in order to avoid the problem of bias in fossilization, preservation and collection (Behrensmeyer and Hill, 1980; Damuth, 1982; Fariña, 1996; Palmqvist et al., 2003). To estimate the population density of each herbivorous species, the general equation in Damuth (1981) was used:

$$\log D = -0.75 \log m + 4.23$$

where D is population density in number of individuals per square kilometre, and m is the body mass expressed in grams. The basal metabolic rate of these herbivores was calculated following the equation in Peters (1983):

$$\log R = -0.25 \log m + 0.6128$$

where R is the per-second mass-specific metabolic rate (in $\mathrm{J\,kg^{-1}\,s^{-1}}$), and m is the body mass expressed in kilograms.

In the case of the carnivores, their density was calculated after the equation in Damuth (1993) for African flesh-eaters (same symbols as above):

$$\log D = -0.64 \log m + 2.23$$

An appropriate equation, also quoted by Peters (1983), was used to estimate the basal metabolic rate of carnivores (but see Discussion; same symbols as above):

$$\log R = -0.27 \log m + 0.6551$$

The population density and metabolic rates of phorusrhacoid birds were conservatively (Nagy, 2001) calculated as if they were mammals of the same size.

The estimates of primary and secondary productivity were made following Fariña (1996).

At a second stage, in agreement with the discussion in Vizcaíno et al. (2006a), the low basal metabolic rate of the xenarthrans was adjusted for using a correction factor of 0.6, since their metabolism falls between 40 and 60% of the rates expected from mass in the relation for placental mammals of Kleiber (1932) (McNab, 1985). In addition, a correction factor of 0.96 was applied to the marsupial carnivores, since their metabolism is somewhat lower than that of eutherians (McNab, 2005).

The on-crop biomass for each species was estimated by multiplying the estimated population density by its body mass. The energy requirements for each species were then obtained by multiplying its on-crop biomass by its basal metabolic rate. Following the normal values recorded for living mammals, a typical assimilation efficiency of 50% (of the edible material) was considered, and average actual maintenance metabolism was taken to be 2.5 times the basal rate (Peters, 1983).

Another approach used to assess primary productivity was the equation given by McNaughton et al. (1989):

$$\log B = 1.52(\log \mathrm{NAP}) - 4.79,$$

where B is on-crop biomass per unit area (in $\mathrm{kJ\,m^{-2}}$) and NAP is Net Above-ground Productivity (in $\mathrm{kJ\,m^{-2}\,year^{-1}}$).

In a third analysis we added another carnivore, the borhyaenid marsupial *Arctodictis munizi* recently recorded in the literature (Goin et al., 2004). See Discussion for further explanation.

3. Results

3.1. Palaeoecology

Table 1 includes all taxa collected by us present in Campo Barranca and Puesto Estancia La Costa and their body masses estimates. In CB 16 species (61.5%) had body mass estimates under 10 kg; 6 species (23%) between 10 and 100 kg, and 4 species (15.4%) above 100 kg. In PLC 15 species (47%) had body mass estimates under 10 kg; 13 species (40.6%) between 10 and 100 kg, and 5 species (15.6%) above 100 kg.

The taxa of body masses greater than 10 kg found in both CB and PLC faunas are listed in Table 2. In CB, there are 9 species of herbivores. Five of them are xenarthrans: two armadillos (*Proeutatus* spp.), and three sloths (*Eucholaeops* sp.1 and *Hapalops* sp. 1 and 2). The list is completed by two notoungulate species (*Nesodon* sp., and

Table 1
List of all the taxa recorded in the localities studied: Campo Barranca (CB) and Puesto Estancia La Costa (PLC), including their body masses estimates with their sources.

	Taxa	CB	PLC	Body mass (kg)	Source
AVES					
Phorusrhacidae	*Phorusrhacus longissimus*	X	X	110	Campbell and Marcus, 1992
Mammalia					
Marsupialia					
Borhyaenidae	*Cladosictis patagonica*	X		3.7	Gordon, 2003; Van Valkenburgh, 1990
	Borhyaena tuberata		X	23.31	Gordon, 2003; Van Valkenburgh, 1990
	Sipalocyon gracilis		X	1.93	Gordon, 2003; Van Valkenburgh, 1990
	Prothylacynus patagonicus		X	13.83	Gordon, 2003; Van Valkenburgh, 1990
Paleothentiidae	*Paleothentes minutus*	X	X	0.083	Dumont et al., 2000,
	P. lemoinei		X	0.363	Dumont et al., 2000
Xenarthra					
Dasypodidae	*Prozaedyus* sp.	X	X	1.12	Vizcaíno et al., 2006b
	Proeutatus sp. 1	X	X	15.28	Vizcaíno et al., 2006b
	Proeutatus sp. 2	X		15.28	Vizcaíno et al., 2006b
	Stenotatus patagonicus	X		3.72	Vizcaíno et al., 2006b
	Peltephilus strepens		X	8.23	Vizcaíno et al., 2006b
Glyptodontidae	*Propalaehoplophorus* sp. 1		X	73.4	Vizcaíno et al., 2006a
Megalonychidae	*Eucholaeops* sp. 1	X	X	80	Bargo et al., 2009
	Eucholaeops sp. 2		X	80	Bargo et al., 2009
Megatherioidea	*Hapalops* sp. 1	X	X	70	Bargo et al., 2009
	Hapalops sp. 2	X	X	40	White, 1997
Astrapotheria					
Astrapotheriidae	*Astrapotherium magnum*	X	X	1021.63	Janis, 1990
Notoungulata					
Toxodontidae	*Adinotherium* sp.	X	X	121.26	Janis, 1990
	Nesodon sp.	X	X	554.61	Janis, 1990
Homalodotheriidae	*Homalodotherium* sp.		X	340	Janis, 1990
Typotheria					
Intheratheriidae	*Protypotherium attenuatum*		X	4.4	Janis, 1990
	Protypotherium australe	X	X	7.8	Janis, 1990
	Interatherium robustum		X	3.5	Janis, 1990
Hegetotheriidae	*Hegetotherium mirabile*		X	14. 23	Janis, 1990
Litopterna					
Proterotheriidae	*Licaphrium floweri*		X	18.14	Janis, 1990
	Thoatherium minusculum		X	21	Janis, 1990
	Diadiaphorus majusculus	X	X	70.25	Janis, 1990
Primates					
	Homunculus patagonicus		X	2.7	Smith and Jungers, 1997
Rodentia					
Neoepiblemidae	*Perimys* sp.	X	X	0.32	Croft, 2000
Dasyproctidae	*Neoreomys australis*	X	X	4.22	Croft, 2000
Eocardiidae	*Eocardia montana*	X	X	0.58	Croft, 2000
	Eocardia excavata	X		0.16	Croft, 2000
	Eocardia sp.	X		0.58	Croft, 2000
	Phanomys mixtus	X		0.58	Croft, 2000
Echimyidae	*Stichomys*	X		0.79	Croft, 2000
	Spaniomys modestus	X	X	0.65	Croft, 2000

Adinotherium sp.), one litoptern (*Diadiaphorus majusculus*) and one astrapothere (*Astrapotherium magnum*), the last one being a megamammal *sensu stricto* (i.e. with body mass above 1000 kg). There are no mammalian carnivores larger than 10 kg, but a carnivorous phorusrhacid bird *Phorusrhacos longissimus* was included.

At PLC there are 14 species of herbivores, three mammalian carnivores, and one phorusrhacoid bird larger than 10 kg. Six of the herbivores are xenarthrans: one armadillo (*Proeutatus* sp.1), one glyptodont (*Propalaehoplophorus* sp. 1), and four sloths (*Eucholaeops* sp.1, *Eucholaeops* sp.2, *Hapalops* sp.1, and *Hapalops* sp.2). There are seven ungulates: three notoungulates (the toxodontids *Adinotherium* sp. and *Nesodon* sp. and the typothere *Hegetotherium mirabile*), three litopterns (*Licaphrium floweri*, *Thoatherium minusculum*, and *Diadiaphorus*), and one astrapothere (*Astrapotherium magnum*). There are two carnivorous marsupials (*Borhyaena tuberata* and *Prothylacynus patagonicus*). As mentioned above, at a second stage we added the borhyaenid marsupial *Arctodictis munizi* (Goin et al., 2004), with a body mass estimated at 37 kg.

Adding up the requirements of all the species considered, and converting the units, it follows that in CB the total herbivore biomass required about 0.56 MJ m^{-2} $year^{-1}$ to fulfil their requirements. In turn, the PLC herbivores must have needed 0.86 MJ m^{-2} $year^{-1}$. The requirements of carnivores were 2.2 kJ m^{-2} $year^{-1}$ and 6 kJ m^{-2} $year^{-1}$, respectively for the CB and the PLC faunas (Table 3).

When the faunas in both localities are considered together as a single local fauna (summing up the species found in one or both faunules), then the herbivores must have needed 0.93 MJ m^{-2} $year^{-1}$, and the carnivores, 6 kJ m^{-2} $year^{-1}$.

Table 2
List of the species considered in this study (above 10 kg) of both localities and their estimates of body mass, population density, on-crop biomass, and basal metabolism.

Species	Body mass (kg)	Population density	On-crop biomass	Basal metabolism	Corrected basal metabolism
Campo Barranca					
Phorusrhacus longissimus	110	0.1	11.09	1.27	–
Proeutatus sp. 1	15.28	12.36	188.81	2.07	1.24
Proeutatus sp. 2	15.28	12.36	188.81	2.07	1.24
Eucholaeops sp. 1	80	3.57	285.61	1.37	0.82
Hapalops sp. 1	70	3.95	276.23	1.42	0.85
Hapalops sp. 2	40	6.00	240.17	1.63	0.98
Astrapotherium magnum	1021.63	0.53	540	0.73	–
Adinotherium sp.	121.26	2.61	316.91	1.24	–
Nesodon sp.	554.61	0.84	463.44	0.84	–
Diadiaphorus majusculus	70.25	3.94	276.48	1.42	–
Puesto La Costa					
Phorusrhacus longissimus	110	0.1	11.09	1.27	–
Borhyaena tuberata	23.31	0.27	6.34	1.93	1.85
Prothylacynus patagonicus	13.83	0.38	5.26	2.22	2.13
Proeutatus sp. 1	15.28	12.36	188.81	2.07	1.24
Propalaehoplophorus sp. 1	73.4	3.81	279.53	1.40	0.84
Eucholaeops sp. 1	80	3.57	285.61	1.37	0.82
Eucholaeops sp. 2	80	3.57	285.61	1.37	0.82
Hapalops sp. 1	70	3.95	276.23	1.42	0.85
Hapalops sp. 2	40	6.00	240.17	1.63	0.98
Astrapotherium magnum	1021.63	0.53	540	0.73	–
Adinotherium sp.	121.26	2.61	316.91	1.24	–
Nesodon sp.	554.61	0.84	463.44	0.84	–
Homalodotherium	340	1.21	410.08	0.95	–
Hegetotherium mirabile	14.23	13.03	185.48	2.11	–
Licaphrium floweri	18.14	10.86	197.09	1.99	–
Thoatherium minusculum	21	9.73	204.43	1.92	–
Diadiaphorus majusculus	70.25	3.94	276.48	1.42	–

The herbivore on-crop biomass was estimated at 2776 kg km^{-2} for CB, 4150 kg km^{-2} for PLC and 4339 kg km^{-2} for both localities combined. The carnivore on-crop biomass was estimated at 11.1 kg km^{-2} for CB, 22.7 kg km^{-2} for PLC and 22.7 kg km^{-2} for both localities combined.

The secondary productivity, as an estimate of the food available for the carnivores, was of around 14 kJ m^{-2} year^{-1} in CB, 21.6 kJ m^{-2} year^{-1} in PLC and 23.1 kJ m^{-2} year^{-1} if both localities are considered as one.

Table 4 shows the results after the application of the correction factors for the lower metabolic rates of both xenarthrans and marsupials, and the calculations made including the marsupial *Arctodictis* in PLC.

4. Discussion

The Santa Cruz Formation is characteristic for having indicators of different climatic environmental conditions Tauber (1997b). On one side, the occurrence of primates and echimyid and erethizontid rodents has been used as indicators of warm and humid conditions and forests (Vucetich, 1986; Pascual and Ortiz-Jaureguizar, 1990). On the other, following Tauber (1997b), the presence of gypsum crystals, mud cracks, and other sedimentological features suggests the existence of open environments in relatively dry conditions. Additionally, to a great extent, the Santa Cruz Formation rocks are a sequence of superimposed mudstones of volcanoclastic origin, although some relatively unaltered tuffs also occur (Bown and Fleagle, 1993). A recent review on the evolution of the early Miocene palaeoflora of Patagonia (Barreda and Palazzesi, 2007) provides evidence consistent with this scenario confirming the existence of both closed and open environments. Following these authors, by the early Miocene in addition to the forests, shrubby and herbaceous elements became progressively important. Although forests remained, probably developing riparian or gallery forests across extra-Andean Patagonia until about the middle Miocene, in the late–early Miocene drier conditions would have prevailed in lowland areas, and the contraction of humid elements coincides with the expansion of xerophytic taxa. Among present environments in South America, certain parts of the East of Chaco show faunal and floral constitutions that fit with the scenario described above, although for the plants the similarity is more in physiognomy than in taxonomic composition. Gómez and Gallopín (1991) provide estimations of above-ground net primary production in present terrestrial ecosystems in Latin America. According to our interpretations the environment of the Santa Cruz Formation would be comparable to their temperate forest and bushland under less than 1000 mm of annual rainfall category (but see a preliminary report by Croft and Townsend, 2005, for an alternative interpretation).

Based on this interpretation, the herbivores of CB must have required a primary productivity between 9.3 and 18.5 MJ m^{-2} year^{-1} if large

Table 3
Energetic requirements and on-crop biomass of both herbivores and carnivores present in Campo Barranca (CB), Puesto Estancia La Costa (PLC), and those localities combined. Secondary productivity in such localities is shown as well.

Locality	Herbivore energetic requirements (in MJ m^{-2} year^{-1})	Herbivore on-crop biomass (in kg km^{-2})	Secondary productivity (in KJ m^{-2} year^{-1})	Carnivore energetic requirements (in KJ m^{-2} year^{-1})	Carnivore on-crop biomass (in kg km^{-2})
CB	0.56	2776	14	2.2	11.1
PLC	0.86	4150	21.6	6	22.7
CB + PLC	0.93	4339	23.1	6	22.7

Table 4

Results of calculations made after applying correction factors for the lower metabolic rates of both xenarthrans and marsupials, and calculations including the marsupial *Arctodictis* in Puesto Estancia La Costa (PLC).

Locality	Herbivore energetic requirements (in MJ m^{-2} $year^{-1}$)	Herbivore on-crop biomass (in kg km^{-2})	Secondary productivity (in KJ m^{-2} $year^{-1}$)	Carnivore energetic requirements (in KJ m^{-2} $year^{-1}$)	Carnivore on-crop biomass (in kg km^{-2})	Carnivore energetic requirements with *Arctodictis* (in KJ m^{-2} $year^{-1}$)	Carnivore on-crop biomass with *Arctodictis* (in kg km^{-2})
CB	0.43	2776	10.8	2.2	11.1	–	–
PLC	0.72	4150	18	5.8	22.7	7.8	30.2
CB + PLC	0.75	4339	18.8	5.8	22.7	7.8	30.2

herbivores consumed between 3 and 6% of the primary productivity, as in modern mammalian faunas (Owen-Smith, 1988). A lower value is obtained using the equations of McNaughton et al. (1989), which are based on on-crop biomass; primary productivity must have been 9.8 MJ m^{-2} $year^{-1}$. In the case of PLC, the herbivores would have needed a primary productivity between 14.4 and 28.8 MJ m^{-2} $year^{-1}$. Using the equations of McNaughton et al. (1989), the primary productivity would have been around 12.8 MJ m^{-2} $year^{-1}$. If both localities are combined, the primary productivity must have been between 15.4 and 31 MJ m^{-2} $year^{-1}$, and using the equations of McNaughton et al. (1989), it must have been of 13 MJ m^{-2} $year^{-1}$. According to these results, the required primary productivity of CB fits rather well with that expected for the environment proposed above for the Santa Cruz Formation, while that of PLC and both localities combined exceeds it.

In our second analysis, (i.e. introducing the correction factors for metabolism of xenarthrans and carnivore marsupials) the primary productivities estimated become lower than those calculated above. In CB the estimate would be between 7.2 and 14.4 MJ m^{-2} $year^{-1}$, in PLC, between 12 and 24 MJ m^{-2} $year^{-1}$, and in both localities combined, between 12.5 and 25 MJ m^{-2} $year^{-1}$. Once again, the primary productivity in CB fits well to that expected for the proposed environment, and PLC and the combination of both localities, do not.

In order for a community to be balanced, the secondary productivity should match the requirements of the carnivores in it (Fariña, 1996). In none of the localities considered (including the combination of CB and PLC), do such values match each other (see Table 3), this being more evident in the case of CB. In the second analysis, the community behaves in a more even way but it does not achieve the expected balance (see Table 4). Almost no difference can be appreciated when the McNaughton et al. (1989) equations are used.

In the third analysis *Arctodictis munizi* was included in PLC, and therefore in the combination of both localities. *Arctodictis munizi* was the largest carnivorous mammal of the Santa Cruz Formation. Although we did not recover it at our localities, recently Goin et al. (2004) stated that two specimens at the collection of the Museo Argentino de Ciencias Naturales "B. Rivadavia" of Buenos Aires (MACN 5915-5917 and 5918-5921) must come from the fossil level 6 at PLC of Tauber (1997a) (Corriguen Aike). Adding this carnivore resulted in a more even community, although it does not balance it (see Table 4). Estimates fall slightly closer when the McNaughton et al. (1989) equations are used.

Although the model applied here fits very well in both present day and northern hemisphere Pleistocene faunas, as La Brea in North America (Fariña, 1996) and Venta Micena in Europe (Palmqvist et al., 2003), in a South American fossil fauna studied previously (the late Pleistocene Luján Local Fauna) it showed a four-fold difference in favour of secondary productivity (Fariña, 1996, but see Prevosti and Vizcaíno, 2006 for a discussion of the model used). Also in South America, at the Plio-Pleistocene boundary, Chapadmalalan faunas seem to be balanced, while Barrancalobian faunas were not, which was explained by the possible environmental stress from a proposed extraterrestrial impact (Vizcaíno et al., 2004).

According to our results, this model produces an imbalance in both CB and PLC faunas which can be seen by comparing the secondary productivity of the ecosystem and the energetic requirements of the carnivores in it. While in CB, the difference between them is six-fold, in PLC this difference is smaller: the secondary productivity around three and a half times the carnivore requirements. The big difference between both localities may be mainly due to the absence of marsupial carnivores in CB, very probably reflecting a sampling and/or taphonomic bias. If both localities are combined, the difference rises to around four-fold in favour of the secondary productivity.

When the correction factors are applied to calculate the basal metabolisms of xenarthrans and marsupials, the communities become slightly more even. In CB, the secondary productivity is five-fold the carnivore requirements. In PLC, such difference is of three to one in favour of the secondary productivity. When both communities are combined, the difference does not vary from that of PLC.

All the calculations concerning the requirements of the carnivores were made according to the equations from Damuth (1993) and Peters (1983). The results obtained in our first analysis were those expected for mammals from the order Carnivora which is not recorded in South America prior to the late Miocene–Pliocene. As mentioned above, the Santacrucian carnivore niche was filled by marsupials and birds. Marsupials are also characterized by mean lower standard metabolism rates (SMRs) than most placental mammals (Dawson and Hulbert 1970), excluding xenarthrans; although some authors argued that lifestyle and diet may be more significant factors in determining standard metabolism rates in marsupials than ancestry (see McNab, 1989). Although the mean SMR value of marsupials is 30% below the mean value for placentals, McNab (2005) stated that Australian marsupials committed to carnivory have basal rates that vary from 82 to 96% of the value expected from mammals generally. This author also indicated that placentals belonging to the order Carnivora have higher basal metabolic rates than those of mammals generally, which means that marsupial carnivores should have basal metabolic rates lower than 82 to 96% , when compared to their placental counterparts. This should be taken into account for the correction factor applied to marsupial carnivores, since it may not have been that used by us, but may be lower. Tyndale-Biscoe (2005: 12) concluded that the lower SMR of living marsupials implies that they have lower food requirements and water turnover rates, which may confer special advantages in adverse conditions or arid environments. In any case, it is difficult to predict how this could affect the model (and empirical observations available are insufficient), as, other factors being equal, lower carnivore metabolisms and consequent lower requirements per individual may result in higher biomass of the marsupial carnivores.

Smaller than average populations or lower metabolic and turnover rates of herbivores, may also account for the disparity, although again the argument just discussed of the consequences of low metabolism as well as the lack of modern analogues calls for caution in the interpretations. About half of the species included in the herbivore guild were xenarthrans. Vizcaíno et al. (2006a) found that they have less tooth occlusal surface area available for triturating food than other placentals of similar size, and related this fact to the low basal metabolic rates characteristic of living xenarthrans. This implies that xenarthrans have required less energy than other placentals and, therefore, for a specific type of food, require lower intakes than other placentals of similar body mass.

Vizcaíno (2009) reasoned that, until about the time of the Great American Biotic Interchange (Webb and Marshall, 1982), medium to large body size guilds among South American faunas must have essentially been dominated by mammals of relatively low metabolic requirements. Besides the marsupials and xenarthrans recorded in Santacrucian levels, at least astrapotheres may have had low metabolism due to their large size and it may also be true for large notoungulates. Consequently, the Santacrucian may have been a "low-metabolism ecology" with no analogues among living mammalian communities, except to some extent to the marsupial's communities from Australia.

Once *Arctodictis munizi* is added, the communities become even more balanced. In CB there is no difference because that species was not recorded there, and hence not added. In PLC the secondary productivity is two-fold the carnivore requirements, and in the combination of both localities that difference is virtually the same as in PLC, though slightly higher.

The suggested lack of carnivores agrees with the observations of Croft (2001, 2006) on the "depauperate nature of the carnivore palaeoguild in South America" mentioned above. However, this condition could be more artificial than real. Croft (2001) analyzed several potential methodological and biological sources of errors on the environmental information that arise from his cenograms, considering especially that the causal nature of the apparent relationship between predators and prey is unknown (i.e. whether predator diversity directly depends on the diversity of prey and/or whether prey diversity is partly limited by the diversity of predators), and hypothesized that pre-interchange faunas could have had greater-than-expected numbers of medium-sized mammals due to the low diversity (and, perhaps, abundance) of mammalian predators. Thus, cenogram statistics computed for a pre-interchange fauna would suggest erroneously high amounts of rainfall (due to the greater-than-expected taxonomic richness of medium-sized mammals) and a possibly erroneous interpretation of a closed habitat (Croft, 2001, but see Croft and Townsend, 2005).

Prevosti and Vizcaíno (2006) provided a different vision on the relationships between taxonomic richness of prey (herbivores) and predators (carnivores), arguing against the use of allometric equations between living carnivore densities and body mass to estimate the densities of fossil communities. Following these authors, the available ecological information on living carnivores, demonstrates the presence of several factors affecting the densities of these mammals in a local scale: climate, prey density and availability, the presence of competitors and predators, epidemics, and population genetic diversity. They report a positive relationship between carnivore density and prey abundance for several carnivores in different habitats (Prevosti and Vizcaíno, 2006 and references therein). These interpretations are based on an exhaustive revision of the literature on the ecology of living carnivorous mammals. However, also based on comparisons with modern faunas, Croft (2006) sustains that South American faunas prior to the Great American Biotic Interchange should include approximately from two to fourteen times as many species of predators as are observed. In addition, predators are represented by remarkably few specimens. After excluding taphonomic biases as a source for this pattern, Croft (2006) considered competition with phorusrhacoid birds as another potential explanation, admitting that data are ambiguous to assert that the presence of these birds might have been a casual factor in the low diversity of pre-Great American Biotic Interchange mammalian predators. Instead, he proposed that the lesser degree of morphological diversity/specialization in their dentition relative to carnivorans may be a primary causal factor in their apparent low taxonomic diversity.

5. Final remarks

Our analysis provides support to the view of Croft (2001, 2006) of the depauperate carnivore paleoguild of the Santacrucian faunas, although perhaps in a less humid environment as proposed by Tauber (1997b). However, the taxonomic deficiency in mammalian carnivores does not strictly imply that there were not enough carnivores. We also considered several caveats to the approach to be addressed in the future, mainly the influence of basal metabolism in the energetic requirements and density of herbivores and non-mammalian carnivores, and different models of carnivore abundance that can be observed in Africa today.

Contrary to the expectations created by the monographs of the Reports of the Princeton University Expeditions to Patagonia edited by Scott between 1900 and 1932 (Simpson, 1948), e.g. those by Hatcher (1903), Scott (1903–1905, 1910, 1912, 1928), and Sinclair (1906, 1909), the Santacrucian localities from the lower member of the formation on the Atlantic coast between the rivers Coyle and Gallegos record a modest number of mammal species of above 10 kg of body mass. In the case of Campo Barranca, a locality that started to be systematically prospected a few years ago, this may be due to currently incomplete sampling or to taphonomic causes. This may account for the lack of mammalian carnivores and, more surprisingly, of glyptodonts. Additional collection effort could help to increase the number of taxa. In the case of Puesto Estancia La Costa, most of the main collections from Santa Cruz made at the end of the 19th century and the beginnings of the 20th century (MACN, YPM, FMNH) include many fossils collected by C. Ameghino, J.B. Hatcher, and others with geographic indications that suggest that the fossils may came from what Tauber (1997a,b) identified as Puesto Estancia La Costa. Although all those specimens could be included in the analysis, the increase in the number of taxa must be offset by the reduced reliability of the result: at that locality fossils are collected in the intertidal zone and, due to more than a century of erosion, we cannot be certain that we are collecting at the same rock levels. If the entire range of Santacrucian localities spans just a short interval of time, there could be some justification for lumping together all the levels, but such a choice would introduce a range of geographic variation in climate and productivity.

As indicated above, one of our main goals is to identify working hypotheses about the Santacrucian mammalian community to be tested using ecomorphological approaches. Some general hypotheses are: (1) the coexistence of so many different lineages of herbivores implies partitioning of vegetation as a food source, reflected in wide morphological variation in the masticatory apparatus; (2) there was competition for plant resources essentially at two levels: the ground — including some armadillos, glyptodonts, probably some sloths, ungulates and some rodents — and the trees — including most sloths, other rodents, primates and probably some ungulates — (see Croft and Anderson, 2008).

Particular hypotheses can be enumerated for the main lineages of Santacrucian herbivores and carnivores. For instance, within xenarthrans: (1) a wide morphological variation in the masticatory apparatus of the cingulates (armadillos and glyptodonts) reflects greater dietary diversity than in extant representatives and explains the coexistence of several taxa in the same area (see Vizcaíno et al., 2006b); and (2) the two basic patterns of mastication recorded in Santacrucian sloths (predominantly vertical in megatherioids and lateral in mylodontids), correlate with variation in food quality (see Bargo et al., 2009). Among ungulates, (3) the coexistence of such different lineages implies a partitioning of vegetation as a food source more pronounced than we see in modern African ungulates, and (4) different lineages developed masticatory mechanics comparable to those of living ungulates, rodents and lagomorphs. Other groups of herbivores not analyzed in this contribution should also be considered: (5) Santacrucian primates were folivorous and frugivorous; (6) Santacrucian rodents (caviomorphs) developed a diversity of diets similar to their living relatives. Among carnivores, (7) the borhyaenoid marsupials were the main predators in the vertebrate communities of the Santa Cruz Formation; (8) they were hypercarnivorous forms, which fed mostly on other mammals; (9) the mammalian carnivore guild was structured mainly by body size and locomotory habit differences (Argot, 2004; Ercoli and Prevosti, 2009a, b). Finally, within birds, the Ralliformes Cariamae (Phorusrhacidae and Cariamidae) were important predators in Santacrucian communities that competed with Borhyaenoidea for a wide range of prey items.

Other aspects of the palaeobiology and palaeoecology of the Santacrucian fauna seem promising. Using other methodologies could be useful to compare these and other fossil and recent faunas. For instance, comparing fossil predator/prey diversity and the distribution of body mass values with local (i.e., a community restricted to one locality or a restricted area) recent faunas through simple graphs (e.g., bivariate plots) could help to explore the predator/prey relationship and body mass pattern. This would avoid the need to use allometric formulas to infer population densities, and their other required parameters. Also, it would be useful to extend the analysis to all homeothermic vertebrates, evaluating how to get reliable estimates of basal metabolism rates for phorusrhacid birds. It is also crucial to evaluate how low metabolism, and/or the phylogenetic signal affects density. Finally, it would be beneficial to study temporal environmental changes through the Santa Cruz Formation and perform detailed taphonomic studies to evaluate the genesis of the assemblages.

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