10 Paleoecology of the Paucituberculata and Microbiotheria (Mammalia, Marsupialia) from the late Early Miocene of Patagonia

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Abstract

This chapter presents a paleoecological analysis of non-carnivorous Santacrucian marsupials of the orders Paucituberculata and Microbiotheria. Different ecological niches are inferred from estimates of body mass, diet, and locomotor behavior. Body masses were estimated using a regression analysis based on living marsupials. Possible dietary preferences were explored by an analysis of the development of molar shearing crests. Inferences about locomotor behaviors of some species with well-preserved postcranial skeletal remains were derived from a published morphofunctional analysis. From the wide range of estimated body masses and diet several niches were inferred: small- to medium-sized insectivores, small- to medium-sized insectivore–frugivores, and medium- to large-sized frugivores. According to our results, Paucituberculata and Microbiotheria of the Santa Cruz Formation constitute an ecologically diverse assemblage that inhabited forested habitats, developed under warm temperatures and seasonal rainfall. These forested habitats could have supported several non-carnivorous marsupial niches, offering diverse resources both in the spatial dimensions and in the trophic ones.

Resumen

En este capítulo se presenta un análisis paleoecológico de los marsupiales no carnívoros del Santacrucense pertenecientes a los órdenes Paucituberculata y Microbiotheria. Para establecer los distintos nichos ecológicos se analizaron las masas corporales, dietas y estrategias locomotoras. El tamaño corporal fue estimado a partir de una recta de regresión linear obtenida a partir de marsupiales actuales. Las posibles preferencias dietarias fueron exploradas mediante un análisis del grado de desarrollo de las crestas cortantes de los molares. Las estrategias locomotoras, en el caso de aquellas especies que poseen un esqueleto postcraneano bien preservado, fueron inferidas a partir de un análisis morfofuncional. A partir del análisis de los resultados de las masas corporales y la dietas, se reconocieron diversos nichos ecológicos: pequeños a medianos insectívoros, pequeños a medianos insectívoros-frugívoros y medianos a grandes frugívoros. Nuestros resultados nos permiten concluir que los Paucituberculata y los Microbiotheria de la Formación Santa Cruz constituyen un agregado ecológicamente diverso que habitó zonas boscosas, desarrolladas bajo un clima cálido y con lluvias estacionales. Estas zonas habrían ofrecido una amplia diversidad de recursos tanto espaciales como tróficos para los diversos nichos ecológicos de los marsupiales no carnívoros. Nuestra reconstrucción paleoambiental es compatible con la existencia de heterogeneidad ambiental durante el Santacrucense, inferencia esta derivada de otros indicadores climático-ambientales.

10.1 Introduction

During the Cenozoic, a high diversity of metatherians occupied a broad range of ecological niches in South America. This array included medium to large carnivorous and carnivorous–omnivorous (i.e. Sparassodonta; Prevosti *et al.*, Chapter 11), small granivorous (e.g. polydolopimorphian Argyrolagoidea; Goin *et al.*, in press), and several small to medium insectivorous and insectivorous–frugivorous species (e.g. didelphimorphian Didelphidae, Paucituberculata; Goin *et al.*, in press, Dumont *et al.*, 2000). All of the larger taxa are now extinct, and a few of the small- to medium-sized insectivorous, insectivorous–frugivorous, and carnivorous taxa (microbiotherians, paucituberculatans, and didelphids) survive to the present.

Paucituberculata and Microbiotheria are two major Marsupialia clades (Fig. 10.1). As a result of all current phylogenies (e.g. Amrine-Madsen *et al.*, 2003; Horovitz and Sánchez-Villagra, 2003; Phillips *et al.*, 2006; Asher *et al.*, 2004; Nilsson *et al.*, 2004; Beck, 2008; Meredith *et al.*, 2008), there is consensus on the close affinities between the extant microbiotheriid *Dromiciops gliroides* and the Australasian marsupials (Australidelphia; Szalay, 1982, 1994). However, the position of *D. gliroides* within Australidelphia is still controversial (Nilson *et al.*, 2010). On the other hand, most

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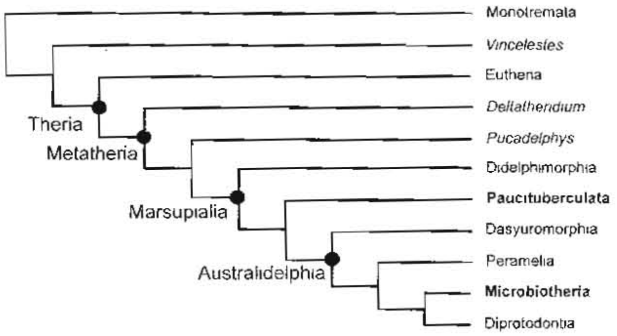

Fig. 10.1. Phylogenetic tree showing the relationships of living marsupial orders (modified from Horovitz and Sánchez-Villagra, 2003).

phylogenetic studies based on molecular or combined data (e.g., Nilson *et al.*, 2004; Asher *et al.*, 2004; Beck, 2008; Meredith *et al.*, 2008), as well as some morphological studies based on cranial, postcranial, and soft tissue anatomy (Horovitz and Sánchez-Villagra, 2003), indicate that Paucituberculata is the sister group of Australidelphia.

Microbiotherians and paucituberculatans are poorly represented in present-day ecosystems (Flores, 2006a, b; Patterson, 2007; Patterson and Rogers, 2007). The only extant microbiotherian is the so-called "monito del monte" (*Dromiciops gliroides*), a small insectivorous marsupial endemic to the temperate forests of southern Chile and Argentina, associated with the southern beech forests (*Nothofagus*) and South American mountain bamboos (*Chusquea*) (Hershkovitz, 1999). *Dromiciops gliroides* is the only South American marsupial reported to exhibit deep torpor or hibernation (Greer, 1966; Bozinovic *et al.*, 2004). In the summer season this species is active during the night, being a common mammal of the understory stratum (Rodríguez-Cabal *et al.*, 2008).

The living Paucituberculata include five species that are grouped in the genera *Caenolestes*, *Lestoros*, and *Rhyncholestes*, all belonging to Caenolestidae ("shrew opossums"). This clade has a disjunct Andean distribution that ranges from Venezuela to northern Peru (*Caenolestes*; Albuja and Patterson, 1996), central Peru and Bolivia (*Lestoros inca*; Anderson, 1997; Ramirez *et al.*, 2007) and southern Chile and Argentina (*Rhyncholestes*; Patterson and Gallardo, 1987; Birney *et al.*, 1996). Caenolestids have a wide latitudinal and altitudinal (up to 4000 meters above sea level) distribution, spanning several biomes including Páramo, Montane forest, and Valdivian forest. Extant caenolestids are small shrew-sized marsupials, which inhabit moist and dense vegetated microhabitats (Kirsh and Waller, 1979; Kelt *et al.*, 1994). The scanty ecological data reported in the literature indicate that caenolestids have a cursorial-leaping locomotion, and a primarily insectivorous diet (Kirsh and Waller, 1979; Barkley and Whitaker, 1984, Patterson and Gallardo, 1987; Patterson, 2007).

The fossil record of Paucituberculata and Microbiotheria indicates that these marsupials had a wider geographic distribution and higher taxonomic diversity than those of the present (Abello, 2007; Goin *et al.*, in press). The oldest-known Paucituberculata and Microbiotheria date from the Paleocene and include forms such as the paucituberculatan *Bardalestes* Goin, Candela, Abello and Oliveira, 2009 (Itaboraian Age, Argentina; Goin *et al.*, in press) and the microbiotherian *Mirandatherium* (Paula Couto, 1952) from Brazil (Itaboraian Age; Goin *et al.*, in press). Both groups achieved their highest taxonomic diversity in the Early Miocene Colhuehuapian and Santacrucian Ages, but the inferred cladogenetic events that gave rise to the Miocene forms seem to have occurred during the Oligocene (Abello, 2007; Goin *et al.*, 2010). By the Early Miocene, microbiotherians are represented by nine species belonging to Microbiotheriidae. At the same time, paucituberculatans are represented for 23 species grouped among Caenolestidae, Pichipilidae, Palaeothentidae, and Abderitidae.

Despite the abundant representation of small marsupials (particularly paucituberculatans) in the Early Miocene (Bown and Fleagle, 1993; Abello, 2007), they are mainly known by mandibular and maxillary remains and isolated teeth. Consequently, the reconstructions of certain paleoecological aspects (e.g. body size, diet) have been derived from the study of dental remains.

Several ecological niches have been identified among Paucituberculata (Dumont *et al.*, 2000): small insectivores (Caenolestidae and Pichipilidae), small- to medium-size insectivore–frugivores (Palaeothentidae), and small- to medium-size frugivores (Abderitidae). As yet only two specimens including postcranial and cranial remains are reported for Pancituberculata (Abello and Candela, 2010). These were referred to two palaeothentid species, *Palaeothentes minutus* Ameghino, 1887 and *Palaeothentes lemoinei* Ameghino, 1887, from the late Early Miocene (Santa Cruz Formation). Curso-saltatorial locomotor strategies were inferred for both species (Abello and Candela, 2010).

In this chapter we summarize previous paleoecological studies of Santacrucian Paucituberculata, and present the results of a new paleoecological analysis of Santacrucian Microbiotheria. Additionally, we evaluate the paleoenvironmental significance of non-carnivorous Miocene marsupials.

10.2 Santacrucian paucituberculatans and microbiotherians

During the South American Miocene, paucituberculatans and microbiotherians coexisted with other metatherians such as Sparassodonta, polydolopimorphian Argyrolagoidea, and Didelphimorphia. Paucituberculatans occur in most Miocene assemblages, but Argyrolagidae and Didelphimorphia are rare or absent as is the case for the late Early Miocene fauna of Santa

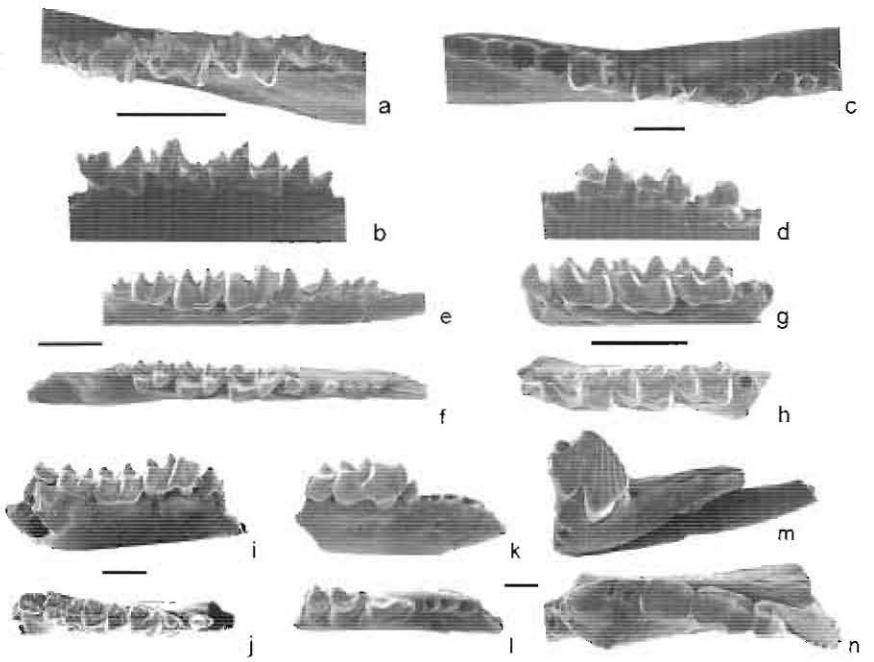

Fig. 10.2. Dentition of selected Paucituberculata and Microbiotheriidae species of the Santa Cruz Formation. a, b, *Microbiotherium acicula* (MACN-A 5727) left mandibular fragment with m1–4 in labial (a) and occlusal (b) views. c, d. *Microbiotherium gallegosense* (type AMNH 9591) right mandibular fragment with p3–m3 in labial (c) and occlusal (d) views. e, f. *Stilotherium dissimile* (type MACN-A 8464) right mandibular fragment with i2, i3 alveolous, three one-rooted teeth and p2–m4 in labial (e) and occlusal (f) views. g, h, *Phonocdromus gracilis* (type MACN-A 8457). left mandibular fragment with p3–m3 in labial (g) and occlusal (h) views. i, j, *Palaeothentes minutus* (MACN-A 5591–5518a), right mandibular fragment with p3–m4 in labial (i) and occlusal (j) views. k, l, *Acdestis owenii* (type MACN-A 1379) mandibular fragment with i2, four alveoli of one-rooted teeth, complete p3–m1 and m2 trigonid in labial (k) and occlusal (l) views. m, n. *Abderites meridionalis*, (m) (MLP 55-XII-13–145) mandibular fragment with i1, four alveolous of one-rooted teeth and p3–m1 in labial view, (n) (type MACN-A 12) mandibular fragment with m1–3 and m4 alveolous in occlusal view. Scale bar, 2 mm.

Cruz beds. To date, microbiotherians (Fig. 10.2a–d) and paucituberculatans (Figs. 10.2e–n and 10.3) are the only non-carnivorous metatherians recorded in the Santa Cruz Formation. Metatherians of this formation were first described by Ameghino (1887, 1891). Sinclair (1906) and Marshall (1976a, 1980, 1982) made significant contributions to the knowledge of the diversity of Santacrucian paucituberculatans and microbiotheriids. Recent revisions include those of Bown and Fleagle (1993), Tauber (1997), Abello (2007), and Abello and Rubilar-Rogers (in press). An updated taxonomic list and the records of paucituberculatans and microbiotheriids from localities of the Santa Cruz Formation are presented in Appendix 10.1.

10.3 Materials and methods

The material studied is listed in Appendix 10.2.

10.3.1 Abbreviations

The generalized metatherian dental formula is: I/i 5/4, C/c 1/1, P/p 3/3, M/m 4/4.

Institutional abbreviations

MACN, Museo Argentino de Ciencias Naturales "B. Rivadavia," Buenos Aires, Argentina. MACN-A, Colección Nacional Ameghino.

MLP, Museo de La Plata, La Plata, Argentina.

AMNH, American Museum of Natural History, New York, EEUU.

MPM-PV, Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina.

10.3.2 Methodology

To estimate body masses and infer dietary preferences of Santacrucian non-carnivorous marsupials, we follow the methodologies of Dumont *et al.* (2000). In the context of an analysis of dietary preferences of Paucituberculata, Dumont *et al.* (2000) studied all available Santacrucian species. Here we summarize the results of these dietary reconstructions, and apply the same methodology to the Santacrucian Microbiotheriidae. In contrast to Dumont *et al.* (2000), we follow Abello and Rubilar-Rogers (in press) in considering *A. meridionalis* Ameghino, 1887 to be a different species from the Colhuehuapian *Abderites crispus* Ameghino, 1902.

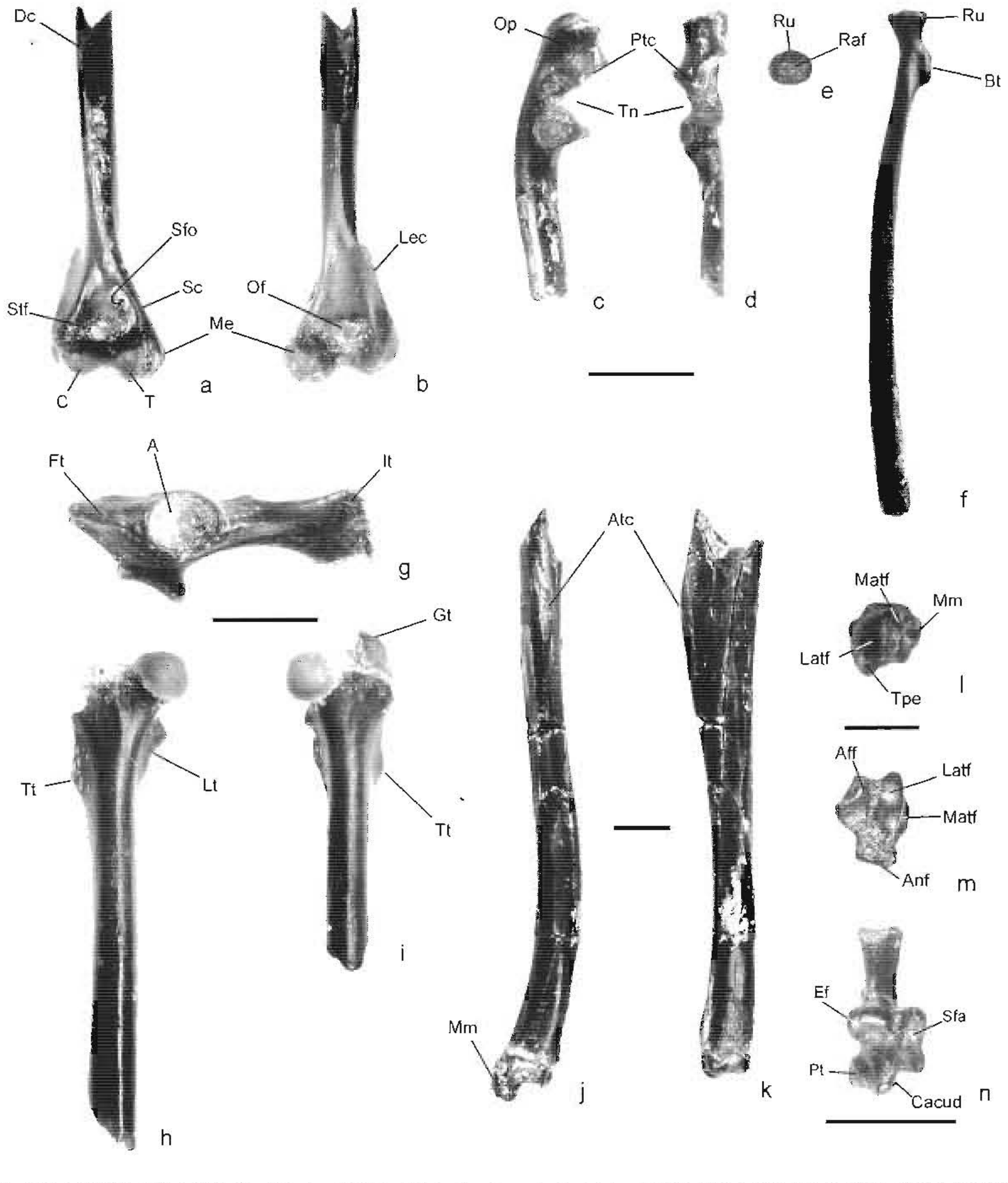

Fig. 10.3. Postcranial skeleton of *Palaeothentes* species. *Palaeothentes minutus*: a, b, right humerus (MACN-A 5619–5639c) in anterior (a) and posterior (b) views; c, d, right ulna (MACN-A 5619–5639e) in lateral (c) and anterior (d) views. e, f, Right radius (MACN-A 5619–5639d) in proximal (e) and medial (f) views. g, Pelvis (MACN-A 5619–5639f) in lateral view; h, right femur (MACN-A 5619–5639g) in anterior view; i, left femur (MACN-A 5619–5639h) in anterior view. *Palaeothentes lemoinei* (MPM-PV 3494): j, k, left tibia in anterior (j) and lateral (k) views; l, right tibia in distal view; m, right astragalus in dorsal view. *Palaeothentes minutus* (MACN-A 5619–5639i); n, right calcaneum in dorsal view. Scale bar, 4 mm. Abbreviations: A. acetabulum; Aff, astragalofibular facet; Auf, astragalouavicular facet; Atc, anterior tibial crest; Bt, bicipital tuberosity; C, capitulum; Cacud, cuboid facet distal half; Dc, deltopectoral crest; Ef, ectal facet; Ft, femoral tubercle; Gt, great trochanter; It, ischial tuberosity; Latf, lateral astragalotibial facet; Lec, lateral epicondylar crest; Lt. lesser trochanter; Matf. medial astragalotibial facet; Me. medial epicondyle; Mm, medial malleolus; Of, olecranon fossa; Op, olecranon process; Pt, peroneal tubercle; Ptc, proximal trochlear crest; Raf, radial articular facet for the capitulum; Ru, radio-ulnar facet; Sc, supracondyloid crest; Sfa, sustentacular facet; Sfo, supracondyloid foramen; Stf, supratrochlear foramen; T, trochlea; Tn. trochlear notch; Tpe. tibial posterior extension; Tt, third trochanter.

Regarding the locomotor habits of *Palaeothentes* species, we present here a synthesis of Abello and Candela's (2010) main results.

Body mass Body masses were estimated from the occlusal area (mesiodistal length × labiolingual breadth) of the second lower molar, using the linear regression equation

$$\ln \text{body mass} = 2.419 + (1.727 \times \ln \text{m2 area}) \qquad \text{(Eq. 10.1)}$$

derived by Dumont *et al.* (2000) for living marsupials. This equation included 27 extant marsupial species whose body masses range from approximately 10 to 1500 g, a wide range encompassing that of Santacrucian marsupials.

Locomotion and use of the substrate To assess the locomotor strategies of *Palaeothentes minutus* and *P. lemoinei*, Abello and Candela (2010) performed a morphofunctional analysis based on comparisons with living South American marsupials.

Palaeothentes minutus (MACN-A 5619–5639a–i) is the most important specimen available, being represented by the humerus, radius, ulna, femur, pelvis, and calcaneum (Fig. 10.3a–i, n). The postcranium of *P. lemoinei* (MPM-PV 3494) preserves the humerus, ulna, pelvis, tibiae, and astragalus (Fig. 10.3j–m). The postcranial features with functional significance, preserved in these fossils, were compared to those of extant marsupials having various locomotor behaviors. Abello and Candela (2010) evaluated traits functionally related to different movements (e.g. flexion/extension, pronation/supination). In this context, special attention was paid in the analysis of articular surfaces (e.g. elbow, cruroastragalar, and hip joints) and areas of muscular attachment. *Caenolestes fuliginosus* and the didelphids *Metachirus nudicaudatus* and *Monodelphis dimidiata* were considered as terrestrial model species. The didelphid *Didelphis aurita* and the microbiotheriid *Dromiciops gliroides* were included as scansorial and arboreal models, respectively.

Feeding habits The dietary habits of the Santacrucian microbiotheriids were investigated following the method of dietary reconstructions proposed by Strait (1993a, b). This approach relies on the assumption that the development of shearing crests on the molars should reflect the physical properties of the foods that must be comminuted (Strait, 1993b; Kay and Hylander, 1978).

Two molar shearing ratios are calculated to discriminate frugivorous from faunivorous small-bodied taxa in a comparative framework with extant mammals whose dietary preferences are well known. Both ratios consider the sum of six shearing crests (crests 1–6 of Kay and Hiiemae, 1974; Fig. 10.4), and two size surrogates: m2 length and the square root of m2 area. The shearing ratio based on area (SRA) is the sum of lengths of crests 1–6 divided by the square root of tooth area, and the shearing ratio based on length (SRL) is the sum of lengths of crests 1–6 divided by molar length.

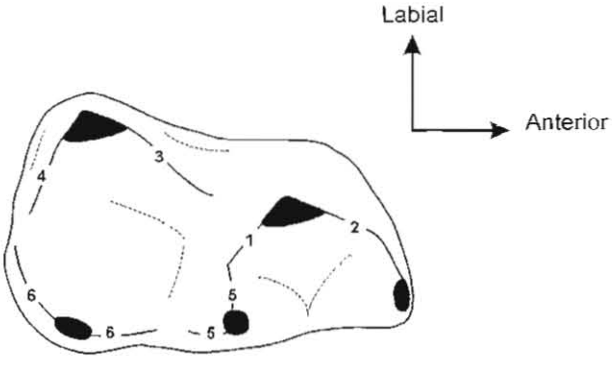

Fig. 10.4. Occlusal view of left lower second molar showing the shearing crests 1–6 (Kay and Hiiemae, 1974) measured in this study.

The present analysis is based on those performed by Dumont *et al.* (2000) for paucituberculatans, who included the following living marsupials as models: four insectivores (the paucituberculatans *Lestoros inca* and *Caenolestes caniventer*, the dasyurids *Antechinus stuartii* and *Sminthopsis crassicaudata*), and two frugivores (the petaurids *Petaurus breviceps* and *Acrobates pygmaeus*). To broaden the comparative sample of extant marsupials, we included here the insectivorous microbiotheriid *Dromiciops gliroides* (Patterson and Rogers, 2007, and references therein).

Living marsupials, especially those of the Australasian region, have a broad dietary diversity including a wide range of food, such as vertebrate and invertebrate prey, vegetative and reproductive tissues of plants, plant exudates, and fungi (Hume, 2006). For the living marsupials several feeding categories may be established (Lee and Cockburn, 1985); however, the definition of strict trophic categories is imprecise (Vieira and Astúa de Moraes, 2003). Taking into account this constraint, we have followed Dumont *et al.* (2000) and used broad dietary categories to infer the diet of the Santacrucian marsupials. These authors used two categories, faunivores and frugivores, but we have preferred to use "insectivores" instead of "faunivores" for two reasons: (1) faunivores is an equivocal term, because it has been used to refer to those carnivorous mammals that eat vertebrates (e.g. Hume, 2003), as well as to those that eat invertebrates (e.g. Heesy, 2008); and (2) all the living species used by Dumont *et al.* (2000) to represent "faunivores" are actually insectivores (= insectivore/omnivore of Lee and Cockburn, 1985) because they feed primarily on arthropods (which may be consumed as adults or juvenile stages) but their diet may include, in some cases, vegetable matter and fungi. On the other hand, the marsupials used by Dumont *et al.* (2000) to represent frugivores feed mainly on plant materials, such as nectar, pollen, exudates (gum, sap, and sugar encrustations produced by sap-sucking insects and known as "manna") and fruits, but their diet may be complemented with insects when seasonally available. In this context, this category includes those exudate feeders/insectivores and frugivores/omnivores of Lee and Cockburn (1985). Finally, Dumont *et al.* (2000) also found a third feeding category (i.e. "mixed feeders" or "frugivorous–faunivorous"), formed by those marsupials that emerge as frugivorous or "faunivorous" depending on shearing ratio (i.e. the caenolestid *Stilotherium dissimile* Amegino, 1887, the abderitid *Pitheculites minimus* Ameghino, 1902, and the palaeothentid *Acdestis lemairei* Bown and Fleagle, 1993). We prefer to use insectivore–frugivore because both "mixed feeders" and "frugivorous–faunivorous" are ambiguous terms. The former is more frequently used to designate those herbivorous mammals that are intermediate between grazers and browsers, eating both browse and grass (e.g. the red deer *Cervus elaphus*, the impala *Aepyceros melampus*, the nyala *Tragelaphus angasi*: Staver *et al.*, 2009). The difficulty with the latter is the ambiguity in the usage of faunivore, as explained above.

Measurements of lower second molar maximum length, maximum width, and the lengths of six of its shearing crests were made on a Carl Zeiss Microscope using a measurement module (Axiovision 4.2 and 4.6).

10.4 Results

10.4.1 Body mass

The estimated body masses were 20 g for *Microbiotherium acicula*, 40 g for *M. patagonicum*, 61 g for *M. tehuelchum*, 147 g for *M. gallegosense*, and 487 g for *Abderites meridionalis*. Table 10.1 shows the current body mass estimations for microbiotherians and *A. meridionalis*, and those previously presented by Dumont *et al.* (2000) for paucituberculatans, with the exception of *A. meridionalis* (see Methodology).

10.4.2 Locomotion and use of substrate

The results of comparative analysis with extant marsupials showed that several postcranial features of *Palaeothentes* species resemble those of modern curso-saltatorial forms

Table 10.1. *Body mass estimates and diet of Santacrucian Microbiotheriidae and Paucituberculata*

	Sample size	m2 area (mm^2)	Body mass	Diet
Microbiotheria				
Microbiotheriidae				
Microbiotherium acicula	1	1.38	20 g	Insectivorous
Microbiotherium patagonicum	1	2.07	40 g	Insectivorous
Microbiotherium tehuelchum	1	2.66	61 g	Insectivorous
Microbiotherium gallegosense	1	4.44	147 g	Insectivorous–frugivorous
Paucituberculata				
Caenolestidae				
Stilotherium dissimile	3	1.48	37 g	Insectivorous–frugivorous
Pichipilidae				
Phonocdromus gracilis	2	1.04	28 g	Insectivorous
Palaeothentidae				
Palaeothentes aratae	13	11.34	860 g	Frugivorous
Palaeothentes minutus	112	3.06	82 g	Insectivorous
Palaeothentes intermedius	30	4.67	192 g	Insectivorous
Palaeothentes lemoinei	28	7.18	425 g	Insectivorous
Palaeothentes pascuali	6	2.25	38 g	Insectivorous
Acdestis owenii	113	6.71	344 g	Frugivorous
Acdestis lemairei	18	5.13	256 g	Insectivorous–frugivorous
Abderitidae				
Abderites meridionalis	15	8.86	487 g	Frugivorous

The sample size and mean m2 area (mm^2) from which the body mass was reconstructed are presented. Inferred diet (Diet) is based on shearing ratio and body mass data.

such as *Caenolestes fuliginosus* and *Metachirus nudicaudatus* (Abello and Candela, 2010). Characteristics of the forelimbs include, among other features, a deep and high humeral trochlea (Fig. 10.3a), a deep olecranon fossa (Fig. 10.3b), and mediolaterally broad proximal trochlear crest (Fig. 10.3c, d). These features indicate a well-stabilized elbow joint. The short lateral epicondylar crest (Fig. 10.3b) and the suboval radial head (Fig. 10.3e) suggest that pronation–supination was limited (Abello and Candela, 2010: 1520). The pelvis, better preserved in *P. minutus*, shows a restrictive acetabulum (i.e. tightly articulating; Szalay and Sargis, 2001), lengthened ischium, and prominent femoral tubercle as well as ischial tuberosity (Fig. 10.3g). The morphology of the pelvis indicates a high stability at the ilio-femoral joint and an increased mechanical advantage of the flexors and extensors of the hip (i.e. *rectus femoris* and hamstring muscles), which are well developed in saltatorial species (Argot, 2003a). The greater trochanter of the femur projects beyond the proximal surface of the femoral head (Fig. 10.3i), indicating that the gluteal muscles were favorably positioned to produce fast extension at the hip joint, as occurs in agile and leaping species. Additionally, the hind limbs of *Palaeothentes* species, like those of curso-saltatorial forms, have features associated with marked stability for flexion and extension in the parasagittal plane. Among these functionally significant traits are the right angle between the medial and lateral astragalotibial facets at the cruroastragalar joint (Fig. 10.3l, m), and the conformation of the transverse tarsal joint, characterized by the distal and proximal calcaneo-cuboid facet forming a right angle (Fig. 10.3n).

10.4.3 Feeding habits

Plots of SRL and SRA show the separation between extinct and extant frugivorous and insectivorous species (Fig. 10.5). Both ratios indicate that most extinct microbiotheriids were insectivorous. *Microbiotherium acicula* is the microbiotheriid with the highest SRA and SRL values, equaling the living insectivorous *Caenolestes caniventer* and *Sminthopsis crassicaudata* in SRA ratio. The SRL value of *Microbiotherium patagonicum* is close to that estimated for *Dromiciops gliroides*, while *M. tehuelchum* and *M. gallegosense* present lesser SRL values than *D. gliroides* and *M. acicula*, indicating a less shearing development in these species. *Microbiotherium gallegosense* has an SRA value comparable to those of the living Australian frugivores *Petaurus breviceps* and *Acrobates pygmaeus*. However, *M. gallegosense* clusters with the modern insectivores based on SRL ratio (Fig. 10.5b).

Among paucituberculatans, three species (*Abderites meridionalis*, *Acdestis owenii* Ameghino, 1887, and *Palaeothentes aratae* Ameghino, 1887) cluster with modern frugivores on the basis of SRA and SRL ratios. Conversely, *Phonocdromus gracilis* Ameghino, 1894 (Fig. 10.2g, h) and the palaeothentids *Palaeothentes pascuali* Bown and Fleagle, 1993, *P. minutus*, *P. intermedius* Ameghino, 1887, and *P. lemoinei* cluster with the living insectivores. Finally, the caenolestid *Stilotherium dissimile* (Fig. 10.2e, f) and the palaeothentid *Acdestis lemairei* are classified as frugivorous or insectivorous depending on shearing ratio (i.e. as insectivore–frugivore, Fig. 10.5a, b).

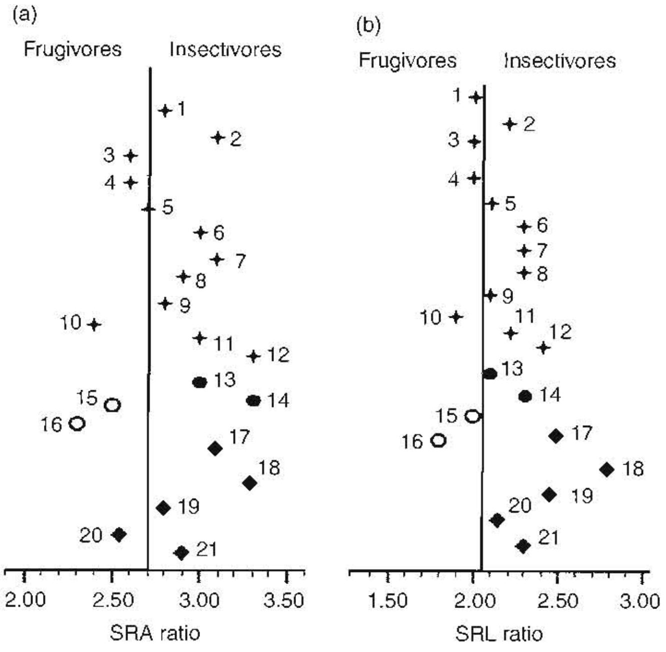

Fig. 10.5. Partition between frugivorous and insectivorous taxa based on SRA (a) and SRL (b) ratios. Paucituberculatans (crosses), petaurids (filled circles), dasyurids (open circles), microbiotherids (diamonds). Species are: 1, *Stilotherium dissimile*; 2, *Phonocdromus gracilis*; 3, *Abderites meridionalis*; 4, *Acdestis owenii*; 5, *Acdestis lemairei*; 6, *Palaeothentes minutus*; 7, *Palaeothentes pascuali*; 8, *Palaeothentes intermedius*; 9, *Palaeothentes lemoinei*; 10, *Palaeothentes aratae*; 11, *Lestoros inca*; 12, *Caenolestes caniventer*; 13, *Antechinus stuartii*; 14, *Sminthopsis crassicaudata*; 15, *Petaurus breviceps*; 16, *Acrobates pygmaeus*; 17, *Dromiciops gliroides*; 18, *Microbiotherium acicula*; 19, *Microbiotherium patagonicum*; 20, *Microbiotherium gallegosense*; and 21, *Microbiotherium tehuelchum*.

10.5 Discussion

10.5.1 Body mass

In a study of extant Neotropical marsupials, Birney and Monjeau (2003) analyzed the distribution of body size among species and established three size categories: (a) small-sized (less than 100 g); (b) medium-sized (from 100 to 499 g); and (c) large-sized (500 g or more). Taking into account these size categories, we found that Santacrucian microbiotheriids were mainly small-sized, with estimated body masses ranging from 20 g in *Microbiotherium acicula* to 147 g in *M. gallegosense* (Fig. 10.2c, d). Santacrucian paucituberculatans show a much greater body-mass range, extending from 13 g in *Phonocdromus gracilis* to 800 g in *Palaeothentes aratae*, and with more than half of the species being small- to medium-sized (Table 10.1).

Throughout the Cenozoic, most South American metatherians were small- to medium-sized (see Goin, 2003). In extant faunas, small- to medium-sized marsupials represent about 90% of the marsupial fauna of the Americas (see Birney and Monjeau, 2003), and they are also abundant in the marsupial fauna of Australasia (Dickman and Vieira, 2006). Our results are in agreement with this pattern, because 52% of the Santacrucian marsupial species are small- to medium-sized (nine paucituberculatans plus four microbiotherian species; see Table 10.1), and 48% are large (one paucituberculatan species plus 11 sparassodont species; see Table 10.1 and Prevosti *et al.*, Chapter 11).

Santacrucian paucituberculatans and microbiotheriids show a body mass overlap in the small and medium size categories (Fig. 10.6a, c). Nevertheless, the differential use of space and food resources may have minimized or avoided competition among species of similar body mass, as in extant marsupial assemblages (Charles-Dominique *et al.*, 1981; Charles-Dominique, 1983; Vieira and Monteiro-Filho, 2003).

10.5.2 Locomotion and use of the substrate

Locomotor strategies constitute an important dimension of a species' niche. For extinct mammals, locomotion may be inferred from fossil postcranial remains, and have implications for species paleoecology. Unfortunately, only two skeletons of non-carnivorous Santacrucian marsupials are known. Both skeletons (pertaining to two different palaeothentid species) were recently analyzed by Abello and Candela (2010) who paid particular attention to the reconstruction of locomotor pattern. As noted earlier, in terms of functionally significant features, the major similarities were found with the extant marsupials *Caenolestes fuliginosus* and *Metachirus nudicaudatus*. The latter is the most terrestrial didelphid (Miles *et al.*, 1981; Delciellos and Vieira, 2006, 2009). This marsupial inhabits a wide range of forest habitats (Miranda *et al.*, 2009), from open scrub

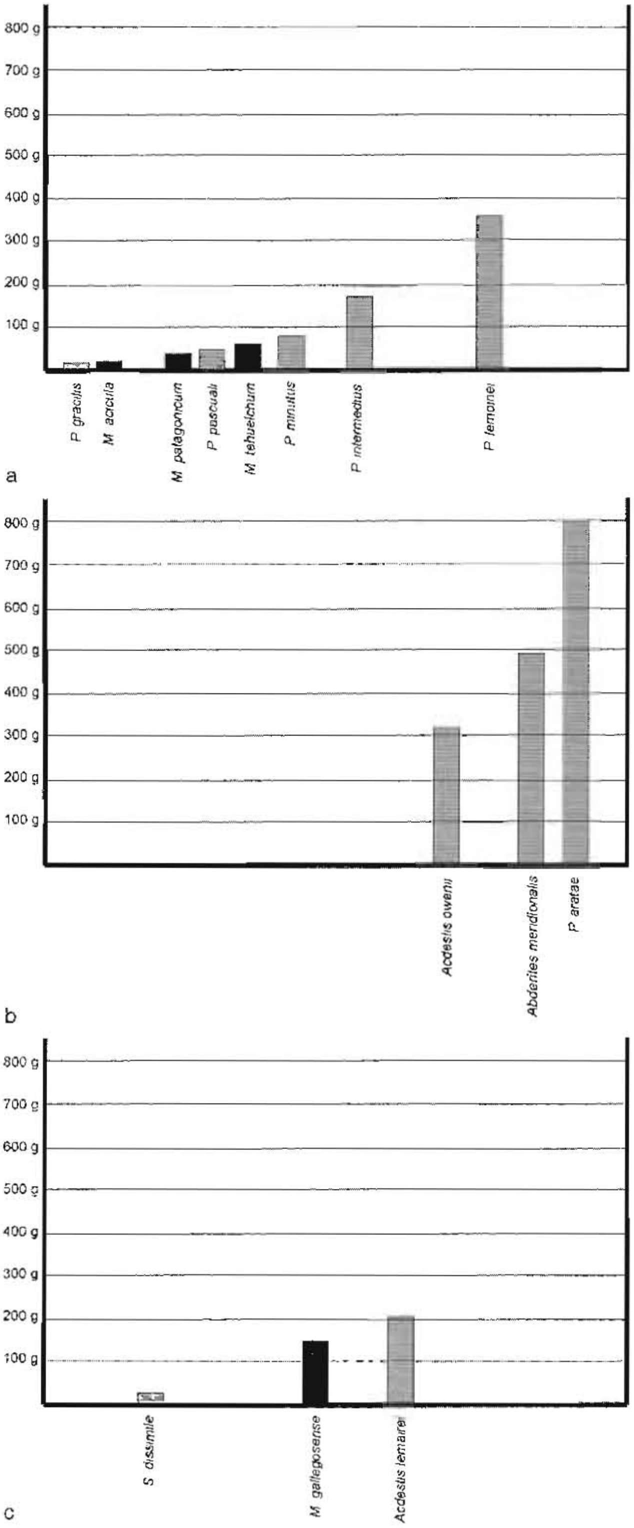

Fig. 10.6. Body mass averages of insectivorous (a), frugivorous (b), and insectivorous–frugivorous (c) non-carnivorous marsupials of Santa Cruz Formation. Gray bars: paucituberculatans; black bars: microbiotheriids. Values from Table 10.1.

vegetation (Miles *et al.*, 1981) to lowland and hillside woodlands (Moraes, 2004). In the wild it was observed bounding on the ground, swiftly negotiating obstacles at high speed (Miles *et al.*, 1981). *Caenolestes* species occur in the Andean highlands biomes such as Montane and Cloud forests, and Páramo. In these biomes caenolestids inhabit forests with or without dense undergrowth, and the grassland–forest ecotone (Kirsh and Waller, 1979; Albuja and Patterson, 1996). *Caenolestes* and its relative *Lestoros* can leap at high speed using anterior and posterior limbs simultaneously (Kirsh and Waller, 1979).

Locomotor behaviors of *M. nudicaudatus* and caenolestids have clear anatomical correlates in their postcranial skeletons (Grand, 1983; Argot, 2003a, b), a particularly important aspect for functional interpretations in fossil species. *Palaeothentes* species exhibit enhanced joint stability and parasagittal movement (Abello and Candela, 2010). Additionally, features associated with fast movements and leaping have been identified. In conclusion, *P. minutus* and *P. lemoinei* were probably agile species with running and leaping abilities resembling *Caenolestes*, *Lestoros*, and *Metachirus*.

Even though the locomotor strategies described by Abello and Candela (2010) were established for only two *Palaeothentes* species, it may be speculated that other species of the genus, such as *P. pascuali* and *P. intermedius*, may have had similar locomotor abilities. In addition, it is possible that scansorial or arboreal locomotor behaviors evolved among non-carnivorous Santacrucian marsupials.

We note that the ecological diversity of non-carnivorous Santacrucian marsupials evaluated here is similar to that of current tropical habitats of South America (see below). In extant ecosystems, ecological diversity is positively correlated with habitat complexity (i.e. with the development of vertical strata in a habitat; August, 1983). In the case of Santacrucian marsupials, the ecological diversity inferred here would seem to reflect a vertical heterogeneity. In this context, it is possible to infer that the vertical space of these habitats could be exploited by Santacrucian marsupials through scansorial and/or arboreal habits. Vertical space offers an additional dimension for niche partitioning, and hence the possibility of more species coexisting in the same area (Miles *et al.*, 1981; Vieira and Monteiro-Filho, 2003; Croft and Eisenberg, 2006 and references therein).

10.5.3 Feeding habits

According to the crown morphology of its molars, Miocene microbiotheriids were considered insectivores or insectivores/frugivores (Pascual and Bond, 1986; Goin, 1997). Based on an analysis of molar wear facets, Goin *et al.* (in press) concluded that Early Oligocene Patagonian members of this family (including *Microbiotherium*, a genus that we analyzed in this study) were insectivores.

According to our results, Miocene microbiotheriids also were mainly insectivores. Only one species, *M. gallegosense*, has shearing ratios that indicate a more limited shearing component, suggesting an insectivorous–frugivorous diet (Fig. 10.5a, b). *Microbiotherium acicula* is the most extreme insectivorous species, showing the highest SRL and SRA values. *Microbiotherium patagonicum* is closer to the extant *Dromiciops gliroides* in SRL values, and it achieved a similar degree of molar crest development as in the living species.

In our analysis, *D. gliroides* is grouped with insectivorous species (Fig. 10.5a, b). This result is consistent with the information of its main dietary preferences in the wild. Analysis of stomach contents indicated that this species feeds primarily on arthropods and other invertebrates (Mann, 1955; Meserve *et al.*, 1988). However, it also feeds seasonally on fruits (Amico *et al.*, 2009). This strategy could be extrapolated to Santacrucian microbiotheriids, as insectivores may consume plant material, either regularly or seasonally, when prey species are scarce or unavailable (Hume, 2003).

According to molar crown morphology, Miocene paucituberculatans were considered insectivores, insectivores–frugivores, and insectivores–phytophages (e.g. Ortiz-Jaureguizar, 2003). Our analysis corroborates this inference, showing that insectivores are more diverse (five species) than insectivore–frugivores and frugivores (including the insectivorous–phytophagous category of Ortiz-Jaureguizar, 2003; see above) (Table 10.1). As Dumont *et al.* (2000) pointed out, folivory seems not to have evolved in paucituberculatans, as no taxon with high shearing ratios has an estimated body mass higher than 600 g (Smith and Lee, 1984).

Most insectivorous paucituberculatans differ markedly in body mass (e.g. *Palaeothentes minutus*, *P. intermedius*, and *P. lemoinei*), suggesting that ecological separation among them may have been achieved by differences in dietary composition and/or consumption of prey of different body size. In living insectivores, such as dasyurid marsupials and soricid placentals, there is a positive correlation between body size of predators and their prey (Fisher and Dickman, 1993; Churchfield *et al.*, 1999). Even so, both small and large dasyurids can exploit a relatively large range of prey sizes, and there is no physical constraint on the size of prey consumed. Consequently, dasyurid species maximized their rates of energy intake by feeding on prey of a selected size (Fisher and Dickman, 1993). Thus, larger dasyurids prefer larger invertebrates because of greater energy return per prey item; conversely, for the smaller dasyurids prey consumption requires more chewing time, and this could result in a fall in the rate of energy intake from each prey (Fisher and Dickman, 1993). Despite small differences in body size and overall ecology, niche overlap is minimized in shrews as they differ in terms of the

Fig. 10.7. Life reconstructions. a, *Abderites meridionalis* and b, *Palaeothentes minutus*. Drawing by Pablo Motta.

percentage of several invertebrate prey in the diet (Churchfield *et al.*, 1999). We expect that dietary composition (as it covaries with body size) would have produced niche separation among extinct insectivorous paucituberculatans.

As mentioned above, the body mass of Santacrucian microbiotheriids and paucituberculatans overlaps to some degree in the small to medium size range (Fig. 10.6a), initially suggesting that some niche overlap may have occurred. However, differences in body size and molar morphology suggest that niche overlap was, in fact, minimal, and it is also possible that differences occurred not only in diet composition, but also in foraging mode (Sanson, 1985; Churchfield and Sheftel, 1994; Churchfield *et al.*, 1999).

Frugivorous and insectivorous–frugivorous marsupials analyzed here do not exhibit body mass overlap (compare Fig. 10.6b with 10.6c). Frugivorous species are paucituberculatans belonging to Palaeothentidae (*Palaeothentes aratae* and *Acdestis owenii*, Fig. 10.2k, l) and Abderitidae (*Abderites meridionalis*, Figs. 10.2m, n and 10.7a), which are quite distinct in dental morphology (Abello, 2007). The dentition of Abderitidae is characterized by the presence of well-developed lophs and a plagiaulacoid complex (Simpson, 1933; Ortiz-Jaureguizar, 2003). The plagiaulacoid complex of *Abderites* was considered by Dumont *et al.* (2000) as a dietary indicator in addition to body mass and extent of molar shearing. According to their analysis, occlusion between P3 and m1 in *Abderites* was a shearing complex that operated in a manner similar to that of living Australian phalangerids such as *Phalanger*, but dissimilar to those of other mammals with plagiaulacoid dentition such as certain Cretaceous to Early Eocene multituberculates (e.g. the cimolodontan *Ptilodus* Cope, 1881) and North American Paleocene plesiadapiform primates (e.g. *Carpodaptes* Matthew and Granger, 1921). In the multituberculates and plesiadapiforms, the shearing teeth mainly exhibit apical wear, because the lower cutting teeth become worn when the food is ground against a cuspate upper tooth. In contrast, in *Phalanger*, and probably also in *Abderites*, the food items are cut between the upper and lower teeth as they shear across one another in a scissor-like fashion (Dumont *et al.*, 2000). A shearing complex similar to that of the abderitids occurs in many extant Diprotodonta, including the *Phalanger* already mentioned as well as *Burramys* and the Potoroidae *Hypsiprymnodon* and *Bettongia*. Related to their function, these dental modifications are adequate to break open food items with a hard covering (Dimpel and Calaby, 1972; Parker, 1973).

On the other hand, *Palaeothentes aratae* and *Acdestis owenii* have a strong shearing crest (paracrista) on m1 (Fig. 10.2k, l), but they lack a plagiaulacoid dentition and lophs. These differences suggest that frugivorous paucituberculatans were distinct not only in body mass but in their diets as well (Ortiz-Jaureguizar, 2003).

10.5.4 Paleoenvironmental implications

From the wide range of estimated body masses and diet of non-carnivorous Santacrucian marsupials, several ecologic niches were reconstructed: small- to medium-sized insectivores, and small to large frugivores and insectivores–frugivores. In regard to a paleoecological reconstruction, this ecological diversity suggests the existence of forested habitats that could have supported the diverse marsupial niches. In modern ecosystems, and particularly in tropical forests, high values of mammalian species richness arise from habitat heterogeneity, mainly owing to the partitioned vertical space (August, 1983; Bakker and Kelt, 2000).

Species richness also tracks plant productivity, with higher productivity leading to more species (Kay *et al.*, 1997).

Paleoenvironmental inferences can also be advanced by analyzing the trophic guild structure of Santacrucian marsupials. In a macroecological study of Neotropical marsupials, Birney and Monjeau (2003) evaluated the latitudinal variation among several biological characters, such as trophic guild structure, habitat use, and body size. Taking into account that latitude is a surrogate for physical environmental variables such as temperature and precipitation, the trophic guild structure of Santacrucian marsupials may offer clues to the Santacrucian paleoenvironments. According to Birney and Monjeau (2003), three guilds were considered: frugivores, carnivores, and insectivores. Current carnivorous marsupials include, among others, the didelphids *Didelphis*, *Lutreolina*, and *Philander*, all of them having body masses less than 2 kg. In the Santacrucian assemblage, carnivores with body masses less than or equal to 2 kg include the sparassodonts *Sipalocyon gracilis* Ameghino, *S. obusta* Ameghino, *Pseudonotictis pusillus* Ameghino, and *Perathereutes pungens* Ameghino (see Prevosti *et al.*, Chapter 11). Thus, small carnivores represent 22% of the Santacrucian marsupial species richness, insectivore–frugivores plus frugivores 33%, and insectivores 45%. Comparing the trophic guild structure of Santacrucian marsupials with those of the modern Neotropics, we find that in the Santacrucian fauna there is a relatively high percentage of frugivores in relation to carnivores, a ratio that occurs at low latitudes in the extant marsupial faunas of South America. Birney and Monjeau (2003) concluded that the thermal range (i.e. the difference between mean maximum extreme temperatures and mean minimum extreme temperatures) is the best predictor of the proportion of frugivores and carnivores. Closer to the equator, the narrower thermal range allows year-long availability of fruits, and the percentage of frugivores is higher than at high latitudes. Additionally, differences in precipitation (i.e. seasonal rainfall) seem to be another important factor influencing the abundance of frugivores (Birney and Monjeau, 2003). If we consider this last factor, the sharp differences between dry and wet seasons in the tropics would have allowed more diversification in the trophic niche than more constant precipitation. On the basis on these ecological similarities, we can infer that Santacrucian marsupials lived in relatively warm climates, but with seasonal rainfall. However, it should be kept in mind that taphonomic bias and time averaging are common factors that affect the composition of fossil assemblages. Consequently, in the absence of a precise evaluation of the incidence of these biases, the inferences derived from a fossil assemblage have a less heuristic value that those based on living assemblages.

In summary, the ecological characteristics of non-carnivorous marsupials of the Santacrucian suggest that they lived in forested habitats developed under warm temperatures and rain seasonality. According to the fossil record of vascular plants, the distribution of megathermal and mesothermal angiosperms expanded their distribution at middle–high latitudes of Patagonia during the Late Oligocene to Early Miocene (Barreda and Palazzesi, 2007; Brea *et al.*, Chapter 7). Nevertheless, the first records of some shrubby and herbaceous angiosperms in southern South America suggest that the vegetation acquired a more complex physiognomy than that of the Early Oligocene (Barreda and Palazzesi, 2007). During the Early Miocene, xerophytic (or mesophytic) vascular plants were dominant in Patagonia, and the development of all these specialized communities was probably related to a water deficit in open forest regions or marginal marine areas. During the late Early Miocene, rainforest trees may have formed riparian or gallery forests in central Patagonia, while drier conditions would have prevailed in lowland areas (Barreda and Palazzesi, 2007). Finally, during the latest Early Miocene, xerophytic elements suffered a geographic retraction in Patagonia, with an increase of megathermals and a dominance of aquatic herbs and hydrophytes. Forests persisted across extra-Andean Patagonia until about the Middle Miocene (Barreda, 2002; Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2007).

If we consider the ecological information provided by all the Santacrucian mammals (Prevosti *et al.*, Chapter 11; Vizcaíno *et al.*, Chapter 12; Bargo *et al.*, Chapter 13; Cassini *et al.*, Chapter 14; Candela *et al.*, Chapter 15; Kay *et al.*, Chapter 16), this fauna was dominated by grazers and mixed-feeders, with frugivores and browsers remaining highly diverse. This distribution of trophic niches indicates that during Santacrucian times a balance existed between grasslands and woodlands, probably represented by a park savanna (Webb, 1978; Pascual and Ortiz-Jaureguizar, 1990; Pascual *et al.*, 1996; Ortiz-Jaureguizar and Cladera, 2006, and references therein). From a climatic point of view, the presence of primates and other warm climate-sensitive vertebrates that have been recorded as far south as 51°S suggests that warm and forested habitats were well developed in Patagonia. Nevertheless, together with these indicators of warm and forested habitats, there were also other mammals such as some rodents that indicate the existence of open habitats encroaching on areas of wet forests in Patagonia (Pascual *et al.*, 1996; Ortiz-Jaureguizar and Cladera, 2006; Pérez, 2010).

Considering the evidence provided by vascular plants and mammals, we may conclude that the ecological diversity of the Santacrucian marsupials is compatible with the existence of habitat patchiness during Santacrucian times, with a balance between closed and open habitats represented by a park savanna. In this scenario, the non-carnivorous marsupial species would have occupied the more forested areas (Fig. 10.7).

10.6 Conclusions

Microbiotheria and Paucituberculata of the Santa Cruz Formation constitute an ecologically diverse assemblage of non-carnivorous marsupials. Among microbiotheriids we recognize small insectivores such as *Microbiotherium acicula* and *M. tehuelchum*, and a medium-sized insectivore–frugivore, *M. gallegosense*. Compared with microbiotheriids, paucituberculatans are taxonomically and ecologically more diverse, having a wider range of body mass and diet. For this group we identify small insectivores such as *Phonocdromus gracilis*, medium-sized curso-saltatorial insectivores such as *Palaeothentes minutus* (Fig. 10.7b) and *P. lemoinei*, the small- to medium-sized insectivores–frugivores *Stilotherium dissimile* and *Acdestis owenii*, the medium-sized frugivore *Abderites meridionalis* (Fig. 10.7a), and the large frugivore *Palaeothentes aratae*.

Regarding the marsupials of the insectivore guild, a minimal niche overlap was inferred from differences in body mass and its relations to prey size and diet composition, as is observed in extant insectivorous mammals. In addition to the inferred terrestrial, curso-saltatorial locomotion of *Palaeothentes minutus* and *P. lemoinei*, scansorial or arboreal locomotor behaviors could have evolved among non-carnivorous Santacrucian marsupials that allowed their exploitation of resources in the vertical space.

From the present study, the ecological diversity of the non-carnivorous Santacrucian marsupial indicates that they lived in forested habitats, under warm temperatures and rain seasonality. Forested habitats could have supported the varied previously mentioned marsupial niches, offering diverse resources in the spatial and trophic dimensions. Considering also the paleoecological information provided by vascular plants and all the mammalian species, we conclude that the ecological diversity of non-carnivorous marsupials is compatible with a patchy environment, with a balance between vegetation typical of closed and open habitats, represented by a park savanna.

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Appendix 10.1 Paucituberculata and Microbiotheria of the Santa Cruz Formation

Microbiotheria Ameghino, 1889

Microbiotheriidae Ameghino, 1887
Microbiotherium acicula (Ameghino, 1891)
Microbiotherium patagonicum Ameghino, 1887
Microbiotherium tehuelchum Ameghino, 1887
Microbiotherium gallegosense Sinclair, 1906

Paucituberculata Ameghino, 1894

Caenolestidae Trouessart, 1898
Stilotherium dissimile Ameghino, 1887
Pichipilidae (Marshall, 1980)
Phonocdromus gracilis Ameghino, 1894
Palaeothentidae Sinclair, 1906
Palaeothentes aratae Ameghino, 1887
Palaeothentes minutus Ameghino, 1887
Palaeothentes intermedius Ameghino, 1887
Palaeothentes lemoinei Ameghino, 1887
Palaeothentes pascuali Bown and Fleagle, 1993
Acdestis owenii Ameghino, 1887
Acdestis lemairei Bown and Fleagle, 1993
Abderitidae (Ameghino, 1889)
Abderites meridionalis Ameghino, 1887

List of Paucituberculata and Microbiotheria from localities of the Santa Cruz Formation

For details of the specimens, localities, data of collection and collectors (Col.) see Marshall (1980, 1982), Bown and Fleagle (1993) and Vizcaíno *et al.* (Chapter 1: Figs. 1.1 and 1.2, and Appendix 1.1).

Gobernador Gregores: *Acdestis owenii.*

Lago Cardiel: *Acdestis owenii.*

Río Chalía – Ea. Viven Aike – (Col. Bown y Fleagle): *Palaeothentes minutus, Palaeothentes intermedius, Acdestis owenii, Acdestis lemairei.*

Monte León (Col. Bown and Fleagle): *Palaeothentes aratae, Palaeothentes minutus, Palaeothentes intermedius, Palaeothentes lemoinei, Acdestis owenii, Acdestis lemairei.*
La Cueva (Col. Ameghino): *Phonocdromus gracilis, Palaeothentes minutus, Palaeothentes intermedius, Palaeothentes lemoinei, Stilotherium dissimile, Abderites meridionalis, Microbiotherium patagonicum, Microbiotherium tehuelchum.*

Yegua Quemada (Col. Ameghino): *Palaeothentes intermedius, Palaeothentes lemoinei, Microbiotherium tehuelchum.*

Santa Cruz (Col. Ameghino): *Palaeothentes aratae, Palaeothentes minutus, Palaeothentes lemoinei, Microbiotherium patagonicum.*

Monte Observación (= Cerro Observatorio. see Marshall, 1976b, and Vizcaíno *et al.*, Chapter 1; Col. Ameghino, Bown and Fleagle): *Palaeothentes aratae, Palaeothentes minutus, Palaeothentes pascuali. Palaeothentes intermedius, Palaeothentes lemoinei, Stilotherium dissimile, Abderites meridionalis, Acdestis owenii, Acdestis lemairei, Microbiotherium acicula, Microbiotherium patagonicum. Microbiotherium tehuelchum.*

Puesto Estancia La Costa (= Corriguen-Aike; Col. MLP-Duke University): *Palaeothentes lemoinei.*
Corriguen-Kaik (Col. Ameghino): *Palaeothentes lemoinei, Microbiotherium tehuelchum.*

Killik-Aike (Col. H. Felton): *Palaeothentes minutus, Microbiotherium tehuelchum.*

Río Gallegos (Col. B. Brown): *Palaeothentes aratae, Palaeothentes minutus.*

Near Feltou's Estancia, along the north bank of the Río Gallegos (Col. Bamum Brown): *Phonocdromus gracilis, Microbiotherium acicula, Microbiotherium gallegosense.*

Sehuen (= Río Chalía; Col. Ameghino): *Palaeothentes aratae, Palaeothentes lemoinei, Palaeothentes intermedius, Stilotherium dissimile. Abderites meridionalis, Microbiotherium patagonicum.*

Appendix 10.2 Material studied

Microbiotheriidae

Microbiotherium acicula (Ameghino, 1891),
MACN-A 5727, a left mandibular ramus with p3–m4. Horizon and locality: Santa Cruz Formation, Monte Observación, Santa Cruz Province.

Microbiotherium patagonicum Ameghino, 1887
MLP 11–30, a right mandibular ramus with m1–4. Horizon and locality: Santa Cruz Formation, collected from "*las barrancas del río Santa Cruz*" (Ameghino, 1889: 264). Santa Cruz Province.

Microbiotherium tehuelchum Ameghino, 1887
MLP 11–36, a right mandibular ramus with p2–m4. Horizon and locality: Santa Cruz Formation, without locality data (see Marshall, 1982), Santa Cruz Province.

Microbiotherium gallegosense Sinclair, 1906
AMNH 9591, a right mandibular ramus with p3–m2. Horizon and locality: Santa Cruz Formation, Estancia Felton, Santa Cruz Province.

Dromiciops gliroides Thomas, 1894
MACN 19142, MACN 22918, MACN 22919, and MACN 13038.

Paucituberculata

Abderites meridionalis Ameghino, 1887
MACN-A 5542, left mandibular ramus with m1–4 and MACN-A 2037, left mandibular ramus with p3–m4. Horizon and locality: Santa Cruz Formation, Monte Observación, Santa Cruz Province; MACN-A 5541, left mandibular ramus with p3–m4 and PU 15079, left mandibular ramus with p3–m3. Horizon and locality: Santa Cruz Formation, Río Chalía, Santa Cruz Province; MACN-A 8248, left mandibular ramus with p3–m3. Horizon and locality: Santa Cruz Formation, La Cueva, Santa Cruz Province; MACN-A 2031, left mandibular ramus with m2; MACN-A 2032, right mandibular ramus with m2–4; MACN-A 2033, right mandibular ramus with m2–4; MACN-A 2034, right mandibular ramus with m1–3; MLP 11–109, right mandibular ramus with m1–2; MLP 11–133, left mandibular ramus with m2–3; MLP 55-XII-13–144, right mandibular ramus with m2; and MACN 11651, right mandibular ramus with p3-m4. Horizon and locality: unknown, Santa Cruz Province.

Palaeothentes minutus

MACN-A 5619–5639a–I, right and left mandibular rami with m3–4, distal portion of right humerus, proximal portion of right ulna, partially complete pelvis, proximal portion of right femur, proximal portion of left femur, and right calcaneum. Horizon and locality: Santa Cruz Formation, Killik-Aike, Santa Cruz Province.

Palaeothentes lemoinei

MPM-PV 3494, right mandibular fragment with m2–4 and left edentulous mandibular fragment, left humerus, left ulna, left fragment of pelvis, fragment of right tibia, fragment of left tibia, and right astragalus. Horizon and locality: Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 5.3, Puesto Estancia La Costa, Santa Cruz Province.

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