<div style="background:#7ec8e3">

CHAPTER 1

</div>

ORIGIN, SYSTEMATICS, AND MORPHOLOGICAL RADIATION

Authors: MARIANO L. MERINO, ROGÉRIO VIEIRA ROSSI

Associate Editor: COLIN GROVES

INTRODUCTION

Deer have always been significant elements of aboriginal cultures in every part of the world where they occur, be it as source of food, hides, and/or medicines. Similarly, the representations of deer in cave paintings, their inclusion in heraldic shields of some countries, their appearance in folkloric legends and innumerable toponymies, illustrate the sociocultural significance of these mammals. At present they are of great interest, both from aesthetic and cynegetic perspectives.

The greatest attraction that deer present for humans lies possibly in the possession of antlers in the males; antlers are used to manufacture diverse utensils. The reindeer (*Rangifer tarandus*) is the only species in which the females also have antlers. Conversely, these are absent in the Chinese water deer (*Hydropotes inermis*), while males of this species have long canine teeth (Putman 1988).

Some controversy surrounds the question of the primitive or derived nature of the presence of antlers and consequently, whether their absence in *Hydropotes* is a derived character (Janis and Scott 1987, Scott and Janis 1987), given that antlers were present in the earliest recorded fossil deer (such as *Dicrocerus*). This hypothesis is supported by the several molecular analyses (Gilbert et al. 2006; Kuznetsova et al. 2005; Pitra et al. 2004; Randi et al. 1998), in which *Hydropotes* appears as sister group to some genera of Odocoileinae. Another perspective proposes that the evolution of antlers took place after the differentiation of the lineage that led to this genus, and that there is no evidence supporting a secondary loss of those structures (Hamilton 1978).

In another phylogenetically close group, the musk deer (*Moschus* spp. - Moschidae), males also lack antlers and possess markedly enlarged canines. However, the members of this genus are currently not considered as "true deer" (see citations in Grubb 2005).

Compared to Eurasian species such as the red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and axis deer (*Axis axis*), the antlers of Neotropical species are smaller and simpler, with the exception of *Blastocerus dichotomus*. This lack of spectacularity, along with other factors such as an historical deficiency of specific research focused on these taxa, may be the reason why Neotropical species have been less studied than their Northern Hemisphere counterparts, for which diverse aspects, including population dynamics, mating systems, reproduction, genetics, habitat requirements and use, have been extensively studied (Barrette 1987; Putman 1988; Geist 1998; Eisenberg 2000).

ORIGIN OF NEOTROPICAL DEER

The place of origin of the family Cervidae would be Eurasia, where some of the earliest representatives, such as the Miocene *Dicrocerus* (Eisenberg 1987), have been recorded. The first cervids were probably small antlerless animals that inhabited tropical forests, similar in many aspects to the modern tragulids and moschids (Eisenberg 1987; Geist 1998). In these taxa, the males exhibited long canines with which they probably fought other males for access to the females, as does the living deer genus *Hydropotes*. Thus, these long teeth were used similarly to the antlers of the head-appendaged cervids.

Another morphotype for an ancestral cervid is infered by Gilbert et al. (2006) from the distribution of morphological characters over a molecular phylogenetic tree. According to these authors, the male ancestor of cervids should have been large, bigger than females, with three-tined antlers, no upper canines, and an open habitat dweller.

Recent molecular phylogenetic analyses (Gilbert et al. 2006; Pitra et al. 2004) have indicated the monophyly of the odocoileines, and a close relationship between at least one species of Mazama and the species of Odocoileus. Gilbert et al. (2006) found two major clades within the group, each of which includes one species of *Mazama*. The first clade links *Mazama americana* to the genus *Odocoileus*, and the second clade includes *Mazama gouazoubira*, *Blastocerus*, *Hippocamelus*, and *Pudu*. These results have been recently confirmed by Duarte et al. (2008) in their molecular phylogenetic analysis of the genus *Mazama*.

Cervids probably entered America from Asia through the Bering Strait, during the early Pliocene. Later, some taxa entered South America from North America through the Panamanian bridge, around 2.5 million years before present (mybp) (Plio-Pleistocene boundary) (Stehli and Webb 1985). Recently, Webb (2000) undertook an interesting analysis of the origin of Neotropical deer, based

on the interpretation of *Eocoileus gentryorum* from the Late Miocene (5 mybp) as the first New World deer. This interpretation rests upon Hershovitz's (1982) statement that the living Neotropical deer of genera *Pudu* and *Mazama* "had diverged from the tiny ancestral odocoileine, which must have lived during the early Pliocene or late Miocene in North America, Central America or South America". This implies a progressive increase of body size and posits the existence of medium-sized forms in the Miocene and Pliocene of Asia and North America that would have been ancestral to the small forms, an idea supported by the known fossil record (Webb 2000). The first deer that entered South America were medium-sized species with branched antlers; these would have given rise to taxa with more conservative appearance, smaller size and simple antlers as in *Mazama* and *Pudu* (Eisenberg 1987). However, these two genera would have evolved independently from each other and are not closely related (Eisenberg 2000). The absence of canines in these species (vestigial canines are occasionally found in brocket deer) and other "modern" characters led to the supposition that the simple antlers and small size are not primitive traits but secondary acquisitions in these species (Eisenberg 1987). Both this ancestral morphotype of South-American cervid and the independent origin of *Mazama* and *Pudu* are also asserted by Gilbert et al. (2006).

Neotropical deer occupy a wide range of habitats. Generally speaking, a distinction can be made between inhabitants of "closed" environments such as *Mazama*, *Pudu*, and *Hippocamelus bisulcus*, and those that occur in "open" environments, such as *Ozotoceros*, *Blastocerus* and, to a lesser extent, *Hippocamelus antisensis*. *Odocoileus virginianus* is a very plastic species with respect to environmental requirements and occupies a great variety of habitats, from grasslands and savannas to diverse types of forests, deserts, and man-altered environments such as tree plantation.

The species in the first group characteristically have small body size; small and needle-shaped antlers; relatively large hindquarters apt for short leaping runs, and shorter forelimbs that facilitate progress in dense forests; small hooves; cryptic coloration; and large antorbital glands used to leave territorial marks. They are solitary or live in small groups, and have a non-seasonal breeding cycle. In contrast, the species in the second group have larger body mass, complex antlers – although never reaching the complexity of European deer such as *Cervus elaphus* - and evenly developed hind and forelimbs. They live in groups that can be fairly large, and their diet, although variable according to habitat type, comprises mainly grasses and forbs, with low proportion of fruits.

SYSTEMATICS

True deer are a diversified group of ungulates that includes species as small as the Northern pudu (*Pudu mephistophiles*) with a body mass of about 6 kg, and as large as the elk or moose (*Alces alces*), with over 600 kg. The family is diagnosed by the following anatomical characters: two orifices in the lacrimal duct, situated at or above the level of the orbit; presence of a lacrimal fossa; and an antorbital fenestra that prevents the lacrimal from

contacting with the nasal bones. Other characteristics of cervids are a brachydont first molar, and the parietal-squamosal suture situated closer to the upper margin of the temporal fossa. All cervid species lack a gall bladder and have a metatarsal gully (Janis and Scott 1987, Scott and Janis 1987).

The metacarpals of the 2nd and 5th digit are only partly present or completely absent in deer. In many species, the distal segments of these bones are present and articulate with the phalanges while the proximal rudiments are absent; this is called *telemetacarpal* condition. Conversely, the absence of distal segments is the *plesiometacarpal* condition. These conditions, as well as the presence of antlers, tarsal glands and vomerine septum, are some of the main characters used to separate the major cervid tribes (Groves and Grubb 1987). The New World deer belong to the subfamily Capreolinae Brookes, 1828, of which Odocoileinae Pocock, 1923 is a synonym (Grubb 2000).

The phylogeny of the group is controversial. Groves and Grubb (1987) proposed a single monophyletic tribe, Odocoileini, for the genera *Pudu*, *Mazama*, *Hippocamelus*, *Blastocerus*, *Ozotoceros*, *Odocoileus*, and *Rangifer*. Hershkovitz (1982) regarded *Pudu* as the most primitive taxon within the group. Based on karyotypic characters, Neitzel (1987) suggested that *Ozotoceros* and *Blastocerus* formed a clade together with *Odocoileus*. However, the derived characters appear to be also shared by *Pudu* and partially by *Mazama* spp. The shape of the antler supports Hershkovitz's (1982) idea that *Odocoileus* is not immediately related to the genera *Ozotoceros*, *Blastocerus* and *Hippocamelus*.

More recently, Webb (2000) split the South American cervids into two tribes: Rangiferini, including the circumboreal *Rangifer* and the South American *Hippocamelus* and *Pudu*; and Odocoileini, including *Odocoileus*, *Blastocerus*, *Ozotoceros* and *Mazama*. The systematic of the groups and species of deer are quite complex and not yet completely resolved, as shown by the many changes the classification scheme has undergone during recent years (Bianchini and Delupi 1979; Duarte and Merino 1997; Groves and Grubb 1987; Grubb 2000; Grubb 2005; Scott and Janis 1987; Webb 2000) and the recent discoveries of new species (Duarte 1996; Duarte and Jorge 2003; Duarte and Merino 1997; Medellín et al. 1998). There are 52 species currently recognized whitin the family Cervidae (Grubb 2005). *Mazama* Rafinesque, 1817, with at least 9 species, is one of the most diverse genera, together with *Muntiacus* (11 species) (Grubb 2005). The taxonomy of the genus *Mazama* is confusing and the inter-specific relationships are not clear (Eisenberg 2000; Groves and Grubb, 1987). Analyzing the phylogenetic molecular evolution of Old World deer, Gilbert et al. (2006) found evidence that the genus *Mazama* is not monophyletic. Furthermore a recent phylogenetic molecular analysis of the Neotropical deer showed an astounding and complex evolutionary pattern and phylogenetic relationships among species, including the paraphyly of the brocket deer (Duarte et al. 2008).

A recent revision of the diversity of Neotropical cervids proposed 16 species (Weber and González 2003), thus

making this tribe the most diversified group of ungulates in the Neotropical region. Some authors recognise three genera in the Neotropics - *Mazama*, *Pudu* and *Odocoileus* (Bianchini and Delupi 1978; Ximenez et al. 1972), or four genera including *Hippocamelus* (Delupi and Bianchini 1995). Grubb (1993) also recognizes the genera *Blastocerus* and *Ozotoceros*. His arrangement is followed by the majority of present-day deer specialists. Surely, molecular taxonomy will be an additional and important tool to understand the patterns of evolution of the Neotropical deer species in which there are many examples of cryptic species as in the brocket deer (Duarte et al. 2008).

The classification of the Neotropical deer, up to the generic level that we adopt herein follows, the scheme proposed by Grubb (2000, 2005), who last reviewed the nomenclature of this group.

Order Artiodactyla Owen, 1848
 Suborder Ruminantia Scopoli, 1777
  Superfamily Cervoidea Simpson, 1931
   Family Cervidae Gray, 1872
    Subfamily Capreolinae Brookes, 1828
     Tribe Rangiferini Brookes, 1928
      † *Agalmaceros* Hoffstetter 1952
      † *Antifer* Ameghino 1889
      † *Epieuryceros* Ameghino 1889
      † *Paraceros* Ameghino 1889
      † *Morenoelaphus* Carette 1922
      † *Charitoceros* Hoffstetter 1963
      Blastoceros dichotomus (Illiger, 1815)
      Hippocamelus antisensis (d´Orbigny, 1834)
      Hippocamelus bisulcus (Molina, 1782)
      Mazama americana (Erxleben, 1777)
      Mazama bororo Duarte, 1996
      Mazama bricenii Thomas, 1898
      Mazama chunyi Hershkovitz, 1959
      Mazama gouazoubira (Fischer, 1814)
      Mazama nana (Hensel, 1872)
      Mazama nemorivaga (Cuvier, 1817)
      Mazama pandora Merriam, 1901
      Mazama rufina (Pucheran, 1851)
      Mazama temama (Kerr, 1792)
      Odocoileus virginianus (Zimmermann, 1780)
      Ozotoceros bezoarticus (Linnaeus, 1758)
      Pudu puda (Molina, 1872)
      Pudu mephistophiles (de Winton, 1896)

EXTINCT SPECIES AND PAST DIVERSITY (Figure 1)

Like living species, extinct deer have been little studied in comparison with other groups of Neotropical mammals; consequently, the phylogenetic relationships between extinct and living taxa have not yet been elucidated.

Very often, fossil skeletal remains are not identified, but some taxonomic information is derived from their morphological resemblance to a known taxon. Unfortunately, while such approach may be sufficient for some groups, it is not sufficient for others. In the case of taxa with highly conservative anatomy such as the members of the family Cervidae, in which skeletal morphological differences between two species are based

mainly on body measurements and morphology of the antlers, this method proves to be inadequate or at best insufficient for taxonomic purposes (Menegaz and Tonni 1985). Consequently, the validity of some of the fossil taxa described to the present is likely to change in the future on the basis of new studies.

We present here a brief description of the extinct South American deer genera, based on available information.

Genus † *Agalmaceros* Hoffstetter, 1952

This genus, known from the single species *A. blicki* (Frick, 1937) from the upper part of the Late Pleistocene, has only been recorded at its type locality in the Andes of Ecuador (Hoffstetter 1952). The large size and robustness of this taxon have been interpreted as adaptations to high altitude mountain habitats, and their habits might have been similar to those of the recent genus *Hippocamelus* (Tomiati and Abbazzi 2002).

Genus † *Antifer* Ameghino, 1889

A large-sized deer, similar in that respect to the living *Blastocerus*, with large robust antlers that are compressed and irregularly dichotomous. The antlers are laterally inclined but medially arched, and bear marked longitudinal grooves.

Three species have been assigned to this genus: 1) *Antifer ensenadensis* (Ameghino 1888), with a biochron restricted to the Ensenadan (late Pliocene – middle Pleistocene); 2) *Antifer ultra* (Ameghino 1888) recorded in the Lujanian (late Pleistocene – Holocene) and the Bonaerian (middle Pleistocene); and 3) *Antifer niemeyeri* Casamiquela, 1984 from the late Pleistocene of Chile (Casamiquela 1984). The main character used for identification of these species is their size. This, coupled with the scarce records, raises some doubts about the validity of these species (Alcaraz and Zurita 2004; Menegaz 2000). Most of the records are for the Argentinean provinces of Buenos Aires, Santa Fe, Entre Ríos, Corrientes, and Formosa (Alcaraz and Zurita 2004; Alcaraz et al. 2005; Menegaz 2000). They also occur in Pleistocene fossil beds in the State of Rio Grande do Sul, southern Brazil (Souza Cunha and Magalhães 1981), and in the Sopas Formation, upper Pleistocene of Uruguay (Ubilla 1985). According to recent interpretations, *Antifer* could have been associated with arid to semiarid environments (Alcaraz and Zurita 2004).

Genus † *Charitoceros* Hoffstetter, 1963

This genus was recorded in Pleistocene deposits of Tarija, Bolivia, from which it was first described (Hoffstetter 1963).

Genus † *Epieuryceros* Ameghino, 1889

These were very large deer, with antlers that are palmate from the base and have 4 to 6 small terminal points. The genus comprises two species: *Epieuryceros truncus* Ameghino, 1889, with palmate antlers arising almost from the pedicle, and *Epieuryceros proximus* Castellano 1945, that has a well-developed pedicle with defined concavity. *E. truncus* is known from the Ensenadan (upper Pliocene - middle Pleistocene), while *E. proximus*
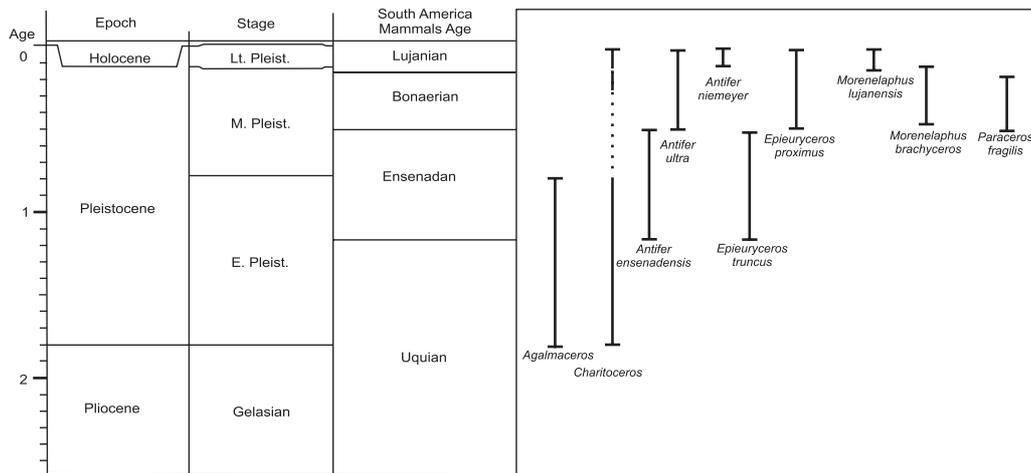
Figure 1 - Stratigraphic chart of South American late Cenozoic land mammal ages and known range distribution of extinct deer species.

occurs in the Belgranan in Santa Fe, which is assignable to the Bonaerian (Cione and Tonni 1999) (middle - late Pleistocene), and the Lujanian of Corrientes (middle Pleistocene – early Holocene) (Alcaraz and Zurita 2004). These species would have been associated with open shrub environments and moist climate (Alcaraz and Zurita, op. cit.).

Some authors have included this genus within *Blastocerus* (McKenna & Bell 1997).

Genus † *Morenoelaphus* Carette, 1922

These were medium-sized to small deer, with large S-shaped antlers. Two species are recognized: *Morenoelaphus brachyceros* H. Gervais and Ameghino, 1880 and *M. lujanensis* Ameghino, 1888. These species are discernible by details of their antler morphology (Menegaz and Ortiz Jaureguizar 1995). The presence of this genus in the fossil record goes back to the Bonaerian (middle-late Pleistocene) and late Lujanian (Menegaz 2000). In South America, fossil remains have been found in Uruguay (Ubilla 1985), Paraguay (Carlini and Tonni 2000; Hoffstetter 1978), southern Brazil (Souza Cunha and Magalhães 1981), and Argentina. There is very little information about paleoecological aspects of this genus, although some authors (Menegaz and Ortiz Jaureguizar 1995) have postulated that it occupied open or partly open environments.

Genus † *Paraceros* Ameghino, 1889

This deer is characterized by antlers 40 cm long at their maximum development. Its size was probably that of a medium-sized to small deer. The slender antlers are curved in a semielliptical or lyre-shape, with lateral

ramifications in a single plane. Their surface is smooth or exhibit weak grooves. The main beam is flattened at the origin of the ramifications, as in *Ozotoceros*, *Blastoceros* and *Hippocamelus*. Only one species, *Paraceros fragilis* (Ameghino 1888), is known, recorded in Buenos Aires and Santa Fe Provinces, Argentina. The oldest stratigraphic record is from the Ensenadan (early Pleistocene).

LIVING SPECIES AND CURRENT DIVERSITY (Figure 2)

The living species of Neotropical cervids are adapted to a wide range of habitats, from dense forests to open environments. Their adaptations include morphological, physiological and behavioural traits that maximize their efficient use of natural resources (Putman 1988). In this section we present brief morphological descriptions and comments about the distribution and ecology of each one of these species.

Marsh deer *Blastocerus dichotomus* (Illiger, 1815)

The marsh deer is the largest South American cervid. Males have an average body mass of 130 kg, while females are 100 kg, reaching a height of 1.3 m at the shoulder (Duarte 1996). This species occurs in seasonally inundated grassland in central South America, northern Argentina, west central and southern Brazil, Paraguay, southern Peru, and eastern Bolivia. It inhabits the lowlands at the edge of rivers, always in the vicinity of marshy regions or wet savannas with tall grasses. Morphological adaptations to their environment include possession of an interdigital membrane as well as long limbs, which enable them to progress swiftly through their flooded environment. The fossil record of this species refers to the Pleistocene of
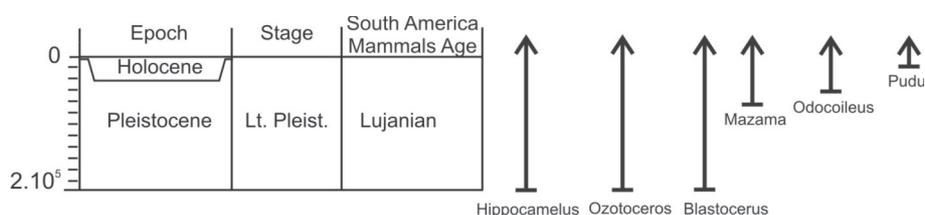
Figure 2 - Stratigraphic chart with known range distribution of living genera of deer.

Brazil (Souza Cunha and Magalhães 1981) and Paraguay (Marshall et al. 1984), whereas the genus has not been found in Argentinean sediments older than Holocene in age (Menegaz and Ortiz Jaureguizar 1995).

North Andean huemul *Hippocamelus antisensis* (d´Orbigny, 1834)

This is the smallest species of the genus, with a body mass ranging from 45 to 65 kg, and 80 cm high at the shoulder (Regidor and Rosati 2001). *H. antisensis* is distributed through the Andes of Peru, Bolivia, northern Chile, and a restricted area in northern Argentina, where it inhabits rocky areas in the Andean mountains and highland fields between 2500 and 4500 meters a.s.l. (Redford and Eisenberg 1992).

South Andean huemul *Hippocamelus bisulcus* (Molina, 1782)

This is a robust deer. Males are larger than females, with body mass ranging from 60 to 100 kg, and height at shoulder from 80 to 100 cm (Serret 2001). *H. bisulcus* occurs in the southern Andes of Argentina and Chile, from 37° S latitude to the Strait of Magellan. It is found mostly at or just below the tree line, and prefers rocky slopes with irregular topography, dense shrub cover, and forest clearings (Redford and Eisenberg 1992).

Hippocamelus occurs in late Pleistocene deposits of Chile, Bolivia and Argentina (Frailey et al. 1980; Marshall et al. 1984; Menegaz and Ortiz Jaureguizar 1995).

Red brocket *Mazama americana* (Erxleben, 1777)

This is the largest and most robust species of *Mazama*, with an average body mass of 30 kg (up to 40 kg), and height at shoulder approximately 65 cm (Duarte 1996). It inhabits thick forested habitats throughout a large distribution area that ranges from northern Colombia to northern Argentina.

Small red brocket deer *Mazama bororo* Duarte, 1996

This brocket was firstly described by Duarte (1996) and Duarte and Merino (1997), and a more accurate description was recently given by Duarte and Jorge (2003). This species is similar to *Mazama americana* though smaller, with an average body mass of 25 kg and a height of 51 cm at the shoulder. *Mazama bororo* lives in fragments of the relictual Brazilian Atlantic Forest in southeastern São Paulo State, adjacent to the northeastern part of Paraná State.

Grey dwarf brocket *Mazama bricenii* Thomas, 1908

This is a small cervid whose biology and ecology are poorly documented. Bisbal (1991) reported a body mass of 13.6 kg for one adult specimen, and Czernay (1987) has restricted the range of this species to the eastern Andean mountain range in western Venezuela and adjacent Colombia. It occurs in moors at 3000 m a.s.l..

Peruvian dwarf brocket *Mazama chunyi* Herkhkovitz, 1959

M. chunyi is the smallest of the Andean dwarf brockets, with only 39 cm high at the shoulder (Eisenberg 2000). It is found in southern Andean Peru (Cuzco, Puno, and Madre de Dios Departments), and northern Bolivia (La Paz and Cochabamba Departments), from 1500 to 3200 m a.s.l. (Rumiz et al. 2006). This is a rare and poorly known species. Details of its ecology are unknown, although it seems to be solitary, active at daytime as well as during the night, and expected to be a browser/frugivore in the forest understory (Weber and Gonzalez 2003).

Grey (brown) brocket *Mazama gouazoubira* (G. Fischer, 1814)

The grey brocket is a small cervid with a body mass of 18 kg (rarely exceeding 20 kg), and 50 cm average height at shoulder (Duarte 1996). This deer species is common in South America, and is widely distributed throughout northeastern, central and southern Brazil, most of Bolivia, Paraguay, Uruguay, and northern Argentina. This large area of occurrence comprises many diverse environments, including Brazilian Atlantic Forest, Cerrado, Caatinga, and Chaco. *M. gouazoubira* feeds on hard, dry fruits during the dry season and soft, fleshy fruits during the wet season, but also eats leaves, buds, flowers, twigs, and roots.

Brazilian dwarf brocket *Mazama nana* (Hensel 1872)

This is a small brocket, with body mass rarely exceeding 15 kg, and 45 cm height at shoulder (Duarte 1996). It occurs at low densities in the mountain areas covered by forests in northeastern Argentina, adjacent areas in Paraguay, and southern Brazil.

Amazonian grey brocket *Mazama nemorivaga* (Cuvier 1817)

M. nemorivaga was considered a valid species by Rossi (2000), confirming the assertions of Duarte (1996), Duarte and Merino (1997), and Duarte and Jorge (1998) about the probable validity of *Mazama rondoni* Miranda-Ribeiro, 1914 (= *M. nemorivaga*). This species is smaller than the grey brocket, with body mass between 14 and 15.5 kg, and height at shoulder varying from 49 to 50.5 cm (Duarte and Jorge 1998). It is distributed in Peru, Ecuador, Colombia, Venezuela, Guyana, Surinam, French Guiana, and northern Brazil (see Rossi et al. in this volume), comprising an area that corresponds primarily to the Amazon Forest, but also to open areas such as the "llanos" (plains) and xeric scrublands in Venezuela.

Yucatan brown brocket *Mazama pandora* (Merriam 1901)

This brocket was restored to a valid-species status by Medellin et al. (1998). Its total body length is 112.5 cm, and height at shoulder is 57.2 cm (Merriam 1901). This species inhabits both dense humid forests and drier, more open forest areas in Yucatan peninsula, Mexico. According to Weber and Gonzalez (2003), no accurate information about its biology and ecology is available.

Dwarf red brocket *Mazama rufina* (Pucheran 1851)

This small red brocket is confined to the central Cordillera of southern Colombia and adjacent areas in Ecuador and extreme north of Peru. *M. rufina* is a solitary deer that prefers moist forest habitats (Eisenberg 1989).

More accurate information about the biology and ecology of this species is completely unknown, partly because it occurs in a sociopolitically conflictive area where research is difficult (Weber and Gonzalez 2003).

Central American red brocket *Mazama temama* (Kerr 1792)

The Central American brocket was raised to the species level by Geist (1998). This species occurs in southern Mexico southward to northern Colombia.

The fossil records of the genus *Mazama* comprise the Pleistocene of Argentina, Ecuador, Peru and southwest Piauí State, Brazil (Churcher 1962; Guerin et al. 2002; Hoffstetter 1952; Noriega et al. 2004).

White-tailed deer *Odocoileus virginianus* (Zimmermann 1780)

This medium-sized cervid occurs in North America, and its distribution also extends over Central and South America to northern Bolivia and northern Brazil. Height at shoulder averages 95 cm and weight ranges from 50 to 120 kg (Eisenberg 2000). According to Smith (1991), height at shoulder varies from 53.3 to 106.7 cm in males, and body mass ranges from 90 to 135 kg in northern United States and southern Canada males. This same author states that the subspecies with smallest body size occur at lower elevations or latitudes nearer to the Equator. This species is tolerant of different habitat types, but favors woodland savannas and edge habitats. Its diet varies according to local conditions.

The first fossil record for this genus comes from the early Pliocene (Kurten and Anderson 1980). The first record for the living species *O. virginianus* dates from the late Pliocene, and it is possibly derived from the extinct *Odocoileus brachyodontus*. According to Hershkovitz (1972), it probably originated in Middle America and its geographic expansion toward South America is comparatively recent. Pleistocene records are known for Colombia, Ecuador, Peru and Brazil (Churcher 1962; Tomiati and Abbazi 2002). A fossil species, *O. salinae*, is known from early Holocene deposits in Ecuador and Peru.

Pampas deer *Ozotoceros bezoarticus* (Linnaeus 1758)

This is a medium-sized cervid, with body mass around 30 kg, and height at shoulder 65 cm (Duarte 1996). The pampas deer occurs as insular populations in western, northern and central Argentina, eastern Bolivia, central and southern Brazil, Paraguay, and Uruguay (Anderson 1997; Cabrera and Yepes 1961; Merino et al. 1997). It is characteristically found in grasslands with none or few trees, and is absent from closed habitats such as dense forests.

Ozotoceros occurs in the late Pleistocene-Holocene of Brazil (Souza Cunha and Magalhães 1981), late Pleistocene of Uruguay (Ubilla et al 2004), and Holocene of Argentina (Menegaz and Tonni 1985).

Northern pudu *Pudu mephistophiles* (de Winton 1896)

The northern pudu is the smaller of the two species of the genus and also the smallest among living deer, with body mass 5.8 kg and height at shoulder 25 to 32 cm (Hershkovitz 1982). It occurs in a discontinuous range throughout the montane forests and grasslands of the Andes in Colombia, Ecuador, and Peru, between 3000 and 4000 m a.s.l. (Hershkovitz 1982). Its actual range is poorly known and the distributional gaps between locality records are unresolved.

Southern pudu *Pudu puda* (Molina 1782)

The southern pudu is a small cervid, with 8.3 to 13.4 kg body mass and 30 to 44 cm height at shoulder (Hershkovitz 1982). This species occurs at low densities in lowlands and montane forests, between sea level and 1700 m a.s.l. in southern Chile and Argentina (Hershkovitz 1982). The distribution of southern pudu in Argentina covers a narrow area adjacent to the Andean mountain range, comprising mainly *Nothofagus dombeyi* forests with dense *Chusquea coleu* understory, over a territory situated below 1,200 m a.s.l. (Meier and Merino 2007)

Fossil records of *Pudu* are known for the Holocene of Chile (Saavedra and Simonetti 1991).

ADAPTIVE RADIATION AND FEEDING STRATEGIES OF LIVING NEOTROPICAL DEER

Ever since their entrance into South America in the late Pliocene-middle Pleistocene, cervids underwent a rapid radiation in the Neotropics, as attested by the presence of diverse extinct and living genera (Menegaz and Ortiz Jaureguizar 1995), always occupying a wide range of habitats. This radiation was possibly influenced by the absence of other artiodactyls such as bovids, an opposite scenario to that in Africa, where bovids reached their highest diversity (Webb 2000).

This diversification was undoubtedly due to the evolution of different feeding strategies, as result of the interaction of several factors both intrinsic (dental morphology, anatomy and physiology of the digestive system) and extrinsic (temporal and spatial distribution of the vegetation, and physicochemical properties of plants) (Gordon 1989 a,b and c; Illius and Gordon, 1993; Jarman 1974).

Hofmann (1973, 1989) and Hofmann and Stewart (1972) recognized that the structure of the digestive tract of ruminants is closely related to the type of food consumed and the manner of its acquisition, and is thus a clear indicator of feeding strategies. These authors proposed three major types of ruminant feeding strategies based on feeding habits, as well as structure, morphology and bacterial flora of the digestive tract, which they designated as "*concentrate selectors*", "*bulk feeders*" and "*intermediate types*". These types are part of a continuum and may partially overlap. The so-called *bulk and roughage feeders* are characterized by their low selectivity and highly efficient cellulose digestion, and are consequently better adapted to consumption of foods with high proportion of low digestible fibers, such as grasses. Their digestive tube is long, with a large stomach for food fermentation. The *concentrate selectors* have a relatively simple digestive tube comprising a small rumen lined with poorly-developed papillae; the food passes through the rumen rapidly to the omasum, which is also

small. The intestine is short. These structures allow digestion of rich forage, which lacks well-developed cell walls that hinder access to cell contents. They use their well-developed sense of smell for the selection of food items and thus benefit from high-quality diets. The *intermediate* ruminants engage in some type of food selection in an opportunistic manner.

This classification was initially developed for the ruminants of Africa, where bovids comprise more than 137 species ranging in body mass from 2 kg (*Neotragus moschatus*) to almost 900 kg (*Syncerus caffer*). Hofmann (1985) adapted the scheme for cervids, providing a new interpretation of their diet. The scheme formulated by this autor includes only three Neotropical genera (*Mazama*, *Pudu* and *Odocolileus*). The most significant limitation for applying Hofmann's classification to the Neotropical deer is the lack of information about their digestive tract anatomies, essential for the use of the categories proposed by Hofmann (1989). These data are almost nonexistent for Neotropical deer, with the exception of *Odocoileus* and some species of *Mazama* (Bodmer 1989a, 1989b, 1991).

Nonetheless, some conclusions about the different feeding strategies evolved among Neotropical deer may be drawn, on the basis of Hoffman's proposals. Merino (2003) analyzed the different feeding strategies within this group, particularly the Southern Cone species, using the concept of forage classes proposed by Pelliza-Sbriller et al. (2001), which allows standardization of the diet of different species. This concept is based on anatomical and morphological features of plant species that are directly related to the ability of deer to ingest and digest them. The forage classes used for this analysis are: Woody Plants (WP), Forbs (F), and Grasses (Poacea) and Graminiforms (Juncaceae and Cyperaceae) (GGr). The composition of species and their populations were later compared by means of the graphic method proposed by Chivers and Hladik (1984). This analysis was based on the diet of wild populations of some Neotropical deer, such as *Blastocerus dichotomus* (Beccaceci 1994;

Beccaceci and Merino 1994; Tomas and Salis 2000), *Hippocamelus bisulcus* (Smith-Flueck 2000), *Mazama americana, M. gouazoubira, M. nemorivaga* (Bodmer 1997; Branan et al. 1985), *Odocoileus virginianus* (Branan et al. 1985; Gallina 1984; Martínez et al. 1997), and *Ozotoceros bezoarticus* (Cosse 2001; Guilietti 1988; Jackson and Rodrigues 1996; Merino 2003; Pinder, 1997). Regarding *Hippocamelus antisensis, Mazama nana* and other species of this genus, as well as the species of *Pudu*, no detailed dietary information is available that would allow their inclusion in this analysis. Finally, the diet of different species and populations was grouped according to the categories of Spencer (1995), which are based on the proportion of different forage classes to describe dietary strategies.

Figure 3 shows three clearly different groups that agree with Spencer's (1995) dietary classes; the 'grass feeder' class is missing. This is an expected outcome, given that according to previous works (Owen-Smith 1997), no cervids are included in this class.

With respect to the species included in the different classes, two groups stand out: those species that are only included in one of the classes, such as *Mazama americana, M. gouazoubira, M. nemorivaga*, and *Hippocamelus bisulcus* among the 'dicot feeders'; and *Blastocerus dichotomus* among the 'mixed dicot feeders'. In contrast, *Odocoileus virginianus* and *Ozotoceros bezoarticus* fall into the three classes, depending on the population studied. These species have wide geographical ranges and occupy a great variety of habitats with different forage offer. *Odocoileus virginianus* is widely distributed from southern Alaska and Canada (60° N) to northern Brazil, southern Peru and northwestern Bolivia (15° S) (Vaughan and Rodrigues, 1994), representing the widest distribution with largest populations among New World deer (Teer 1994). This species is highly versatile and inhabits grasslands, savannas, deciduous forests, conifer and tropical forests, and deserts, as well as artificially forested areas associated with agricultural exploitation. Its diet is extremely variable depending on environmental conditions, and includes
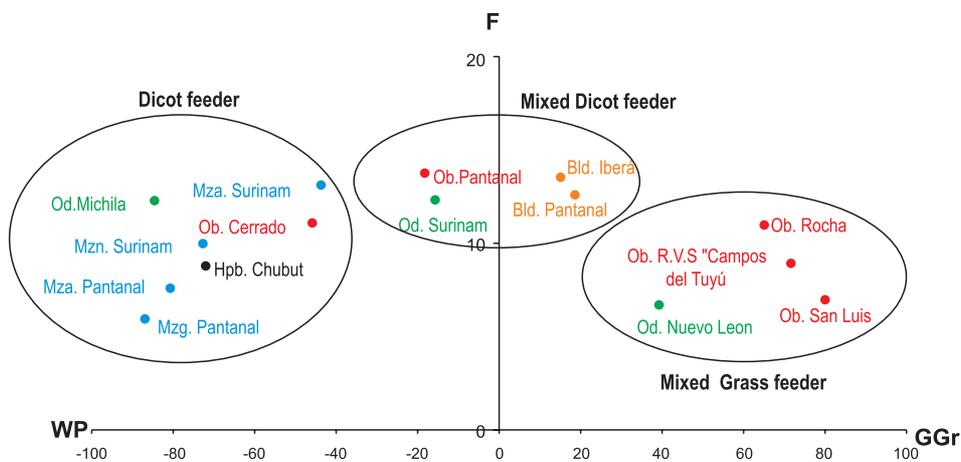
Figure 3 - Annual diet of different population of six species of Neotropical deer represented within a triangle. The composition of annual diet in terms of percentage of Woody Plants **(WP)**, Forbs **(F)** and Grasses and Graminiforms **(GGr)**. In a circle different plant food preference followed Spencer (1995). **Ob.:** *Ozotoceros bezoarticus*, **Bld.:** *Blastocerus dichotomus*, **Mza**.: *Mazama americana*, **Mzg.:** *Mazama guoazoubira*, **Mzn**.: *Mazama nemorivaga* and **Od.:** *Odocoileus virginianus*.

shoots, new leaves, forbs, grasses and fruits, in proportions that vary according to geographical location; in any case, they always select the most nutritive and easiest to digest species or parts of plants (Branan et al. 1985; Gallina, 1984; Martinez et al. 1997).

Ozotoceros bezoarticus has a wide distribution that ranges from 1° S to 43° S. This large geographical area comprises a wide variety of 'open' environments where food offer is very diverse; this factor favors the diversity of trophic behavior in this species. Nevertheless, in this case its diet is restricted to green and highly nutritive parts of plants.

While this is a first approximation to understand the feeding strategies of Neotropical deer, the addition of new dietary data for different species in different environments, and detailed descriptions of the digestive system of deer species are required for more in-depth analyses. Their results may provide essential information on the Neotropical deer diet and the subsequent assessment of available food resources, possible environmental management strategies, and the influence of the latter over deer populations.

LITERATURE CITED

ALCARAZ, M. A., and A. E. ZURITA. 2004. Nuevos registros de cérvidos pocos conocido: *Epiceuryceros* cf. *proximus* Castellanos y *Antifer* sp. (Mammalia, Artiodactyla, Cervidae). Revista del Museo Argentino Ciencias Naturales 6:41-48.

ALCARAZ, M. A., B. S. FERRERO, and J. I. NORIEGA. 2005. Primer registro de *Antifer ultra* Ameghino 1889 (Artidactyla: Cervidae) en el Pleistoceno de Entre Ríos. Pp. 65-69 in Temas de la Biodiversidad del Litoral fluvial argentino II (F. G. Aceñolaza, ed.). Tucumán, Argentina.

ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of American Museum of Natural History 231:1-652.

BARRETTE, C. 1987. The comparative behavior and ecology of chevrotains, musk deer, and morphologically conservative deer. Pp. 200-213 in Biology and Management of the Cervidae (C. M. Wemmer, ed.). Smithsonian Institution, Washington, DC.

BECCACECI, M. D. 1996. Dieta del ciervo de los pantanos (*Blastocerus dichotomus*), en la Reserva Iberá, Corrientes, Argentina. Mastozoologia Neotropical 3:193-198.

BECCACECI, M. D., and M. L. MERINO. 1994. Dieta del ciervo de los pantanos en la Reserva Iberá, Corrientes, Argentina. Pp. 129-136 in Population & Habitat Viability Assessment for Cervo-do-pantanal (*Blastocerus dichotomus*) (L. Pinder and U. Seal, eds.). IUCN/SSC Conservation Breeding Specialist Group, Apple Valley Minnesota, USA.

BIANCHINI, J., and L. DELUPI. 1979. El estado sistemático de los ciervos neotropicales de la tribu Odocoileni Simpson 1945. Physis C 38:83-89.

BISBAL, F. J. 1991. Distribución y taxonomía del venado matacán (*Mazama* sp) en Venezuela. Acta Biologica Venezuelica 13:89-104.

BODMER, R. 1997. Ecologia e conservacao dos veados mateiro e catingueiro no amazonia. Pp. 70-77 in Biologia e conservacao de Cervideos Sul-americanos; *Blastocerus, Ozotoceros e Mazama* (J. M. Barbanti Duarte, ed.). FUNEP, Jaboticabal.

BODMER, R. E. 1989a. Frugivory in Amazonian Artiodactyla: evidence for the evolution of the ruminant stomach. Journal of Zoology 219:457-467.

BODMER, R. E. 1989b. Ungulate biomass in relation to feeding strategy within Amazonian forest. Oecologia 81:547-550.

BODMER, R. E. 1991. Influence of digestive morphology on resource partitioning in Amazonian ungulates. Oecologia 85:361-365.

BRANAN, W., M. WERKHOVEN, and R. MARCHINTON. 1985. Food habits of brocket and white-tailed deer in Suriname. Journal Wildlife Management 49:972-976.

CABRERA, A., and J. YEPES. 1961. Los mamíferos Sudamericanos. Ediar, Buenos Aires: 1- 370.

CARLINI, A. A., and E. P. TONNI. 2000. Mamíferos Fósiles del Paraguay. Cooperación Técnica Paraguayo-Alemana. Proyecto Sistema Ambiental del Chaco-Proyecto Sistema Ambiental Región Oriental: 1-108.

CASAMIQUELA, R. 1984. Critical catalogue of some Chilean fossil vertebrates I. The Deers: Complementary considerations on Antifer (*Antifer niemeyeri* n.sp.), the Pleistocene Giant Deer. Pp. 41-50 in Quaternary of South America and Antarctic Peninsula (J. Rabassa, ed.). A. A. Balkema, Rotterdam.

CHIVERS, D. J., and C. M. HLADIK. 1984. Diet and gut morphology in primates. Pp. 213 -230 in Food acquisition and processing in primate (D. J. Chivers, B. Wood and B. Bilborough, eds.). New York, Plenun Press.

CHURCHER, C. S. 1962. *Odocoileus salinae* and *Mazama* sp. from the Talara tar seeps, Peru. Royal Ontario Museum Contribution 31:3-26.

CIONE and TONNI 1999. Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean Area, Argentina. Pp. 23-52 in (J. Rabassa and M. Salemme, eds.) Quaternary of South America and Antarctic Peninsula 12.

COSSE LARGHERO, M. 2002. Dieta y solapamiento de la población de venado de campo "Los Ajos" (*Ozotoceros bezoarticus* L. 1758) (Artiodactyla: Cervidae). MSc. thesis, Universidad de la República Oriental del Uruguay.

CZERNAY, S. 1987. Spiesshirshe und Pudus: Neue Brehm. Bücherei, 581:1-84.

DELUPI, L. H., and J. J. BIANCHINI. 1995. Análisis morfológico comparado de los caracteres cráneo-faciales en el ciervo de las pampas *Odocoileus bezoarticus* y formas relacionadas. Physis C 50:23-36.

DUARTE J.M.B. 1996. Guia de Identificação de Cervídeos Brasileiros. FUNEP, Jaboticabal:1-8.

DUARTE, J. M. B., and M. L. MERINO. 1997. Taxonomia e evolução. Pp. 1-21 in Biologia e conservação de cervídeos Sul-Americanos: *Blastocerus, Ozotoceros* e *Mazama*. (J.M.B Duarte, ed.). FUNEP, Jaboticabal.

DUARTE, J. M. B., and W. JORGE. 1998. Análise citotaxonômica dos *Mazama* cinzas do Brasil (*Mazama gouazoubira* e *Mazama rondoni*). No page in Análise citogenética e taxonômica do gênero *Mazama* (Cervidae; Artiodactyla) no Brasil (J. M. B Duarte, author). Ph. D. dissertation, Universidade Estadual Paulista, Botucatu, Brasil.

DUARTE, J. M. B., and W. JORGE. 2003. Morphologic and cytogenetic description of the small red brocket (*Mazama bororo* Duarte, 1996) in Brazil. Mammalia, 67:403-410.

DUARTE, J. M. B.; S. GONZALEZ, and MALDONADO J. E. 2008. The surprising evolutionary history of South American deer. Journal of Molecular Phylogenetics and Evolution 49:17-22.

EISENBERG, J. F. 1987. The evolutionary history of the Cervidae with special reference to the South American radiation. Pp. 60-64 in Biology and Management of the Cervidae (C. Wemmer, ed.). Smithsonian Institution Press, Washington D.C.

EISENBERG, J. F. 1989. Mammals of the Neotropics. The Northern Neotropics. Vol. 1. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press. 449.

EISENBERG, J. F. 2000. The contemporary Cervidae of Central and South America. Pp. 189-202 in Antelopes, deer, and relatives. Fossil record, behavioral ecology, systematic, and conservation (E. S. Vrba and G. B. Schaller, eds.). Yale University Press, New Haven and London.

FRAILEY D., K. E. CAMPBELL, and R. G. WOLF. 1980. Additions to knowledge of *Hippocamelus*, *Ctenomys* and *Myocastor* from the middle Pleistocene of the Tarija Basin, Bolivia. Occasional Paper of the Museum of Natural History. The University of Kansas. 85(1-14).

GALLINA, S. 1984. Ecological aspects of the co-exploitation of deer *Odocoileus virginianus* and cattle. Acta Zoologica Fennica 172:251-254.

GEIST, V. 1998. Deer of the world. Their evolution, behaviour, and ecology. Stackpole Books, Pennsylvania.

GILBERT, C., ROPIQUET, A., and HASSANIN, A. 2006. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): Systematics, morphology and biogeography. Molecular Phylogenetics and Evolution 40:101-117.

GORDON, I. J. 1989a. Vegetation community selection by ungulates on the isle of Rhum. I. Food supply. Journal of Applied Ecology 26:35-51.

GORDON, I. J. 1989b. Vegetation community selection by ungulates on the isle of Rhum. II. Vegetation community selection. Journal of Applied Ecology 26:53-64.

GORDON, I. J. 1989c. Vegetation community selection by ungulates on the isle of Rhum. III. Determinants of vegetation community selection. Journal of Applied Ecology 26:65-79.

GROVES, C. P., and P. GRUBB. 1987. Relationships of living deer. Pp 21-59 in Biology and Management of the Cervidae (C. Wemmer, ed.). Smithsonian Institution Press, Washington D.C.

GRUBB, P. 2000. Valid and invalid nomenclature of living and fossil deer, Cervidae. Acta Theriologica 45:280-307.

GRUBB, P. 2005. Order Artiodactyla. Pp. 637-722 in Mammal species of the world, a taxonomic and geografic reference (D. E. Wilson and D. M. Reeder, eds.). 3rd edition. The John Hopkins University Press, Baltimore.

GUERIN, C., M. FAURE, P. SIMÕES, M. HUGUENEY, C. MOURER-CHAUVIRE. 2002. Toca de Janela da Barra do Antonião, São Raimundo Nonato, PI. Pp. 131-137 in Sitios Geológicos e Paleontológicos do Brasil (C. Schobbenhaus, E. T. Queiroz, M. Winge, and M. L. C. Berbert-Born, eds.). DNPM/CPRM-Comissão Brasileira de Sítios e Paleobiológicos, Brasília, Brasil.

HAMILTON, W. R., 1978, "Cervidae and Palaeomerycidae", 495-508, in "Evolution of African mammals" (Maglio, V. J, and Cooke, H. B. S., eds.) Harvard University Press, Cambridge, England, xiv-641.

HERSHKOVITZ, P. 1972. The recent mammals of the Neotropical Region: a zoogeographic and ecologycal review. Pp. 311-431 in Evolution, mammals and southern continents (A. Keast, F. C. Erk and B. Glass, eds). State University of New York Press, Albany.

HERSHKOVITZ, P. 1982. Neotropical deer (Cervidae). Part I. *Pudus* genus Gray. Fieldiana Zoology 11:1-86.

HOFFSTETTER, R. 1952. Les mammifères pleistocènes de la République de L'Equateur. Mémoires de la Societé Géologique de France Nouvelle Serie. Tome XXXI, fasc. 1-4, Feuilles 1 a 49 : 1-391.

HOFFSTETTER, R. 1963. La faune pléistocène de Tarija (Bolivie). Bulletin du Muséum National D'Histoire Naturelle 2ª serie, tome 35:194-203.

HOFMANN, R. R. 1973. The ruminant stomach. Stomach structure and Feeding habits of east African game ruminants. East African Monographs in Biology 2:1-364.

HOFMANN, R. R. 1985. Digestive Physiology of the Deer – their morphophysiological specialization and adaptation. Pp. 393-407 in Biology of Deer Production (P. F. Fennessy and R. K. Drew, eds.). Royal Society of New Zeland.

HOFMANN, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

HOFMANN, R. R., and D. R. M. STEWART. 1972. Grazer or browser: A classification based on the stomach-structure and feeding habits of east African ruminants. Mammalia 36:226-240.

ILLIUS, A. W., and I. J. GORDON. 1990. Constrains on diet selection and foraging behaviour in mammalian herbivores. Pp. 369-393 in Behavioural mechanisms of food selection (R. N. Hughes, ed.). Springer–Verlag, Berlin.

JACKSON, J. E., and J. GIULIETTI. 1988. The food habits of pampas deer *Ozotoceros bezoarticus celer* in relation to its conservation in a relict natural grassland in Argentina. Biological Conservation 45:1-10.

JANIS, C. M., and K. M. SCOTT. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. American Museum Novitates, 2893:1-85.

JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215-267.

KURTEN, B. and E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press , New York. 442pp.

KUZNETSOVA, M. V., KHOLODOVA, M. V., and DANILKIN, A. A. 2005. Molecular phylogeny of deer (Cervidae: Artiodactyla). Russian Journal of Genetics 41:910-918.

MARSHALL, L. G., et al. 1984. Mammals and Stratigraphy: Geochronology of the continental mammal-bearing quaternary of South America. Palacovertebrata, Montpellier.

MARTÍNEZ, A. M., V. MOLINA, F. S. GONZÁLEZ, J. S. MARROQUÍN, and J. NAVAR. 1997 Observations of white-tailed deer and cattle diets in Mexico. Journal of Range Management 50:252- 257.

McKENNA, M., and S. K. BELL. 1998, Classification of Mammals, above the species level. Columbia University Press, New York.

MEDELLÍN, R. A., A. L. GARDNER, and J. M. ARANDA. 1998. The taxonomic status of the Yucatán brown brocket, *Mazama pandora* (Mammalia: Cervidae). Proceedings of The Biological Society of Washington 111:1-14.

MEIER D. and M. L. MERINO 2007. Distribution and habitat features of southern pudu (*Pudu puda* Molina, 1782) in Argentina. Mammalian Biology 72:204-212.

MENEGAZ, A. N. 2000. Los Camélidos y Cérvidos del Cuaternario del Sector Bonaerense de la Región Pampeana. Ph.D dissertation, Universidad Nacional de La Plata, Argentina.

MENEGAZ, A. N., and E. P. TONNI. 1985. *Ozotoceros bezoarticus* (Mammalia, Cervidae) in the Quaternary of Buenos Aires Province, Argentina. Pp. 43-53 in Quaternary of South America and Antarctic Peninsula (J. Rabassa, ed.). A. A. Balkema, Rotterdam.

MENEGAZ, A. N., and ORTIZ JAUREGUIZAR. 1995. Artiodactyla. El registro continental de la evolución climática y biológica de los últimos 5 millones de años entre el Hemisferio Norte y el Hemisferio Sur. Pp. 311-337 in Monografías del Museo Nacional de Ciencias Naturales 12 (M. T. Alberdi, G. Leone and E. P. Tonni, eds.). Madrid.

MERINO M. L. 2003 Dieta y uso de hábitat del venado de las pampas, *Ozotoceros bezoarticus celer* Cabrera 1943 [Mammalia - Cervidae] en la zona costera de Bahía Samborombón, Buenos Aires, Argentina. Implicancias para su conservación. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, UNLP, La Plata. 198 pp.

MERINO, M. L., S. GONZALEZ, F. LEEUWENBREG, F. H. G RODRIGUES, L. PINDER, and W. TOMAS. 1997. Veado campeiro (*Ozotoceros bezoarticus* Linneus 1758). Pp. 42 –55 in Biologia e Conservacao de Cervideos Sul-Americanos; *Blastocerus*, *Ozotoceros* e *Mazama* (J. M. Barbanti Duarte, ed.) FUNEP, Jaboticabal.

MERRIAM C. H. 1901. A new brocket from Yucatan. Proceeding of the Biological Society of Washington XIV: 105-106.

NEITZEL, H. 1987. Chromosome evolution of Cervidae: Karyotypic and molecular aspect. Pp. 90-112 in Cytogenetics, basic and applied aspects (G. Obe and A. Basler, eds.) Springer-Verlag, New York.

NORIEGA J. I., A. CARLINI, and E. P. TONNI. 2004. Vertebrados del Pleistoceno tardio de la Cuenca del Arroyo Ensenada (Departamento Diamante, Provincia de Entre Ríos). INSUGEO Miscelánea. 12:71-76.

OWEN-SMITH, N. 1997. Distinctive features of the nutritional ecology of browsing versus grazing ruminants. Proceedings of international Symposium on Physiologie and Ethology of Wild and Zoo Animals, Suppl. II:176-191.

PELLIZA-SBRILLER, A., P. WILLEMS, and M. MANACORDA. 2001. Dietary structural types of polygastric herbivores at different environments and seasons. Journal of Range Management 54:330-337.

PINDER, L. 1997. Niche overlap among brown brocket, pampas deer and cattle in the Pantanal of Brasil. Ph.D. dissertation, University of Florida, Gainsville USA.

PITRA, C., J. FICKEL, E. MEIJAARD, and P. C. GROVES. 2004. Evolution and phylogeny of old world deer. Molecular Phylogenetics and Evolution 33:880-895.

PUTMAN, R. 1988. The natural history of deer. Cristopher Helm, London United Kingdon.

RANDI, E., N. MUCCI, M. PIERPAOLI, and E. DOUZERY. 1998. New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome b gene. Proceedings of the Royal Society of London 265:793-801.

REDFORD, K., and J. EISENBERG. 1992. Mammals of the Neotropics. The Southern Cone. Chile, Argentina, Uruguay, Paraguay, University of Chicago, Chicago.

REGIDOR, H., and V. ROSATI. 2001. Taruca. Pp 75-82 in Los ciervos autóctonos de la Argentina y la acción del hombre (Dellafiore C. and N. O. Maceira eds.) Grupo Abierto Comunicaciones, Buenos Aires.

RODRIGUES, F. H. G. 1996. Historia Natural e Biologia comportamental do veado campeiro (*Ozotoceros bezoarticus*) em cerrado do Brasil central . Universidad Estadual de campiñas - UNICAMP. Msc. Thesis.

RODRIGUES, F. H. G., and E. L. A. MONTEIRO-FILHO. 1999. Feeding behavior of the Pampas deer: a grazer or a browser?. Deer Specialist Group News. 15:12-13.

ROSSI, R. V. 2000. Taxonomia de *Mazama* Rafinesque, 1917 do Brasil (Artiodactyla, Cervidae). MSc. thesis, Universidad de São Paulo, São Paulo.

RUMIZ, D. I., et al. 2006. New records and a status assessment of a rare dwarf brocket deer from the montane forests of Bolívia. Journal of Zoology 271:428-436.

SAAVEDRA, B., and J. A. SIMONETTI. 1991. Archaeological evidence of *Pudu pudu* (Cervidae) in central Chile. Zeitschrift für Säugetierkunde 56:252-253.

SERRET A. 2001. Huemul. Pp.57-66 in Los ciervos autóctonos de la Argentina y la acción del hombre (Dellafiore C. and N. O. Maceira eds.) Grupo Abierto Comunicaciones, Buenos Aires.

SCOTT, K. M., and C. M. JANIS. 1987. Phylogenetic relationships of the Cervidae, and the case for a superfamily "Cervoidea". Pp. 3-20 in Biology and Management of the Cervidae (C. Wemmer, ed.). Smithsonian Institution Press, Washington D.C.

SMITH W. P. S.1991. *Odocoileus virgiunianus.* Mammalian Species 338:1-13.

SMITH-FLUECK, J. 2000. Food habits of the Patagonian Huemul. Pp. 93-96 in The Patagonian huemul. A mysteriosus deer on the brink of extincion (N. Diaz and J. A. Smith-Flueck, eds.). L.O.L.A. Buenos Aires, Argentina.

SPENCER, L. M. 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. Journal of Mammalogy 76:448-471.

STEHLI, F. G., and S. D. WEBB. 1985. The great American Biotic Interchange. Plenum Press, New York and London.

SOUZA CUNHA, F. L. and R. M. M. MAGALHAES. 1981. Cervideos pleistocenicos de Santa Victoria do Palmar, Río Grande do Sul. II Congreso Latino Americano de Paleontología (Porto Alegre) Anais II: 795 -803

TEER, J. 1994. El venado cola blanca: historia natural y principios de manejo. Pp. 32-48 in Ecología y manejo del venado cola blanca en México y Costa Rica (C. Vaughan and M. Rodriguez, eds.). Serie Conservación Biológica y Desarrollo Sostenible Nº 2, Heredia, Costa Rica.

TOMAS, W. M., and S. M. SALIS. 2000. Diet of the marsh deer (*Blastocerus dichotomus*) in the Pantanal wetland, Brazil. Studies of Neotropical Fauna and Environment 35:165-172.

TOMIATI, C., and L. ABBAZZI. 2002. Deer fauna from Pleistocene and Holocene localities of Ecuador (South America). Geobios 35:631-645.

UBILLA, M. 1985. Mamíferos fósiles, Geocronología y Paleoecología de la Formación Sopas (Pleistoceno sup.) del Uruguay. Ameghiniana. 22:185-196.

UBILLA, M., D. PEREA, C. GOSO AGUILAR, and N. LORENZO. 2004. Late Pleistocene vertebrates from northern Uruguay: tools for biostratigraphic, climatic and environmental reconstruction. Quaternary International 114:129- 142.

VAUGHAN, C., and M. A. RODRÍGUEZ. 1994. Ecología y manejo del venado cola blanca en México y Costa Rica. Serie Conservación Biológica y Desarrollo Sostenible Nº 2, Heredia, Costa Rica.

WEBB, S. D. 2000. Evolutionary history of new world deer. Pp. 38-64 in Antelopes, deer, and relatives. Fossil record, behavioral ecology, systematic, and conservation. (E. S. Vrba and G. B. Schaller, eds.). Yale University Press, New Haven and London.

WEBER, M., and S. GONZALEZ. 2003. Latin American deer diversity and conservation: a review of status and distribution. Écoscience 10:443-454.

XIMENEZ, A., A. LANGGUTH, and R. PRADERI. 1972. Lista sistemática de los mamíferos del Uruguay. Anales del Museo de Historia Natural de Montevideo 5:1-49.