The Broken Zig-Zag: Late Cenozoic large mammal and tortoise extinction in South America

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Abstract: During the latest Pleistocene-earliest Holocene, South American terrestrial vertebrate faunas suffered one of the largest (and probably the youngest) extinction in the world for this lapse. Megamammals, most of the large mammals and a giant terrestrial tortoise became extinct in the continent, and several complete ecological guilds and their predators disappeared. This mammal extinction had been attributed mainly to overkill, climatic change or a combination of both. We agree with the idea that human overhunting was the main cause of the extinction in South America. However, according to our interpretation, the slaughtering of mammals was accomplished in a particular climatic, ecological and biogeographical frame. During most of the middle and late Pleistocene, dry and cold climate and open areas predominated in South America. Nearly all of those megamammals and large mammals that became extinct were adapted to this kind of environments. The periodic, though relatively short, interglacial increases in temperature and humidity may have provoked the dramatic shrinking of open areas and extreme reduction of the biomass (albeit not in diversity) of mammals adapted to open habitats. Many populations were surely close to a minimum level of population viability. During the longer glacial periods, mammals populations recovered. This alternation of low and high biomass of mammals from open and closed areas is what we refer to as the Zig-Zag. During the present interglacial, humans entered South America and broke the Zig-Zag when killed all the megamammals and almost all the large mammals during their less favourable periodic lapse.

Key words: Extinction, South America, Pleistocene, Holocene, Mammalia, Man, Climate.

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It is well known that South American mammal communities underwent marked changes in diversity during the late Cenozoic (Pascual *et al*., 1965; Marshall *et al*., 1984; Tonni *et al*., 1992; Cione & Tonni, 1995, 2001; see papers in Tonni & Cione, eds., 1999). The last and most important turnover occurred in the late Pleistocene-Holocene, when about 80 % of large mammal species (weighting over 44 kg) and 100% of megamammal species (weighting over 1,000 kg, both herbivore and carnivore; see Owen-Smith, 1987) became extinct (Tables 1, 2, 3). South American communities had included at least some megamammals since the Paleogene but during the middle Pleistocene-earliest Holocene the remarkable figure of more than 35 megamammal species was documented. For a comparison, only 4 megamammal species (and the giraffe, close to a ton in body mass) occur in Africa today and in South America there are no megamammal today. The largest terrestrial mammal in the continent is the tapir *Tapirus bairdii* (with some individuals slightly surpassing 300 kg; Nowak & Paradiso, 1983). A few small mammals also disappeared, but no other metazoan or plant is known to have been affected by the extinction. Consequently, this extinction event is different to others such as the K-T event.

The late Pleistocene and earliest Holocene South American mammal fauna was very different to the Recent not only by the presence of many very large mammals but also because the glacial climates provoked a different distribution of many species (e.g. Tonni & Cione, 1997; Tonni *et al*., 1999a). In summary, the present composition and distribution is the result of extinction of large mammals and the biogeographic shifting and extirpation in some areas of most of the biota, caused by dramatic climatic changes.

For explaining the latest Cenozoic extinction, many hypotheses have been proposed, such as extinction due to climatic change and habitat destruction (Ficcarelli *et al*., 1997; Ochsenius, 1997; Coltorti *et al*., 1998), coevolutionary disequilibrium (Graham & Lundelius, 1984), overkilling by humans (with or without "blitzkrieg;» Martin, 1967, 1984; Alroy, 2001), the «keystone herbivore» hypothesis (Owen-Smith, 1987), and the infection

Table 1. Mammal taxa present in presumed Lujanian (sensu Cione & Tonni, 1999) beds in South America that became extinct. Asteriscs indicate those taxa that occur in archaeological sites.

Megamammals

Cuvieronius humboldti *	*Glossotherium tropicorum*	*Megatherium medinae*
Cuvieronius hyodon	*Glyptodon clavipes*	*Mixotoxodon larensis*
Doedicurus clavicaudatus *	*Glyptodon perforatus*	*Mylodon darwinii*
Eremotherium carolinense	*Glyptodon reticulatus*	*Mylodon listai* *
Eremotherium laurillardi	*Glyptodon sp.* * (from archaeo-	*Neothoracophorus depressus*
Eremotherium mirabile	logical site)	*Panochthus frenzelianus*
Eremotherium rusconii	*Haplomastodon guayasensis*	*Panochthus morenoi*
Glossotherium (Oreomylodon)	*Haplomastodon waringi*	*Panochthus tuberculatus*
wagneri	*Hemiauchenia paradoxa* *	*Plaxhaplous canaliculatus*
Glossotherium lettsomi	*Lestodon armatus*	*Stegomastodon platensis*
Glossotherium	*Lestodon trigonidens*	*Toxodon burmeisteri*
(Pseudolestodon) myloides	*Macrauchenia patachonica* *	*Toxodon platensis* *
Glossotherium robustum *	*Megalonyx sp.*	
	Megatherium americanum *	

Large mammals

Antifer niemeyeri	*Holmesina paulacoutoi*	*Pampatherium typum*
Arctotherium bonariense	*Hoplophorus euphractus*	*Paraceros fragilis*
Arctotherium brasiliense	*Lama gracilis* *	*Parapanochthus jaguaribensis*
Arctotherium tarijense	*Morenelaphus lujanensis*	*Propraopus grandis*
Brasiliochoerus stenocephalus	*Mylodopsis ibseni*	*Propraopus humboldti*
Equus (A.) andium	*Neochoerus aesopy*	*Propraopus magnus*
Equus (A.) insulatus	*Neochoerus sirasakae*	*Scelidodon cuvieri*
Equus (A.) lasallei	*Neuryurus n. sp.*	*Scelidodon chiliensis*
Equus (A.) neogeus *	*Nothropus priscus*	*Scelidodon reyesi*
Equus (A.) santa-elenae	*Nothrotherium roverei*	*Scelidotherium leptocephalum*
Eulamaops paralellus	*Ocnopus gracilis*	*Sclerocalyptus sp.* *
Eutatus seguini *	*Ocnotherium giganteum*	*Smilodon populator*
Glyptotherium sp.	*Onohippidion saldiasi* *	*Tapirus cristatellus*
Hippidion principale *	*Palaeolama niedae*	*Trigonodops lopesi*
Holmesina occidentalis	*Palaeolama weddelli*	*Xenorhinotherium bahiense*
	Pampatherium humboldti	

Medium sized mammals

Canis dirus	*Protocyon orcesi*	*Protopithecus brasiliensis*
Canis avus	*Protocyon troglodytes*	*Valgipes deformis*

Small mammals

Eligmodontia n. sp.	*Microcavia robusta*	*Desmodus draculae*

hypothesis (Ferigolo, 1999). Both more arid (Ochsenius, 1997) and more humid (Oliveira, 1999) conditions were found to be important for explaining the extinction. Opponents of the theory that large mammal extinctions were caused by climatic change state that there were many other similar and periodic climatic changes during the late Pleistocene that did not triggered massive extinctions (see Roy, 2001). Besides, counters of the "blitzkrieg" hypothesis carried out by human immigrants main-

tain that there are few bones of extinct mammals in the early archaeological sites (Politis et al., 1995). With respect to the infection hypothesis, immigrants that could carry infection vectors to the local fauna have been entering South America since the beginning of the Great American Interchange (ca. 3,000,000 YBP) and thus cannot readily explain a much later, short event.

It is not our goal to discuss the other hypotheses (there is abundant casuistic about it; see

Table 2. Present large mammals in South America (Nowak & Paradiso, 1983).

Blastocerus dichotomus	*Lama vicugna*	*Tapirus terrestris*
Catagonus wagneri	*Lama guanicoe*	*Tapirus pinchaque*
Hippocamelus antisensis	*Panthera onca*	*Tapirus bairdii*
Hippocamelus bisulcus	*Priodontes maximus*	*Tremarctos ornatus*
Hydrochoerus hydrochaeris	*Puma concolor*	

Table 3. Present large mammals in North America (Nowak & Paradiso, 1983).

Alces alces	*Odocoileus hemonius*	*Panthera onca*
Antilocapra americana	*Odocoileus virginianus*	*Puma concolor*
Bison bison	*Oreamnos americanus*	*Rangifer tarandua*
Canis lupus	*Ovibos moschatus*	*Ursus americanus*
Cervus elaphus	*Ovis canadensis*	*Ursus maritimus*
Enhydra latris	*Ovis dalli*	*Ursus arctos*

above) but proposing a new one, the Broken Zig-Zag hypothesis. In this paper, we analyze the bio-stratigraphic pattern of the large continental mammals and tortoises in South America during the late Pleistocene-earliest Holocene, and suggest that the extinction was caused by human hunting activities, but within a particular environmental framework.

METHODS

We rely heavily on the middle-late Pleistocene-Holocene biostratigraphic record (and radiometric dating) of the Pampean area of central Argentina, because it is the best known in South America (see articles in Tonni & Cione, 1999, eds.; Figure 1). Most of the previous analyses took the «Lujanian» mammals *in toto* for the analysis of the extinction process (see Marshall *et al*., 1984) and considered the Lujanian South American Land Mammal «Age» as including the Bonaerian and Lujanian *sensu stricto* (see the discussion below). We discuss occurrences in uppermost Cenozoic beds, including those of putative Holocene age. Presently, there are many radiocarbon dates in the upper Pleistocene and Holocene beds of the Pampean area, many derived from bones (Tonni *et al*., 2003). Dates given here are uncalibrated (RCYBP: radiocarbon years before present; see below).

For comparison of the general vegetation for the Recent and the Last Glacial Maximum (LGM) we designed two maps where three arbitrary categories of vegetational structure were used: open, medium and closely vegetated areas. The present distribution of these categories was approximately

Fig. 1. Map of South America depicting most of the sites mentioned in the text. 1. Taima Taima; 2. Talara; 3. Cupisnique; 4. Huargo; 5. Ayacucho complex; 6. Río Juruá; 7. Minas Gerias; 8. Sauce; 9. Tapalqué; 10. Cerro La China; 11. Arroyo Seco; 12. Los Toldos and Piedra Museo; 13. Las Buitreras; 14. Cueva del *Mylodon*, Cueva Lago Sofía, Cueva del Medio, Cueva Fell, Pali Aike and Tagua Tagua.

calculated on the basis of the biogeographic analysis of South America by Cabrera & Willink (1973; Figure 2). We did not include territories above 2000 m in this estimate. For the LGM, we designed a map showing the distribution partially following Clapperton (1993a; his Figure 23.10; our Figure 3). The continental surface area during the LGM was larger because sea level dropped about 120 m (Fray & Ewing, 1963; Fairbanks, 1989; Bard *et al*., 1990; Cione & Barla, 2000). In our reconstruction, the southwestern area of South America is shown as covered by ice. Present shelf areas that emerged during the LGM were depicted with the adjacent type of vegetation.

In addition to Clapperton (1993, his Figure 23.10), we used the following literature sources:

Fig. 3. Map depicting plant distribution in South America during the Last Glacial Maximum (modified from Clapperton, 1993b, and Tonni & Scillato, 1997). The boundaries of vegetation areas are tentative. The South American area was larger than present due to the sea level drop of ca 120 m. Symbols as in Fig. 2.
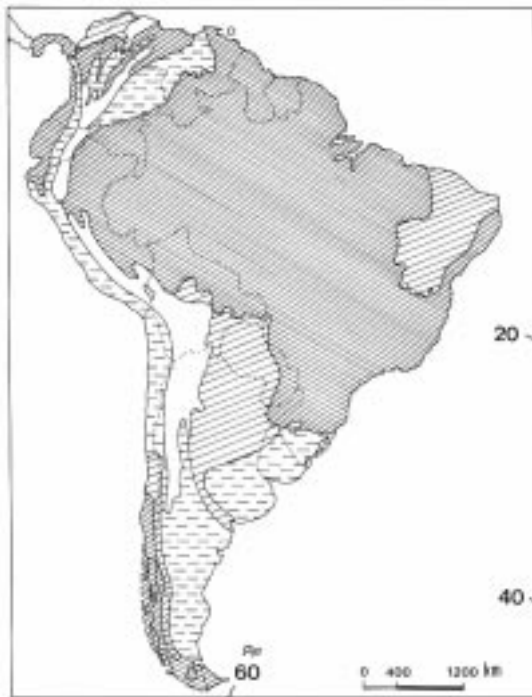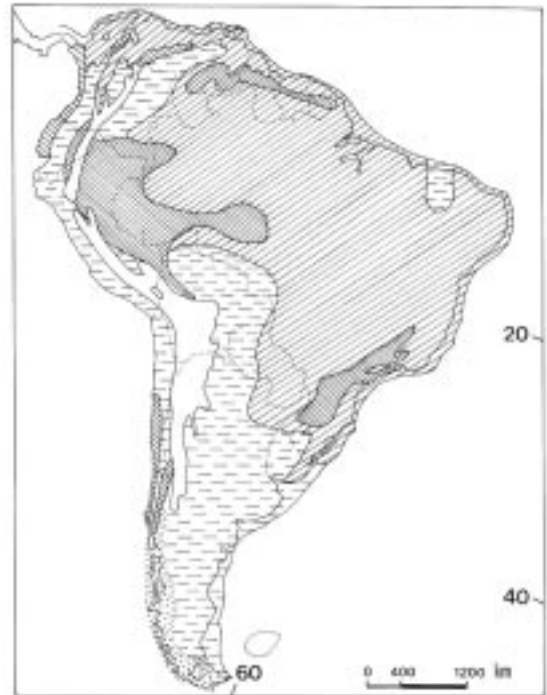

Fig. 2. Map depicting plant distribution in Recent South America following Cabrera & Willink (1973). We subdivided the vegetation types in 1) open areas (horizontal broken lines; Provincias Sabana, Desierto, Monte, Pampeana, Patagónica, Altoandina, Páramo, Puneña, Prepuneña, Guayana; in this subdivision mountains are included), 2) intermediate vegetated areas (oblique lines from right to left; Provincias Caatinga, Chilena, Espinal, Chaqueña), and 3) forested areas (oblique lines from left to right; Provincias Amazónica, Cerrado, Paranense, Yungas, Pacífica, Atlantica, Subantártica, Venezolana). Blank areas depict territory 2,000 m above sea level.

Venezuelan Guyana. Aridity during late Pleistocene and Holocene (Linares, 1993).
Llanos del Orinoco. Colombia and Venezuela; sand and loess mantle (Iriondo, 1997).
General Amazonia. Savanna-type vegetation and savanna forest replaced the rain forest during the late Pleniglacial ca. 22,000-13,000 RCYBP; the Amazonian forest may have been split into one major wet Amazonian and several other medium-sized forest areas (van der Hammen & Absy, 1994; see also Thompson *et al*., 1995). Savanna in the Amazonian area (Ochsenius, 1997; see also Turcq *et al*., 1997). During the Younger Dryas, the Amazon Basin was extremely dry, and Amazon River discharge was low (Maslin, 2000).
Western Amazonia. Presence of camelids (Rancy, 1992). In the Río Juruá: open country or savanna habitat (Webb & Rancy, 1992; Latrubesse & Rancy, 1997).
Northern Ecuador. Loessic sediments of periglacial areas (Ficcarelli & Borselli, 1993).
Central Brazil. From 32,400 to about 20,000

RCYBP a treeless grassland replaced the arboreal cerrado and the gallery forest, suggesting that humidity increased but temperature probably decreased. Humidity started to decrease at ca. 18,500 RCYBP and the period from ca. 18,500 to ca. 11,500 RCYBP was very dry. A sparse vegetation was growing in the region during that time. The dry climate continued until 6,500 RCYBP (Salgado-Laboriau *et al.*, 1997).

Southeastern Brazil. Late Glacial records from S Brazilian highlands document the predominance of grasslands (campos) where *Araucaria* forests occur today. Records from SE Brazil show that during pre- and full-glacial times modern tropical semideciduous forest and cerrado (savanna to dry forest) were mostly replaced by grassland and some subtropical gallery forest (Behling, 2002; Behling *et al.*, 2002; see also Behling, 1997; Behling & Negrelle, 2001).

Southern South America. General aridity; «sea» of loess, «sea» of sand (Clapperton, 1993 a, b; Iriondo & García, 1993; Tonni & Cione, 1994, 1995; Markgraf *et al.*, 1995; Iriondo, 1997; Tonni *et al.*, 1999a).

THE STRATIGRAPHIC AND FAUNISTIC FRAMEWORK

Biostratigraphy and climate

The periodic climatic alternation of glacial and interglacial epochs during the middle-late Pleistocene dramatically modified the distribution, composition and biomass of plant and animal communities in South America as in other regions of the world (Tonni & Fidalgo, 1978; Tonni & Politis, 1980; Graham, 1986; Tonni & Cione, 1997; Whitlock & Bartlein, 1997; Tonni *et al.*, 1999a; Haynes, 2002). The global inception of the glacial periods that characterize the middle and late Pleistocene is chronologically related to an important turnover in the South American mammal fauna.

The Pliocene to Recent continental faunistic sequence of the Pampean area of eastern Argentina gave the basic framework for the South American chronological scale (Cione & Tonni, 1999). The above mentioned turnover is represented by the boundary between the *Tolypeutes pampaeus* and *Megatherium americanum* biozones in the stratigraphic sections of the Pampean area and in Bolivia (Cione & Tonni, 1999; Cione *et al.*, 1999; MacFadden, 2000; Figure 6). Both units provide the biostratigraphic basis for the Ensenadan and Bonaerian stages. According to magnetostratigraphic analyses in the Pampean area and Bolivia, the base of the Bonaerian is younger than 0.78 Ma (Tonni *et al.*, 1999a, b; Cione

& Tonni, 1999, 2001; MacFadden, 2000; Nabel *et al.*, 2000; Figure 6).

A much smaller turnover permits to define a biostratigraphic unit in the Pampean area: the *Equus (Amerhippus) neogeus* biozone (Figures 4,6). This unit is the basis of the Lujanian Stage and is dated from about 130,000 to perhaps 7,000 RCYBP. It is characterized by the first record of some mammal taxa and the extinction of other (Pardiñas *et al.*, 1996; Cione & Tonni, 1999). Overlying the *Equus (Amerhippus) neogeus* biozone is the *Lagostomus maximus* biozone which constitutes the basis for the Platan Stage, dated from about 7,000 RCYBP to the XVI century (Figure 5). In this zone, only autochtonous Recent mammals occur, except for the peculiar occurrence of the canid *Canis avus* during this period (see below). Consequently, the deposition of sediments representing this stage appears to have occurred after the mammal mass extinction in South America. In the *Lagostomus maximus* biozone there are introduced mammals from the Old World, such as the cows, sheep and horse.

In the conceptual framework of «Land Mammal Ages,» Pascual *et al.* (1965) had recognized
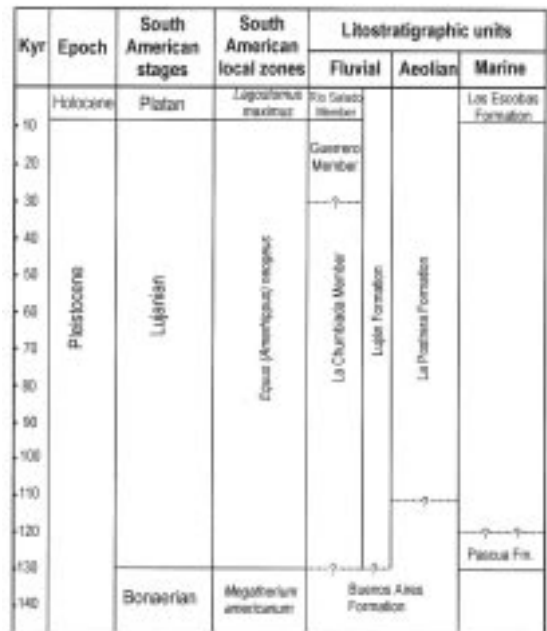

Fig. 4. Chronological chart of the late Pleistocene-Recent in southern South America depicting mammal zones and lithostratigraphic units from the Pampean area mentioned in text (modified from Cione & Tonni, 1999 and Tonni *et al.*, 1999b).
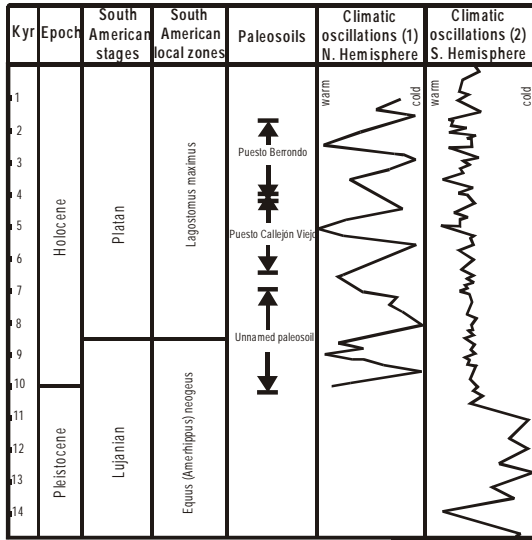
Fig. 5. Chronological chart of the latest Pleistocene-Recent in southern South America including paleosoils mentioned in text (modified from Tonni *et al*., 2001) and climatic oscillations represented by [18]O from a Northern Hemisphere site (Broecker, 2001) and a Southern Hemisphere site (Thompson, 2000).
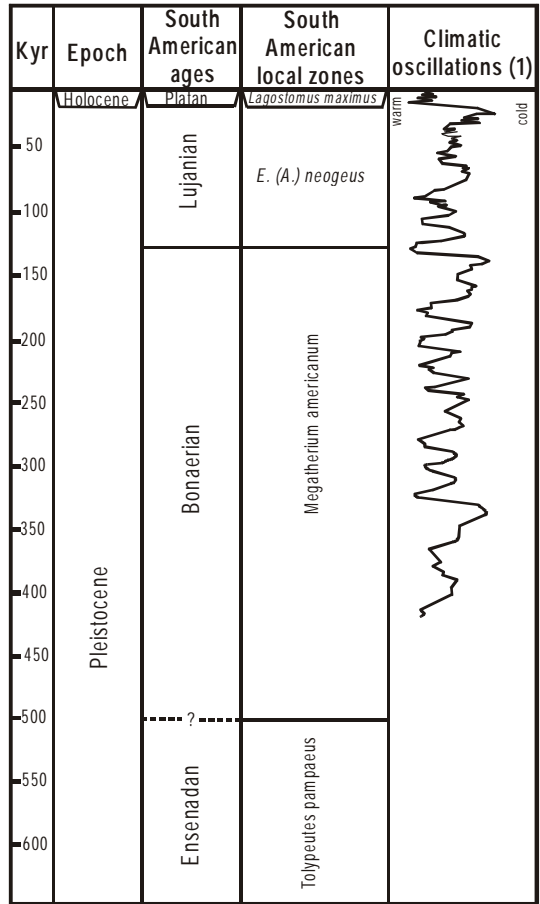

Fig. 6. Chronological chart of the middle Pleistocene-Recent in southern South America depicting mammal zones (modified from Cione & Tonni, 1999) and the climatic oscilations represented by [18]O of Vostok, Antarctica (Petit *et al*., 1999).

only the Ensenadan and Lujanian in the Pleistocene of South America. We have resurrected the Bonaerian and Lujanian of former authors as equivalent of the Lujanian of Pascual *et al*. (1965) in the Pampean area and Argentine Mesopotamia (Cione & Tonni, 1999). Additional biostratigraphic research should be done to demonstrate if these units can be recognised in the rest of South America. For this, we refer to as Bonaerian-Lujanian for the time between the Ensenadan and Platan in other parts of the continent except when there are radiometric dates available.

Mammal diversity during the middle-late Pleistocene

A remarkable feature of the South American Cenozoic terrestrial fauna is the presence of a very diverse endemic fauna of gigantic mammals (Ameghino, 1889; Simpson, 1980). The large size of individuals is striking in the Ensenadan, but also continues to be marked in the Bonaerian and Lujanian (Tonni *et al*., 1992). During the Neogene, until the establishment of the Isthmus of Panama at about 3 Ma, these very large mammals were mainly endemic notoungulates, litopterns and xenarthrans. However, mostly during the Pliocene Chapadmalalan and Marplatan Ages and the Pleistocene Ensenadan Age, many other taxa of Holarctic origin appeared in South America, most of them represented by already endemic genera and species (Cione & Tonni, 1995; 1996). Many of the Holarctic mammals that invaded South America were large (eg. several felids, ursids, tayassuids, equids, camelids, and cervids) and some other fall in the category of megamammals (gomphoteriids, other ursids).

The South American middle Pleistocene-earliest Holocene (Bonaerian-Lujanian) mammal diversity was significantly higher than that of the middle Holocene to Recent because at this moment it can be presumed that most of the extant mammals (243 genera; 73 genera if we exclude Chiroptera, Rodentia, Lagomorpha, Marsupialia and Insectivora; Nowak & Paradiso, 1983) were present together with those mammals that be-

came extinct in the continent (52 genera, see Table 1). In the particular case of the Pampean area, the faunal composition during most of the middle and late Pleistocene was also different to the Recent one because many of the extant mammals occurring there during this interval (except for interglacial times) corresponded to those presently living in arid and/or colder areas to the south and west. At least 24 species of mammals of the Platan or the Recent were documented as inhabiting the Pampean region during at least part of the late Pleistocene (*Lestodelphys halli, Didelphis albiventris, Lama guanicoe, Lyncodon patagonicus, Pseudalopex culpaeus, Dusicyon gymnocercus, Panthera onca, Puma concolor, Chaetophractus villosus, Zaedyus pichiy, Dasypus hybridus, Tolypeutes matacus, Abrothrix illuteus, Akodon azarae, A. iniscatus, Calomys laucha, C. musculinus, Eligmodontia typus, Graomys griseoflavus, Necromys benefactus, N. lactens, Oxymycterus rufus, Reithrodon auritus, Microcavia australis, Dolichotis patagonum, Galea musteloides*; Cione *et al.*, 1999)**.** Only one «non-analogue» association (see Graham et al., 1996) was documented in the Bonaerian and other in the Platan from the Pampean area (Cione & López Arbarello, 1994; Pardiñas, 1999). The lack of more examples of this kind of association could be due to poor sampling. During interglacial times, mammals from warmer climates occupied the region and during the glacial times, Patagonian and western taxa occurred there (Pardiñas *et al.*, 1996; Tonni *et al.*, 1999a).

Ninety-one extinct species and 52 extinct genera of large mammals and megamammals occur in presumed Lujanian beds of South America (from 130,000 yr to about 7,000 RCYBP; Table 1). We refer them as of «presumed» Lujanian age because there is some stratigraphic inaccuracy in several parts of South America outside Argentina and some records could correspond to Bonaerian beds. This means that some of these species might not have been involved in the massive extinction at the end of Lujanian. However, the Lujanian of the Pampean region appears to be characterized primarily by new occurrences, with few extinctions in the top of the Bonaerian (Cione *et al.*, 1999).

The total mammal generic diversity present during Lujanian times could have been as high as 295 genera (52 extinct genera plus Recent 243 genera; Tables 1, 2). The total large mammal (and megamammal) diversity present during Lujanian times could have been as high as 96 species distributed into 58 genera (the extinct 82 species distributed into 48 genera plus the Recent 14 species distributed into 10 genera; Tables 1, 2). Most

of the Lujanian taxa that became extinct were large mammals and megamammals.

The uppermost levels of the Lujanian (dated between 20,000 RCYBP to the earliest Holocene), comprising the well studied Guerrero Member of the Luján Formation in the Pampean area and other units in different parts of South America with radiometric dates include at least 44 species distributed into 37 genera of extinct taxa (41 large and megamammal species plus 3 smaller mammal species and 34 large and megamammal genera plus 3 smaller mammal genera; see detail below).

Present evidence indicates that the large and megamammal fauna was very well diversified at the end of the Pleistocene and did not suffer from any kind of declining trend in previous time intervals. Some clades such as notoungulates and litopterns were declining in number of taxa, but the total number of species did not diminish. Moreover, the number of megamammals in South America was the largest in the world at this moment.

Giant tortoises during the late Cenozoic

The presence of very large terrestrial tortoises (larger than a small glyptodont such as *Sclerocalyptus*) along with the large mammals and megamammals in South America is not widely known. These reptiles were of the size of a Galapagos tortoise, but were characterized by a remarkable robust caparace (thickness reaching to about 50 mm; Marcelo de la Fuente, personal communication). They have been found in the provinces of Santa Fe, Buenos Aires and Entre Ríos of Argentina (de la Fuente, 1999). The youngest record of a large tortoise (cf. *Chelonoidis*) comes from Lujanian beds in the Arroyo Perucho Verna, Entre Ríos, Argentina (de la Fuente, 1999).

Youngest record of extinct mammals in South America

The youngest beds where now-extinct mammals (with the exception of *Canis avus*) have been found in South America are Lujanian in age (that is older than 7000 RCYBP). Several of these Lujanian localities could be early Holocene in age. In North America, there is agreement that all the extinctions took place before the beginning of the Holocene (before 10,500 RCYBP; Roy, 2001; Haynes, 2002) because many of the putative Holocene dates were considered unreliable (Mead & Meltzer, 1984).

In the river valleys of the South American Pampean region, no extinct mammal was found in the typical Río Salado Member of the Luján Formation or correlative units, excepting for the

peculiar case of *Canis avus* (see below; Figure 4). The *Lagostomus maximus* biozone (and the Platan) begins in the base of this member (Cione & Tonni, 1995). The Río Salado Member is correlated with at least the middle Holocene Las Escobas Formation marine beds which were dated between ca. 6,500 to ca. 2,000 RCYBP. Their deposition coincides with the high sea-level of the Hypsithermal event (Tonni & Fidalgo, 1978; Fidalgo, 1992; Aguirre & Whatley, 1995). Eleven ^{14}C ages based on molluscan shells and total organic matter were obtained from transitional beds between the Guerrero and Río Salado members of the Lujan Formation in sections at the Arroyo Tapalqué (central Buenos Aires province; Figure 1) ranging between 9710 ± 110 and 8810 ± 140 RCYBP (Figini *et al*. 1995; Zárate *et al*. 1995; Cione *et al*., 2001).

In the divides of the Pampean region, no extinct mammal occurs in the uppermost beds of La Postrera Formation (of middle to late Holocene age).

Certainly, the best-known mammal faunas in the South American upper Pleistocene are those found in the Guerrero Member of the Luján Formation, the La Postrera Formation in the Pampean area, and the correlative Dolores Formation of Uruguay (Table 4). According to stratigraphic relationships and isotopic dating, the Guerrero Member was deposited between 21,000 and 10,000 RCYBP (Tonni *et al*., 2003 and papers cited therein). The localities most accurately dated are Tapalqué and Paso Otero (Tonni *et al*., 2003). The composite assemblage includes at least 36 extinct species distributed in 28 genera of large mammals (plus at least 3 species and genera of extinct smaller mammals and many other extant species; Ameghino, 1889; Prado *et al*., 1987; Alberdi *et al*.,

1988; Tonni *et al*., 1992; Martínez, 1997; Cione *et al*., 1999; Ubilla & Perea, 1999; see Table 4).

In addition to those records, in the uppermost Pleistocene beds (dated between 20,000 and 10,000 RCYBP) of several sites in Argentina, Chile, Peru, Uruguay and Venezuela, the following extinct species were documented: *Mylodon listai* (Cueva del *Mylodon*; southern Chile; Borrero, 1997), *Megatherium tarijense* (Ayacucho complex, Peru, dated 18,000-15,000 RCYBP; Hoffstetter, 1986:230), Megatheriidae indet. (Ayacucho complex, Perú, dated in 12,200 RCYBP, Mc Neish *et al*., 1970); *Glyptodon* sp. (Taima Taima, Venezuela, Gruhn & Bryan, 1984), *Eutatus seguini* (Cerro La China, Cueva Tixi, Buenos Aires, Argentina, Flegenheimer & Zárate, 1997; Mazzanti, 1997), *Scelidodon* sp. (Talara, Peru; 13,616 ± 600 RCYBP and 14,418 ± 500 RCYBP; Hoffstetter, 1970; Marshall *et al*., 1984; F. Pujos, personal communication; Cupisnique, Peru; Marshall *et al*., 1984; 24,000-16,000 RCYBP, F. Pujos, personal communication).), *Scelidotherium* sp. (Huargo, Perú, dated 13,400 ± 700 RCYBP; Hoffstetter, 1986:230), *Holmesina* sp. (Talara, Peru; Hoffstetter, 1970; Marshall *et al*., 1984; F. Pujos, personal communication), *Eremotherium* sp. (Cupisnique, Peru; Marshall *et al*., 1984; F. Pujos, personal communication), *Lestodon* sp. (Sauce, Uruguay, Arribas *et al*, 2001), *Macrauchenia* sp. (Cueva del *Mylodon*, southern Chile; Borrero 1997:91; Taima Taima, Venezuela, Gruhn & Bryan, 1984), *Onohippidion saldiasi* (Cueva del *Mylodon*, Piedra Museo, Los Toldos, Las Buitreras, Cueva Lago Sofía, Cueva del Medio, Fell, Pali Aike, Cerro Sota; southern Chile and Argentina; Alberdi & Prado, 1992; Miotti, 1993; Borrero, 1997; Alberdi *et al*., 2001; Huargo, Perú, cited as *Parahipparion*, dated 13,400 ± 700

Table 4. Large mammals and megamammals in the Guerrero Member of the Luján Formation and correlative units in the Pampean area.

Arctotherium bonariense	*Hippidion principale*	*Pampatherium typum*
Arctotherium tarijense	*Lama gracilis*	*Panochthus morenoi*
Doedicurus clavicaudatus	*Lestodon armatus*	*Panochthus tuberculatus*
Equus (A.) neogeus	*Lestodon trigonidens*	*Paraceros fragilis*
Eulamaops paralellus	*Macrauchenia patachonica*	*Plaxhaplous canaliculatus*
Eutatus seguini	*Megatherium americanum*	*Propraopus grandis*
Glossotherium myloides	*Megatherium lundi*	*Scelidotherium leptocephalum*
Glossotherium robustum	*Morenelaphus lujanensis*	*Sclerocalyptus sp.*
Glyptodon clavipes	*Mylodon darwinii*	*Smilodon populator*
Glyptodon perforatus	*Neochoerus aesopy*	*Stegomastodon platensis*
Glyptodon reticulatus	*Neothoracophorus depressus*	*Toxodon burmeisteri*
Hemiauchenia paradoxa	*Neuryurus n. sp.*	*Toxodon platensis*

RCYBP; Hoffstetter, 1986:230), *Lama gracilis* (Los Toldos, Piedra Museo; southern Patagonia; Miotti & Cattáneo, 1997; Borrero, 1997; Borrero *et al.*, 1998*), Equus (Amerhippus) neogeus* (Tagua Tagua; Casamiquela, 1999), *Equus andium* (Ayacucho complex, Perú; Hoffstetter, 1986:230), *Equus* sp. (Taima Taima, Venezuela, Gruhn & Bryan, 1984), *Hippidion* sp. (Taima Taima, Venezuela, Gruhn & Bryan, 1984), *Cuvieronius humboldti* (Monte Verde; 11,900 ± 200 RCYBP; Borrero, 1997), *Haplomastodon* sp. (Taima Taima, Venezuela, R. Casamiquela in Gruhn & Bryan, 1984; Talara, Perú; Hoffstetter, 1970), *Palaeolama* sp. (Cupinisque, Peru; F. Pujos, personal communication; Monte Verde, Chile, Casamiquela y Dillehay, 1989 fide Borrero 1997: 91), *Antifer niemeyeri* (Tagua Tagua, Chile; Casamiquela, 1999), *Canis avus* (Cueva las Buitreras, Cueva Tixi; Mazzanti, 1997; Borrero, 1997; Borrero *et al.*, 1998), *Smilodon* sp., Cueva Lago Sofía, southern Argentina; Borrero 1997), *Arctotherium tarijense* (Soibelzon, 2002, Prevosti *et al.*, 2003) were documented. Many of these records were based on dates obtained from bones and the other where dating was carried out on the basis of other elements are here sufficient to support that they correspond to the last 20,000 RCYBP.

There are several other records that are doubtful, at best. The identification of *Lama* cf. *owenii* is here dismissed (Nami & Nakamura, 1995). The Bonaerian genus *Antifer* was incorrectly cited for the latest Pleistocene of Buenos Aires and Chile by Aramayo (1997) and Casamiquela (1999). The *Mylodon* species that is recorded in Patagonia appears to be *M. listai* and not *M. darwinii* (Gustavo Scillato Yané, personal communication). *Panthera onca mesembrina* is here considered as indistinguishable from the living jaguar (*Panthera onca*).

At least 16 different extinct taxa were documented in dated South American units of putative early Holocene age: *Doedicurus clavicaudatus*, *Sclerocalyptus* sp., *Glyptodon sp.*, Scelidotherinae indet*., Megatherium americanum,* probably *Glossotherium robustum, Equus (Amerhippus) neogeus, Hippidion* sp., *Toxodon platensis, Macrauchenia patachonica, Hemiauchenia* sp., Gomphotheriidae*, Canis avus* (Pampean area, Tucumán, and Patagonia of Argentina and southern Chile; Fidalgo *et al.*, 1986; Collantes *et al.*, 1993; Politis *et al.*, 1995; Borrero, 1997; Borrero *et al.*, 1998; Politis & Gutiérrez, 1998) and *Eremotherium mirabile*, *Haplomastodon waringi* and *Arctotherium brasiliense* (Cedeño District, Venezuela; Linares, 1993; personal communication). However, these records have been discussed and many doubts persist about their consistence.

The youngest dated remains of extinct fauna in South America (excepting *Canis avus*) occur in the Estancia La Moderna site and the Arroyo Seco 2 sites, both in the Pampean area. The fossils recorded at the Estancia La Moderna include the glyptodonts *Sclerocalyptus* and *Glyptodon*, and an indeterminate mylodontid. They occur in a bed (UL a' of Zetti *et al.*, 1972; see discussion in Politis & Gutiérrez, 1998) transitional between two members of the typical Luján Formation: the Guerrero Member (with youngest dates ca. 10,000 RCYBP) and the Holocene Río Salado Member. According to Politis *et al.* (1995) and Politis & Gutiérrez (1998), bones of the glyptodont *Doedicurus clavicaudatus* yielded dates between 7,500 to 7,000 RCYBP. Other authors suggested that some young contaminants could have rejuvenated the samples (Borrero *et al.*, 1998). However, Politis & Gutiérrez (1998), even mention that a sample that gave an older date (LM-2-4; 12,350 ± 370 RCYBP) was redated with a better treatment and gave younger dates (7,010 ± 100 and 7,510 ± 370 RCYBP; Beukens, 1992, unpublished report fide Politis & Gutiérrez, 1998).

In the Arroyo Seco 2 site, a diverse extinct fauna was dated from 11,590 ± 90 to 7,320 ± 50 RCYBP (Politis *et al.*, 1995). It includes *Megatherium americanum,* cf. *Mylodon, Glossotherium robustum, Equus (Amerhippus) neogeus, Hippidion* sp., *Toxodon platensis, Macrauchenia patachonica* and *Hemiauchenia* sp. (Fidalgo *et al.*, 1986; Tonni, 1990; Politis *et al.*, 1995; Politis & Gutiérrez, 1998). Only *Megatherium americanum* and *Equus (Amerhippus) neogeus* were proved to have been a human food resource in this locality (Politis & Gutiérrez, 1998). In the same site, a human burial accompanied by a funeral trousseau dated at 7,800 to 6,300 RCYBP included a *Glyptodon* osteoderm close to the human skull with which it seemed to be contemporaneous (Politis & Gutiérrez, 1998). However, recent redating of samples did not confirm the Holocene age of Arroyo Seco 2 extinct fauna (G. Politis, personal communication).

A Holocene date (8639 ± 450 RCYBP) based on bones of *Mylodon*, *Lama* and horse found at Pali Aike, Santa Cruz, Argentina was considered as a minimal age for that site (see Borrero, 1997).

Gomphotheriidae and Scelidotherinae remains were found in a bed overlying mylodontine remains dated 8,660 ± 150 RCYBP in Tafí del Valle (Tucumán; Collantes *et al.*, 1993).

Bones of *Canis avus*, without evidence of human association were recovered from levels dated at 4,865 ± 65 RCYBP in the Cueva Tixi and also in Zanjón Seco 2, both in the Pampean area (Politis *et al.*, 1995; Mazzanti & Quintana, 1997). The late disappearance of the species *Canis avus* was

not considered as a real extinction but a hybridation with other canids (Berman & Tonni, 1987). A date of 4,300 RCYBP for a caparace of a glyptodont (Rosello *et al.*, 1999) was considered unsupported by Cione *et al.* (2001).

In summary, we counted at least 55 species and 40 genera of confirmed extinct mammals and reptiles in beds deposited between 20,000 to 10,000 (perhaps 7,000) RCYBP in South America. These taxa certainly disappeared in the last massive extinction. There are many other mammals documented in Lujanian beds of South America for which we have not certitude if they reached this period (Table 1). Future work will confirm or reject this hypothesis.

Oldest human presence in South America
In South America, archaeological evidence indicates that the continent was occupied by several distinct groups at the end of the Pleistocene (Gruhn, 1997). «A late date for the arrival of human groups, around 13,000-11,000 RCYBP, can be defended if we include, in addition to the evidence (from Argentina), that from Monte Verde (Chile) and other sites in South America» (Borrero *et al.* 1998:196). Some of the dated sites with humans for this period are: Taima Taima (ca. 13,000 RCYBP) and El Jobo complex (both sites in the Estado de Falcón,Venezuela; see Gruhn & Bryan, 1984; Politis & Gutiérrez, 1998); Tibitó, Bogotá basin, Colombia, dated at 11,740 ± 110 RCYBP (see Gruhn, 1997); four different cultural complexes in Peru dated between 10,000 and 12,000 RCYBP (Cardich, 1997); Quereo, near Los Vilos, Chile, dated at 11,600 ± 190 RCYBP (see Gruhn, 1997); Tagua Tagua, Chile, 10,200 RCYBP and 9,900 RCYBP (Núñez *et al.*, 1993); Monte Verde, a site with mastodont and paleocamelid remains located in southern Chile dated ca. 12,000 RCYBP (Dillehay, 1989; however see Fiedel, 1999); Pedra Pintada, Amazonia, Brazil, ca. 11,100 RCYBP (Roosevelt *et al.*, 1996); Lapa do Boquete, Minas Gerais, Brazil, 12,070 RCYBP to 11,000 RCYBP (see Gruhn, 1997); Abrigo de Santana do Riacho, Minas Gerais, Brazil, 11,960 ± 250 RCYBP (see Gruhn, 1997); for supposed dates of ca. 13,000 RCYBP in southern Brazil, see Schmidt Dias & Jacobus (2002); Los Toldos (11 level of Los Toldos, Santa Cruz, Argentina, dated at 12,600 ± 600 RCYBP; Cardich (1977); Cueva del Lago Sofía (Santa Cruz, Argentina; 12,990 ± 490 RCYBP and 11,570 ± 60 RCYBP; Politis *et al.*, 1995), Tres Arroyos (Tierra del Fuego, Argentina; 11,800 ± 250 RCYBP; Politis *et al.*, 1995:199); Cerro La China and Cerro El Sombrero, Argentina, dated at ca. 11,000-10,000 RCYBP (Flegenheimer & Zárate, 1997); the Piedra Museo site (Santa Cruz,

Argentina) corresponds to a time between 11,100 and 10,300 RCYBP (Miotti, 1993; Borrero *et al.*, 1998; Ramírez Rozzi *et al.*, 2001).

In the Holocene, there are many localities with cultural remains or human bones. Some of them, of putative early Holocene age, include extinct fauna (see above).

The oldest widely accepted human presence in North America is dated at 11,500 RCYBP (Pielou, 1992: 112; Ward, 1997; Haynes, 2002; but see Fiedel, 1999).

THE BROKEN ZIG -ZAG HYPOTHESIS

We propose that megamammal and large mammal (and tortoise) extinction in South America during the late Pleistocene-earliest Holocene was occasioned by human foragers. However, we believe that the slaughtering of the large mammals would have been accomplished in a particular circumstance: total biomass (not diversity) and distribution of open areas adapted mammals was extremely reduced in response to the periodic shrinking of this kind of environments (the Zig-Zag) which was provoked by the last (the present) interglacial periodic rising of temperature and humidity.

This hypothesis is supported by the climatic evolution of the continent, the positive biostratigraphical evidence, the adaptation to open environments of those mammals that became extinct which also were probably k-adapted, the complete disappearance of megamammals and most large mammals, the protected environments where the few surviving large mammals live, and the fact that American mammals did not coevolution with humans.

DISCUSSION

The Zig-Zag
The periodic severe changes in Pleistocene climate provoked dramatic modifications in the distribution and biomass of the biota in South America and other continents (probably 18 times during the LGM; Ward, 1997; Blunier & Brook, 2001; Figure 6). We used the expression Zig-Zag to stress in the periodicity of a phenomenon that actually has almost not been considered in the literature.

To determinate the impact of changes, we evaluated the possible modification of the distribution of vegetation types. Modern South America encompasses 18% open areas, medium vegetated areas 15% and closed areas 67% (Figure 2). Using the reconstruction of South America during the LGM, we calculated that open areas could encom-

pass 31% of the territory, medium 54% and closed 15% (Figure 3). Simberloff (1986 fide Raup, 1992: 136) had calculated that areas of wet forests were reduced by 84 % during this time. We understand that the most difficult definition is that of the «medium vegetated areas». In this item, cerrados, chaco, monte and other relatively closed areas are included along with some more open areas (see Clapperton, 1993a, his Figure 23.10). For this, we consider that the geological, floristic and faunistic evidence from the present densely vegetated areas suggest that open areas were even larger than that depicted by Clapperton (1993a, his Figure 23.10).

We commented above that during the late Pleistocene the mammal diversity was higher especially because many different species of large and megamammals were thriving in the Pampean area and the rest of South America. However, although the taxonomic diversity was elevated, the number of individuals per species and the total biomass in each location probably was not high because the glacial ecosystems should not have been very productive. During the glacial times, while climate was colder and drier, open areas expanded and animals and plants adapted to these environments augmented their distribution and biomass (Tonni & Cione, 1997; Tonni *et al.*, 1999a). During the shorter interglacial periods, when temperature was even higher than present (Thompson, 2000; Blunier & Brook, 2001), an expansion of the forested areas may be expected, and with this an increase the biomass of forest dwelling animals, including those that survived the Pleistocene-Holocene extinction, such as tapirs (Pardiñas *et al.*, 1996; see above).

Remarkably, the fossil record does not suggest that these cyclic environmental changes either produced depletion of niches or caused massive extinction of mammals (Cione *et al.*, 1999; Tonni *et al.*, 1999b; Nabel *et al.*, 2000). In the short integlacial periods, open areas adapted mammals had not necessarily been starving, but populations were surely remarkably reduced in number of individuals and under ecological stress. Some populations possibly were close to the minimal viable number and some populations surely became isolated and genetic flux greatly diminished among them, reducing variability. The persistence of South American mammal species through a prolonged lapse of important environmental changes could be explained according to the Plus Ça Change Model, in which morphological stasis over geological timescales tends to arise not from the stability of physical environments, but from their instability (Sheldon, 1998).

Climate when humans entered in South America

Global climate began to ameliorate after the 20,000-18,000 RCYBP cold peak (LGM; Clapperton, 1993; Petit *et al.*, 1999; Thompson, 2000; Blunier & Brook, 2001). After the LGM, climate appears to have continued being relatively dry in South America during several thousand years and humans seems to have entered southern South America when climate was still relatively dry (Figures 4,5; Iriondo, 1997; Tonni *et al.*, 1999a). Arid climates lasted at least until the end of the Pleistocene (Iriondo, 1997, 1999; Carignano, 1999; Tonni *et al.*, 1999a). Ice cores in South America, Greenland and Antarctica indicate that there was a peak of temperature followed by a decrease at about 12,700 and 10,300 RCYBP (the Antarctic Cold Reversal and the Younger Dryas, see McCulloch *et al.*, 2000). After this, there was a steep increase in temperature near the Pleistocene-Holocene boundary (Figures 4, 5; Thompson, 2000; McCulloch *et al.*, 2000). In the Pampean area, at about 10,000 RCYBP, development of dated paleosoils indicates a change to wetter conditions (Fidalgo *et al.*, 1975; Tonni & Fidalgo, 1978; Zárate *et al.*, 1995; Prieto, 1996; Tonni *et al.*, 1999a; Cione *et al.*, 2001; Figure 5). This series of climatic events are in agreement with ice cores and other temperature evidence (Thompson, 2000; McCulloch *et al.*, 2000). Consequently, a substantial change to warmer and wetter climate occurred in South America at about 10,000 RCYBP.

Which animals became extinct?

In North America, some very large mammals (below the size of megamammals, but weighing almost a ton) survived the great extinction (eg. bison, polar bear). In South America, however, there are no very large mammals, because no megamammal survived and the largest present mammal (*Tapirus bairdii*) weighs less than one third of a ton (Table 3).

Respecting the extinct taxa in South America, more than 70% of megamammal species and 55% of the large mammal species were xenarthrans. No megaxenarthran and only one large xenarthran survived. On the contrary, no small xenarthran became extinct notwithstanding that there were many medium-sized and small xenarthrans present (as today; Table 2). Besides, the last notoungulates, litopterns, and gomphotheriids disappeared.

Of the 14 species of large mammals that presently occur in South America, 12 are of Holarctic origin and 2 are of South American origin. There

was a larger proportion of extinct mammals of South American origin because almost all the large xenarthrans, and all litopterns and notoungulates disappeared (Tonni *et al.*, 1992; Cione *et al.*, 1999). Only one large xenarthran (*Priodontes maximus*) and a caviomorph (*Hydrochoerus hydrochaeris*) survived the large mammal extinction (Table 2).

A small number of extinct mammals with a body mass under 44 kg is documented as follows: the carnivores *Canis dirus* (Lujanian of Peru; Hoffsteter, 1970), *Canis avus* (Lujanian-Platan of Argentina)*, Protocyon orcesi* (Bonaerian-Lujanian of Ecuador; Hoffsteter, 1970)*, Protocyon troglodytes* (Lujanian of Brazil; Cartelle, 1994) and *Valgipes deformis* (Lujanian of Brazil; Cartelle, 1994); the rodents *Eligmodontia* n. sp. (Lujanian of Argentina; Pardiñas, 1999) and *Microcavia robusta* (Lujanian of Argentina; Quintana, 1996), the vampire bat *Desmodus draculae* (Lujanian of Brazil; Morgan 1999), and the primate *Protopithecus brasiliensis* (Cartelle, 1994).

Consequently, the latest Quaternary extinction in South America was biased towards large mammals and megamammals (about 90% of the species; Table 1), both those of South American and of Holarctic origin but also the giant terrestrial tortoises disappeared (see above).

Extinct mammals were adapted to open environments

Although the at least 83 species of large and mega-mammals and the big terrestrial tortoises that became extinct in South America involve species with different feeding habits, nearly all seem to have been adapted to open environments (Webb & Marshall, 1982; Marshall *et al.*, 1984; Bond *et al.*, 1995; Tonni & Scillato Yané, 1997; Table 1). Moreover, many were even adapted to arid environments. A possible exception is the capybara *Neochoerus aesopy* of presumed amphibious habit.

Glyptodonts, tardigrades, toxodonts, equids, and camelids were grazers; litopterns and perhaps gomphotheriids were browsers; daypodiids are omnivores; smilodons, ursids, and the canid *Canis avus* were carnivores; in addition, some authors considered the ground sloth *Megatherium americanum* as a carnivore (Fariña & Vizcaíno, 1999). Mastodonts have been traditionally considered as browsers, but grass phytolith assemblages in feces from three individual mastodonts contained similarly high concentrations of pooids, suggesting that these grasses were a significant part of the diet. Abundant pooid phytoliths, in addition to diatoms, indicate that these mast-

odonts grazed in a cool, moist, possibly near water, late Pleistocene environments (Gobetz & Bozarth, 2001: 115).

Many extinct mammals were k-adapted animals

Many of the extinct mammals were large but low in abundance. Females probably attained sexual maturity late, with a very long gestation period (one year or more) and prolonged parental care, implying one offspring in two or three years, and a total low number of offsprings during life.

Which of the large mammals survived in South America?

No megamammal survived in this continent and the only relatively large mammals that avoided extinction are inhabitants of areas of relatively difficult access for humans such as 1) forests and cerrados (tapirs, *Tapirus terrestris*; large armadillos, *Priodontes giganteus*; peccaries, *Catagonus wagneri*; and some deers, *Blastoceros dichotomus; Hippocamelus bisulcus*); 2) mountainous areas (spectacled bear, *Tremarctos ornatus*; other tapirs, *Tapirus pinchaque* and *Tapirus bairdii*; vicuña, *Lama vicugna*; and deer, *Hippocamelus antisensis*); and 3) wetlands (carpinchos, *Hydrochoerus hydrochaeris*; cervids, *Ozotoceros bezoarticus*). Among those large tetrapods that survived are the more fully aquatic vertebrates such as river dolphins, manatees, seals, sealions, and caimans. The other survivors are some eurytopic species such as large carnivoran (*Panthera onca*, *Puma concolor*), and the camelid guanacos (*Lama guanicoe*) (Table 2). Guanacos are fast, numerous and have montane populations. In addition, there is evidence in the Andean region of early domestication of the guanacos (Pires Ferreira *et al.*, 1976; F. Pujos, personal communication). The jaguar and puma include a large variety of prey in their diets and certainly were not especially adapted to feed on those big herbivores that became extinct.

American mammals were not adapted to humans

South American large and heavy Pleistocene megaherbivores have been mostly considered relatively clumsy and slow animals (Romer, 1966; for a different view see Fariña & Vizcaíno, 1999). However, notwithstanding that most of the survivors were of Holarctic origin, it is certain that none of these animals first evolved in contact with humans. Quite certainly, these animals had not developed prevention reflexes against human hunting practices. Besides, there is no doubt that

paleoindians both in North and South America were big-game hunters notwithstanding that they also could use other resources for their subsistence (Martin & Klein, eds., 1984; Neves & Cornero, 1997; Borrero *et al*., 1998; Politis & Gutiérrez, 1998; Haynes, 2002). In some cases, there was even ritual burials as it is the case of bears in North America (Mather, 2002). Even those mammals that do not appear in archaeological sites were hunted, especially when their large size impeded transportation. Indirect evidence of hunting of some large mammals not recorded in archaeological contexts was obtained from blood present in lithic points (Kooyman *et al*., 2001).

In summary.

· The distribution and biomass of the fauna and flora had strongly fluctuated many times during the middle-late Pleistocene in a Zig-Zag but no mass extinction event was recorded in the continent until the boundary Pleistocene-Holocene.

· All megamammals (36 species distributed into 18 genera) and most large mammals (46 species distributed into 30 genera) present in the Lujanian (latest Pleistocene) became extinct in South America.

· Pleistocene megamammals and large mammals were mostly adapted to open areas and were probably k-adapted organisms.

· Almost all the few large mammals that survived (14 species distributed into 10 genera) are adapted to forests, mountainous areas or wetlands or at least they have populations in this kind of environments.

· When humans entered South America, climate was changing and open areas were shrinking strongly (with the correlative diminution in number of open areas-adapted mammals).

· It is documented that humans hunted many of the mammals that became extinct.

· The extinction appears to have been more concentrated in taxa of South American origin, mainly because a large proportion of xenarthrans disappeared.

We believe that in the particular situation of a dramatic shrinking of geographic range and populations of large, native, and mostly slow and clumsy mammals and tortoises, a relatively small number of latest Pleistocene active foragers with specialized weapons would have been able to exterminate nearly all of them after several thousand years of cohabitation. Quite certainly, when populations diminished to a threshold, they became not viable anymore. We agree with Politis *et al*. (1995: 200) in that this process seems to have not been a "blitzkrieg" because it took several

thousand years (perhaps 5,000 yr.) to be completed in South America. Actually, there are other objections to the "blitzkrieg" hypothesis (e.g. absence of an advancing front; see Beck, 1996).

COMMENTS

Large carnivores such as the short-faced bears *Arctotherium* and the large saber-tooth cat *Smilodon populator* also became extinct (Soibelzon, 2002). We interpret that this extinction was a cascade effect related to the disappearance of their prey (see also Haynes, 2002). We do not discard that some herbivores could also have been exterminated by cascade effects (see Owen-Smith, 1987).

Certainly, the disappearance of such a remarkable series of megamammals and large mammals should have had a profound effect on the rest of the biota in South America, perhaps as important as those effects in North America (see Haynes, 2002). Megamammals and large mammals exerted dominance over the communities in South America. Many of the megamammals and large mammals exploited similar niches and formed guilds. The large glytodonts are an example. These niches disappeared completely. When all megamammals and large mammals were erased, open areas were only occupied by guanacos, cervids, some carnivores and smaller animals. This important change had to have a great ecological influence and it should be most relevant to learn what happened with the open areas vegetation, the small mammals and the carrion eater birds after the massive extinction. For example, in North America it was postulated that when megamammals were gone, natural processes such as woody regeneration and shrub invasions of grassy glade progressed unimpeded (Haynes, 2002).

Based on the supposition that the native fauna was in process of reduction, some authors suggested that humans had a secondary role in the extinction of fauna in the Pampean area (Politis *et al*., 1995). This could be certain for litopterns and notoungulates, but not for xenarthrans which were highly diversified during the late Pleistocene. Moreover, from the 91 extinct mammal species, 51 were edentates (Table 1). Actually, there was a process of replacement of local mammal fauna by other taxa of Holarctic origin, especially ungulates (which included many endemic genera and species; Tonni *et al*., 1992; Cione & Tonni, 1995; Cione *et al*., 1999). The fauna was certainly able to cope with the environmental conditions present in the continent prior to the major extinction event, even during the glacial time (Tonni *et al*.,

1992). Moreover, many new endemic taxa appear for the first time in the latest Pleistocene (e.g. *Doedicurus clavicaudatus* which is known from the base of the *Equus (Amerhippus) neogeus* biozone in the Pampean area; Cione & Tonni, 1999). Doubtless, the extinction was due to new ecological causes and neither was a coup de grâce nor accelerated a process already underway before human arrival in South America. Raup (1992) suggested that fluctuations in the rain forest should have provoked fluctuations in the global diversity. However, no massive extinction was observed in large mammals through the Pleistocene glaciations in South America. There is no sound evidence indicating that the present interglacial was fundamentally different from older ones, except for that it was proposed that it lasted more than the other warm periods in the middle-late Pleistocene (Petit *et al*., 1999 but see Kukla, 2000) and the modifications occasioned by the expansion of human activities. Graham (1986) discussed the possibility that the Holocene was not as warm as the last interglacial. However, climatic differences with other interglacial periods seem to have been relatively small (Pardiñas *et al*., 1996).

From a biogeographic point of view, if humans entered South America from North America, and if the extinction was occasioned by them, it would have to be accomplished earlier in North America than in South America. Accordingly, the youngest records of extinct mammals in North America were dated at 10,370 RCYBP (i.e. latest Pleistocene (Beck, 1996) while in South America, the youngest records appear to correspond to the early Holocene. However, the dispersion of humans in South America could have been very fast. Youngblood (2002) calculated that humans could have traveled from Beringia to central Chile in 250 years. Available evidence suggests that the extermination process lasted longer in South America than in North America. This long lasting process could have been related to the peculiar climatic history and biocenotic evolution of each continent.

Finally, we would like to stress that the extinction event in South America was the largest in the world at the moment and perhaps the youngest one. Besides, it appears plausible that without human hunting, the extraordinarily varied fauna of large mammals and megamammals that characterized South America in the late Pleistocene would have recovered and survived, as it had occurred after each of the previous numerous interglacial periods.

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