TROPHIC RELATIONSHIPS AMONG LUJANIAN MAMMALS

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ABSTRACT: The South American Lujanian megafauna is analysed from the points of view of the body mass of its members, and of the ecological implications of these body sizes. Using equations relating body size to population density and basal metabolic rate, it is proposed that the normally assumed trophic requirements of such a community could not have been fulfilled, and, therefore, that the accepted environments could not have supported this on-crop biomass. Further, it will be proposed here that a large flesh-eater (probably a carrion-eater) trophic niche would be at least partially empty, based on the paucity of large carnivorous species relative to the number of large herbivores. If this view is correct, it should be concluded that this fauna did not function like modern faunas. A possible explanatory hypothesis is that there are carnivores among those mammals currently regarded as megaherbivores. The ground sloths appear as the best candidates among the presumed herbivorous members of this fauna to have a more diverse diet.

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Introduction

The South American mammalian fauna of the late Pleistocene-early Holocene (Lujanian Land-mammal Age) is considered impressive relative to any modern or extinct mammalian fauna (Patterson & Pascual 1972; Simpson 1980). Among the more than one hundred and twenty genera compiled in Marshall et al. (1984), the estimated adult masses of 38 extinct herbivore genera exceeded 100 kg; about 20 of them were megaherbivores, that is, their masses were measured in megagrams, or metric tonnes (Owen-Smith 1988). No other fossil mammalian fauna is known to contain that number of megaherbivores. In contrast, the whole African continent, indisputably the most diverse mammal fauna known today, has only four species of megaherbivores: the African elephant (*Loxodonta africana*), the white rhinoceros (*Ceratotherium simum*), the black rhinoceros (*Diceros bicornis*), and the hippopotamus (*Hippopotamus amphibius*). A fifth species, the giraffe (*Giraffa camelopardalis*), might also be considered as belonging to this category. The Lujanian mammalian megafauna appears to be more comparable to dinosaur faunas, which of course had species of even larger body size. But even these dinosaur faunas not very often contained so many large-bodied species in a relatively short span of time and a limited area.

Many of the members of this obviously unique mammalian fauna have been well known for over a century (Owen 1838; Burmeister 1866-67; Ameghino 1887, 1889, 1895; see also Kraglievich 1940). However, this megafauna has not been extensively studied from a palaeobiological point of view; the exceptions are a number of papers regarding the Great American Biotic Interchange (see Stehli & Webb 1985; Marshall 1988; Lessa & Fariña 1992, and references therein). Darwin (1839) commented on this megafauna with his usual accurate insight. He stated in the subtitle of Chapter V of his journal of the Beagle's Voyage that "Large animals do not require luxuriant vegetation", and made many comparisons between the diversity and abundance of Lujanian and African faunas. This peculiar abundance of large-sized forms must have had important consequences; the distinctions, especially in many aspects of their ecology, between animals reaching a mass of or above 1000 kg and those of smaller sizes have been well documented and discussed by Owen-Smith (1987, 1988).

In this paper, I address the question of the trophic relations of the Lujanian megafauna, following the general ecological relationships between population density and body size (Damuth 1981a, 1987, 1991), and between basal metabolic rate and body size (Kleiber 1932; McNab 1980). On those grounds, I suggest that my analysis is valid for South America as a whole, or at least for a large temperate region. A particular fossil assemblage, the Luján local Fauna, was chosen as a case study. The Luján Formation in Argentina has long been recognised as being a source of fossils of animals living together at a single time (late Pleistocene-early Holocene, Lujanian Land-mammal Age) in a single habitat (Pascual et al. 1965). Its time span ranges from 300 ky BP- 8.5 ky BP. The Guerrero Member corresponds to the Pleniglacial (18 ky BP- 8.5 ky BP). The species contained in this formation were widespread in South America at this time (Patterson & Pascual 1972).

Four local faunas have been defined in the upper, richly fossiliferous, Guerrero Member of this formation for the Buenos Aires Province, Argentina; Luján, Paso Otero, Confluencia Quequén Salado-Indio Rico (Tonni et al. 1985), and Empalme Querandíes (Bargo et al. 1986). The local fauna discussed here was the preferred one for this study because it has been a focus for the collection of fossil material.

Material and Methods

Body mass and diet

All of the species found in the Luján local Fauna and listed in Tonni et al. (1985) were classified according to their probable diet. The masses of the extinct species were taken from previous estimations in the literature (Fariña 1993, 1995b; Fariña & Artigas 1993), or estimated following various procedures (Fariña 1995a; Fariña et al. in prep.). The masses of *Tayassu tajacu* and of *Lama guanicoe*, the two living species represented in the assemblage analysed here, were taken from Nowak (1991). Those species whose masses were estimated as less than 10 kg were not considered in order to avoid the problem of the biases in fossilisation, preservation, and collection (Behrensmeyer & Hill 1980; Damuth 1982). The justification of this is as follows: it seems highly unlikely that in a well studied formation, with a century-long history of collection, many new large forms remain to be found. The same cannot be assumed about smaller species. Although the figure of 10 kg appears to be an arbitrary cut-off, there are good taphonomical and ecological reasons to employ this limitation.

Population density

To estimate the population density of each herbivorous species, the general equation in Damuth (1981a) was used:

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

where D is population density in number of individuals per square kilometre, and m is the body mass expressed in grams. This equation is empirical. It was obtained from the study of many diverse modern ecosystems. The standard error of the slope is 0.026. If the average minus one s.e. were used rather than -0.75, there would be no important differences in the results.

It could be argued that the equation for tropical savannah herbivores in Damuth (1987) should be used rather than the general one, because African savannah is the only modern example of an ecosystem with high numbers of megaherbivore species. However, this might introduce serious biases in the understanding of past faunas. Indeed, so little is known from the Lujanian ecology that it seems more sensible to use values obtained from the whole universe of studied modern faunas. In any case, a cursory analysis using this other equation showed that the results and conclusions would alter very little.

On the other hand, abundance could have been estimated from the fossil record itself, as in Damuth (1982). This approach gives relative abundance only, and is more susceptible to taphonomic biases than is presence/absence. In addition, it would have required a thorough checking of the collected material, which would have been impractical. The use of theoretical calculations of population densities from algorithms derived from modern ecosystems has the advantages that the data are more easily available, and that there is sound theory supporting it. For further discussion, see Damuth (1981a, 1982, 1987, 1993) and Nee et al. (1991).

The basal metabolic rate of these herbivores was calculated following the equation in Peters (1983):

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

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

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

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

An appropriate equation, also quoted by Peters (1983), was used to estimate the basal metabolic rate of these species of the order Carnivora (same symbols as above):

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

Results

The herbivorous mammals of body masses greater than than 10 kilograms found in the Luján local Fauna are listed in Table 1. There are 30 species, more than half of them (16) being edentates: nine glyptodonts (*Neothoracophorus depressus*, *N. elevatus*, *Plaxhaplous canaliculatus*, *Doedicurus clavicaudatus*, *Panochthus tuberculatus*, *Glyptodon reticulatus*, *G. perforatus*, *G. rudimentarius*, *G. clavipes*), one pampathere (*Pampatherium typum*), six ground sloths (*Megatherium americanum*, *Scelidotherium leptocephalum*, *Glossotherium robustum*, *G. myloides*, *Lestodon trigonidens*, *L. gaudryi*). The list is completed by one rodent (the extinct giant capybara *Neochoerus sulcidens*), four members of the extinct South American Order Notoungulata (all of them belonging to the genus *Toxodon*: *T. bilobidens*, *T. burmeisteri*, *T. platensis*, and *T. paradoxus*), one litoptern (*Macrauchenia patachonica*), one perissodactyl (the horse *Equus (Amerhippus) curvidens*), six artiodactyls (the tayasuid *Tayassu tajacu*, the camelids *Eulamaops parallelus*, *Hemiauchenia paradoxa*, and *Lama guanicoe,* and the cervids *Morenelaphus azpeitianus* and *M. lujanensis*), and the gomphothere proboscidean *Stegomastodon superbus*.

They range in mass from 25 kilograms in the case of the peccary (one of the two living herbivorous species), to four tonnes in the cases both of the giant ground sloth *Megatherium* and the *Stegomastodon*. The on-crop biomass for each species was obtained by multiplying the calculated population density by its body mass. The total on-crop biomass for these species was 15434 kg km^{-2}, or 106 kJ m^{-2}. The figures for the megaherbivores alone were 11260 kg km^{-2}, or 78 kJ m^{-2}.

The energy requirements for each species (Table 1) were obtained by multiplying its on-crop biomass by its basal metabolic rate. A typical assimilation efficiency of 50% (of the edible material) was assumed, and average actual maintenance metabolism was taken to be 2.5 times the basal rate (Peters 1983). Adding up the requirements of all the species considered, and converting the units, it follows that they must have needed some 1.8 MJ m^{-2} year^{-1}, or 33 g C m^{-2} year^{-1}, in habitat primary productivity. The megaherbivores alone account for the consumption of almost 1.2 MJ m^{-2} year^{-1}, or 22 g C m^{-2} year^{-1}.

Table 2 lists the four large Carnivora species in the Luján local Fauna; the extinct canid *Canis avus*, a living felid (jaguar, *Panthera onca*), the extinct sabre-toothed felid *Smilodon populator*, and the extinct ursid *Arctodus*. They range in mass from 30 kg (*Canis avus*) to some 500 kg in the case of *Arctodus*. The on-crop biomass for each species was obtained by multiplying the calculated population density by its body mass. The total on-crop biomass for these carnivores was 50.34 kg km^{-2}, or 352 J m^{-2}. The requirements for each species (Table 2) were obtained by multiplying its on-crop biomass by its basal metabolic rate. Adding up the requirements of all the large carnivore species, and converting the units, it follows that they must have needed about 3.6 kJ m^{-2} year^{-1} as habitat secondary productivity to bear their basal metabolism, if an assimilation efficiency of 50 % was assumed. It was also assumed that the actual maintenance metabolism was 2.5 times as high as the basal rate. Therefore, the energy required to carry their maintenance metabolism was about 9 kJ m^{-2} year^{-1}.

Discussion

Primary productivity

A primary productivity of 7300 kJ m^{-2} year^{-1}, or 130 g C m^{-2} year^{-1}, is considered high for present-day open-country habitats (Margalef 1980). As a matter of fact, the best present-day natural field in Uruguay reaches a figure for primary productivity of 6600 kJ m^{-2} year^{-1}, or 120 g C m^{-2} year^{-1} (Cayssials 1979; see also Panario & May 1994).

If the Lujanian mammals scaled as predicted by Damuth's (1981a) average equation, some 28% of this quantity would have been needed to support the species larger than 10 kg, and about 18% to support the megaherbivores. This is unusually high: if it were so, it would be difficult to explain how the smaller mammals, birds, reptiles, insects and other consumers could get their nourishment. The highest average rate of consumption efficiency by large herbivores (i.e., larger than 50 kg) in Rwenzori National Park was 7.5 % in 1973 (Owen-Smith 1988).

Moreover, the highest net above-ground primary productivity value presented in McNaughton et al. (1989) for an open ecosystem predicts a herbivore on-crop biomass equivalent to 52 kJ m^{-2}. The biomass of the mammals studied here would have been twice as much as this. Considering the megaherbivores alone, the value would be 78 kJ m^{-2}.

These unbalanced figures deserve an extensive discussion of its many implied consequences.

Climate and productivity

If the primary productivity of of the Lujanian habitat had been as productive as the African savannah is today, about 38 MJ m^{-2} year^{-1}, the consumption efficiency would fall to average levels. However, there is a considerable body of evidence against this conjecture. Indeed, from 18000 to 8500 years BP, the latest Glacial Maximum was established. As a result of extensive glaciation in the Andes, a dry, cool climate occurred in the Chaco-Pampa plain (Clapperton 1983). Over that interval, the sediments (mainly loess) composing the fossiliferous Guerrero Member of the Luján Formation were deposited. Evidence from faunal analysis (Tonni 1990), sedimentology (Cantú & Becker 1988), and archaeology (González 1960) supports this palaeoclimatic scenario.

Further, sedimentological analyses of the Pampean plains suggest that aeolian activity deflated and redeposited large masses of silt and fine sand of periglacial origin, which had been deposited initially by floods in La Pampa province, Argentina, between 37ºS and 39ºS. Wind fields relating to the South Pacific Anticyclone, augmented by katabatic winds generated from the ice-cap of the North Patagonian Cordillera, formed a sand-sea in the southwestern half of the Pampa and a broad loessic belt over the remainder of the area (Iriondo 1990). Also, the remains of the still-extant mammals, i.e., those whose habitat preference can be safely assigned, belong to species confined to Central and Patagonian faunistic provinces (Tonni 1985; Prado et al. 1987; Alberdi et al. 1989). The same can be said about the birds of this age (Tonni & Laza 1980), and analyses of pollen and ostracods have yielded congruent results (Quattrocchio et al. 1988; Markgraf 1989).

The limits of this semi-arid environment were set by Iriondo & García (1993). The shift was of about 750 km relative to present conditions. According to this proposal, Luján would have had climatic conditions similar to the climate which exists today in Choele-Choel (39ºS). This suggests a mean annual temperature lower by 2.5-3ºC, with more marked seasonality. Rainfall must have been considerably lower, about 350 mm per year, which amounts to less than half of today's receipts.

Because of its high edaphic quality (and perhaps due also to water bodies which might have increased humidity locally), primary productivity in the Pampean region might have been higher than that in today's Choele-Choel area. However, it seems highly unlikely that it could have been higher than the best present-day cattle field of Uruguay, and, hence, it must have been dramatically lower than the African savannah.

Another comparison can be made using some values given by Owen-Smith (1988). Locally, the total biomass of large herbivores in African game parks exceeds the figures calculated for the Lujanian fauna in two cases; the Manyara Park in Tanzania supports 22000 kg km^{-2} (11000 kg km^{-2} of megaherbivores), and the Rwenzori Park in Uganda supports almost 19000 kg km^{-2} (10000 kg km^{-2} of megaherbivores). A third Park, Virunga in Zaire, bears more or less the same amount of large herbivore biomass as the Lujanian fauna, 16000 kg km^{-2} (10000 kg km^{-2} of megaherbivores). However, the general situation in the remaining 14 African national parks appears to be quite different: the biomass of large herbivores never exceeds 10000 kg km^{-2}, and usually is much lower. In no case does the observed biomass of megaherbivores exceed the one calculated here for the Lujanian fauna, which I suggest is valid as an ecological density for a long period and for a large area.

Scaling equations

It could be argued that the chosen scaling factor for computing population density is not realistic, and that in fact the species scaled with a lower exponent. However, similar present-day ecosystems, such as wooded savannahs and other open-country habitats, are reported to have usually higher, and even positive, exponents (Damuth 1981a, 1993). This is particularly true for the way African large and mega-herbivores are reported to scale (Owen-Smith 1988). Owen-Smith discussed four possible reasons why large animals use a disproportionately large fraction of food resource relative to smaller animals: 1) large animals tolerate a lower-quality food; 2) acceptable food patches are more continuously distributed for larger species than for smaller species, with fewer lacunae or unsuitable habitats; 3) large animals are less influenced by predation, so they usually attain densities closer to the saturation capacity of the food resource than do smaller species; 4) larger animals dominate smaller ones in competition for food.

Moreover, the use of lower exponents would require the assumption that megaherbivores were very rare; small populations are highly prone to extinction (Soulé 1987; Pimm 1991). Of course, this whole fauna eventually became extinct, but it lasted several thousand years. The situation was not very different in the previous Land-mammal Age, the Ensenadan, and probably during the whole Pleistocene (see Tonni et al. 1992).

Finally, the metabolic rates could have been overestimated in this study, but they would have to have been substantially different to improve the situation, if it is taken into account that many species ranging widely in size were used. Moreover, South American climatic conditions during the Lujanian were consistently colder than those of today, as discussed above. Therefore, climate was even colder than in modern Africa. Thus, other things being equal, Lujanian mammals would have had to spend more energy in maintaining their body temperature than modern African mammals do, and thus would be expected to have had relatively high metabolic rates. For further discussion, see McNab (1989).

Faunal composition

Another potential source of bias is in taxonomic oversplitting. If fewer species existed than those listed here, all of the calculations would be inflated. However, the number of species in the Lujanian fauna is probably accurate, as this fauna has been the subject of numerous taxonomic studies. Already a century ago, Lydekker (1894) proposed many synonymies, but this was bitterly attacked by Ameghino (1895). More recent compilations (which included partial revisions) have changed the species number very little (see Marshall et al. 1984; Tonni et al. 1992). Moreover, if all the Lujanian species of the same genus were considered synonyms, the consumption efficiency would fall only to a 15% of the primary productivity of the cattle field mentioned above.

As an additional consideration, the presence of transient species might dramatically alter these calculations. Such transients, however, would probably not represent a large source of error, because the problem remains valid when a larger geographic scale is taken into account. This should be particularly valid for the larger species, which have a larger home range (McNab 1963; Lindstedt et al. 1986; Reiss 1988; Swihart et al. 1988), especially if they have a complex social organisation (Jarman 1974; Damuth 1981b). For instance, clans of more than one hundred individuals of African elephants are reported to share a home range up to 700 km^2, with little overlap between different clan areas (Owen-Smith 1988, and references therein).

Predators

The distinctiveness of the Lujanian mammals is particularly noticeable in the large-sized forms, because most of the smaller mammals found there are members of the modern South American fauna. As can be seen in Table 1, 28 large species out of 30 from the Luján local Fauna itself are extinct, and a similar proportion of extant to extinct large mammals applies to South America as a whole (Lessa & Fariña 1992). Thus, it can be assumed that the trophic relationships that hold today among the smaller members of the fauna were also valid in the Lujanian.

It seems strange that a fauna containing such a diversity of large extinct herbivores did not also contain a diversity of large extinct carnivores. In Africa, where a relatively much less diverse fauna of large mammals exists today, there are four predators with masses greater than 50 kilograms: lion, leopard, spotted hyaena, and cheetah. In the Luján local Fauna, as well as in the whole Lujanian of South America, there were two large extinct carnivores: the sabre-tooth felid *Smilodon* and the bear *Arctodus*. There is also one living species, the jaguar. A fourth, although probably less important, predator must have been the much smaller extinct canid *Canis avus*, perhaps a pack hunter, as are many modern species of the genus.

Admittedly, active carnivores may not be so important in a consideration of predation upon megaherbivores, at least as regards adult individuals, because very large animals escape predation due to their size alone. Even so, glyptodonts must have been experienced some predation, despite their size, complete armours, and defensive behaviour (Fariña 1993). Indeed, the presence of more than one species in this local fauna, as well as in many others, can be compared with the prediction of the cropping theory (Paine 1966). This theory states that, in the absence of predation, the most efficient species of a guild would eventually become the single one. On the contrary, predation, when it exists, would be exerted on this dominant species, given its higher probability of being found. Therefore, predation would allow the other species to develop. This also applies to toxodonts and other megaherbivore genera, but such predation must have been restricted to juveniles.

Nevertheless, it seems odd that, with such a diversity of megaherbivores, there should not have been a diversity of carnivores which could have filled at least the role of scavenging carrion feeders. Is it possible that only a few relatively small scavengers, mammals and birds, could have taken advantage of the resource provided by dead megaherbivores? If so, they must have been less efficient than a larger carnivore. Large size is more efficient for opening carcasses and cutting tendons, and a large number of individuals is no compensation. Secondly, smaller scavengers would have had to wait for their food if a larger predator were feeding first, much in the way hyaenas have to do until lions are satisfied.

As stated earlier, the metabolic requirements of the four species of carnivores would have been fulfilled with 9 kJ m^{-2} year $^{-1}$. The secondary productivity predicted by the appropriate equations in McNaughton et al. (1989) for an ecosystem able to support the herbivore biomass inferred above is at least four-fold greater. If a growth efficiency of 0.025 is assumed (Peters 1983), comparable results are obtained.

This leads to the impression that the niche of a big carnivore (probably a scavenger) was largely unoccupied; it does not seem likely that the sabretooth, the jaguar, the bear, and the canid could have occupied it completely. This niche might have been fulfilled by birds, such as vultures, but the available evidence does not support this view. The adequacy of palaeontological record of birds is usually doubtful. However, Tambussi et al. (1993) claimed that there are enough remains from the South American late Cenozoic to draw some conclusions. In that study, they demonstrated that South American vultures (family Cathartidae) are not an exception to the general Cenozoic trend of diversity of birds. Indeed, vultures are less diverse in the Pleistocene than in the late Pliocene, following the same pattern as the rest of the class Aves.

In addition, the abundance of hypercarnivore canid species in the South American Pleistocene stated by Van Valkenburgh (1991) is not apparent in this local fauna. Another interesting peculiarity of this fauna is the absence of any cheetah-like predator, in contrast to the presence of them in other open habitats, i.e. *Acinonyx jubatus* in Africa, the fossil *Acinonyx pardinensis* in the Pleistocene of Europe, and the genus *Miracinonyx* in the Plio-Pleistocene of North America (see Van Valkenburgh 1990).

Cryptic scavengers?

From the above, I contend that the Lujanian fauna cannot be well understood using modern ecosystems as a paradigm. However, other fossil faunas are well explained by the approach, which seems to have failed in this case.

Some preliminary calculations on the Rancho La Brea fauna in North America were taken as an example of this. This fauna is approximately from the same age as the Lujanian, and it is from a moderately high latitude habitat as well. The list of species was taken from Stock (1956) and the body masses of their carnivores from unpublished data kindly supplied by Dr. Blaire Van Valkenburgh. Applying the equations given above and making the same assumptions, this fauna turned out to be easier to sustain than the Lujanian. The metabolic requirements of the megaherbivores would have been fulfilled with a primary productivity of 0.6 MJ m^{-2} $year^{-1}$, which is congruent with the inferred habitat. Indeed, a conifer parkland habitat is proposed for the La Brea site (see Marcus and Berger 1984, and references therein). Assuming a primary productivity of 11 MJ m^{-2} $year^{-1}$ (Margalef 1980), the consumption efficiency of the large mammals would have been 5.5%, a figure within the normal range. Furthermore, given a production efficiency of 2.5 %, the secondary productivity must have been some 15 kJ m^{-2} $year^{-1}$. This is *exactly* the predicted requirements of the carnivores. Of course this fauna is biased as a carnivore trap, but such bias has to do with the abundance of specimens rather than with the actual species diversity.

Having emphasised the unusual guild structure of the Lujanian fauna, I now wish to offer an explanatory hypothesis for its most remarkable aspects: excess of herbivores for the primary productivity, and scarcity of carnivores, given the high number of large herbivores.

As in Gaston Leroux's (1977) detective story "Crime in the yellow room", the explanation should be sought within the community. I propose that there must have been one or more large-bodied species that ate carrion opportunistically (scavengers in disguise), even though their diet also included plants.

However, the serious problem of identifying a potential scavenger remains. Glyptodonts, capybaras, toxodonts, *Macrauchenia*, big artiodactyl ungulates, and mastodonts are unlikely candidates, because of their known palaeoautecology (Ferigolo 1985; Fariña 1985, 1988; Fariña & Alvarez 1994), or because their living relatives show no preference for animal food. *Pampatherium* might be a potential candidate, because some living Dasypodidae usually eat carrion (Redford 1985) and even juveniles of other mammals (Newman & Baker 1942; McBee & Baker 1982). However, their high-crowned, lobated teeth, and the entire structure of their masticatory apparatus, strongly suggest that they were grazers (Vizcaíno & Fariña 1994).

By a process of elimination, this leaves the ground sloths as the remaining candidates. Indeed, their strange dentitions, though not typical of a carnivore, are also atypical for a herbivore.

A comparison with the living relatives of the ground sloths, the tree sloths, does not rule them out as the possible scavengers in disguise. The Recent sloths are relictual and specialised examples of a once very diverse group. They occupy a very particular niche, hanging upside down from the canopy of the trees in the Amazonian forest, while the ground sloths were among the most energy-controlling species of the plains of their time. Additionally, they are between two or three orders of magnitude smaller than their extinct relatives.

There are many species of ground sloths, and only a few North American forms have been the subject of detailed masticatory morphofunctional studies (Naples 1987, 1989). Certainly, they are poorly adapted for carnivory if compared with large felids, but they may have had no need to be so efficient. Moreover, *Glossotherium* optimised its shearing efficiency (Naples 1989), and, more in general, some ground sloths (megatheriids, megalonychids, and nothrotheriids) have transverse crests on their teeth which could conceivably have been used for chewing up animal flesh. Notwithstanding this, they lack the sharp cutting surfaces typical of the sectorial dentitions of extant mammalian carnivores. However, there is no *a priori* reason to assume that these teeth could not have been used to consume meat, especially if meat was taken in an opportunistic fashion, and not used for bone cracking on a regular basis. By way of example, euphrachtine dasypodids manage to use their cone-shaped teeth with a fair degree of efficiency to consume flesh (Vizcaíno & Fariña 1994).

Besides, ichnological evidence strongly supports bipedal standing and locomotion for ground sloths (Casamiquela 1974; Aramayo & de Bianco 1987, 1993). The biomechanics of their forearms (Aramayo 1988) and the development of their brains (Dozo 1989) suggest that the ground sloths were capable of a very active and precise use of their forearms. Their strong claws could have been used to rip carcasses (and perhaps even living smaller animals) and to cut pieces of flesh small enough to be swallowed without much oral comminution. Indeed, even in the context of a herbivorous diet, *Nothrotheriops* was described by Hansen (1978) and Naples (1987) as swallowing large pieces. Additionally, the brains of ground sloths appear to have been bigger, and with a greater degree of telencephalic development, than expected for xenarthrans of their size (Dozo 1989). This feature would be better explained by predatory or scavenging habits than by the traditionally accepted diet of exclusive herbivory (see Jerison 1973).

It is not proposed here that ground sloths were full-time scavengers, as their dentitions and skull architecture are not like those of ossiphagous hyaenas. Still, opportunistic scavenging could have accompanied a primarily browsing diet.

If ground sloths were removed from the Lujanian herbivore community, 4989 kg km^{-2}, or 34 kJ km^{-2} - some 35% of the biomass -, would be removed from the primary consumer level, and 4587 kg km^{-2} or 31 kJ km^{-2}, some 41 % of the megaherbivore biomass. In connection with the energy flux, the ecosystem could have lowered its primary productivity by 23 % (32 % of the megaherbivore-bearing production). A mixed diet would naturally yield intermediate figures, but even so some relief could be given to an otherwise very stressed habitat.

A hypothetical flesh-eater of four tonnes would need only to make a kill (or to find a carcass and drive the vultures, small canids, and other competitors away) every 16 days, if the killing-rate equation given by Peters (1983) could be extrapolated. Certainly, it would be unwise to make too literal a projection from these equations, but their application suggests that the need for animal food for the largest ground sloths, as *Megatherium,* would nonetheless be very low. This would apply even if totally carnivorous habits were proposed, admittedly a thermodynamically problematic suggestion (for discussion, see Colinvaux 1980).

The diet of the ground sloths has been stated for a long time to be herbivorous (Burmeister 1879), and proposals about their having an insectivorous or snail-based diet were jocularly discarded by Cabrera (1926, 1929). The alternative hypothesis presented here is not devoid of problems. The first one comes from the evidence of diet obtained from faeces (Markgraf 1985, and references therein); pollen and plant cuticles found there suggest that they were either grazers (a specimen of *Mylodon* found in Ultima Esperanza, Southern Chile) or xerophytic browsers (a North American species of *Nothrotheriops*). There is no evidence of a carnivorous diet, like little pieces of bone or hair. However, those are examples from either a marginal environment (Patagonia), or from a less stressed habitat (southern North America, see above). No faeces are known from the members of the Lujanian fauna.

In addition, there are many specialisations of the digestive tract in herbivorous mammals, including living tree sloths. All species feeding on low-quality, high-fibre forage must develop a fermentation chamber within the digestive system for a symbiotic association with cellulase-producing microorganisms. Large ground sloths would have been able to tolerate low-quality forage, because of their large sizes, but in order to be truly effective at feeding on browse at their size, they would have had to evolve modifications to their digestive tract as all other large herbivores have done. A stomach and intestine partly full of carrion and partly full of poor-quality plant material would not be able to digest either optimally, for they are such different kinds of food (although caecal fermentation should not be ruled out, see Janis 1976). So, if ground sloths were eating appreciable carrion more or less simultaneously with plant material, they must have also been relatively poor herbivores. Bears are a possible analogue but have never attained the size of the largest ground sloths. Nevertheless, the Lujanian fauna's trophic composition was certainly peculiar, and it might have been the appropriate circumstance for a very large herbivore to adopt this kind of diet. Finally, this more diverse diet might have been a late acquisition in their evolutionary history, and therefore might be poorly reflected in their anatomy.

Generally speaking, the choice of diet is related to the potentiality of the morphology, but also to the chance to select food items. To put it in the words of Peters (1983:106, emphasis added): "it should be noted that the distinctions between herbivores and carnivores ought not to be drawn too rigidly. Most, if not all, herbivores will eat meat when available and *often seem to prefer it*". If my analysis is correct, availability of meat does not appear to have been a problem in Lujanian times.

Conclusions

According to the evidence given here and the discussion of its consequences, the strongly counter-intuitive proposal that ground sloths were at least opportunistically carrion-eaters is advanced. Nevertheless, there is still much palaeoecological work to do on this surprisingly neglected fauna, and, therefore, this study must be taken as a first approximation to a very complex and interesting problem. In this proposal, the ground sloths, particularly the larger forms as *Megatherium*, would become the largest flesh-eating land mammals known to have existed.

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Table 1. Herbivorous mammals larger than 10 kg found in the Luján local Fauna, their current status (living or extinct), their estimated mass, their calculated on-crop biomass, and their mass-specific basal metabolic rate.

Species	Extant	Mass (kg)	On-crop biomass ($kg\ km^{-2}$)	Basal metabolic rate ($J\ kg^{-1}\ s^{-1}$)
Neothoracophorus depressus	No	1100	550	0.71
Neothoracophorus elevatus	No	800	506	0.77
Plaxhaplous canaliculatus	No	1300	573	0.68
Doedicurus clavicaudatus	No	1300	573	0.68
Panochthus tuberculatus	No	1100	550	0.71
Glyptodon reticulatus	No	1200	562	0.70
Glyptodon perforatus	No	1600	604	0.65
Glyptodon rudimentarius	No	800	506	0.77
Glyptodon clavipes	No	2000	639	0.61
Pampatherium typum	No	200	359	1.09
Megatherium americanum	No	4000	803	0.51
Scelidotherium leptocephalum	No	600	473	0.82
Glossotherium robustum	No	1300	573	0.68
Glossotherium myloides	No	1200	562	0.70
Lestodon trigonidens	No	3000	707	0.55
Lestodon gaudryi	No	1300	573	0.68
Neochoerus sulcidens	No	150	334	1.17
Toxodon bilobidens	No	1100	550	0.71
Toxodon burmeisteri	No	1100	550	0.71
Toxodon platensis	No	1100	550	0.71
Toxodon paradoxus	No	1000	534	0.73
Macrauchenia patachonica	No	1100	550	0.71
Equus (A.) curvidens	No	300	397	0.98
Tayassu tajacu	Yes	25	214	1.83
Eulamaops parallelus	No	150	334	1.17
Hemiauchenia paradoxa	No	1000	534	0.73
Lama guanicoe	Yes	90	294	1.33
Morenelaphus azpeitianus	No	50	254	1.54
Morenelaphus lujanensis	No	50	254	1.54
Stegomastodon superbus	No	4000	803	0.51

Table 2. Species of the order Carnivora larger than 10 kg found in the Luján local Fauna, their current status (living or extinct), their estimated mass, their calculated on-crop biomass, and their mass-specific basal metabolic rate. See text.

Species	Extant	Mass (kg)	On-crop biomass ($kg\ km^{-2}$)	Basal metabolic rate ($J\ kg^{-1}\ s^{-1}$)
Arctodus bonariensis	No	500	19.2	0.84
Smilodon populator	No	300	15.9	0.97
Felis onca	Yes	50	8.3	1.57
Canis avus	No	30	6.9	1.80