

THE EXTINCTION OF THE MEGAFUNA: A SUPRA-REGIONAL APPROACH

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Summary

Most discussions on the extinction of the Pleistocene megafauna in southern South America depend on dates determined for deposits within which the bones were recovered. An analysis based on taxon-dates (Grayson, 1987), the majority of which are from recent work in the Ultima Esperanza region, Southern Chile, suggests that the chronological framework for the rest of Fuego-Patagonia needs to be revised. In addition, some implications for the assessment of the model of Coevolutionary Disequilibrium are introduced.

Résumé

Extinction de la grande faune : une approche supra-régionale.

La plupart des discussions relatives à l'extinction de la grande faune pléistocène dans l'extrême sud de l'Amérique du Sud repose sur des datations faites dans les dépôts d'où proviennent les os. Une étude fondée sur le concept de "taxon-dates" (Grayson, 1987), et pour laquelle la majorité des données provient d'un récent travail effectué dans la région d'Ultima Esperanza, dans le Chili austral, suggère la nécessité de réorganiser le cadre chronologique du reste de la Patagonie et de la Terre de Feu. De plus, des implications pour l'évaluation du modèle de déséquilibre co-évolutionnaire sont introduites.

Zusammenfassung

Das Aussterben der Großfauna: eine überregionale Betrachtung.

Bei den meisten Diskussionen bezüglich des Zeitpunktes des Aussterbens der pleistozänen Großfauna des südlichen Südamerikas werden Daten verwendet, die aus Materialien der Schichten gewonnen wurden, aus denen die Knochen stammen. Eine auf Taxondaten (Grayson 1987) basierende Untersuchung belegt, daß eine Umorganisation des chronologischen Rahmens Feuerlands nötig ist. Die verwendeten Daten beruhen auf jüngeren Untersuchungen in der Region Ultima Esperanza, Südchile. Einige Überlegungen gelten dem Modell des Koevolutionären Disequilibriums.

Key Words

Pleistocene megafauna, Fuego-Patagonia, Coevolutionary Disequilibrium.

Mots clés

Grande faune pléistocène, Terre de Feu, Patagonie, Déséquilibre coévolutionnaire.

Schlüsselworte

Pleistozäne Großfauna, Feuerland, Koevolutionäres Disequilibrium.

Introduction

The chronology of the Fuego-Patagonian late Pleistocene extinctions will be discussed. Recent studies with faunas recovered at the region of Ultima Esperanza (Chile) will be used to support the need for a different approach. The taxon-date concept will be emphasized in order to replace the current use of radiocarbon dates that can only be referred to deposits. It will be shown that this change substantially transforms our current perception of the extinction issue.

On the basis of radiocarbon dates that apply to deposits that contain Pleistocene megafauna bones, it was previously suggested that: (1) *Mylodon darwini* (Saxon, 1976; Borrero,

1977) and other species (Ochsenius, 1985) survived up to mid-Holocene times, (2) horse and an extinct camelid (*Lama (Vicugna) gracilis*) survived up to early Holocene times (Cardich, *et al.* 1973; Miotti, 1993a), and (3) most of the extinctions took place between 11,000 and 10,000 bp. Actually, none of these claims can be supported.

It is now clear that the complications of the archaeological record are sufficient to cast doubt on results sustained on the basis of the mere physical association of bones of Pleistocene megafauna and charcoal samples recovered from the same deposits. Even when some cases are moderately controlled, and offer some reliability, most cases are not well sustained. For example, the applicability

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of the radiocarbon dates of Los Toldos -widely used to substantiate so called "pre-Clovis" dates and also to support the survival of megafauna- can be seriously questioned. Isolated pieces of charcoal were used, and the samples even lack a laboratory reference number. In addition, formation processes must be seriously taken into account before any of those associations between megafauna and radiocarbon dates is accepted. This problem not only applies to Los Toldos, but to most of the involved sites.

A taxon-date refers to trustworthy chronological information related with the latest record for any given species (Grayson, 1987). The reorganization of the current information focusing on taxon-dates not only cast serious doubts on the more accepted sequence of extinction events, but also show the difficulties associated with the discussion of different extinction models, such as the model of Coevolutionary Disequilibrium (Graham and Lundelius, 1984; Lundelius, 1989).

Chronology of the extinctions

I will briefly examine the chronological evidence available for the most important species of megafauna recovered in Fuego-Patagonia settings.

Hippidion saldiasi. Horse bones were recovered at Cueva del Mylodon (Alberdi and Prado, 1992), Piedra Museo (Miotti, 1993b), Los Toldos (Miotti, 1993b), Las Buitreras (Sanguinetti, 1976), Cuevas Lago Sofía 1 and 4 (Prieto, 1991), Cueva del Medio (Nami and Menegaz, 1991) and Fell, Pali-Aike and Cerro Sota (Bird, 1988). Charcoal is usually the dated material, with some cases in which bones of unspecified species were used (tab. 1). No taxon-dates are presently available. On the basis of this evidence it was sustained that horse disappeared in Patagonia as recently as in early Holocene times. The applicability of the dates of these deposits to the horse remains is open to question. Outside Patagonia, in the Argentine pampas there is one taxon-date for *Equus cf. (Equus americanus)* of TO-1504: 8,890 ± 90 bp (Politis and Beukens, 1991: 152).

Mylodon darwini. Several sites with deposits containing mylodon bones are dated (tab. 2), but also a number of taxon-dates are available (tab. 3), all of them coming from sites on the Ultima Esperanza region. Sites containing mylodon bones, but lacking radiocarbon dates, include Las Buitreras Cave (Sanguinetti, 1976), Pali-Aike and Cerro Sota (Bird, 1988).

Table 1: Radiocarbon dated deposits containing *Hippidion saldiasi* bones in Fuego-Patagonia.

* = Bones assigned to *Hippidion* sp. were recovered below the dated deposits.

Site	Date bp	Laboratory	Observations
Piedra Museo AEP 1	10,400 ± 80	AA-8428	Camelid vertebrae
Los Toldos, Nivel 11	12,600 ± 600	No lab reference	Charcoal
Los Toldos, Nivel 9	8,750 ± 480	No lab reference	Charcoal
Cueva del Mylodon	Several	-	Mylodon taxon-dates, see table 3
Dos Herraduras 3	11,380 ± 150	LP-421	Mylodon rib
Cueva del Medio	9,595 ± 115	PITT-0344	Charcoal
	9,770 ± 70	Beta-40281	Bone
	10,310 ± 70	GrN-14913	Charcoal
	10,550 ± 120	GrN-14911	Burnt bone
	10,930 ± 230	Beta-39081	Charcoal
	12,390 ± 180	PITT-0343	Burnt bone
Cueva Lago Sofía 1	11,570 ± 60	PITT-0684	Charcoal
Cueva Lago Sofía 4	11,590 ± 100	PITT-0940	Mylodon vertebrae
Cueva Fell	10,080 ± 160	I-5146	Charcoal
Cueva Fell	10,720 ± 300	W-915	Charcoal
Cueva Fell	11,000 ± 170	I-3988	Charcoal
Pali Aike	8,639 ± 450	C-485	Guanaco, Mylodon and horse bones
Tres Arroyos*	11,880 ± 25	Beta-20219	Charcoal
Tres Arroyos*	10,420 ± 420	Dic-2733	Unspecified bone
Tres Arroyos*	10,280 ± 110	Dic-2732	Camelid bone

Table 2: Radiocarbon dated deposits containing *Mylodon* sp. (exclusive of taxon-dates) (see tab. 3).

Site	Date bp	Laboratory	Observations
Cueva Lago Sofía 1	11,570 ± 60	PITT-0684	Charcoal
Cueva Fell	Several	–	See Table 1
Tres Arroyos	Several	–	See Table 1
Cueva del Medio	Several	–	See Table 1

Table 4: Radiocarbon dated deposits containing *Lama* (*Vicugna*) *gracilis*.

Site	Date bp	Laboratory	Observations
Piedra Museo AEP 1	10,400 ± 80	AA-8428	Camelid vertebrae
Los Toldos Nivel 11	12,600 ± 600	No lab number	Charcoal
Los Toldos Nivel 9*	8,750 ± 480	No lab number	Charcoal
* = Salemme y Miotti (1987: 45)			

Table 3: Taxon-dates for *Mylodon* sp. (Borrero *et al.*, 1988).

* = Last taxon-date for a given species/site.

Site	Date bp	Laboratory	Observations
Dos Herraduras 3*	11,380 ± 150	LP- 421	Mylodon rib
Cueva del Mylodon*	10,200 ± 400	Sa-49	Mylodon dung
Cueva del Mylodon	10,400 ± 330	A-1391	Mylodon hide
Cueva del Mylodon	10,575 ± 400	GX-6248	Mylodon dung
Cueva Lago Sofía 1*	12,990 ± 490	PITT-0939	Mylodon bones
Cueva del Mylodon	10,832 ± 400	C-484	Mylodon dung
Cueva del Mylodon	10,880 ± 300	GX-6243	Mylodon dung
Cueva del Mylodon	11,775 ± 480	GX-6246	Mylodon dung
Cueva del Mylodon	11,810 ± 229	BM-1210	Mylodon dung
Cueva del Mylodon	11,905 ± 335	GX-6247	Mylodon dung
Cueva del Mylodon	12,020 ± 460	GX-6244	Mylodon dung
Cueva del Mylodon	12,240 ± 150	A-2447	Mylodon dung
Cueva del Mylodon	12,270 ± 350	A-2445	Mylodon dung
Cueva del Mylodon	12,285 ± 480	GX-6245	Mylodon dung
Cueva del Mylodon	12,308 ± 288	BM-1210B	Mylodon dung
Cueva del Mylodon	12,496 ± 148	BM-1209	Mylodon dung
Cueva del Mylodon	12,552 ± 128	BM-1375	Mylodon dung
Cueva del Mylodon	12,870 ± 100	A-2448	Mylodon dung
Cueva del Mylodon	12,984 ± 76	BM-728	Mylodon collagen
Cueva del Mylodon	13,183 ± 202	BM-1208	Mylodon collagen
Cueva del Mylodon	13,260 ± 115	LU-794	Mylodon collagen
Cueva del Mylodon	13,470 ± 189	A-2446	Mylodon dung
Cueva del Mylodon	13,500 ± 470	NZ-1680	Mylodon hide
Cueva del Mylodon	13,560 ± 180	A-1390	Mylodon dung
Cueva del Mylodon	11,330 ± 140	LP-255	Mylodon dung
Cueva del Mylodon	12,570 ± 160	LP-257	Mylodon dung
Cueva del Mylodon	10,812 ± 325	LP-34	Mylodon dung
Cueva del Mylodon	10,377 ± 481	LP-49	Mylodon collagen
Cueva del Mylodon	13,500 ± 410	R-4299	Mylodon hide

Lama (Vicugna) gracilis. This species was recorded within dated deposits at Los Toldos, Levels 11 and 9 (Salemme and Miotti, 1987: 45; Miotti, 1993b) and Piedra Museo (Miotti, 1993b) (tab.4). It is also recorded, but without dates at El Ceibo (Miotti, 1993a). There are no taxon-dates.

Palaeolama. Recorded at Fell's Cave (Miotti, 1993a) and Monte Verde (Casamiquela and Dillehay, 1989). There are no taxon-dates.

Lama sp. Recorded at Cueva del Medio (Nami and Menegaz, 1991) and Tres Arroyos (Mengoni Goñalons, 1987). In both cases deposits are dated (see tab. 1), but taxon-dates are lacking. Bone specimens attributed to *Lama* sp. are larger than those of guanaco (*Lama guanicoe*) but are difficult to assign to *Hemiauchenia* or *Palaeolama* (Nami and Menegaz, 1991: 122).

Macrauchenia sp. There is only one record, a second phalanx recovered at Cueva del Mylodon, level C (Nordenskiöld, 1900: 16). No taxon-dates are available.

Dinamyidae ("*Megamys*" sp.). It is a medium sized rodent, erroneously classified as *Megamys* sp. It was recovered at Cueva del Mylodon (Nordenskiöld, 1900) and Cueva Lago Sofía 4 (Prieto, 1991). No taxon-dates are available.

Smilodon sp. A fragment of maxillar was found at Cueva Lago Sofía 4 (Canto, 1991). Some fragments from Cueva del Mylodon are also assigned to this taxon, but with doubts (see Prieto, 1991). No taxon-dates are available.

Canis (Dusicyon) avus. Specimens which are now attributed to this taxon (Caviglia, 1985-1986) were previ-

ously assigned to *Canis familiaris* (Cardich *et al.*, 1978; Clutton-Brock, 1988). In addition to its presence in the dated deposits compiled on table 5, it was recorded at Cueva Las Buitreras (Caviglia, 1976-1980), Cueva del Medio (Borrero *et al.*, 1988) and Los Toldos (Cardich *et al.*, 1978). Massone (1987: 51) suggested that the specimen from Level III at Tres Arroyos was redeposited by rodents. There are no taxon dates available. In spite of this situation, and on the basis of evidences from Punta Bustamante (Miotti and Berman, 1988) and perhaps Tres Arroyos (Caviglia, 1985-1986), a late Holocene survival may be defended. A similar situation is recorded in Pampa (Tonni and Politis, 1981).

Panthera onca mesembrina. The date from Cueva del Mylodon (tab. 6) is the only one directly referable to a deposit containing a panthera metapodial. However, it is not clear that the date applies to the bone. Additional bones were recovered in other deposits of the cave, to which datings on Mylodon dung generally apply (tab. 3). The findings from Cueva del Medio are below the dated deposits. There are no taxon-dates available. If it is accepted that pantheras were involved in the formation of the deposits of Cueva Lago Sofía 4, then there is circumstantial proof for pantheras around 11,600 bp.

Cuvieronius sensu Casamiquela (Mastodon). There is one taxon-date from Monte Verde, 11,990 ± 200 bp (TX-3760) made on collagen from a humerus (Dillehay and Pino, 1989).

Table 5: Radiocarbon dated deposits containing *Canis (Dusicyon) avus*.

Site	Date bp	Laboratory	Observations
Pali Aike	8,639 ± 450	C-485	Guanaco, Mylodon and horse bones
Los Toldos 3	7,260 ± 350	No lab number	<i>Canis familiaris</i> in Cardich <i>et al.</i> (1978)
	4,850 ± 90	LP-136	
Tres Arroyos	Several	-	Level V, see Table 1
Tres Arroyos	700 ± 70		Charcoal, Level III
Punta Bustamante	ca. 3,000		Mansur-Franchomme, 1988
Cueva Fell	Several for the inferior levels	-	See Table 1
Cueva Fell	6,485 ± 115	I-5140	Charcoal
Cueva Fell	6,560 ± 115	I-5141	Charcoal
Cueva Fell	6,740 ± 130	I-5138	Charcoal
Cueva Fell	8,180 ± 135	I-5142	Charcoal
Cueva Fell	8480 ± 135	I-5143	Charcoal
Cueva Fell	9030 ± 230	I-5145	Charcoal and sediment
Cueva Fell	9100 ± 150	I-5144	Charcoal
Cueva del Mylodon	ca. 5,500		Charcoal; probably redeposited (Borrero <i>et al.</i> , 1991)

Table 6: Sites with deposits containing *Panthera onca mesembrina*.

Site	Date bp	Laboratory	Observations
Cueva del Mylodon	13,183 ± 202	BM-1208	Mylodon collagen, Trench 2, Level 10 (Saxon, 1979)
Cueva del Medio	Below dated deposits	–	See Table 1

Gliptodontidae. There is only one reference for a gliptodon bone in association with archaeological remains from Fell's Cave (Emperaire, 1988: 82). This bone is best explained as a Tertiary fossil, which was naturally incorporated within the archaeological deposits after weathering from the rock on which the cave is formed (Marshall and Salinas, 1989-90).

Discussion

In sum, there are taxon-dates only for mylodon and mastodon. The date of the final presence in Fuego-Patagonia for most of the Pleistocene species is unknown. Lack of control on postdepositional processes prevents from using most of the non-taxon dates. It is ironical that the more cited evidence for Holocene survival of megafauna concerns the *Mylodon darwini* (Borrero, 1977; Saxon, 1976, 1979; Ochsenius, 1985; Sutcliffe, 1985), which is the only taxon for which a number of taxon-dates support a late Pleistocene date for its last living representatives. Considering that the literature is full of references to the Holocene survival of different taxa, including horse (i.e., Alberdi and Prado, 1992: 278; Menegaz *et al.*, 1990: 156), a conceptual reorganization is necessary.

In general, there is better control in Ultima Esperanza than in the rest of Fuego-Patagonia, with isolated exceptions, such as the mastodon at Monte Verde. It is interesting and instructive that the Ultima Esperanza panorama of extinctions differs from that usually accepted, as outlined at the beginning of this paper. On the basis of admittedly limited data it can be defended that the Patagonian panthera disappears before 12,000 bp. Mylodon, as already mentioned, went extinct by 10,000 bp. Perhaps the case of the horse is similar, on the basis of well defined archaeological associations at Cueva del Medio and Cueva Lago Sofía 1, but there are no taxon-dates to support this. The case for the extinct fox is not well defined in this region, with most findings from deposits which are ambiguously dated.

On the contrary, except for the case of the mastodon, we lack taxon-dates for the rest of Fuego-Patagonia. The more trustworthy dated deposits, those from open air sites overlying Holocene geoforms, suggest that the extinct fox survived up to late Holocene times. The disappearance dates for the rest of the taxa are poorly known.

It is interesting to mention, for the sake of comparison, that there are taxon-dates in the pampas which suggest that gliptodonts disappeared around 12,000 bp, that other species like megaterium and horse survived until the beginning of the Holocene, and that the extinct fox survived up to late Holocene times.

One way of explaining this differences is assuming the existence of regionally different extinction patterns. But perhaps the quality of information is part of the explanation. For example, there is nothing bizarre in postulating that horse survives in Fuego-Patagonia beyond the Pleistocene-Holocene Transition, only that we completely lack any evidence to substantiate it. A comparison made with the situation in the Pampa region was instructive, in that real differences with the case of Ultima Esperanza appear, including the Holocene survival of different species, and perhaps the early loss of other species. But it must be kept in mind that some species are poorly represented in late Pleistocene records (i.e., *Palaeolama*, Patagonian panthera) because their numbers probably dwindled before 12,000 bp (see Grayson, 1987).

The case of Ultima Esperanza and limited evidence from other Patagonian regions show that the period of extinction is larger than usually accepted, with mastodon and panthera probably disappearing before 12,000 bp, with other species abundantly represented until Transition times, and finally with extinct foxes arriving to the late Holocene.

The period of extinction is larger than usually accepted by most authorities. Then, instead of swift extinction, we must accept that this process is spread across thousands of years (Grayson, 1987, 1989). A major implication resulting from the acceptance of a larger period of extinction is that classic global models (human impact, climatic change) used to account for the extinction should be transformed. This is probably the case in Fuego-Patagonia.

Disharmonious or averaged faunas?

The larger time scale offered to account for extinctions in Fuego-Patagonia implies not only that it is not an event, but also that probably more than one process is implicated. The essentialist position that places ecosystems with "Pleistocene megafauna" on one side, and ecosystems without that fauna in the other side is no longer tenable.

Graham and Lundelius (1984) and Lundelius (1989) defended a modern version of the climatic hypothesis using the concept of “Disharmonious faunas” in order to account for the extinctions. This model sustains that during the Pleistocene there was greater climatic equability and habitat diversity, which sustained in turn a larger faunal diversity. According with this model, faunas that today have allopatric ranges were sympatric in late Pleistocene times. Extinction and allopatry are two results of the diminution of habitats. The model gains applicability in Fuego-Patagonia, on the basis of evidence suggesting the existence of habitats lacking modern analogs in the late Pleistocene. The model has explanatory power, but its use is prevented by the lack of knowledge on formation processes. It is clear that the latter is a prerequisite for the application of the model.

Miotti (1993b) found bones of two different species of flightless birds that today are allopatric (*Rhea americana* and *Pterocnemia pennata*) at Piedra Museo, both in a deposit dated around 10,500 bp (tab. 1). Is this evidence for the past presence of disharmonious faunas? Or we have just another averaged deposit including faunas that never coexisted? The model of Coevolutionary Disequilibrium is heavily dependent on answering this kind of questions. Previously to this finding of Piedra Museo, the available evidence in the region pointed toward *Rhea americana* being replaced by *Pterocnemia pennata* at some point during the Holocene. Accordingly it was speculated that “the ecological niche left by the former species... was occupied by *P. pennata*” (Salemme and Miotti, 1987: 45-46). The situation was taken as indicative of environmental deterioration. Actually it is difficult to choose between the two competing explanations of replacement and late Pleistocene sympatry.

Similar situations exist in the Pampean area at Cueva Tixi, with the coexistence of Brazilian and Patagonian faunas (Tonni *et al.*, 1988: 108) and at La Toma, with the coexistence of Pampasic and Patagonian/Central faunas (Salemme and Miotti, 1987: 46). Cases like this were considered in the light of the Coevolutionary Disequilibrium model (Tonni, 1990), while the case of La Toma was taken as representative of the prey of “hunters... in a transitional adaptive situation” (Salemme and Miotti, 1987:

46). Once again, the alternative of averaged samples needs to be considered.

In general, I think that discussion of postdepositional factors and dating on bones, hide or dung are needed in order to eliminate the hypothesis that the samples are averaged. Once this is done, it will be possible to assess the applicability of the Coevolutionary Disequilibrium model. As a final comment on this model, it must be stressed that the cases of Cueva Tixi and La Toma concern purely Holocene samples containing bones of modern faunas. This means that the model may be lacking in temporal specificity. In other words, climatic equability may not be restricted to Pleistocene times. The survival of the extinct fox until the late Holocene in the Pampas, Patagonia and Tierra del Fuego point in the same direction, since it can be suggested that rather than a real extinction it is a case of transformation (Berman and Tonni, 1987).

Conclusions

Both the model of Coevolutionary Disequilibrium and the timing of the losses of Pleistocene fauna are in need of dates made on bones, hide or dung. The admittedly limited available evidence from Ultima Esperanza, complemented with scattered information from the rest of Fuego-Patagonia informs us that the discussion of samples and models in a short, ecological time scale is not appropriate for long-term phenomena like the extinction of the megafauna. Fuego-Patagonia offer a number of opportunities to study the insertion of different faunas over previously glaciated regions, many of them within the range of radiocarbon analysis. Accordingly, first dates for all the involved taxa will also be required. More mature discussions will probably depend from the adoption of a chronological framework concordant with the scale of the phenomena under analysis.

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