

Evolutionary pattern of land mammal faunas during the Late Cretaceous and Paleocene in South America: a comparison with the North American pattern

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Using families, this paper reviews the pattern of mammal fauna changes in South America throughout the late Cretaceous–Paleocene span, comparing them with the changes in North America. Although there are as yet no records of land-mammal fauna of the latest Cretaceous in South America, the unique Alamitian (Campanian – early Maastrichtian?) and the late early Paleocene Tiupampian land-mammal faunas provide eloquent evidence that abrupt changes occurred during this lapse of time. The known late Cretaceous–Paleocene land-mammal faunas of North America show no such abrupt changes. In North America, a major change occurred between the “middle” Cretaceous Paluxian and the late Cretaceous Aquilan. In both North and South America another major change occurred during the first half of the Paleocene, the Puercan–Torrejonian change and the Tiupampian–Itaboraian change, respectively. The different North and South American scenarios are related to quite different geological histories. The physical (and biotic) Cretaceous–Cenozoic South American history is characterized by long periods of isolation (late Jurassic–early late Cretaceous, and early middle Paleocene–Pliocene), alternating with brief connections. This explains why the history of the South American Cretaceous–Present terrestrial biota is characterized by relatively few episodes (Simpson’s Faunal Strata), which, as a rule, are sharply and clearly separable.

1. Introduction

Strata of continental origin of either the latest Cretaceous or early Paleocene are known in several regions of the world, but there are few areas

in which apparently uninterrupted accumulation of continental deposits took place through this entire interval of the earth’s history. For that reason, virtually all that is known of the vertebrates of this time, particularly the evolutionary

patterns of the mammals, comes from continental deposits in the Western Interior of North America (see Clemens & Archibald 1980, Archibald 1981, 1987, Archibald & Clemens 1984, Clemens 1986, Fox 1987). On the basis of this evidence Archibald & Clemens (1984) and Clemens (1986) claimed that changes in the mammalian fauna from the Cretaceous to the Paleocene, in contrast to those affecting the reptiles, were similar to what is usually seen in any given succession of North American land mammal ages. The question is, did the mammal communities all over the world have a similar pattern during the Cretaceous–Tertiary transition?

In South America, until recently there were no records of mammals representing the Cretaceous–Tertiary transition. However, during the last years this crucial gap has been closed by two important finds on the continent, the first within beds reputed to be late Campanian–early Maastrichtian (see Bonaparte 1986a, and references therein), and the second in the early Paleocene (see Pascual & Ortiz Jaureguizar 1990, and references therein). Unfortunately, these records are few and sparse in space and time, but enough to show that the mammal communities changed more markedly than on the North American continent (see Bonaparte & Pascual 1987). This fact was recently confirmed by us (Ortiz Jaureguizar & Pascual 1989) in a paper in which we analysed the changes affecting mammal communities, to the ordinal level, throughout the Late Cretaceous–Paleocene interval. In that paper we:

- 1) stated the intra- and intercontinental relationships of faunistic similarity;
- 2) using different geological and paleobiological evidence, inferred the climatic–environmental conditions of this interval during which the South American mammal fauna evolved; and
- 3) recognised the relationship of the faunistic changes with the (likewise) changing climatic–environmental conditions.

It must be emphasized that the evidence of the different pattern of changes in South America throughout the Late Cretaceous–Paleocene lapse was very limited. Likewise, it should be pointed out that this pattern was revealed by analysis of the taxonomic rank of order. This procedure permitted identification of the overall intra- and in-

tercontinental similarities of the South American and North American land mammal faunas, because the orders have more extended biochronological ranges. But the relative magnitude of change is more accurately expressed at the level of families. Actually, the only unquestionable late Cretaceous record of mammals from South America (Bonaparte 1986a, Bonaparte & Pascual 1987, Bonaparte et al. 1987) shows that a marked endemism had occurred at the familial level. Thus, to evaluate more accurately the magnitude and peculiarity of the changes affecting the mammal communities during the Cretaceous–Paleocene transition, we will now use the families so far known.

2. Methodology

We used multivariate analytical techniques for determining the faunistic similarity relationships. As operational units (OTU) we employed the same 11 of the 12 Land-Mammal Ages recognized by us previously (Ortiz Jaureguizar & Pascual 1989) for the North and South American Cretaceous and Paleocene: 7 North American Land-Mammal Ages (NALMA) and 4 South American Land-Mammal Ages (SALMA) (see Fig. 1). Although we still maintain that the Hauterivian–Barremian eupantothere *Vincelestes neuquenianus* (Vincelestidae) is so peculiarly advanced as to suggest that it actually characterises a different stage in the evolution of the South American Cretaceous mammals, i.e. the Amar-gian SALMA (see Ortiz Jaureguizar & Pascual 1989), we will now disregard this SALMA, mainly because it is irrelevant to the specific purpose of this essay.

The data consisted of 82 “characters”, i.e. mammalian families, scored for each 11 OTU, i.e. the late Cretaceous plus Paleocene SALMA and NALMA. All the characters are qualitatives (presence/absence). The data, as in our previous paper (Ortiz Jaureguizar & Pascual 1989), were taken from:

- a) Clemens et al. 1979, just the Paluxian NALMA;
- b) Lillegraven & McKenna 1986, the Aquilan, Judithian, and Lancian NALMA;

Time (Ma)	Chronostratigraphy	Biochronology		South American chronofaunas (faunistic cycles) ²			
		NALMA	SALMA	Subcycles	Cycles	Supercycles	Megacycles
60 –	TERTIARY Eocene Paleocene	CLA	CAS	Pancasamayoran	Prepatagonian	Infracenozoic	Paleocenozoic
		TIF	RIO ITA	Panriochican	Eopatagonian		
		TOP PUE LAN	TIU	Tiupampian	Cochabambian	Protocenozoic	
70 –	CRETACEOUS Late	JUD ¹	ALA	Alamitian	Somunchurian	Cuadradian	Verdian
		AQU					
80 –							
90 –							
100 –	Early	PAL					

Fig. 1. Correlations Cretaceous – Early Eocene North American and South American land-mammal ages, and South American chronofaunas (from Ortiz Jaureguizar & Pascual 1989:A233). — Abbreviations: NALMA = North American Land-Mammal Ages; SALMA = South American Land-Mammal Ages; CLA = Clarkforkian; CAS = Casamayoran.

¹ including “Edmontonian” (see Lillegraven & McKenna 1986);

² the recognition and concepts of the South American faunistic “episodes” so far distinguished, i.e. chronofaunas, were treated by Pascual (1984), Ortiz Jaureguizar (1986), Pascual & Ortiz Jaureguizar (1990) and Ortiz Jaureguizar & Pascual (1989). For other abbreviations, see Table 1.

- c) Archibald et al. 1987, just the Puercan, Torrejonian and Tiffanian NALMA;
- d) Bonaparte & Pascual 1987, just the Alamitian and Itaboraian SALMA;
- e) Marshall & de Muizon 1988, Tiupampian SALMA; and
- f) Ortiz Jaureguizar 1986, Riochican SALMA.

The taxonomic list and the temporal range of each family were updated by us in accordance with the most recent available bibliography.

The data were arranged in a basic data matrix (BDM) of 11 OTU by 82 characters (see Table 1). This BDM was partitioned into two secondary BDM. The first with 4 OTU (SALMA) by 82 characters (i.e. the first four rows of the original BDM, Table 1), and the second with 7 OTU (NALMA) by 82 characters (i.e., the last seven rows of the original BDM, Table 1).

The original BDM and the two secondaries were transformed into three similarity association matrices (SAM) among the OTU using the Jaccard coefficient (see Cheetham & Hazel 1969). Each one of these three SAM was clustered by the unweighted pair-group method, using arithmetic averages (UPGMA; see Sokal & Michener 1958, Rohlf 1963), and the cophenetic correlation was computed for the three resulting phenograms, using the Cophenetic Correlation Coefficient (CCC) of Sokal & Rohlf (1962). More details about the multivariate analytical techniques employed can be found in Sneath & Sokal (1973), Crisci & López Armengol (1985) and Sokal (1986).

The computational work was done on an IBM-PC using the NTSYS-PC 1.40 library of numerical taxonomy computer programs (Rohlf 1988) at the LASBE in the Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

3. Results

3.1. SALMA relationships

The phenogram in Fig. 2 shows that the SALMA more directly involved in the Cretaceous–Tertiary transition are grouped into two clusters:

1. Alamitian; and
2. Tiupampian + Itaboraian + Riochican.

Cluster 2 is likewise divisible into two groups:

- 2.1. Tiupampian; and
- 2.2. Itaboraian + Riochican.

The CCC value is 0.99764.

3.2. NALMA relationships

The phenogram in Fig. 3 shows that the NALMA are grouped into two clusters:

4. Paluxian; and
5. Aquilan + Judithian + Lancian + Puercan + Torrejonian + Tiffanian.

The second cluster is divisible into two groups:

- 5.1. Aquilan + Judithian + Lancian + Puercan; and
- 5.2. Torrejonian + Tiffanian.

Group 5.1 is likewise divisible into two sub-groups:

- 5.1.1. Aquilan + Judithian; and
- 5.2.2. Lancian + Puercan.

The CCC value is 0.85339.

3.3. Relationships between SALMA and NALMA

The phenogram depicted in Fig. 4 shows two groups of SALMA and NALMA:

6. Alamitian + Paluxian; and
7. Tiupampian + Itaboraian + Riochican + Aquilan + Judithian + Lancian + Puercan + Torrejonian + Tiffanian.

Group 7 is divisible into two subgroups:

- 7.1. Tiupampian + Itaboraian + Riochican; and
- 7.2. Aquilan + Judithian + Lancian + Puercan + Torrejonian + Tiffanian.

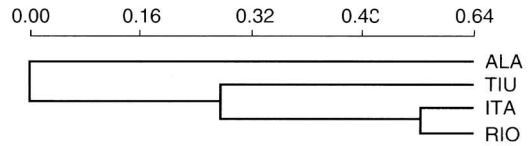


Fig. 2. Phenogram of Cretaceous and Paleocene SALMA from the UPGMA cluster analysis (CCC = 0.99764). For abbreviations, see Table 1.

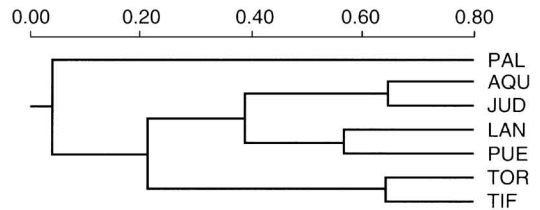


Fig. 3. Phenogram of Cretaceous and Paleocene NALMA from the UPGMA cluster analysis (CCC = 0.85339). For abbreviations, see Table 1.

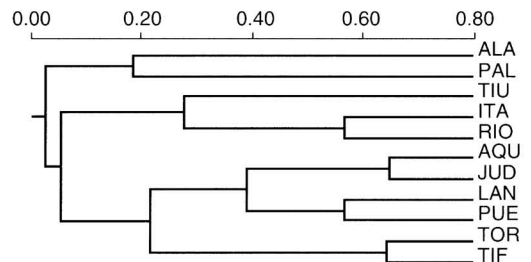


Fig. 4. Phenogram of Cretaceous and Paleocene SALMA and NALMA from the UPGMA cluster analysis (CCC = 0.91083). For abbreviations, see Table 1.

Subgroup 7.1 is divisible into two clusters:

- 7.1.1. Tiupampian; and
- 7.1.2. Itaboraian + Riochican.

Subgroup 7.2 is likewise divisible into two clusters:

- 7.2.1. Aquilan + Judithian + Lancian + Puercan; and
- 7.2.1. Torrejonian + Tiffanian.

The CCC value is 0.91083.

4. Discussion

We must bear in mind (see Bonaparte 1986a, b, Bonaparte & Pascual 1987, Ortiz Jaureguizar & Pascual 1989) that the Alamitian fauna was almost exclusively composed of pre-tribosphenic mammals (again, except for the enigmatic Gondwanatheria, see Table 1), whereas during the late Cretaceous NALMA the pre-tribosphenic mammals were decreasing, so that only the multituberculates persisted until the end of the Cretaceous (even till the early Oligocene). Furthermore, the Albian Paluxian NALMA yielded records of the first Theria of metatherian–eutherian grade (see Kielan–Jaworowska et al. 1979a), and later on the marsupials (middle Cenomanian, see Cifelli & Eaton 1987), and the eutherians (Aquilan NALMA. See Lillegraven & McKenna 1986). In South America, by contrast, the first unquestionable eutherians and metatherians were first recorded during the Tiupampian, conventionally regarded as early Paleocene, and represented by fairly advanced taxa (Table 1).

The different North and South American Cretaceous patterns are graphically expressed (Fig. 4) by the major similarity between the late Cretaceous Alamitian SALMA and the “middle” Cretaceous Albian Paluxian NALMA (see Results, 3.3). On the one hand, the taxa common to the two Americas appear to be relicts of a Pangaeian Mesozoic biota. On the other hand, the taxa exclusive to each of the Americas support the conclusion that by the late Jurassic–earliest Cretaceous the two continents were unconnected (see Bonaparte 1986b, Bonaparte & Pascual 1987). If we accept the conventional dates assigned to the SALMA and NALMA (Fig. 1), the major compositional changes on the two American continents were diachronic, taking place between the Paluxian and Aquilan in North America, and between the Alamitian and Tiupampian in South America (Figs. 2, 3 and 4). It is possible that a pronounced change occurred between the Hauterivian–Barremian Amargian and the Campanian–Maastrichtian Alamitian SALMA, but if so, it is unlikely to have been as profound as the North and South American ones. According to the records, it must be attributed merely to the pre-tribosphenic mammals, disregarding the uncertain Gondwanatheria.

The change between the Alamitian and Tiupampian is fairly drastic, so that the first may be recognized as the most clearly distinguishable SALMA. Furthermore, in our opinion (Ortiz Jaureguizar and Pascual 1989) this age characterizes the last known Cretaceous Faunistic Cycle, the Somuncurian (see references in Fig. 1). Its distinctness from the next, the first Cenozoic Cochabambian Cycle, is clearly expressed by the fact that they have no families in common (Fig. 2). Moreover, the uniqueness of the Cochabambian Faunistic Cycle, that is to say the beginning of the “Age of Mammals” in South America, is illustrated by the following facts: (1) it marks the complete extinction of pre-tribosphenic mammals in South America; and (2) besides the expected forbears of later Paleocene groups, there are representatives of two or three families of condylarths (Hyopsodontidae, Mioclaenidae and Phenacodontidae or Didolodontidae) and two orders (Proteutheria and Pantodonta) which are unknown in South America after this time, whereas some of these were known earlier or later in Asia and North America (Pascual & Ortiz Jaureguizar 1990). None of them are related to any known African taxa. These South American records suggest a more diverse dispersal regime (if not an extended range) between South America and North America (Gingerich 1985), quite probably related to geographical connections, caused by diastrophic events and/or sea level changes. It may be inferred that these geographical changes were related to concomitant climatic changes (Pascual & Ortiz Jaureguizar 1990). Thus, the time from the late Cretaceous to the early middle Paleocene in South America reveals a marked compositional change: from wholly pre-tribosphenic mammals (except for the uncertain Gondwanatheria) to wholly metatherian and placental ones (again except for the Gondwanatheria). In North America, by contrast, the same span reveals a gradual change, with an absence of pre-tribosphenic mammals (Table 1). We realize that there are no records of mammal faunas representing the Cretaceous–Tertiary transition, and that material is lacking for a crucial and relatively long time span (latest Cretaceous – earliest Paleocene). But, if an early (although not the earliest) Paleocene age is assumed for the Tiupampian fauna, it is unquestionable

that dramatic changes occurred in the mammal communities in South America if not precisely in the Cretaceous–Tertiary transition, then during the latest Cretaceous and earliest Paleocene.

The Eopatagonian Faunistic Cycle (Fig. 2) marks the beginning of the most autochthonous part of the history of mammals in South America. As we wrote (Pascual & Ortiz Jaureguizar 1990):

... the basic regional diversification had been achieved. All adaptive types were monopolized by only three different mammalian stocks: Marsupialia, Xenarthra, and varied native “ungulates”. The different ecological niches within the adaptive zones were occupied by very peculiar types. The resulting communities, and surely the biocenosis to which they belonged, were unique and quite unmatched by any contemporaneous ones from the rest of the world (Pascual et al. 1985). Notably, the Cochabambian “northerners” ungulates are absent, apparently related more to a holarcticward range retreat than to a dispersal event from South America to Holarctica, as has been suggested by Marshall & de Muizon (1988).

Another quite plausible explanation is that they evolved regionally, giving rise to some of the endemic South American “ungulate” orders.

The first endemic Cochabambian mammalian taxa and the completely endemic mammal fauna characterizing the Eopatagonian Faunistic Cycle show that the Cenozoic South American continental isolation had evidently begun some time before the middle Paleocene (Fig. 1), though transitory and selective geographical connections with the North American continent occurred (see Gingerich 1985, Marshall & de Muizon 1988, Bonaparte & Pascual 1987). It appears that such connections began by the late Cretaceous, even before the time covered by the Late Cretaceous Somuncurian vertebrate records, and apparently in an even more selective way (Bonaparte 1984, 1986b, Bonaparte 1987, Bonaparte & Pascual 1987).

Our analysis of the mammal families characterizing the late Cretaceous and the Paleocene NALMA supports the conclusion of Archibald & Clemens (1986) that the Cretaceous–Paleocene transition was not abrupt, since the Lancian and the Puercan are very similar (0.64, see Fig. 3). However, the phenograms depicted in Figs. 3 and 4 show that the mammalian familial changes between the Lancian and Puercan were not similar “... to that usually seen between any given succession of North American land mammal ages”,

as pointed out by Archibald & Clemens (1984). At least they are not similar to that between the Puercan and Torrejonian. That is to say, there was a much more marked change between the early and middle Paleocene. If we accept that the Tiupampian SALMA represents the earliest Paleocene (Fig. 1), the mammal changes between this Age and the conventionally middle Paleocene Itaboraian Age (Figs. 2 and 4), appear *prima facie* to be similar and correlative to those recorded between the Puercan and Torrejonian NALMA (Figs. 3 and 4). It seems that these coincident evolutionary phenomena could be related to global physical changes.

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