Paleoecology of the Santa Cruz Formation (Lower Miocene) in the extreme southwest of Patagonia

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INTRODUCTION

The Santa Cruz Formation is one of the stratigraphic units with the greatest quantity and diversity of continental vertebrates in South America. Its combined paleofauna is one of the most-studied, and includes numerous collections made since the last century (see Marshall, 1976). Not withstanding, there has been a deficiency in the vertebrate fossil record of this formation, due to lack precise stratigraphic position data for fossil material and, in many cases, a lack of precise geographic data, with the exception of the more modern collections studied by Bown and Fleagle (1993) and Tauber (1991, 1994, 1996, 1997).

This characteristic of the record has impeded knowledge of the natural taphonomic associations and the lithologic features of the fossil-bearing layers and has made the construction of dependable paleoecological interpretations difficult. For these reasons, hypotheses have been proposed that are difficult to verify, refute, or contrast with evidence or hypotheses contributed by other lines of paleontology or sedimentology. Moreover, circular reasoning is frequent in our body of knowledge, especially in reference to paleoecological aspects, as a consequence of the lack of precision in the data of the record. Detailed synecological studies of the Santa Cruz Formation will make an essential contribution to the analysis of eventual "Faunistic Cycles" (Ortiz Jaureguizar, 1986; see Tauber, 1997) and the relation that they will have with the

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"diastrofic" phases (e.g. "diastrofic" phase Quecha, Pascual, 1984; Pascual et al., 1985; Pascual and Ortiz Jaureguizar, 1990; Tauber, 1994), the climatic modifications, the variations in sea level or other phenomena produced during the Cenozoic in the extreme south of our continent.

The objective that is pursued with the present work is to make a preliminary paleoecological analysis of the Santa Cruz Formation in the Atlantic coast zone between the Rio Gallegos and the Rio Coyle, with an intent to verify or refute hypotheses formulated previously (Tauber, 1994, 1996), for example:

HYPOTHESIS 1. A deterioration was produced during the deposition of the lower member of the Santa Cruz Formation (Estancia La Costa Member).

HYPOTHESIS 2. The faunistic association of the lower levels of the Estancia La Costa Member indicates the existence of predominantly forested environments.

HYPOTHESIS 3. The upper part of the Estancia La Costa Member (fossiliferous levels 8 to 10, e.g. Tauber, 1996) was deposited in a predominantly grassland environment.

RESULTS

Two members within the Santa Cruz Formation in the study zone have been recognized: the Estancia La Costa (120 m thick) where 18 fossiliferous levels are recorded and the Estancia Angelina Member (103 m of thickness) with 4 fossiliferous levels (Tauber 1994, 1996).

Remains of 500 fossil vertebrate specimens were collected, from which the most representative of the recorded species were selected. These specimens come from 7 localities: cañadón del Indio (CL: 50° 59' 27" S and 69° 06' 32.4" E), Estancia La Costa (ELC: 51° 04' 58" S and 69° 08' 13" E), cañadón Silva (CS: 51° 09' 16.6" S and 69° 04' 9.73" E), Puesto de la Estancia La Costa (PLC: 51° 12' 8.2" S and 69° 03' 35.6" E = Corriguen Aike, see Tauber, 1991), Monte Tigre (MT: 51° 20' 36" S and 69° 01' 24.3" E), cañadón Las Totoras (CS: 51° 21' 18" S and 69° 0' 35.6" E), and cabo Buen Tiempo (CS: 51° 33' 22" S and 68° 57' 27" E) (Figure 1). The partial stratigraphic columns of these localities with the precise position of the fossiliferous levels and some paleontological materials were illustrated previously (Tauber 1991, 1994, 1996).

The fossil remains used in this study are deposited in the Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, of the Universidad Nacional de Córdoba

(CORD-PZ); the specimen numbers are those that appear in brackets. The abbreviation FL signifies fossiliferous level. A list of taxa recorded by fossiliferous level and the studied materials are cited in the appendix.

DISCUSSION

One of the most interesting themes that has been called to the attention of investigators of the Santa Cruz Formation is the great diversity and quantity of fossil vertebrates that this unit contains (e.g. Marshall, 1976, 1985; Marshall et al., 1983, 1986). Another peculiarity of this formation is that it has indicators of very different climatic and environmental conditions, such as the presence of Echimyidae, Erethizontidae (Rodentia), Primates, etc., used as indicators of warm, moist conditions and forested environments (Vucetich, 1986; Pascual and Ortiz Jaureguizar, 1990). On the other hand, the record of Octodontidae (Rodentia), the presence of probable paleodunes (Bown and Larriestra, 1990), of gypsum crystals, of desiccation cracks (Tauber, 1996) or of non-channel fluvial deposits (Tauber, 1994), suggest the existence of arid climatic conditions and open environments.

Investigations of paleoecology with mammals are seen as difficult due to the great quantity of fossils that are necessary in order to undertake studies with confidence. In that sentiment, Wolff (1975) made estimates in order to determine the size of specimens so that the analyses of the ecology of mammal fossils would be representative, comparing the fauna of the late Pleistocene and the recent in the region of Rodeo, in California. In the case of the Santa Cruz Formation that seems to be aggravated by the lack of precise stratigraphic provenance of the old collections and, consequently, by the lack of knowledge of the true temporal spans among the different species of vertebrate fossils. Moreover, the paleoecological studies of the Santa Cruz Formation seem difficult because of the 30 families of mammals recorded, only 36.6% are represent today. This estimate was created considering the family Palaeothentidae in place of Caenolestidae, following the criteria of Bown and Fleagle (1993).

With respect to the locality data of the old collections of vertebrate fossils of the Santa Cruz Formation, which are rather imprecise, there exist some indications in the bibliography that allow them to be assigned in a general way to the Estancia La Costa Member (Tauber 1994, 1996). In fact, the strata of the Estancia Angelina Member are exposed in inaccessible places;

nevertheless, they have been prospected, scarce remains of vertebrate fossils having been recorded. Moreover, the scarcity of vertebrate fossils in the Estancia Angelina Member would be tied to dry climatic conditions, present during its deposition following the interpretations based on sedimentological data.

Following Ameghino (1902) the producing levels in the intertidal zone are positioned horizontally and would correspond to only a single level (see Tauber, 1994). That prompted various authors to consider all the taxa recorded in the intertidal zone of the study region as a natural association. Nevertheless, as was already described (Tauber 1994, 1996), the producing layers in the study area correspond, in general, to levels stratigraphically lower toward the north, higher in front of Cabo Buen Tiempo and above all, at Monte Tigre - cañadón Las Totoras. That signifies that the majority of the collection studied in this work, and the materials collected by Hatcher and Ameghino in the zone, come from the Estancia Angelina Member.

The collection of fossils that is analyzed in this work (250 specimens) is reduced in order to make an exhaustive paleoecological examination; not withstanding, it is considered an example of good taxonomic diversity, if one considers that 60 species, 44 genera, 25 families, and 13 orders are represented. This represents 38.7% of the mammal genera and 37.6% of the vertebrates, including frogs and birds, considered of "Santacrucian Age", that is to say those of the "Astrapotherium Level", those of the "Notohippus Level" and those of the "Santacrucian Level" (following the data of Bondesio, 1986; Fleagle, 1990). This record gives us an idea in preliminary form and along general lines of the probable evolution of the communities of vertebrate fossils of the Santa Cruz Formation in the studied area ("Santacrucian Level") and its eventual relation with environmental and climatic changes.

Hatcher (1897), during his first trip to Patagonia, made observations that permitted him to propose the existence of some variations within the fauna of the Santa Cruz Formation. Following this author, the "Santacrucian Level" should be divided in two parts, distinguishing the lower section exposed in the valley of the Rio Santa Cruz by the high contents of birds and herbivorous marsupials and the upper section, corresponding to the strata that are exposed between the Coyle and Gallegos Rivers with scarce remains of birds and herbivorous marsupials but with abundant carnivorous marsupials, edentates, rodents, and notoungulates; nevertheless, this could not be confirmed subsequently. Bown and Fleagle (1993) have found that in the zone of Monte León and Monte Observación there are two fossiliferous levels that, by their contained nests of [?beetles] and of solitary wasps and by the frequent remains of phororhacid birds, suggest areas with open vegetation.

The new paleontological record examined demonstrates interesting variation among the associations of taxa of each level, whose paleoenvironmental and paleoecological significance will be analyzed later, with respect to the hypotheses put forth in the introduction. This new record was partially illustrated previously (Tauber, 1994, 1996), considering the distribution of the taxa recovered in 20 fossiliferous levels and distributed among 7 localities.

In order to analyze these differences among the associations of each level, some variables observed in the cenograms of Legendre (1986) were taken into account. It has been observed in these cenograms of African fauna: that greater taxonomic diversity exists in tropical forest environments, with respect to an arid and open environment; that a discontinuity is produced in the distribution of species of medium size in open environments; that taxa of small size (less than 500 g) are more abundant in tropical forest environments and that the species of large size are less abundant in arid zones.

One of the principal characteristics of this record is spotlighted in Figures 2 and 3, where the quantity of species and genera, respectively, were represented by each fossil level. These demonstrate that the number of recorded species is greater in the lower levels (e.g. 1 and 6) than in the upper levels (e.g. 8.1 and 10). If the number of families and orders in each fossil level is considered, it is observed that that difference in taxonomic diversity among the principal fossil levels is as great (Tauber, 1994).

If it is taken into consideration that the fossiliferous levels 1, 6, 8.1, and 10 were collected with the same intensity, the difference in taxonomic diversity among them is suggestive, interpreting that the greater variety of taxa of FL 1 and 6 indicate paleoclimatic conditions more warm and humid that those of FL 8.1 and 10. It is necessary to clarify that the fossiliferous levels 1 and 10 demonstrate taphonomic and sedimentological evidence that indicate a low rate of sedimentation (Tauber, 1994), and that their associations of fossils would represent a perthotaxis, that is to say “a death assemblage with the animal corpses in various stages of destruction by the set of processes normally operative under the environment concerned” (Clarke and Kietzke, 1967, p. 155; Clark and Guensburg, 1970, p. 411).

In the lower fossiliferous levels (1 to 6) the taxa of small size are more abundant, with body weights probably less than 500 g, such as *Microbiotherium patagonicum*, *Palaeothentes* *minutus*, *Acarechimys minutissimus*, *Spaniomys riparius*, *Stichomys regularis* and *Acarechimys minutus* (NF ?6); while in the upper levels *Palaeothentes* sp. and *Sciamys* sp. (NF 11) have been recorded, that would also have weights less than 500 g.

This decrease in diversity among the taxa of small size would be related to paleoenvironmental changes, from forested environments with a humid, warm climate and stable conditions in the lower fossiliferous levels (1 to 4) to plains with more open vegetation with a drier climate and more variable seasonal conditions in the upper fossiliferous levels (8.1 to 11).

In the high levels of the Estancia La Costa Member (8.1 to 10) partial dissolution of the bony elements is frequently observed that would have influenced the preservation of remains of small-sized taxa. Nevertheless, the high frequency of bony fragments of ≤ 2 mm diameter preserved in levels 8.1 to 10 allows one to infer that the scarcity of remains of remains of taxa of small size is due to paleoenvironmental causes and not taphonomic ones (Tauber 1994, 1995).

Among the distribution of organisms of large size the differences among the lower levels and the upper ones is due to the record of *Homalodotherium cunninghami* (brachydont, FL 5.1) and of *Theosodon lallemanti* (mesodont, FL 1 and 3). In agreement with the cenograms of Legendre (1986) this would indicate that the deposition of the lower levels had been produced under more humid and warm climatic conditions with respect to the upper levels.

On the other hand, there should exist a discontinuity in the distribution of species of medium size, as that which Legendre (1986) demonstrates for open environments. This discontinuity would be given by the difference of diversity and size between the Proterotheriidae and the combined Megatheriidae-Megalonychidae. In fact, in the lower levels 4 species of diverse sizes are recorded in fossiliferous level 1 (*Diadiaphorus robustus*, *Licaphrium floweri*, "*Proterotherium*" *cavum* and *Thoatherium minusculum*) and only a species of smaller size in fossiliferous level 10 (*Thoatherium minusculum*). Various authors have demonstrated the correlation between the dimensions of the teeth and body size in mammals (Creighton, 1980), utilizing as the variable the natural logarithm of crown area (length x width); the first upper molar (M1) or lower molar (m1) has been selected by being considered teeth with less variability of size in mammals (Gingerich, 1974; Legendre, 1986) although this does not always hold, as in the case of the Megatheroidea (Table 1).

Among the group of the Megatheriidae and Megalonychidae a decrease in size among the species recorded in the lower levels (*Hapalops longiceps*: FL 3, *Hapalops elongatus*: FL 2 and

Eucholoeops fronto: FL 6) and the upper ones (*Hapalops indifferens*: FL 8.1, *Hapalops gracilidens*: FL 8.1, *Pseudhapalops rutimeyeri*: FL 8.1 and 8.5, *Pelecyodon cristatus*: FL 8.1, *Megalonychotherium atavus*: NF 8.1 and *Eucholoeops* sp. FL 8.5) also is produced.

Another important aspect to analyze is the height of the tooth crowns of the different species, following the criteria of Mones (1982), who distinguished four types according to increasing height: brachydont, mesodont, protohypsodont, euhypsodont.

The height of the tooth crowns, the dental morphology, and the type of growth, in the case of mammals that consume plants and especially the ungulates, vary following the different grades of adaptation to wear. These variables have been linked fundamentally with the type of diet, composed of fruits, leaves, stems, roots and principally by grasses that contain abrasive elements (Patterson and Pascual, 1968, 1972; Ortiz Jaureguizar, 1986; Janis, 1988; Pascual and Ortiz Jaureguizar, 1990; Tauber, 199 6), although there exist other natural inorganic elements that produce wear. Considering that these adaptations for dental wear are related indirectly to environments with open vegetation, the distribution of the taxa according to the height of their tooth crowns was analyzed.

The criteria of Ortiz Jaureguizar (1986) have been followed in this analysis excluding the Dasypodidae Stegotheriini and Euphractini (in this case the species of *Prozaedyus*) because although they possess euhypsodont teeth, they would correspond to very specialized organisms with diets of ants and insects, respectively (Scott, 1913; Patterson and Pascual, 1968; Scillato Yané, 1986), but the Eutatini *Proeutatus lagena* and *Proeutatus oenophorus* are included by the probable inclusion of plants in their diet (Vizcaíno and Fariña, 1993), being perhaps grazers (Scillato Yané, 1986). In the case of the Eocardiidae and the species of *Perimys*, they are considered euhypsodont.

In Figure 4, the number of taxa that would have diets composed of vegetation is illustrated, grouped according to their dental morphology by fossil level. In Figure 5 the same numbers are represented in percentages. Because the record is very incomplete in most of the levels, only those better known and more intensely collected ones have been represented. It can be observed in both figures that there exists a greater number of taxa with euhypsodont in FL 8.1, while the number of species with brachydont and brachydont-mesodont teeth decreases from the lower to upper levels. This permits it to be inferred that the environment of deposition of the upper levels, especially 8.1, would have been more open than the environment of deposition of the lower levels, with greater development of grasses.

The fossiliferous levels 1 to 4, exposed in the Estancia La Costa, would have been deposited under similar climatic environmental conditions (Tauber, 1994), moreover, they are encountered in very close stratigraphic positions and their fossils were collected in the same locality. Taking this into account, the total numbers of species with distinct types of teeth recorded in those levels were represented (Figure 6). The same occurs with the fossiliferous levels 5 to 7 (CS-PLC) and in the fossiliferous levels 8 to 10 (MT-CT). The results obtained are more eloquent if one considers that in various levels the record is deficient.

If the Tardigrada Megatheriidae and Megalonychidae are excluded in these estimates, given their euhypsodont dentition and the probability that their diet would have been composed predominantly by leaves, the percentages of euhypsodont teeth also tends to increase from the lower levels (FL 1:31.3%, FL 6: 41.7%) to the upper (FL 8.1: 45%, FL 10: 40%). Moreover, the number of species with protohypsodont dentition increases among the mammals of medium and large size. In particular, the Toxodontidae are particularly abundant and more diverse in levels 8.1to 10, the species *Adinotherium ovinum*, *Adinotherium robustum*, and *Nesodon imbricatus* being recorded there.

Another noticeable aspect in the distribution of the fossil organisms in the stratigraphic column is the diversity of sizes represented by tooth type. Particularly, the taxa with brachydont teeth, coming from the lower levels (1, 2, 3, 4, 5.1) have greater diversity of sizes, the smaller mammals being present for example" *Microbiotherium patagonicum*)(FL 1), *Palaeothentes minutus* (FL 1), *Acarechimys minutissimus* (FL 1), *Acarechimys minutus* (FL 6?), *Spaniomys riparius* (FL 2, 3, 4, and 4.1), *Steiromys detentus* (FL 1?, 3, 4, and 5.2) and *Stichomys regularis* (FL 5, and 5.1), to those of large size such as *Homalodotherium cunninghami* in FL 5.1. In contrast to this, in the upper levels (8 to 11) brachydont teeth are present in *Palaeothentes* sp., *Sciamys* sp., both having very small sizes. The species with brachydont teeth, *Prothylacynus patagonicus* (FL 8.1) and *Arctodictis munizi* (FL 9), would have been carnivore-scavengers, therefore they are not considered for the moment to interpret the paleoenvironment.

The Glyptodontidae determined to specific level are rather scarce, but are important to highlight because, according to our record, in the upper fossiliferous levels (FL 10) two species of greater size of the Santa Cruz Formation are recorded; these are: *Eucinepeltus petestatus* and

Ecinepeltus complicatus, in contrast to the record of *Propalaehoplophorus australis* in fossiliferous level 1, this last one being of smaller size. This fact is significant if one considers that these organisms possess euhypsodont teeth and were very specialized for a grazing habit (Scillate Yané, 1986). On the other hand, *Cochlops debilis* was recorded in FL 8.1, one of the smallest species among the Glyptodontidae of the Santa Cruz Formation, for that reason, apparently, there existed greater taxonomic and size diversity among the Glyptodontidae of the upper levels, with respect to the lower.

In summary, this analysis indicates *a priori* the existence of paleoenvironments with greater quantity of tree or shrub vegetation during the deposition of the lower levels (1 to 4) and paleoenvironments more open with grasses in the upper levels (8.1 to 10). The climatic conditions would have been variable in the same sense, from warm, humid and of greater stability to a more dry climate with well marked seasonal variations during the deposition of the upper level of the Estancia La Costa Member (FL 8.1 to 10). These hypotheses verify the conclusions obtained based on functional morphological analysis of the species of *Protypotherium* (Tauber, 1996).

The presence of immature paleosols and a very mature paleosol in the lower half of the Estancia La Costa Member in conjunction with calcite, desiccation cracks (FL 10) and small crystals of rosette-type gypsum (FL 8.4) toward the top of this member (FL 8 to 10) appear to verify this hypothesis of a deteriorated climate from one of stabile, warm and humid conditions to drier conditions with well-marked seasonality during the deposition of the Estancia La Costa Member (Tauber, 1996). The morphologic and lithofacies variations of the fluvial deposits of this member also verify this hypothesis (Tauber, 1994).

CONCLUSIONS

The paleontological record of the Santa Cruz Formation indicates that in general terms, the following changes between the lower and upper fossiliferous levels were produced:

1) General decrease in taxonomic diversity

2) Decrease in taxonomic diversity, especially among small-sized organisms with body weights probably less than 500g (*Microbiotherium patagonicum*, *Palaeothentes minutus*,

Acarechimys minutissimus, *Spaniomys riparius* (FL 1 to 4), *Acarechimys minutus* (FL 6), *Palaeothentes* sp. and *Sciamys* (FL11).

3) Decrease in taxonomic diversity of organisms of large size such as *Theosodon lallemanti* (FL 1 and 3) and *Homlaodotherium cunninghami* (FL 5.1)

4) Increase in the taxonomic diversity and size of Glyptodontidae and Toxodontidae in the upper levels (8.1 and 10), although the record of the former is rather poor

5) Decrease in the percentage of organisms with brachydont dentition and brachydont-mesodont in the upper levels

6) Increase in the percentage of organisms with euhypsodont dentition

7) In the lower levels the species with brachydont dentition have diverse sizes from small to large while in the upper levels they are only small

8) Decrease in the size of the Megatheriidae and Megalonychidae recorded in the upper levels (8.1 and 10) with respect to the lower levels (2, 3, and 5.1)

9) Decrease in taxonomic and body size diversity, in general, among the Proterotheriidae

10) During the deposition of the Estancia La Costa Member a deteriorated climate had been produced, especially in the type of moisture, varying from warm, moist, stable conditions to drier conditions with quite different seasons

11) During the deposition of the Estancia La Costa Member changes had been produced from environments with predominant tree or shrub vegetation to environments more open with predominantly grassy vegetation