Sauropods crossing formations: biostratigraphical implications for patagonian faunal assemblages

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Introduction

The biostratigraphy of Cretaceous non-marine tetrapods from South America is particularly problematic since entire stratigraphic levels containing faunal assemblages are not well dated by magnetostratigraphy, palinology, microfossils or invertebrates. In this context; the correlation with the European marine stages is problematic and then, the precise age of these strata are doubtful in most cases. Inside the Neuquén Group, an example is the discrepancy regarding the precise age of the different stratigraphical units, as evidenced by the Candeleros Formation, which varies from Albian (i.e., Calvo, 1999) to Cenomanian (i.e., Leanza *et al.*, 2004), a discrepancy of more than eighteen million years. The same problem is also present in other units of the group, with the possible exception of the Huincul and Anacleto formations (Dingus *et al.*, 2000, Corbella *et al.*, 2004).

In basis to both, the lack of precise age determination for most of the fossiliferous stratigraphic units and the absence of precise guide fossils, in the past decades some authors favored the recognition of local ages and assemblages based on land animals for northern Patagonia. The purpose of the present work, is to discuss about different problems concerning to local ages and local assemblages (definitions, similarities and differences in the composition, etc).

Local ages and assemblages

The Cretaceous "land vertebrate ages" (here VA) as the "land mammal ages" was erected with the purpose of establishing a more precise range. Particularly, for land vertebrate ages, two local ages were erected by Bonaparte (1986, 1991; Bonaparte *et al.*, 1987) and include two important local faunas: the upper levels of the Bajo de La Carpa Formation at Neuquén city area at Neuquén province, called Neuquenian VA, and the middle levels of the Los Alamitos Formation at Arroyo Verde area, in the south of Río Negro province, called Alamitian VA. These faunal assemblages were discussed by Bonaparte (1992); indicating that comprise two temporally distant faunas. The problem is evident when the Neuquenian and Alamitian ages are compared as originally

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established. Since the first VA was defined based on the unusual presence of small theropod dinosaurs (including birds) and crocodyliforms; the Alamitian was defined based on the great abundance of mammals, unknown in the Neuquenian VA. Later, Ortiz Jaureguizar and Pascual (1989) defined the existence of two South American local mammal ages for the Cretaceous, the Amargan and Alamitian. These ages represented the most ancient periods of a more complete succession that included the Cenozoic age. These two Cretaceous units, defined only on the basis of their mammalian record, are more restricted in comparison with the local ages, as noted by Bonaparte (1992). In fact, most of the Cretaceous faunas from South America do not contain mammals or are represented by scarce material (Rougier *et al.*, 2009).

A reinterpretation of the Cretaceous land vertebrate ages was made by Juárez Valieri (2003a), redefining the extant local ages and creating two new ages: the Limayan and the Portezueloan. This new interpretation utilized the composition of megaherbivores, such as neosauropod and hadrosaurid dinosaurs, because these include the most abundant fossils among different Cretaceous stratigraphical units in Patagonia. The oldest VA, the Limayan, contains the faunas recovered at the Candeleros and Huincul Formations, and they are defined based in the abundance of rebbachisaurid respect to the titanosaurian sauropods, which are represented by basal forms. The second age, the Portezueloan, comprise the Portezuelo Formation and possibly also the Bajo Barreal Formation. This VA is defined by the notorious apparent complete absence of diplodocimorphs, perhaps with only a single possible exception in the Bajo Barreal Formation, plus the absence of saltasaurine titanosaurs among the faunas. The Neuquenian age, redefined by Juárez Valieri (2003a) to comprise not only the Bajo de la Carpa Formation, but also the Anacleto Formation. This VA includes derived titanosaurs, including saltasaurines, but with the absence of hadrosaurid dinosaurs. Finally, the Alamitian fauna involves the Los Alamitos and Allen Formations, and possibly the Loncoche, Coli Toro and La Colonia Formations. This age retains the same sauropod groups as the Neuquenian, but the younger Alamitian also includes a notable abundance of hadrosaurid dinosaurs. These continental ages represent a process of faunistic successions of megaherbivorous from the "Middle" to the Late Cretaceous of Patagonia. Several authors (e.g. Lamanna et al. 2001) arrived to similar conclusions on faunal replacement of the Cretaceos of Patagonia.

An alternative to use vertebrates ages was given by Juárez (2003b) and he proposed to use biozones of megaherbivores. The biozones of zenith (here BZ) are in accordance with the Código Argentino de Estratigrafía (CAE, 1992). These biozonones of zenith interpret the abundance of particular taxa among the faunal assemblages. Four biozones were recognized: Diplodocoidea BZ, represented from the upper section of Candeleros Formation to the lower section of Huincul Formation; Titanosauria non-Eutitanosauria BZ, represented in the Portezuelo Formation; Saltasaurinae BZ, represented in the top of Bajo de la Carpa Formations; Hadrosauridae BZ, represented in the middle section of Los Alamitos Formation and in the lower section of the Allen.

Posteriorly, Leanza *et al.* (2004) dismissed the use of land vertebrate ages and proposed the creation of successions of local tetrapod assemblages (here TA): the Amargan TA, comprises La Amarga Formation; the Lohancuran TA comprises Lohan Cura and Rayoso Formations; the

Limayan TA, includes the Río Limay Subgroup; the Neuquenian TA, comprises the Río Neuquén Soubgroup; the Coloradoan TA, includes the Río Colorado Subgroup, and the Allenian TA, includes the Allen, Los Alamitos, and other Senonian patagonian Formations. Respect to the faunal differences between assemblages, the authors characterized these TA based on the composition of suprageneric tetrapod taxa, including to diverse sauropod groups as one of the principal elements for comparison; for instance, Rebbachisauridae, Eutitanosauria or Saltasaurinae.



Figure 1. Simplified stratigraphical succession in the Neuquén Basin, containing an approximate disposition of the principal sauropod localities in the area and the successive classifications of land vertebrate ages, biozones of zenith and land tetrapod assemblages.

Discussion

Leanza *et al.* (2004, p. 64) explain that their tetrapod assemblages are not equivalents to local ages. However, both reflect different faunal associations that lived thorough the time and were recovered in successive stratigraphical units; therefore, they show that have the same utility. The basic differences in the definition between the local ages given by Bonaparte (1986, 1991; Bonaparte *et al.*, 1987) and posteriorly by Juárez Valieri (2003a) and the local assemblages presented by Leanza *et al.* (2004) is evidenced in the fact that tetrapod assemblages comprises complete stratigraphical secuences. The vertebrate ages, instead, are restricted to the fossiliferous stratigraphical sections of each unit.

One important point to take into account when we talk about the continuous sequence of the tetrapod assemblages is that from the upper section of the Huincul Formation to the middle of the Portezuelo Formation there is not a variation of local faunas comparables to those present in the under- and overlaying units. Actually, the tetrapod assemblages are currently defined as the direct correlation between the change of depositional units and the change in their assemblages. For instance, in the case of sauropods, the existence of Rebbachisauridae is recorded from the Amargan to the Limayan TA and it is absent in the Neuquenian and posterior TA. The absence, and probable extinction, of Rebbachisauridae could have been occurred in the border between the Limayan and the Neuquenian. The last evidence of rebbachisaurids recorded during the Limayan is in the middle part of the Huincul Formation, and the following record is located in the upper part of the Portezuelo Formation, then the hiatus between these two levels can not be characterized by the tetrapod assemblages. The same is true for all the limits among tetrapod assemblages. A second problem is constituted by mistakes in the characterization of tetrapod assemblages based in misinterpretations of both the stratigraphic provenance of some fossils and the absence of fossil record (ghost lineages). The first case is evidenced by MUCPv 204; a basal titanosaurid with amphyplatian mid-caudals (Salgado e Calvo, 1993, Juárez Valieri e Calvo, this volume). This form was considered by Leanza et al. (2004) as coming from the Neuquenian, but a recent revision of the area, where the same was collected, demonstrates that this sauropod came from the base of the Bajo de la Carpa Formation. Therefore, we have to discard the absence of basal forms during the Coloradoan TA, which at the moment is correct only for the top of the Bajo de la Carpa and younger units. The presence of long-rate ghost lineages are evident in several clades of titanosaurids, as exemplified here with Aeolosaurini, which is recorded in the Allenian but shares a minimum common origin with the Rinconsauria (Calvo et al., 2007), which are reported in the Neuquenian. To this respect; for instance, the upper section of Bajo Barreal Formation, previously dated as Conician or Santonian, is now assigned to a late Campanian - early Maastrichtian in basis to the presence of an Aeolosaurus species (Casal et al., 2007). An alternative conclusion, here proposed, is that Aeolosaurus colhuehuapensis represents the first pre-Campanian Aeolosaurini known in concordance with the ghost line of the group. The absence of Aeolosaurini, previous to the Alamitian VA or the Allenian TA, is evidently an effect of a long-rate ghost lineage; therefore, we have to be careful with respect to the absence of these groups in older stratigraphical units. The same can be said for almost all of the remaining sauropod (and tetrapod) supraspecific taxa.

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Figure 2. Two simplified phylogenetic trees including the diplodocimorphs and titanosauriforms found in the basin. Ref: **state 1**: slightly procoelic anterior caudal vertebrae; **state 2**: strongly procoelic anterior caudals; **state 3**: strongly procoelics anterior and middle caudal vertebrae.

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The use of supraspecific taxa, for defining both ages and assemblages, could generate problems in their application since these groups, even at generic level, present extensive biochrons. A typical example is the sauropod *Limaysaurus* (*Rebbachisaurus* sensu Calvo and Salgado, 1995). Although originally described in the contact of the Candeleros and Huincul Formations, it has been reported from the basalmost section of the Aptian age, Lohan Cura Formation (Salgado *et al.*, 2004) to the middle section of the Cenomanian age, Huincul Formation (Calvo *et al.*, 2005). Therefore, a taxon with a long biochron is not optimal for elucidate precise correlations with another sedimentary basins. In turn, the species *Limaysaurus tessonei* remain as present in a more restricted lapse of time. A similar problematic situation is evidenced by other sauropod titanosaurids such as *Neuquensaurus*.

Lastly, nomenclatural problems appear between Vertebrate Ages and Tetrapod Assemblages. The Neuquenian age of Bonaparte (upper section of the Bajo de La Carpa Formation) does not represent the same stratigraphical units that use Leanza *et al.*, (Portezuelo and Plottier Formation) even in part. Respect to the use of biozones, it present potentiality as there are recognized as valid units under the Argentinian Estratigraphic Code, opposite to the informal character of the vertebrate ages, are not simply the compilation of fossils registered in an entire stratigraphic unit, as present in the tetrapod assemblages. The biozones present in Juárez Valieri (2003b) has been supported by the increase of fossil remains of the last six years, but a substantially more complete fossil record is required for generate viable statistical basis.

Conclusions

Although far of being complete, the abundance of sauropods allows to recognize a succession of specific and supraspecific taxa among the stratigraphical units of the Neuquén basin and related units. It presents a good opportunity of helping with the clarification of the relationships among faunal assemblages from one to other areas of South America. To accomplish this purpose, the sauropod species can be utilized as primary indicators of equivalent age between local faunas. We consider that the restriction of units, in well known local faunas in partial formational sequences, improves a better knowledge of their faunal content, generating a more informative basis for temporal and real comparisons. Additionally; many of the problems, described previously, could be reduced using species-level taxa for reference since their biochrones are notoriously shorter than those of more inclusive taxa, and they appear reduced in broad ghost lineages.

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