SHOULD WE ABANDON THE NAME TITANOSAURIDAE? SOME COMMENTS ON THE TAXONOMY OF TITANOSAURIAN SAUROPODS (DINOSAURIA)

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ABSTRACT

Titanosaurs were the most abundant and widespread of Cretaceous sauropod dinosaurs. A derived subset of titanosaurian genera, historically termed the Titanosauridae, is beset with multiple taxonomic problems. Because the genus *Titanosaurus* is founded upon nondiagnostic material, the International Code of Zoological Nomenclature opposes the continued use of the term Titanosauridae. Nevertheless, the newly proposed Phylogenetic Code of Biological Nomenclature advocates the retention of Titanosauridae. To stabilize the taxonomy of derived titanosaurs, I consider Titanosauridae as a node-based taxon and Epachthosaurinae and Eutitanosauria as stem-based taxa, and thereby establish a node-stem triplet at Titanosauridae. I phylogenetically define additional titanosaurian clades including Titanosauroidea, Andesauroidea, Eutitanosauria, Saltasaurinae, and Opisthocoelicaudinae. Finally, I return "*Titanosaurus*" *araukanicus* to the genus *Laplatasaurus*.

Keywords: Titanosauridae, taxonomy, phylogenetic definitions.

RESUMEN

Los titanosaurios fueron los dinosaurios saurópodos cretácicos más abundantes y los más ampliamente distribuidos. Un subgrupo de titanosaurios derivados, históricamente conocidos como los Titanosauridae, posee múltiples problemas taxonómicos. Debido a que el género *Titanosaurus* está fundado a partir de material no diagnóstico, el Código Internacional de Nomenclatura Zoológica se opone al uso de Titanosauridae. De todas maneras, el recientemente propuesto Código Filogenético de Nomenclatura Biológica favorece el mantenimiento de ese término. Para estabilizar la taxonomía de los titanosaurios derivados, se considera Titanosauridae como un taxón basado en el nodo (node-based taxon) y Epachthosaurinae y Eutitanosauria como taxones basados en la rama (stem-based taxon) y, de este modo, se establece un triplete nodo-rama (NST) en la base de Titanosauridae. Se definen filogenéticamente clados de titanosaurios adicionales, incluyendo Titanosauroidea, Andesauroidea, Eutitanosauria, Saltasaurinae y Opisthocoelicaudinae. Finalmente, "*Titanosaurus*" *araukanicus* es regresado a *Laplatasaurus*.

Palabras clave: Titanosauridae, taxonomía, definiciones filogenéticas.

INTRODUCTION

The monophyly of Titanosauridae [defined by Salgado (2000) as titanosaurian sauropods closer to *Saltasaurus* Powell than to *Andesaurus* Calvo and Bonaparte] has been explicitly or implicitly accepted by virtually all authors (e.g., Huene, 1929; Powell, 1986; McIntosh, 1990; Salgado *et al.*, 1997; Bonaparte, 1999). However, several taxa traditionally included in this clade of sauropod dinosaurs are based upon material that is not diagnostic. The case of *Titanosaurus indicus* Lydekker, the type species of the genus *Titanosaurus* Lydekker, illustrates this situation. Lydekker (1877) diagnosed *Titanosaurus* on the basis of procoely in its caudal vertebrae, which at the time was known only in that taxon. Since 1877, a number of forms related to *Titanosaurus indicus* have been discovered, and it is now known that procoelous caudals characterize a large group of sauropods: the Titanosauridae.

In view of this situation, an increasing number of

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authors have avoided the name Titanosauridae and used alternative names, in order to satisfy the standards of the International Code of Zoological Nomenclature.

In this paper I summarize the many diagnoses of Titanosauridae, *Titanosaurus* and the species assigned to it, and propose new phylogenetic definitions for Titanosauria and clades within. My aim is to standardize the usage of names in order to prevent confusion, and, at the same time, to maintain, as much as is possible, the terminology formerly proposed.

HISTORY OF THE GENUS *TITANOSAURUS* AND THE TITANOSAURIDAE

The type species of *Titanosaurus*, *Titanosaurus indicus*, was founded upon two procoelous caudal vertebrae (designated as the holotype) and an isolated femur (designated as the cotype) from the Lameta Formation at Jabalpur, India (Lydekker, 1877). Although he did not provide a formal diagnosis of *Titanosaurus*, Lydekker (1877) described the caudal vertebrae of *Titanosaurus indicus* as laterally compressed and strongly procoelous. He stated "the forms of the articular surfaces of the vertebrae are quite sufficient to distinguish the Indian genus from all other genera of Dinosauria" (Lydekker, 1877: 40). In this manner, although *Titanosaurus* included only one species, Lydekker understood that procoely was a character of the genus.

Later, Lydekker (1879) applied the same generic name to a new species (*Titanosaurus blanfordi* Lydekker), based on another isolated procoelous caudal vertebra from the Lameta Formation, at Pisdura, India.

In a book that appeared in 1888, Lydekker announced the discovery of bones referable to *Titanosaurus* sp. from the Wealden of the Isle of Wight [subsequently, Friederich von Huene erected a new species, *Titanosaurus valdensis* Huene, the first European titanosaurid to be recognized (Huene, 1929)]. Therein, Lydekker provided short characterizations of *Titanosaurus* and *Titanosaurus indicus*, which can be regarded as diagnoses. For *Titanosaurus*: "postmedian caudal vertebrae procoelous; femur apparently like that of *Cetiosaurus*" (Lydekker, 1888: 134). For *Titanosaurus indicus*: "centra of posterior caudal vertebrae much compressed laterally, and facets for chevrons strongly marked" (Lydekker, 1888: 134). Thus, "caudal procoely", was confirmed as a character applicable at the genus level. In turn, the lateral compression of the caudal vertebrae was established by Lydekker (1888: 134), as part of the diagnosis of the type species (*Titanosaurus indicus*).

When the family Titanosauridae was formally erected by Lydekker in 1893, *Titanosaurus* contained four species: *Titanosaurus australis* Lydekker and *Titanosaurus* (?) *nanus* Lydekker (based on one cervical and two dorsal vertebrae) from the Upper Cretaceous of Patagonia, and the two Indian species mentioned above (Lydekker, 1893). Titanosauridae also included *Argyrosaurus superbus* Lydekker, 1893 and *Microcoelus patagonicus* Lydekker, 1893, the first titanosaurids to receive generic names other than *Titanosaurus* (*Hypselosaurus* Matheron, 1869, a *nomen dubium*, was in fact named earlier, but was not recognized as a member of the Titanosauridae until the early 20th century [Huene, 1929]).

Although Lydekker (1893) stated that *Titanosaurus australis* and *Titanosaurus indicus* belonged to the same genus, he noted differences in caudal morphology between the two taxa. In *Titanosaurus indicus*, distal caudal vertebrae were characterized by strong lateral compression (it must be remembered that the character was first proposed as diagnostic of the type species in 1877), whereas in *Titanosaurus australis* such compression was absent.

Lydekker (1893: 3) diagnosed the new family Titanosauridae as follows: "...sauropodous dinosaurs in which the caudal vertebrae, with the exception of the first, are procoelous, the presacrals opisthocoelous, and the lumbars without lateral cavities; the superior extremities of the chevron-bones being open." Thus, the main diagnostic character of *Titanosaurus* and *Titanosaurus indicus* proposed by Lydekker in 1877, the procoelous condition, was subsumed in his 1893 diagnosis of Titanosauridae. This reflected a change from his earlier opinion, as stated in his 1888 paper ["the procoelous character of the caudals has been regarded as indicating a distinct family, but this does not appear a necessary conclusion" (Lydekker, 1888: 134)].

In his 1929 monograph "Los Saurisquios y Ornitisquios del Cretáceo Argentino" Huene accepted the validity of both *Titanosaurus* (creating the new species *Titanosaurus robustus*) and *Argyrosaurus,* and erected three more titanosaurid genera: *Campylodon* Huene (later emended to *Campylodoniscus* by Kuhn [1961]), *Antarctosaurus* Huene (with the species *A. wichmannianus* Huene and *A. giganteus* Huene), and *Laplatasaurus* Huene. The last was named for remains from Cinco Saltos (in Río Negro Province), and a series of fragmentary bones originally assigned by Lydekker to *Titanosaurus* from several northern Patagonian localities. Huene perceived that the family Titanosauridae included a large diversity of genera (7 in total).

Huene (1929) was the first to recognize the close relationships of *Macrurosaurus semnus* Seeley from the Cenomanian of Barnwell (England), originally described by Seeley in 1869, and *Hypselosaurus priscus* (France), described by Matheron in 1869, with the Titanosauridae.

Huene accepted the inclusion of *Titanosaurus australis* and *Titanosaurus indicus* within the same genus, based on their caudal morphology: "It is always a risky thing to express identity founded only on middle caudal vertebrae. However, the characteristic features are so extraordinary and attractive that, at the moment, they can and they should be enough to satisfy us in this point" (p. 90). According to Huene (p. 90), the only difference between *Titanosaurus australis* and *Titanosaurus indicus* was the lateral compression of the caudal centra of the last species, as noted earlier by Lydekker (1893).

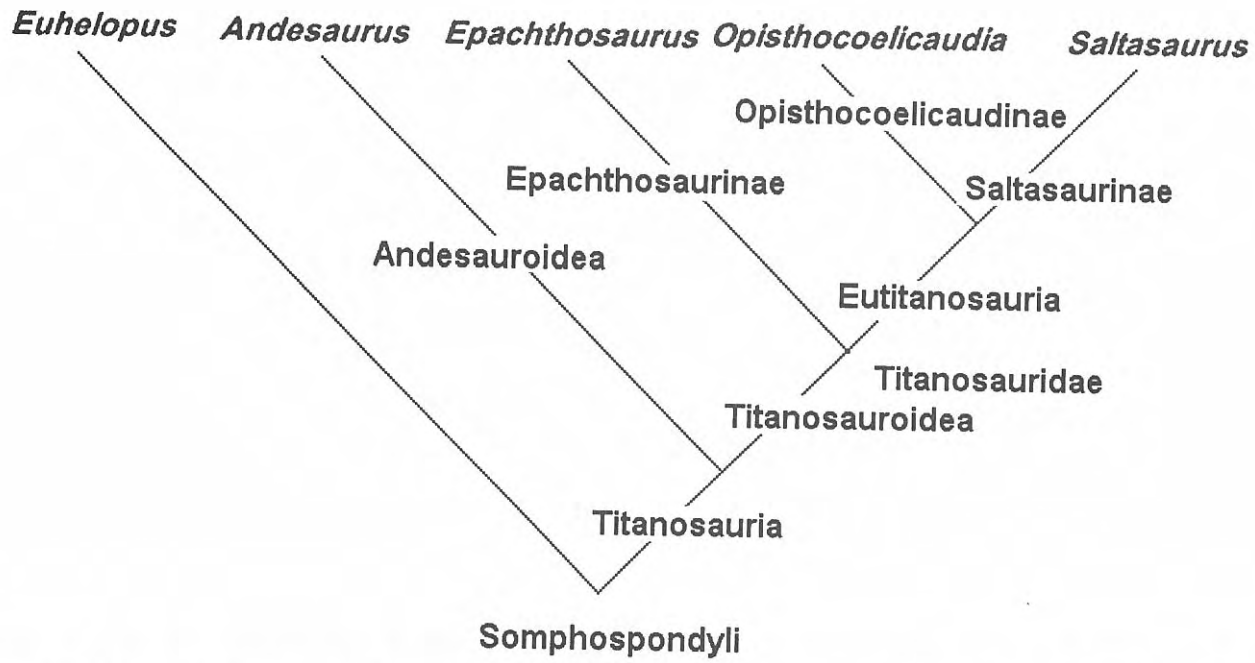

Figure 1. Phylogenetic relationships of titanosaurs and clade names within Titanosauria, according to the proposal given in the text.

Likewise, the differences invoked to separate *Titanosaurus* from *Laplatasaurus* were observed in their caudal morphology. Huene's diagnosis of *Titanosaurus* included the following caudal characters: "(the caudal vertebrae have the) posterior articular cone pointed and wide (with the exception of the subspherical first)" (p. 84), whereas the diagnosis of *Laplatasaurus* included a "high and pointed articular cone" (p. 85). For the characterization of the caudal vertebrae in titanosaurids, Huene stated that "the following (vertebrae distal to the first caudal) are procoelous with the articular cone behind" (p. 86), that is, for him, the presence of procoelous caudal vertebrae was indicative of Titanosauridae.

Huene (1929) also observed differences between *Titanosaurus madagascariensis* Deperet, 1896 and *Titanosaurus australis+Titanosaurus indicus*; for this reason, he proposed to reassign the first species to the genus *Laplatasaurus*, though he never provided adequate evidence of a close relationship with *Laplatasaurus araukanicus* (the type species of the genus).

Huene and Matley (1933) described two vertebrae and many poorly preserved and dissociated appendicular bones from Bara Simla and Silondi, India, and assigned all of this material to *Titanosaurus indicus*. These authors (*op.cit.*: 55) provided a diagnosis of *Titanosaurus indicus*: "post-median procoelous caudal vertebrae with flat, lateral sides (...) (1), a longitudinal groove below (2), and a low longitudinally stretched neural arch growing only from the anterior half of the centrum (3). The deeply bifurcated and open haemapophyses of this region have double articulations on each ramus (4). Tibia with thick head (5). Fibula also very broad and with a strongly developed attachment for the peroneus muscle (6). Femur (if belonging to it) thick and very broad in upper part (7)". Actually, most of these characters are present in nearly all titanosaurids (Powell, 1986; McIntosh, 1990). Huene and Matley (1933) also referred the vertebrae described by Lydekker (1879) as *Titanosaurus blanfordi* to cf. *Laplatasaurus madagascariensis* Deperet.

In his exhaustive revision of South American titanosaurids, Powell (1986) did not invalidate the genus *Titanosaurus* nor its type species (*Titanosaurus indicus*). Instead, he advocated a change in nomenclature in order to define *Titanosaurus* upon observations made principally on caudal morphology. First, Powell (1986, 1992) observed that *Titanosaurus australis* and *Titanosaurus robustus*, with their low caudal vertebrae with dorsoventrally convex lateral faces, had more in common with *Saltasaurus loricatus* Bonaparte and Powell, 1980 (a species from northwestern Argentina), than with *Titanosaurus indicus*. He then created a new subfamily, the Saltasaurinae, to accomodate these three species. In turn, Powell (1986) grouped *Laplatasaurus araukanicus* (Huene, 1929), *Aeolosaurus rionegrinus* Powell, 1987 and *Titanosaurus indicus* in the subfamily Titanosaurinae, united by their high caudal vertebrae with dorsoventrally concave lateral surfaces. Second, given the fact that *Titanosaurus australis* and *Titanosaurus robustus* pertain to a different subfamily than *Titanosaurus indicus*, Powell named the genus *Neuquensaurus* to be applied to the first two species. He replaced *Laplatasaurus* with *Titanosaurus*; *Titanosaurus araukanicus* was thus the name proposed for *Laplatasaurus araukanicus*. The names *Titanosaurus* and Titanosaurinae, thus, were reserved for sauropods with the same caudal morphology as the type species: *Titanosaurus indicus*.

Jain and Bandyopadhyay (1997) described a new species (*Titanosaurus colberti* Jain and Bandyopadhyay)

based on a single, partially disarticulated specimen from Dongargaon (India). It is undoubtedly the best-preserved specimen from the Cretaceous of India assigned to *Titanosaurus*. These authors recognized the presence of three species of *Titanosaurus* in India: *Titanosaurus indicus*, *Titanosaurus blanfordi* and *Titanosaurus colberti*. They stated that differences between these species are found in the shape of the middle caudal centra, the diameter of the articular faces of the centra, and in the placement of the facets for the haemapophyses. Jain and Bandyopadhyay (1997) accepted Huene's (1929) proposal that *Titanosaurus australis* and *Laplatasaurus araukanicus* were valid species, and assumed a phylogenetic relationship between certain Patagonian and Indian titanosaurs (the species of the genus *Titanosaurus*). They provided a new diagnosis of *Titanosaurus*: "Large advanced sauropods with strongly procoelous caudals throughout the series (1); cervical and dorsal vertebrae opisthocoelous with well-marked pleurocoels (2); transverse process of cervicals robust, directed laterally, very wide posteriorly in the shoulder region (3); transverse processes in dorsals narrow and directed outward and little upward (4); neural spine not bifid, directed posteriorly (5); sacrum with six co-ossified vertebrae and ribs (6); first and sixth sacral centra convex anteriorly and posteriorly respectively (7); midcaudal and part of distal caudals with prominent variable chevron facets (8); robust prezygapophyses extending to the anterior margin of the caudals (9); first sacral rib extended outward below the iliac blade (10); preacetabular process of the ilium projecting outward becoming almost horizontal (11); bladelike ischium transversely expanded in the middle (12); shaft of slender radius perpendicular to the axis of the expanded distal ends (13); ulna robust and triangular in cross section (14); humero-femoral ratio 0.74 (15); tibio-femoral ratio 0.65 (16); femur without any lateral prominence (17); moderate development of nuchal crest of braincase (18); transverse ridge on parietal (19); high buttress ridge below the paraoccipital process (20)." (p. 134).

However, many of these characters (1-8,10-12,14) were also proposed as diagnostic of the species *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997: 117), or are widely distributed within the Sauropoda (1-11). Others have an unknown distribution within Titanosauridae (13-20). At the moment, there is no strong evidence to support the referral of the three species from India to the same genus. Furthermore, the presence of more than one titanosaurid species in India has not yet been fully demonstrated, at least by published osteological evidence (see Sahni *et al.*, 1994 for an evaluation of the ichnological evidence). This conclusion agrees with that of Chatterjee and Rudra (1996).

THE ALTERNATIVES TO TITANOSAURIDAE

Because the vertebrae upon which *Titanosaurus indicus* was erected in 1877 do not show clear differences with other non-saltasaurine titanosaurids, both *Titanosaurus indicus* and *Titanosaurus* should be considered *nomina dubia.* Moreover, although the name Titanosauridae has a long usage, it could be abandoned, because it was founded upon a poorly-known type genus (International Code of Zoological Nomenclature 1999 [ICZN], Article 39, Recommendation 64A: 65).

The authors that have discontinued the use of the name Titanosauridae have employed a series of alternative, though not always equivalent, designations.

The first author to dismiss the name Titanosauridae was Sereno (1998). He and others (Wilson and Carrano, 1999; Wilson *et al.*, 1999) used the term Saltasauridae instead of Titanosauridae. Saltasauridae was defined as "*Opisthocoelicaudia, Saltasaurus,* their most recent common ancestor and all of its descendants".

Sereno's Saltasauridae was conceived to encompass "nearly all titanosaurs with the unusual biconvex caudal vertebra". He acknowledged that this clade is not based on diversity, morphology, or tradition, the three criteria for the emplacement of a "node-stem triplet" (NST).

Bonaparte (1999) used the terms Titanosauridae and Andesauridae, both grouped within the Titanosauria. He did not define these groups phylogenetically but rather by their taxonomic content, including *Argentinosaurus* Bonaparte and Coria and *Andesaurus* Calvo and Bonaparte, 1991 within the Andesauridae, and other Late Cretaceous titanosaurs in the Titanosauridae.

Sanz *et al.* (1999) avoided the use of Titanosauridae, employing terms such as Titanosauroidea, Titanosauria and Eutitanosauria. Sanz *et al.*'s (1999) Titanosauria (defined as the most recent common ancestor of *Epachthosaurus* Powell, 1990, *Saltasaurus* Bonaparte and Powell, 1980, *Argyrosaurus* Lydekker, 1893, *Lirainosaurus* Sanz, Powell, Le Loeuff, Martínez and Pereda-Suberbiola, 1999, plus the Peirópolis titanosaur and all of its descendants) is basically equivalent to Titanosauridae of Salgado *et. al* (1997) (defined as the clade including the most recent common ancestor of *Epachthosaurus sciuttoi, Malawisaurus dixeyi, Argentinosaurus huinculensis,* Titanosaurinae indet. (DGM "Serie B), *Opisthocoelicaudia skarzynskii, Aeolosaurus, Alamosaurus sanjuanensis* and Saltasaurinae and all of its descendants). In turn, based on its taxonomic content, Sanz *et al.*'s (1999) Titanosauroidea is equivalent to Upchurch's (1995) Titanosauroidea, although neither of these authors defined the taxon phylogenetically [Upchurch (1995), contrary to Sanz *et al.* (1999) employs both Titanosauroidea and Titanosauridae]. Finally, Eutitanosauria is defined as "the most recent common ancestor of *Saltasaurus*, *Argyrosaurus*, *Lirainosaurus*, plus the Peirópolis titanosaur and all its descendants." (Sanz *et al.*, 1999: 252). This clade does not have a clear counterpart in other phylogenetic schemes. Based on its taxonomic content and diagnosis, it would be equivalent to "unnamed taxon II" of Salgado *et al.* (1997: 22).

Titanosauridae was also not used by Curry Rogers and Forster (2001). The new Malagasy genus *Rapetosaurus* Curry Rogers and Forster is designated a saltasaurine.

However, Curry Rogers and Forster's Saltasaurinae is not equivalent to Powell's Saltasaurinae; paradoxically, Curry Rogers and Forster's Saltasaurinae is more generically inclusive than Sereno's Saltasauridae.

Smith *et al.*'s (2001) usage of Titanosauridae is basically the same as that of Salgado *et al.* (1997).

DISCUSSION

If the preexisting code based upon the Linnaean system of nomenclature is to be followed, any invalid name should be replaced by another of the same hierarchical category. In other words, the invalid name of a group (namely, a family name) should be replaced by a new name, which must be applicable to the same group. The taxonomic change proposed by Sereno (1998) is twofold: first, an invalid name (Titanosauridae) is abandoned, and second, a new group, less inclusive than Titanosauridae, is created, to which a new name, Saltasauridae, is applied. According to Sereno's (1998) phylogenetic definition of the group ("*Opisthocoelicaudia*, *Saltasaurus*, their most recent ancestor and all its descendants"), Saltasauridae is a group less inclusive than Titanosauridae. In short, Saltasauridae and Titanosauridae are not equivalent groups. Most recent titanosaur phylogenies consider *Opisthocoelicaudia* as the sister group of *Alamosaurus* Gilmore plus Saltasaurinae *sensu* Powell (1992) (Salgado, 2000), or even as the sister group of Saltasaurinae *sensu* Powell (1992) (Curry Rogers and Forster, 2001). If accepted, the changes proposed by Sereno would exclude a number of taxa traditionally grouped in the Titanosauridae from the Saltasauridae, including *Aegyptosaurus* Stromer, 1932, *Aeolosaurus* Powell, 1987, *Antarctosaurus*, *Argyrosaurus*, *Epachthosaurus*, *Magyarosaurus* Huene, 1932, *Malawisaurus* Jacobs, Winkler, Downs and Gomani, 1993, *Paralititan* Smith, Lamanna, Lacovara, Dodson, Smith, Poole, Giegengack and Attia, 2001, *Titanosaurus colberti* Jain and Bandyopadhyay, and the Peiropolis titanosaur(s).

Sereno (1998) justified the first change (the abandonment of the name Titanosauridae) with the invalidity of the generic name *Titanosaurus*. The second (the erection of a new group, the Saltasauridae) was claimed to be based upon the necessity to stabilize the higher taxonomy of derived titanosaurs (traditionally designated titanosaurids) and the inconvenience of situating a NST at the base of Titanosauria, which would require using a poorly-known genus, such as *Andesaurus*, as a reference taxon.

Sereno's (1998) first argument, that the name Titanosauridae is unavailable, may not be tenable. According to the newly proposed Phylogenetic Code of Biological Nomenclature, or PhyloCode, "supraspecific names do not have types in the sense that this term is used in the preexisting codes." (Cantino and de Queiroz, 2000). Conversely, the PhyloCode also states that "a clade whose name is converted from a genus name under a preexisting code, or is derived from the stem of a genus name, should include the type of the genus name. Therefore, when a clade name is converted from a preexisting genus name or is a new or converted name derived from the stem of a genus name, the definition of the clade must use the type species of that genus as an internal specifier" (Cantino and de Queiroz, 2000: Article 11.8). If this recommendation is followed, *Titanosaurus indicus* should be used as an internal specifier of those clades whose names are derived from *Titanosaurus* including Titanosauriformes, Titanosauria, Titanosauroidea, Titanosauridae, and Eutitanosauria. However, because *Titanosaurus indicus* is a *nomen dubium*, it cannot be used as an internal specifier for any clade name. That notwithstanding, the PhyloCode (Recommendation 11.8B) also states that "If it is questionable whether the type specimen of a preexisting name belongs to the clade to be named (e.g., because of the fragmentary nature of the specimen), then that preexisting name (or its type) should not be used as a specifier ... and the corresponding name should not be converted to a clade name." This is not the case of the type species of *Titanosaurus*; because of its procoelous condition, it is clearly a titanosaurian.

Finally, in Recommendation 10A, the PhyloCode states that "clade names should be selected in such a way as to minimize disruption of current usage". Therefore, according to this recommendation of the PhyloCode, the name Titanosauridae should not necessarily be abandoned.

With respect to the second argument, I believe that, if the use of the name Titanosauridae is maintained, as stated above, it is possible to place a NST at its base, and thus stabilize the higher taxonomy of titanosaurs. To do this, however, a node-based definition of Titanosauridae is needed. Salgado's (2000) stem-based definition potentially includes titanosaurs with amphiplatyan to platycoelous middle caudal vertebrae, a situation that should be avoided. In contrast, Salgado *et al.*'s (1997) node-based definition seems more adequate for this purpose. Therein, *Epachthosaurus* is chosen as reference taxon for the definition of Titanosauridae. However, to place a NST at the base of Titanosauridae (Titanosauridae= Epachthosaurinae + Eutitanosauria), a new clade, Epachthosaurinae, and Eutitanosauria should be defined as stem groups. The NST is not diversity-based (see Sereno, 1998: 54), given the single genus *Epachthosaurus* on one side of the dichotomy.

In summary, there is no need to abandon the traditional titanosaurian group Titanosauridae. It should be defined to include only titanosaurians with procoelous middle caudal vertebrae (the opisthocoelous condition in *Opisthocoelicaudia* apparently evolved from the procoelous condition). In this way, the name Titanosauridae and its most commonly associated character, caudal procoely, would remain in association.

CONCLUSION: A UNIFYING PROPOSAL

We propose to adopt the following taxonomic scheme for Titanosauria (Figure 1):

Titanosauria Bonaparte and Coria, 1993

Definition: All somphospondylians closer to *Saltasaurus* than to *Euhelopus* Romer.

Titanosauroidea Upchurch, 1995

Definition: All titanosaurs closer to *Saltasaurus* than to *Andesaurus*.

Andesauroidea nov.

Definition: All titanosaurs closer to *Andesaurus* than to *Saltasaurus*.

Titanosauridae Salgado, Coria and Calvo, 1997

Definition: *Epachthosaurus*, *Saltasaurus*, their most recent common ancestor and all of its descendants.

Epachthosaurinae nov.

Definition: All titanosaurs closer to *Epachthosaurus* than to *Saltasaurus*.

Eutitanosauria Sanz, Powell, Le Loeuff, Martínez and Pereda-Suberbiola, 1999

Definition: All titanosaurs closer to *Saltasaurus* than to *Epachthosaurus*.

Saltasaurinae Powell, 1992 (*sensu* Sereno, 1998)

Definition: All eutitanosaurs closer to *Saltasaurus* than to *Opisthocoelicaudia*.

Opisthocoelicaudiinae Sereno, 1998

Definition: All eutitanosaurs closer to *Opisthocoelicaudia* than to *Saltasaurus*.

FINAL COMMENT

The group Titanosaurinae (including the genera *Titanosaurus* and *Aeolosaurus*), as defined by Powell (1986), was recognized as a paraphyletic assemblage by Salgado and Calvo (1993) and Salgado *et al.* (1997), because its supposedly diagnostic characters (high caudal vertebrae with dorsoventrally concave lateral faces, narrow ventral faces and laterally compressed neural spines) are present in a wide range of sauropods. *Titanosaurus* is also paraphyletic, since the diagnoses of *Titanosaurus* and Titanosaurinae are basically the same. Given the fact that *Titanosaurus indicus* and *Laplatasaurus araukanicus* do not form a monophyletic group (because there are no valid diagnostic characters of *Titanosaurus*), the replacement of this last denomination with *Titanosaurus araukanicus* was not justified.

Therefore, I propose to exchange the name *Titanosaurus araukanicus* Huene for its senior synonym, *Laplatasaurus araukanicus* Huene. The type material of this species is the same as proposed by Powell (1986: 82-83).

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