

DISTAL TAIL SEGMENT OF A TITANOSAUR (DINOSAURIA: SAUROPODA) FROM THE UPPER CRETACEOUS OF MENDOZA, ARGENTINA

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Titanosaurs constitute approximately half of known sauropod genera and are the only sauropod lineage to survive into the Late Cretaceous. Despite their abundance and global distribution, the origins and interrelationships of titanosaurs have remained obscure since their discovery more than a century ago. Titanosaurs traditionally have been grouped with diplodocid sauropods primarily on the basis of narrow tooth crowns and an erroneous, *Diplodocus*-like reconstruction of the skull of the South American titanosaur *Antarctosaurus* (Huene, 1929; Romer, 1956; Steel, 1970; Gauthier, 1986; Upchurch, 1995). Aspects of the titanosaur postcranial skeleton, accordingly, have been reconstructed on a diplodocid body plan, such as a long tail presumed to end in a “whiplash” composed of numerous elongate, biconvex caudal vertebrae (Gauthier, 1986). Little evidence of distal caudal vertebrae, however, has been found to support or refute this inference.

New titanosaur remains were discovered in 1996 by a joint University of San Juan-Museo Juan Cornelio Moyano de Mendoza-University of Chicago expedition to the Upper Cretaceous Río Colorado Formation of Mendoza Province, Argentina. These beds have previously yielded remains of the titanosaurs *Argyrosaurus*, *Antarctosaurus*, and *Titanosaurus* (Huene, 1929). The specimen discussed here represents the first described articulated distal tail of a Gondwanan titanosaur and confirms the presence of biconvex distal caudal vertebrae in titanosaurs. The short series of abbreviate biconvex caudal vertebrae at the end of the titanosaurian tail is quite distinct from the elongate “whiplash” tail of diplodocids.

Institutional Abbreviations—CM, Carnegie Museum of Natural History, Pittsburgh; MCNA, Museo de Ciencias Naturales y Antropológico Juan Cornelio Moyano, Mendoza, Argentina.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878

TITANOSAURIA Bonaparte and Coria, 1993

SALTASAURIDAE Powell, 1992

Referred Specimen—MCNA-PV 3136, an isolated distal caudal series consisting of 10 articulated vertebrae.

Locality—Cañadon Amarillo, Department of Malargüe, Mendoza Province, Argentina.

Horizon and Age—Río Colorado Formation, Late Cretaceous: ?Cenomanian.

Description—Although their exact position in the caudal series cannot be determined, the absence of neural arches on the last three vertebrae and the absence of chevron facets on all centra suggest that these are distalmost caudal vertebrae. In diplodocids such as *Apatosaurus*, the last caudal vertebra with a neural arch is followed by up to 40 “archless” vertebrae (Gilmore, 1936:pl. 28). The elongation of these archless vertebrae tends to increase distally up to the last few, which become less elongate. In *Camarasaurus* and the titanosaur *Opisthocoelicaudia*, however, there are usually fewer than seven archless caudal vertebrae whose centra become less elongate distally (Gilmore, 1925:pl. 14; McIntosh et al., 1996:fig. 56; Borsuk-Bialynicka, 1977:pl. 6, figs. 3, 6). The tail segment from Mendoza includes only three archless centra that become less elongate distally, as in *Camarasaurus* and *Opisthocoelicaudia*. Thus, this sequence of ten caudal vertebrae probably represents the distal segment of a tail that had a short, archless tip.

The most anterior preserved caudal vertebra will be referred to as “caudal 1” and successive centra are numbered in sequence. Centrum length decreases along this series of 10 distal caudal vertebrae, with the last preserved centrum approximately 80 percent the length of the first (Fig. 1). Centrum height and width decrease markedly across the first five vertebrae and more gradually across the last five vertebrae (Table 1). The first two caudal vertebrae have procoelous centra, whereas the remaining eight are biconvex. Neural arch rudiments are present on all but the last three caudal vertebrae.

The first caudal is strongly procoelous, with a slightly concave anterior face and a strongly convex posterior face. The centrum is arched in lateral view, such that its posterior face is offset ventrally from the anterior face by approximately 2 cm. At midlength the centrum has a subtriangular cross-section, with a flattened dorsal margin and a ventral aspect that narrows to a rounded keel. A small circular pit is present on the dorsal margins of both the anterior and posterior central faces, so they appear notched in anterior or posterior views (Fig. 2). These pits are not known to occur in caudal centra of other sauropods and may be diagnostic for this species. The neural arch of caudal 1 is incomplete, but its pedicles are preserved and situated on the anterior portion of the centrum. They are positioned asymmetrically: the left pedicle is flush with the anterior margin of the centrum whereas the right is displaced somewhat posteriorly.

Caudal 2 is complete and similar in many respects to caudal 1. The posterior face of the centrum is strongly convex. Its anterior face, however, is rounded peripherally but gently cupped centrally, and thus appears transitional between the concave and convex state (Fig. 2). The articular faces are slightly offset in lateral view, though to a lesser extent than in caudal 1. Caudal 2 has a subcircular cross-section at midlength and well defined pits are present at the dorsal margins of the anterior and posterior extremes of the centrum. The neural arch is complete and composed of two subequal halves that approach each other but do not meet above the neural canal. The more robust left pedicle of the neural arch is nearly twice as broad as the right and much taller, projecting slightly over the midline of the centrum. A horizontally oriented ridge is present near the base of the lateral aspect of the neural arch (Fig. 2). Like caudal 1, the left neural arch pedicle is placed at the anterior extreme of the centrum and is positioned slightly in advance of the right side.

Caudal 3 and all successive vertebrae are biconvex. The anteriorly positioned pedicles of the neural arch are complete and do not meet above the neural canal. The two halves of the neural arch have subequal transverse widths, but the left is still positioned slightly forward of the right. As in caudal 2, a well defined ridge is present on the lateral surface of the neural arch. The vertebral pit is well developed posteriorly but retained only as a shallow notch anteriorly.

Caudals 4 through 6 are very similar in structure. The centra are strongly biconvex with a rounded central apex. The pits described in the preceding caudal centra are absent, although the dorsal aspects of the both the anterior and posterior faces of the centra are slightly notched. The centra are broader transversely than tall dorsoventrally, and have flattened dorsal and ventral surfaces (Table 1). The neural arch is persistent and situated just anterior of mid centrum.

The neural arch is absent on caudals 7 through 10. The dorsal emar-



FIGURE 1. Piece of tail of the titanosaur from Mendoza Province (MCNA-PV 2136) in left lateral view. Scale bar equals 5 cm.

gination, which was present at the extremes of caudals 4 to 6, is absent in these distalmost vertebrae. The ends of the centra are progressively less convex, so that the posterior articular surface of caudal 10 is only gently rounded and without an apex.

Phylogenetic Affinities—Although the Mendoza specimen (MCNA-PV 2136) is not sufficiently complete to demonstrate that procoely extended throughout the entire caudal series, the presence of procoelous distal caudal centra provides strong evidence supporting its placement within Saltasauridae, a subgroup of Titanosauria (Fig. 3). Caudal procoely extending into the distal portion of the tail characterizes several titanosaurs, including *Saltasaurus*, *Alamosaurus*, *Ampelosaurus*, *Neuquensaurus*, *Magyarosaurus*, *Titanosaurus indicus*, *T. colberti*, and *T. araukanicus* (the latter three may not actually pertain to the same genus). Basal titanosaurs such as *Malawisaurus* and *Andesaurus* have amphiplatyan or platycoelous distal caudal centra (Jacobs et al., 1993:fig. 2; Calvo and Bonaparte, 1991:fig. 4a). Among dinosaurs, the sole occurrence of procoelous distal caudal vertebrae outside of Titanosauria appears to be in *Mamenchisaurus hochuanensis*, in which a single procoelous distal caudal vertebra follows a succession of 17 platycoelous or amphicoelous middle and posterior caudal vertebrae. Procoelous distal caudal vertebrae have yet to be described in other specimens of this genus (Young and Chao, 1972:figs. 8–10). The precise phylogenetic affinities of *Mamenchisaurus* are uncertain, although the high dentary tooth count of at least one species, *M. sinovanadorum* (19; Russell and Zheng, 1994:2088), is consistent with its placement as a basal sauropod (Wilson and Sereno, 1998). Caudal procoely extending to the distal caudal vertebrae thus represents an unambiguous synapomorphy of Saltasauridae, a subgroup of titanosaurs more derived than *Andesaurus* and

Malawisaurus. Aside from their singular occurrence in the Late Jurassic Chinese sauropod *M. hochuanensis*, procoelous distal caudal centra are restricted to Saltasauridae.

As elaborated below, the distalmost tip of the tail in the Mendoza specimen and other saltasaurids is composed of biconvex, rather than procoelous, vertebrae. Biconvex distal caudal vertebrae are only known to characterize saltasaurids among titanosaurs, but complete tails are not known for basal titanosaurs (Calvo and Bonaparte, 1991; Jacobs et al., 1993). The presence of biconvex caudal vertebrae in the Mendoza specimen is therefore consistent with its interpretation as a saltasaurid. New discoveries of distal portions of tails of basal titanosaurs will constrain the distribution of this feature.

DISCUSSION

Biconvex caudal centra are present only in sauropods among dinosaurs. Together with the tail club of *Shunosaurus* (Dong et al., 1989), a flexible tail tip composed of biconvex vertebrae represents an important tail specialization of sauropods that was modified within subgroups. The distribution and morphology of biconvex caudal centra provides insight into the evolution of tail morphology within Neosauropoda.

Distribution of Biconvex Caudal Vertebrae

Biconvex distal caudal vertebrae are restricted to Neosauropoda, a sauropod subclade including diplodocoids, *Camarasaurus*, brachiosaurs, *Euhelopus*, and titanosaurs (Fig. 3). Within this group, biconvex distal caudal vertebrae are present in all diplodocoids (*Apatosau-*

TABLE 1. Measurements (mm) of the caudal centra of the Mendoza saltasaurid (MCNA-PV 2136). **Abbreviation:** *, element incomplete or damaged.

Caudal #	1	2	3	4	5	6	7	8	9	10
Length	58.8	59.4	61.7	56.0	60.3	53.7	47.6*	54.4	51.0	46.6
Anterior height	31.5	29.0	26.1	22.0	20.7	17.5	—	16.9	16.6	15.3
Anterior width	29.3*	31.4	28.1	23.0	22.7	18.3*	—	18.1	17.2	15.7
Posterior height	32.0	28.8	24.9	22.1	18.2	16.6	16.6	15.9	15.2	12.7
Posterior width	31.3	30.1	25.6	21.5	19.2	17.4	17.8	16.7	16.3	15.3
Minimum height	23.6	20.8	16.9	16.1	12.7	10.9	10.6	9.1	9.3	8.9
Minimum width	20.5	20.6	20.0	17.1	15.1	13.8	13.0	13.8	12.3	12.0
Total height (incl. neural arch)	30.8*	45.5	29.6	26.4	16.9*	13.9	10.6	9.1	9.3	8.9

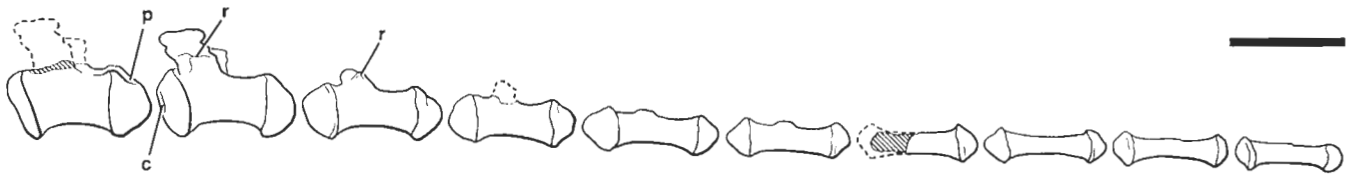


FIGURE 2. Mendoza tail in left lateral view. Cross-hatching indicates broken bone surface. **Abbreviations:** c, concavity; p, pit; r, ridge. Scale bar equals 5 cm.

rus, *Barosaurus*, *Diplodocus*, *Dicraeosaurus*, *Rayosaurus tessonei* [= "*Rebbachisaurus" tessonei*, Wilson and Sereno (1998:18)], the basal neosauropod *Cetiosauriscus*, and saltosaurid titanosaurs (*Neuquensaurus*, *Opisthocoelicaudia*, *T. araukanicus*, the Mendoza specimen). *Camarasaurus* is the only neosauropod that lacks biconvex distal caudal vertebrae (Gilmore, 1925), but distal portions of tails are not known in several other genera (e.g., *Haplocanthosaurus*, *Brachiosaurus*). Biconvex distal caudal vertebrae have an equivocal optimization among neosauropods (Fig. 3); they are present in basal neosauropod taxa (*Cetiosauriscus*, Diplodocoidea) and a distantly related neosauropod clade (Saltosauridae). Although the exact affinities of *Cetiosauriscus* and the condition in other neosauropods will affect the overall pattern, the distribution of biconvex distal caudal centra among neosauropods affords two equally parsimonious optimizations, each requiring two evolutionary steps. Delayed transformation (preferring parallelism over reversal) suggests that biconvex distal caudal centra were acquired independently in diplodocoids and titanosaurs. Accelerated transformation (preferring reversal over parallelism) implies that this feature arose as a neosauropod synapomorphy that was lost in *Camarasaurus*.

Comparisons of Biconvex Caudal Vertebrae Among Neosauropods

The ratio of total length to height of biconvex distal caudal vertebrae ranges between 2.5 and 9.5 within Neosauropoda (Table 2). Diplodocoids are characterized by elongate distal caudal vertebrae having length-to-height ratios between 4 and 9.5. Among diplodocoids, this ratio is highest in *Diplodocus* (7–9.5) and lowest in *Apatosaurus* (4.3–6). Length-to-width values of other diplodocoids are slightly greater

than 5. Other neosauropods have length-to-width metrics much lower than those of diplodocoids. The basal neosauropod *Cetiosauriscus* has relatively short biconvex caudal centra that are only three times longer than tall. The proportions of saltosaurid biconvex distal caudal vertebrae are similar to that of *Cetiosauriscus*, ranging from 2.5 to 4 in *Opisthocoelicaudia*, *Neuquensaurus*, *T. araukanicus*, and the Mendoza saltosaurid. The distribution of centrum shape among neosauropods suggests that the low length-to-width ratio of biconvex caudal vertebrae present in *Cetiosauriscus* and saltosaurids is primitive for neosauropods, whereas the high ratio is probably a derived feature characterizing Diplodocoidea (Fig. 3).

The number of consecutive biconvex distal caudal vertebrae also varies within neosauropods. The distal region of the tail of the diplodocids *Apatosaurus* and *Diplodocus* comprises more than 30 biconvex caudal vertebrae. One specimen of *Apatosaurus* (CM 3378), which preserves 82 articulated caudal vertebrae, has 45 biconvex centra (Gilmore, 1936:pl. 28). Other diplodocoids (*Barosaurus*, *Dicraeosaurus*, *Rayosaurus*) preserve only isolated biconvex centra. Non-diplodocoid neosauropods have comparably fewer biconvex vertebrae. *Cetiosauriscus* has a series of 10 biconvex caudal centra (Woodward, 1905), whereas the saltosaurids *Opisthocoelicaudia* and the Mendoza specimen have seven (Borsuk-Bialynicka, 1977). The distribution of this feature among neosauropods suggests that a relatively short series of biconvex caudal vertebrae (10 or fewer) at the tip of the tail is primitive, whereas a long series (more than 30) is an ambiguous diplodocid synapomorphy (Fig. 3).

"Whiplash" Tails

The tails of the diplodocids *Apatosaurus* and *Diplodocus* end in a terminal "whiplash," which has been interpreted as a defensive (e.g.,

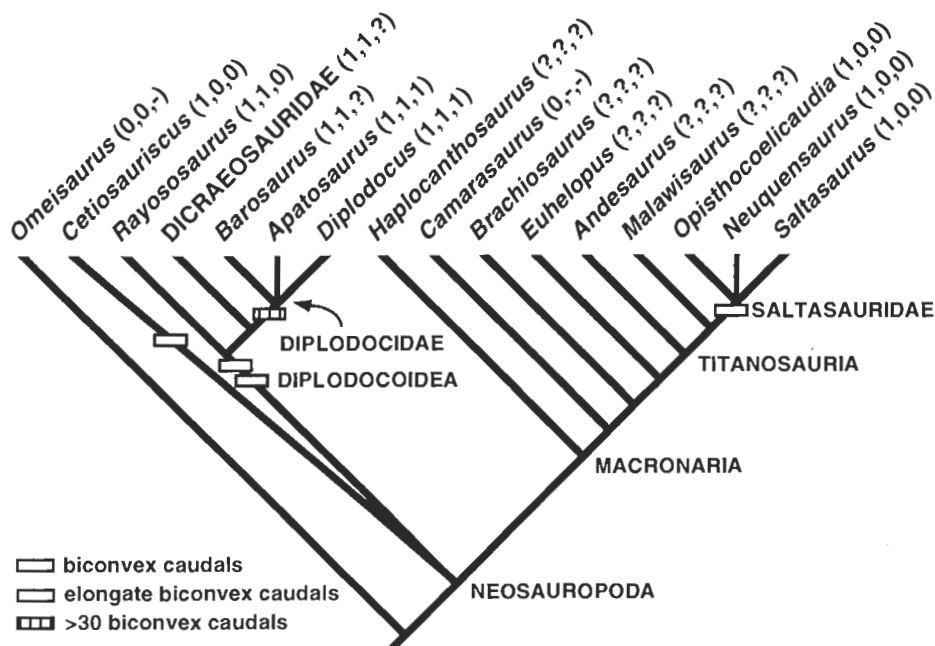


FIGURE 3. Cladogram of neosauropod relationships (modified from Wilson and Sereno, 1998) indicating the distribution of biconvex caudal vertebrae, elongate biconvex caudal vertebrae, and a series of 30 or more biconvex caudal vertebrae. Numbers in parentheses following terminal taxa specify scoring of each of these features, respectively: "0" = absent; "1" = present; "?" = unknown; "-" = not applicable.

TABLE 2. A comparison of length-to-height proportions of biconvex caudal centra of various neosauropod taxa.

Taxon	L : H Ratio	Source
Diplodocoids		
<i>Diplodocus</i>	7–9.5	Holland (1906:pl. 29)
<i>Apatosaurus</i>	4.3–6	Gilmore (1936:pls. 27–28)
<i>Dicraeosaurus</i>	5.5	Janensch (1929:figs. 18, 19)
<i>Rayosaurus</i>	5.2	Calvo and Salgado (1995:fig. 11c)
<i>Cetiosaurus</i>	3	Woodward (1905:243)
Saltasaurids		
<i>Opisthocoelicaudia</i>	2.3–3	Borsuk-Bialynicka (1977:tab. 3)
<i>Neuquensaurus</i>	3.5–4.1	Huene (1929:pl. 5, figs. 11–14)
<i>Titanosaurus</i>	2.6–4	Huene (1929:pl. 22, figs. 12–13, 15–16)
Mendoza saltasaurid	2.5–3.7	—

Holland, 1915) or noisemaking (Myhrvold and Currie, 1997) adaptation. A "whiplash" tail is defined here as a sequence of 30 or more elongate, biconvex distal caudal vertebrae. This complex feature can be resolved into three independently varying, binary characters: (1) centrum shape—short or elongate; (2) articular face shape—platycœlous or biconvex; and (3) consecutive biconvex vertebrae—10 or fewer, or more than 30. The distribution of these three characters on a cladogram (Fig. 3) suggests that biconvex distal caudal vertebrae are more generally widespread than either elongate caudal centra or a series of 30 biconvex vertebrae. Presence of biconvex distal caudal vertebrae alone, then, cannot justify the inference of a "whiplash" tail nor provide unambiguous support for diplodocid affinities. Thus defined, a "whiplash" tail currently characterizes only the diplodocids *Apatosaurus* (Gilmore, 1936:pls. 27–28) and *Diplodocus* (Holland, 1906:pl. 24). Although the diplodocoids *Barosaurus lentus* (Lull, 1919:29), *Dicraeosaurus* (Janensch, 1929:figs. 18–20; McIntosh, 1990:392), and *Rayosaurus* (Calvo and Salgado, 1995:fig. 11c) are known to possess elongate distal caudal centra, the length of the series of these terminal caudal vertebrae is not known, and they cannot yet be ascribed "whiplash" tails.

CONCLUSIONS

The Mendoza saltasaurid documents the first articulated tail tip described for a Gondwanan titanosaur. As in other saltasaurids, the caudal vertebrae are procoelous and become biconvex in the distal portion of the tail. Biconvex distal caudal vertebrae are present in the saltasaurids *Neuquensaurus*, *Opisthocoelicaudia*, and *T. araukanicus*, as well as in diplodocoids and *Cetiosaurus*. The distribution of this feature on a well corroborated cladogram of sauropod relationships suggests two equally parsimonious interpretations for the evolution of biconvex distal caudal vertebrae in neosauropods: (1) a neosauropod synapomorphy with a reversal in *Camarasaurus*; or (2) parallel acquisition in diplodocoids and saltasaurids. Both the number of biconvex vertebrae at the end of the tail and the shape of these centra varies within Neosauropoda. The "whiplash" tail of diplodocids, a series of 30 or more elongate biconvex centra, involves changes in the shape of the articular face, the shape of the centrum, and the number of vertebrae in the series. The distribution of biconvex distal caudal vertebrae is broader than the distribution of the specialized "whiplash" tail. A short and highly flexible tail tip arose early in sauropod evolution—by the Middle Jurassic with the appearance of the first neosauropods. By the Late Jurassic, this early tail specialization was elaborated and greatly lengthened into the characteristic "whiplash" tail of diplodocids.

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