

Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia

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Abstract: We report the discovery of a new titanosaurian taxon, *Puertasaurus reuilli* gen. et sp. nov., from Maastrichtian beds of SW Patagonia. Four vertebrae were recovered (i.e., cervical 9, dorsal 2, and two mid-caudals). The new form is diagnosed on the basis of an inflated neural spine on cervical vertebra, and extremely short second dorsal vertebra, among other features. *Puertasaurus* is one of the largest known sauropod dinosaurs, with dorsal vertebra 2 measuring 168 cm in transverse width. This is the first time that a cervical vertebra is reported for a giant titanosaur, giving a new insight on neck anatomy of neosauropod dinosaurs.

Key words: Sauropoda, Titanosauria, Cretaceous, Patagonia.

The Titanosauria is a diverse and geographically widespread clade of Cretaceous neosauropods, abundant in Upper Cretaceous rocks of South America (Salgado *et al.*, 1997; Powell, 2003; Wilson & Upchurch, 2003). Many titanosaurs were large, but just a few (e.g., the Cenomanian *Argentinosaurus huinculensis* and the Turonian «*Antarctosaurus*» *giganteus*; Huene, 1929; Bonaparte & Coria, 1993) are known to have attained truly gigantic sizes (up to 35 meters long and around 80 tons). Because known specimens of these giant sauropods are incomplete, many aspects of their anatomy and systematics remain obscure. Here we report the discovery of a new Patagonian sauropod, *Puertasaurus reuilli* gen et sp. nov., one of the largest of these giant tetrapods. This is the first time in which a cervical vertebra is reported for a giant titanosaur, making it possible to compare it with smaller members of the clade.

We follow the taxonomy proposed by Salgado (2003).

SYSTEMATIC PALEONTOLOGY

Sauropoda Huene, 1932

Titanosauriformes Salgado, Coria & Calvo, 1997

Titanosauria Bonaparte & Coria, 1993

Titanosauridae Lydekker, 1893

Puertasaurus reuilli gen et sp. nov.

Etymology. In honor to Pablo Puerta and Santiago Reuil, remarkable fossil-hunters who discovered and prepared the specimen.

Holotype. MPM (Museo Padre Molina, Río Gallegos, Santa Cruz) collection number 10002, consisting of four disarticulated vertebrae, including most of a cervical vertebra, a complete dorsal 2, and the centra of two caudal vertebrae.

Locality and Horizon. Cerro Los Hornos, La Leona, Santa Cruz Province, Argentina. Pari Aike Formation, early Maastrichtian (Kraemer & Riccardi, 1997; Novas *et al.*, 2004a). Vertebrae were found *in situ* in a fine, gray sandstone lens, containing highly carbonized plant remains classified as cycads and conifers on the basis of cuticular morphology (L. Villar de Seoane, pers comm.). Dinosaurs recorded in the Pari Aike Formation are the basal iguanodontian

Talenkauen santacruzensis (Novas *et al.*, 2004a) and a large, yet undescribed, derived tetanuran theropod (Novas *et al.*, 2004b).

Diagnosis. *Puertasaurus reuilli* is diagnosed on the basis of the following combination of characters: gigantic size; cervical neural spine considerably inflated, being transversally wider than the vertebral centrum and bearing strong dorso-lateral ridges; caudal cervicals with spinoprezygapophyseal laminae transversely thick and dorsoventrally deep; cranial dorsal vertebrae extremely short, more so than in other sauropods (e.g., centrum width/centrum length:1; in all other titanosauriforms, this ratio is less than 1).

Description. For the first time a cervical vertebra of a giant titanosaur is documented (Fig. 1). The neck vertebra (presumably cervical 9) is 118 cm long (between pre- and postzygapophyses) and although mid-cervicals of the Early Creta-

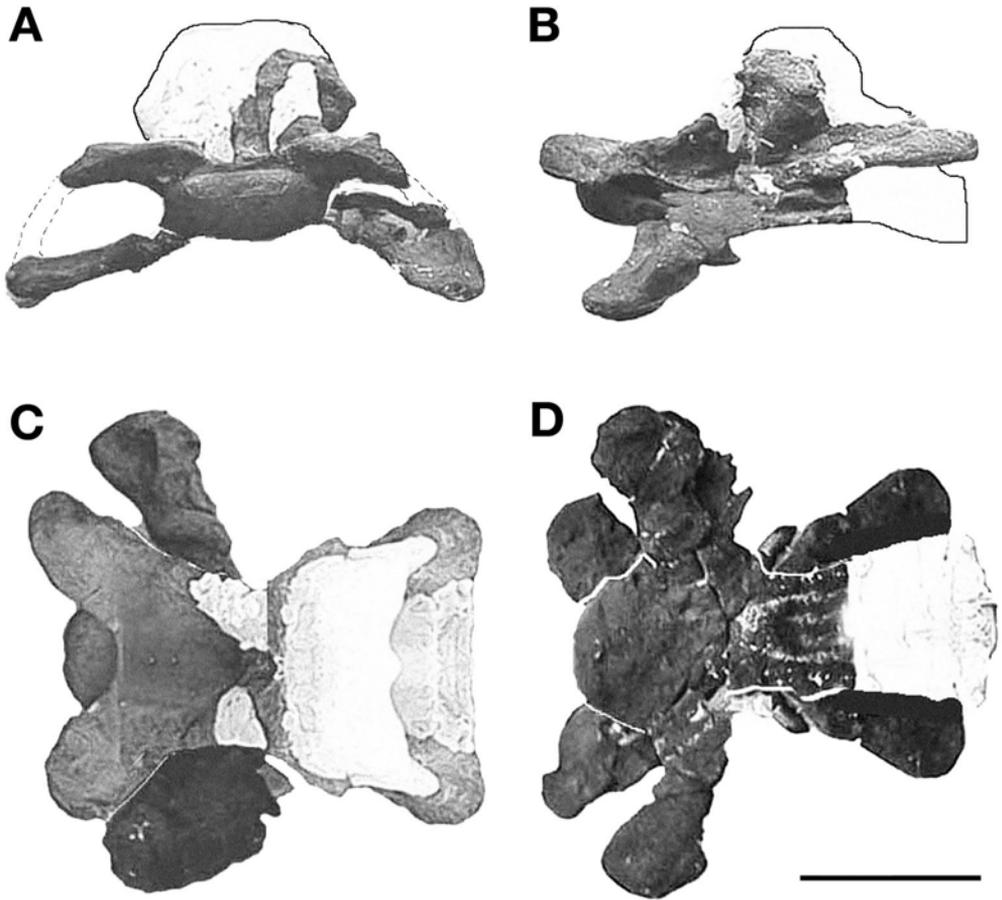


Fig. 1. A-D, *Puertasaurus reuili* gen. et sp. nov. (MPM-10002, Río Gallegos), cervical 9 in cranial (A), lateral (B), dorsal (C), and ventral (D) views. Scale bar 50 cm.

ceous brachiosaurid *Sauroposeidon* (Wedel *et al.*, 2000) are longer than the cervical of the new titanosaur, the latter one is exceptionally wide with a transverse width of 140 cm (including fused ribs). The neural spine bears deep and wide pre- and postspinal fossae for cradling well-developed interspinous ligaments, as well as a considerably inflated distal end, suggesting a powerful neck ligament and cervical muscles. Such characters are insinuated in smaller titanosaurs, but they reach an extreme development in the new form. The dorsal enlargement of the neural spine is derived with respect to the transversely narrower neural spine of all other titanosauriforms (*e.g.*, *Brachiosaurus*, *Euhelopus*, *Neuquensaurus*; Fig. 3), and sharply differs from the bifid spines of diplodocoids. This peculiar neural spine is associated with a set of titanosaurian features (*e.g.*, Upchurch, 1999), such as laterally projecting diapophyses and parapophyses, and a low neural arch with a high neural spine. In the

new specimen, the zygapophyseal articulations are positioned low on the neural arch, and the centrum is even more depressed than in other titanosaurids (*e.g.*, *Saltasaurus*). Consequently, the system of bony struts on the sides of the vertebra (and the pneumatic fossae they define) are dorsoventrally flattened. The cervical vertebra is poorly pneumatized and lacks pleurocoels.

The available dorsal (dorsal 2) vertebra is craniocaudally short, in sharp contrast with the cervical described above (Fig. 2). The centrum is strongly opisthocelous and proportionally shorter than in other Titanosauridae. Hyposphenyantrum articulations are absent. Although the lack of these structures is diagnostic of Titanosauridae (Salgado *et al.*, 1997; Bonaparte, 1999), their absence in *Puertasaurus* may be due to the cranial position of this vertebra.

Dorsal 2 of *Puertasaurus* is 106 cm in height but 168 cm from the ends of the wing-like transverse processes, thus exceeding by nearly 45 cm

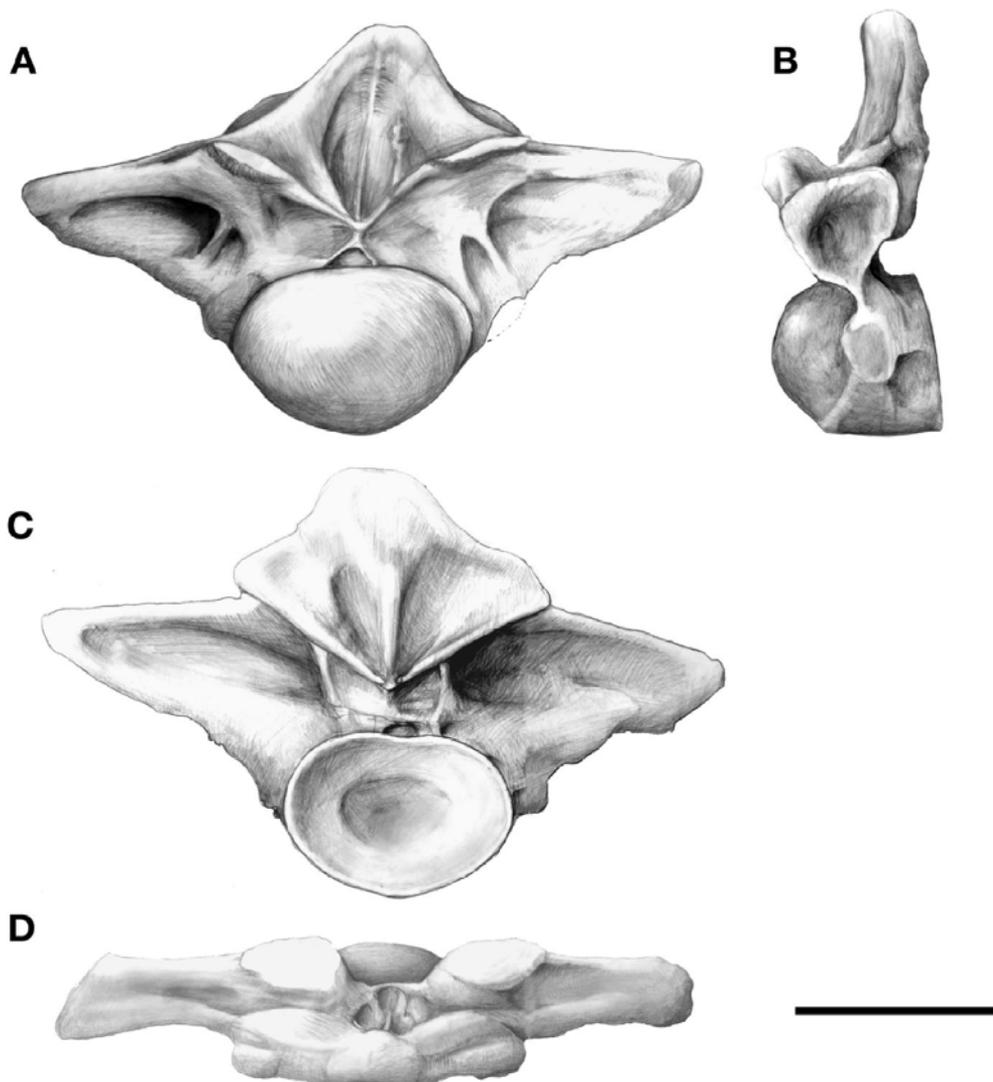


Fig. 2. A-D, *Puertasaurus reuili* gen. et sp. nov. (MPM-10002, Río Gallegos), dorsal 2 in cranial (A), left lateral (B), caudal (C), and dorsal (D) views. Scale bar 50 cm.

dorsal 4? of *Argentinosaurus huinculensis*, considered to be one of the biggest dinosaurs (Bonaparte & Coria, 1993; Paul, 1994). This dorsal is considerably wider (in absolute terms) than in other known sauropod. Transverse processes are dorsoventrally deep at their bases, resulting in a wing-like appearance in cranial view (Fig. 2), as in the basal titanosauriform *Euhelopus* (Wiman, 1929). In *Puertasaurus* the transverse processes of dorsal 2 are perpendicular to the axial plane (Fig. 2D), as is the case in *Argentinosaurus* and *Euhelopus*, instead of being laterocranially oriented as in more derived titanosaurids (e.g., *Saltasaurus*, Titanosauridae

indet. «Series B»; Powell, 2003). The neural spine is dorsoventrally low but transversely expanded, as usually found among Titanosauridae (Powell, 2003). The neural spine is vertically oriented, being perpendicular in respect to the craniocaudal axis of centrum, thus resembling *Argentinosaurus*, for example. The system of laminae in the neural arch is reduced but robust, and it shows pre- and postspinal laminae diagnostic of titanosaurids (Upchurch, 1999). The pre- and postspinal fossae of *Puertasaurus* are wider and deeper than in more derived titanosaurids (e.g., *Saltasaurus*, *Opisthocoelicaudia*; Powell, 2003; Borsuk-Bialynicka, 1977), resembling in this fea-

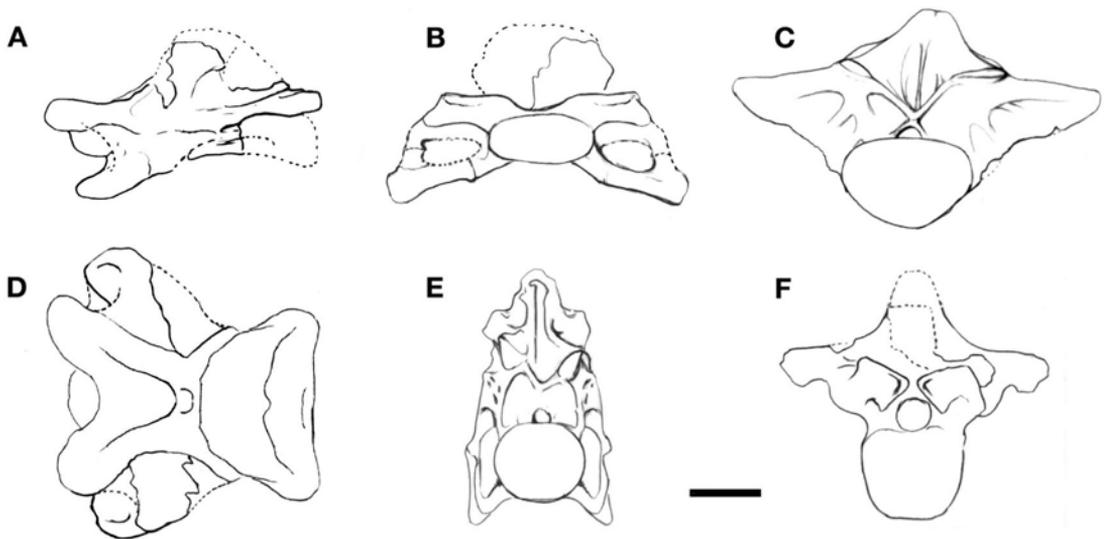


Fig. 3. Comparison among cervical and dorsal vertebrae of some selected sauropods. A, B, D, *Puertasaurus reuili* gen. et sp. nov., cervical 9 in lateral (A), cranial (B), and dorsal (D) views. C, *Puertasaurus reuili* gen. et sp. nov., dorsal 2 in cranial view; E, *Brachiosaurus brancai*, cervical vertebra in cranial view (Janensch, 1950); F, *Argentinosaurus huinculensis*, dorsal ? in cranial view (modified from Bonaparte & Coria, 1993). Scale 50 cm.

ture basal titanosauriforms such as *Euhelopus* and *Brachiosaurus* (Bonaparte, 1999).

Two mid-caudal centra are preserved. They are procoelous, a common feature among Titanosauridae (Salgado *et al.*, 1997).

Discussion. *Puertasaurus reuili* exhibits the following synapomorphic features of Titanosauriforms: 1) deep and wide pre- and postspinal fossae in cervical and dorsal vertebrae; 2) very elongated cervical centra (Wilson, 2002); 3) reduced cervical neural arch lamination; and 4) presence of prespinal laminae in dorsal vertebrae (Salgado *et al.*, 1997). *Puertasaurus* is referred to Titanosauria because it shows the following derived features: 1) cervicals with laterally projecting diapophyses and parapophyses (Upchurch, 1999); 2) low neural arch with a relatively high neural spine (Salgado *et al.* 1997; Bonaparte, 1999); and 3) dorsal vertebrae with robust pre- and postspinal laminae (Upchurch, 1999). *Puertasaurus* exhibits two titanosaurid features: 1) neural spines of dorsal vertebrae dorsoventrally low and transversally expanded (Salgado *et al.* 1997; Bonaparte, 1999); and 2) procoelous mid-caudal vertebrae. Moreover, the new taxon bears a well developed prespinal lamina in dorsal 2, a feature interpreted as diagnostic of Eutitanosauria (Salgado, 2003). Nevertheless, *Puertasaurus* lacks some of the synapomorphies of Titanosauridae: for example, cranial dorsals of the new taxon retained vertical neural spines and transverse processes that are perpendicularly

oriented, and neural arches that lack the complex system of laminae and pneumatic depressions characteristic of derived titanosaurids. In conclusion, *Puertasaurus* is interpreted as a possible basal titanosaurid.

Puertasaurus and *Argentinosaurus* are the largest known sauropods. However, *Puertasaurus* differs from the latter one in having dorsal vertebrae with large, wing-like transverse processes, lower neural spine, thick postspinal laminae, and cranial dorsals craniocaudally shorter. We consider such distinctions enough to distinguish both taxa, a conclusion that is in agreement with the stratigraphical provenance of these dinosaurs: *Puertasaurus* comes from Maastrichtian beds, while *Argentinosaurus* is Cenomanian in age.

The evidence at hand suggests that basal titanosaurian clades were prone to attain big sizes. In contrast, more derived Titanosauridae include not only medium sized members, but also the smallest adult known sauropods (e.g., *Neuquensaurus*, *Saltasaurus*, *Magyarosaurus*; Jianu & Weishampel, 1999). It was suggested (Bonaparte & Coria, 1993) that in South America sauropods attained their maximum sizes between Aptian and Coniacian times. The discovery of *Puertasaurus* in Maastrichtian beds demonstrates that gigantic sizes of South American sauropods endured up to the end of the Mesozoic Era, an interpretation that is in agreement with other findings of big sauropod bones in the Pari Aike Formation (Lacovara *et al.*, 2004). Exeption

southernmost Patagonia, the remaining Maastri-
 trichtian fossil sites with sauropods in South
 America (Powell, 2003), Madagascar (Curry-
 Rogers & Forster, 2001), and Europe (Jianu &
 Weishampel, 1999), the documented titanosaurs
 are consider-ably smaller than *Puertasaurus*.

Up to now, the biggest Cretaceous dinosaurs
 (e.g., *Argentinosaurus huinculensis*, «*Antarcto-
 saurus*» *giganteus*, and *Puertasaurus reuili*) were
 documented in South America. Why such gigan-
 tic vertebrates evolved in this continent is puzz-
 ling. We suggest that this may reflect the evolu-
 tion in progressive isolation of sauropods on this
 continent during the Cretaceous.

The discovery of *Puertasaurus* demonstrates
 that disparity in neck anatomy among sauropod
 dinosaurs is greater than suspected (Fig. 3). The low
 and wide titanosaurian cervicals differ from the deep
 cervicals of the remaining neosauropods (e.g.,
 diplodocids, *Brachiosaurus*, and *Euhelopus*) in that
 the latter exhibit rounded articular surfaces of the
 centra, ribs mostly ventrally oriented, and zygapo-
 physes occupying an elevated position with respect
 to the centrum (Fig. 3E). Such anatomical distinc-
 tions, not recognized before, remain unexplored
 from mechanical, postural and movemental points of
 view, and may have important consequences for
 functional studies of sauropod necks (Wedel et al.,
 2000; Stevens & Parrish, 1999).

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