Two Late Cretaceous sauropods reveal titanosaurian dispersal across South America

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South American titanosaurians have been central to the study of the evolution of Cretaceous sauropod dinosaurs. Despite their remarkable diversity, the fragmentary condition of several taxa and the scarcity of records outside Patagonia and southwestern Brazil have hindered the study of continental-scale paleobiogeographic relationships. We describe two new Late Cretaceous titanosaurians from Quebrada de Santo Domingo (La Rioja, Argentina), which help to fill a gap between these main areas of the continent. Our phylogenetic analysis recovers both new species, and several Brazilian taxa, within Rinconsauria. The data suggest that, towards the end of the Cretaceous, this clade spread throughout southern South America. At the same locality, we discovered numerous accumulations of titanosaurian eggs, likely related to the new taxa. With eggs distributed in three levels along three kilometres, the new site is one of the largest ever found and provides further evidence of nesting site philopatry among Titanosauria.
Titanosaurian sauropods are a group of large, long-necked, herbivorous dinosaurs with a complex evolutionary history. During the Late Cretaceous, they underwent an extensive evolutionary radiation worldwide. Most of their record in South America is restricted to Argentine Patagonia (e.g., Neuquén, Golfo San Jorge and Austral basins) and the Bauru Basin of SW Brazil, although there are remarkable faunistic differences between Patagonian and Brazilian titanosaurians. Similarly, other contemporaneous tetrapods, such as pleurodiran turtles and notosuchian mesoeucrocodylians, also show heterogeneous distributions.

By the Late Cretaceous, vast regions of South America remained flooded by epicontinental seas, and although there are high-rank taxonomic similarities, the evidence of eventual connections between northern and southern terrestrial faunas are still scarce. The ubiquity of the clade Titanosauria in a geographically intermediate area is validated by the occurrence of the saltasaurid titanosaurian Yamanasaurus from Ecuador—plus a putative record of Neuquensaurus—from NW Argentina, along with fragmentary accounts of sauropod dinosaurs in the latter region. However, saltasaurids have not been documented so far in the Bauru Basin nor other units in Brazil, and the non-saltasaurid specimens in NW Argentina are too fragmentary to allow determination of paleobiogeographic relationships. In addition to saltasaurids, the other high-level clade amongst titanosaurians is the Colossosauria, recently stemmed defined as the most inclusive clade containing Mendozaurus but not Saltasaurus, nor Epachthosaurus. It includes the subclades Rinconsauria and Lognkosauria (plus a few related taxa), whose taxonomic composition has fluctuated over the years. The fossil record of colossosaurians has, so far, a disparate distribution, with most of its members reported in Patagonia and SW Brazil.

Herein, we report the discovery of new dinosaurs from the Upper Cretaceous red beds of the Quebrada de Santo Domingo locality (QSD) in the Andes of La Rioja, NW Argentina. We recovered three partial skeletons that belong to two new derived titanosaurian dinosaur species in different stratigraphic positions of the Ciénaga del Río Huaco Formation. Moreover, we found titanosaurian egg clutches and eggshells in an intermediate stratigraphic position, distributed in three levels. With an overwhelming abundance of eggs, QSD is one of the largest nesting sites documented worldwide. The results of our phylogenetic analysis incorporating the two new taxa suggest that they have Patagonian and Brazilian affinities, reinforcing the hypothesis of a close relationship between the titanosaurian sauropod faunas from northern and southern South America during the Late Cretaceous.

Fig. 1 Titanosaurian record in South America, map of the study area and skeletal reconstructions of the new titanosaurian species. a Percentage diversity of Cretaceous titanosaurian sauropods in three main regions of South America: Patagonia (purple), NW Argentina (green), and SW Brazil (yellow) (Supplementary Table 3). The yellow ring corresponds to the record of the saltasaurid titanosaurian Yamanasaurus in Ecuador. Map modified from Scotese. b Location of the discoveries. c Punatitan coughlini gen. et sp. nov. d Bravasaurus arrierosorum gen. et sp. nov. Preserved elements are coloured in red in c, d. Scale bar: 100 km in b, and 1 m in c, d.
Results

Systematic palaeontology.

Sauropoda Marsh, 1878
Titanosauria Bonaparte and Coria, 1993
Colossosaurus González Riga et al., 2019
Punatitan coughlini gen. et sp. nov.

Etymology. 'Puna' is the local name that distinguishes the oxygen-depleted atmosphere typical of the high Andes, and 'coughlini' refers to the geologist Tim Coughlin, who reported the first dinosaur fossils in the area.

Holotype. CRILAR-Pv 614 (Paleovertebrate Collection of Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Argentina), partial skeleton composed of the anterior portion of posterior cervical vertebra (likely C12), two middle dorsal vertebrae (likely D6–D7), partial sacrum, 13 articulated caudal vertebrae (some with articulated haemal arches), right pubis, left ischium, and several dorsal ribs.

Horizon and type locality. Sandstone levels 170 m above the base of the Ciénaga del Río Huaco Formation (Campanian-Maastrichtian) at QSD, La Rioja, NW Argentina (Geological Setting in Supplementary Information).

Diagnosis. A medium-sized titanosaurian sauropod characterised by the following combination of features (autapomorphies marked with an asterisk): (1) middle dorsal vertebrae (likely D6–D7) with anterior and posterior spinoprezygapophyseal laminae (spdl) forming wide and flat surface, between aliform and transverse processes; (2) accessory posterior centrodiaepophyseal lamina (apcdl) crossing over by the posterior centroparapophyseal (pcpl) lamina, forming a X-shaped intersection in D6–D7; (3) pcpl reaches the bottom of posterior centrodiaepophyseal lamina (pcdl) in D6–D7; (4) extra-depression ventrally to intersection of pcpl and apcdl in D6–D7; (5) deep postzygodiapophyseal centrodiapophyseal fossa (pcdf) in D6–D7; (6) neural spine of D6 tapering dorso-posteriorly, forming an inverted "V" profile in anterior/posterior view; (7) caudal transverse processes persist beyond Ca15; (8) slightly anteriorly inclined neural spines in anterior-middle caudal vertebrae (Ca5–6 to Ca10); and (9) distally expanded prezygapophyses in anterior-middle caudal vertebrae.

Description and comparisons of Punatitan. Most diagnostic features are in the axial skeleton of Punatitan (Fig. 2), allowing us to distinguish the new taxon from other titanosaurians. The holotype CRILAR-Pv 614 represents a medium-sized individual, larger than the holotypes of *Overosaurus* 24, *Saltasaurus* 25, *Neuquensaurus* 26,27, and *Trigonosaurus* 28, about the same size as the holotype of *Uberabatitan* 29, and smaller than *Aeolosaurus* 30, *‘Aeolosaurus’* 31, *Mendozasaurus* 3 and giant taxa (e.g., *Argentina

A cranial portion of a posterior cervical vertebra is only available (Fig. 2a, b). It may correspond to C12, based on *Overosaurus* and *Trigonosaurus* (MCT 1499-R 28). The centrum is shorter dorsoventrally than it is wide transversely, with its anterior surface strongly convex. The base of the right parapophysis is level with the ventral border of the centrum and ventrally delimited the deeply concave lateral surface of the centrum. The prezygapophyses are anterolaterally projected and well separated from each other. Their anterior edge is placed slightly anterior to the level of the articular surface. Both are mediolaterally connected by a sharp interzygapophyseal lamina (tprl) that forms an open U-shaped edge in dorsal view. The right base of a rounded dorsomedially projected spinoprezygapophyseal lamina (sprl) is preserved. Although the neural arch is incomplete, the position and development of the prezygapophyses, together with the position, orientation, and robustness of the sprl, suggest a wide and concave spinoprezygapophyseal fossa (sprf). Overall, the cervical vertebra of *Punatitan* is similar to that of most titanosaurians. The robust sprl is more similar to that of *Malawisaurus* 31, *Mendozasaurus* 3, *Futalognkosaurus* 32, and *Dreadnoughtus* 33 than to *Overosaurus* 24, in which the lamina is weakly developed, and the floor of the sprl is reduced. In *Trigonosaurus* 28 the sprl is also conspicuous but relatively short, thus defining a small sprl.

Two dorsal vertebrae are known for *Punatitan*, interpreted as D6 (Fig. 2c, d) and D7 (Fig. 2e), based on comparisons with *Overosaurus* 24 and *Trigonosaurus* 28 (e.g., the relative position of parapophysis and diapophysis, orientation of neural spine). The centra are opisthocoelous, almost as high as wide. Laterally, they show deep and partitioned pleurocoels that have tapering, acute caudal margins. They are located dorsally, near the neurocentral junction. The neural arches are fused to the centrum, without a sign of suture.

The diapophyses are robust and well projected laterally, while the parapophyses are more anteriorly and slightly ventrally positioned, as occurs in middle dorsal vertebrae (e.g., D5–D7 of *Overosaurus* 24). Below these processes, the neural arches are notably intricate, showing a broad, deeply excavated fossa (Fig. 2c) with a conspicuous asymmetry in both lateral sides, as seen in other sauropods (e.g., *Trigonosaurus* 28, *Lirainosaurus* 34).

The pcpl and its anterior projection, the apcdl, plus the well-developed pcdf are the most conspicuous traits in the lateral aspects of these vertebrae (Fig. 2c), as seen in several titanosaurians, such as *Malawisaurus* 31, *Elaltitan* 35, *Overosaurus* 24, *Trigonosaurus* 28, and *Dreadnoughtus* 33. The pcpl projects posteriorly to reach the posterodorsal border of the centrum. The apcdl projects anteriorly from the dorsal edge of this lamina, contacting the anterodorsal border of the centrum. The accessory lamina is crossed over by the pcpl, forming an X-shaped intersection that is evident on the right side of D6 and D7 (on left sides of both, the pcpl finishes when contacting the apcdl, forming a Y-shaped pattern). The pattern observed in D6–D7 of *Punatitan* is roughly observed in D7 of *Overosaurus* 24 (other dorsal vertebrae have no clear X-pattern) and *Petrobrasaurus* 36, but not in other titanosaurians such as *Malawisaurus* 31, *Elaltitan* 35, *Trigonosaurus* 28, *Lirainosaurus* 34, and *Dreadnoughtus* 33. Conspicuously, these laminae define deep fossae in *Punatitan*. The deep, subtrigusl fossa, dorsally delimited by the pcpl and apcdl is identified as posterior centrodiaepophyseal fossa (pcdf-f) 33. It is deeper in *Punatitan* than in *Overosaurus* 24, *Trigonosaurus* 28, *Muylenlaurus* 37, and *Dreadnoughtus* 33.

The anterior centroparapophyseal lamina (acpl) and pcpl project ventrally and posteroventrally, respectively, from the parapophysis. The pcpl is truncated on the left side of D6–D7 when touching the apcdl; consequently, on this side, the pcdf-f is much larger than on the right side. In both dorsal vertebrae, the acpl and pcpl also define a deep but small fossa.

The oval-shaped prezygapophyses are connected mediolaterally by transversely short tprl (Fig. 2e). They are detached from the diaepophyseal body by a marked step that dorsally elevates their articular surface. In anterior view, the centroprezygapophyseal lamina (cpl) has a sharp border, and it widens dorsally. This lamina and the acpl define a deep fossa that faces anterolaterally. The sprl in these dorsal vertebrae are present as blunt structures that are poorly preserved. They connect the prespinal lamina (prsl) medially, without obstructing its path. A similar condition was inferred for *Barrosasaurus* 38, and a posterior dorsal vertebra referred to as *Trigonosaurus* 39, but they can correspond to accessorla laminae rather than to the true sprl, which is usually seen in more anterior vertebrae 40.
The postzygapophyses are higher than the lateral tip of the diapophysis in D6–D7, and there is no direct contact between the postzygapophyses and the diapophyses. Instead, there is a lamina that starts at the postzygapophysis and projects anterodorsally to connect to the spine, closer to the base of the spine than to the base of the diapophysis. The homology of this lamina is debated; it is here interpreted as the podl. This lamina is similar to the podl observed in dorsal vertebrae of *Malawisaurus*<sup>31</sup>, *Choconsaurus*<sup>(D6?42)</sup> and *Dreadnoughtus*<sup>33</sup>, and its unusual connection with the spine may be related to changes of the neural spine inclination and the relative position of the postzygapophyses and diapophyses in middle dorsal vertebrae<sup>41</sup>. At this point, this short podl delimits ventrally a very small postzygapophyseal fossa (posdf), which faces laterally (Fig. 2c). A similar small fossa is present in the anteriormost dorsal of *Rapetosaurus*<sup>43</sup> and the mid-posterior dorsal of *Bonitasaura*<sup>44</sup>. It differs from the condition seen in *Lirainosaurus* and *Neuquensaurus*, in which the posdf is well developed and faces more posteriorly. The postzygapophyses in D6 slope dorsally to the neural spine without a spinopostzygapophyseal fossa (spol), differing from the condition of *Dreadnoughtus*<sup>33</sup>, *Mendozasaurus*<sup>3</sup> and *Elaltitan*<sup>35</sup>, which have a sharp lamina. The centropostzygapophyseal lamina is also well developed, contacting the pcdl near the level of the neural canal. Both laminae define a large and deep pocdf.

The neural spine is complete in D6 of *Punatitan*. It is somewhat inclined posteriorly, with the tip extending as far posteriorly as the posterior border of the centrum (Fig. 2c). It is anteroposteriorly narrow and tapers dorsally. In anterior view, the contour of the tip is rounded, without any expansion, forming an inverted V-shaped profile, with a slightly sigmoid outline owing to the presence of aliform processes. The neural spine bears a prsl and a postspinal lamina (posl). The prsl is sharp in the basal half of the spine, separating two deep, wide fossae, laterally delimited by the prominent spdl. The posl is also sharp and expands over almost all the neural spine, delimiting two deep, narrow fossae, laterally bordered by the postzygapophyses, and

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**Fig. 2** *Punatitan coughlini* gen. et sp. nov. (CRILAR-Pv 614). a, b Cervical vertebra (C12) in dorsal a and anterior b views. c, d Dorsal vertebra (D6) in right lateral c and posterior d views. e Dorsal vertebra (D7) in anterior view. f Articulated series of caudal vertebrae (Ca5–Ca17). g Detail of Ca8–Ca12. acpl anterior centroparapophyseal lamina, apcdl accessory posterior centrodiapophyseal lamina, dp diapophysis, nc neural canal, ns neural spine, pcdl posterior centrodiapophyseal lamina, pcpl posterior centroparapophyseal lamina, pocdf postzygapophyseal centrodiapophyseal fossa, posdf postzygapophyseal spinodiapophyseal fossa, posl postspinal lamina, poz postzygapophysis, pp parapophysis, prsl prespinal lamina, prz prezygapophysis, spdl spinodiapophyseal lamina, spol spinopostzygapophyseal lamina, sprl spinoprezygapophyseal lamina, tprl interprezygapophyseal lamina. Circled numbers correspond to apomorphies numbered in the text. Measurements in Supplementary Table 1. Scale bars: 100 mm.
the aliform processes (Fig. 2d). The neural spine of D6 in *Punatitan* differs from that of most titanosaurians, which have expanded (e.g., *Dreadnoughtus* [25]) or squared (e.g., *Chocodusaurus* [24], *Overosaurus* [24], *Trigonosaurus* [28]) neural spines.

The still unprepared sacrum of *Punatitan* is incomplete and will be described elsewhere. However, it was possible to observe an ossified supraspinous rod placed over the preserved neural spines (two or more). This structure is known for *Epachthosaurus*, *Malawisaurus*, and basal titanosauriforms [45]. The holotype of *Punatitan* also preserves 13 articulated caudal vertebrae as well as several haemal arches (Fig. 2b). The first preserved caudal possibly represents Ca5. As in most titanosaurians, these caudal vertebrae have strongly procyeoloeus centra [46]. The centra are dorsoventrally tall, differing from the depressed centra of saltasaurines [25,26]. Their anterodorsal border is anteriorly displaced from the anterventral one, resulting in an oblique profile in lateral view. They have slightly concave lateral surfaces, with transversely thin ventrolateral ridges that delimit a deeply concave ventral surface that is devoid of lossae. The internal tissue of the caudal centra is spongy, and the neural arches are apneumatic.

In the anterior caudal vertebrae, a suture is present above the transverse processes (Fig. 2g). It forms a conspicuous ridge, which is not evident in related taxa, although it resembles the dorsal tuberosity described for *Baurutitan* [47], and also CRILAR-Pv 518c from Los Llanos, east La Rioja [43]. The neural arch of each caudal vertebra is situated over the anterior two-thirds of the centrum, and each is relatively tall with well-developed prezygapophyses and neural spines. The transverse processes are sub-rectangular to laminar and gradually change from laterally to posterolaterally projected along the vertebral column. The prezygapophyses are long and project anterodorsally. The postzygapophyses contact the neural spine via a short spur and are located almost at the midline of the centra. This condition differs from the much more anteriorly placed postzygapophyses of the Patagonian *Aeolosaurus* [40]. The neural spine is rectangular in cross-section and anteroposteriorly longer than transversely wide (including prsl and posl). The spines are tall in the anterior caudal vertebrae and become shorter and square in the posterior ones. They also project slightly anteriorly, especially in Ca8–Ca10 (Fig. 2g). Some degree of anterior inclination of the neural spines is also reported for *Trigonosaurus* [28] and *Aeolosaurus* [40], contrasting with the most common condition amongst titanosaurians, i.e., vertical or posteriorly oriented neural spines (e.g., *Baurutitan* [47], *Dreadnoughtus* [33], *Saltasaurus* [25]). The available haemal arches are opened Y-shaped, with no expanded pedicles, as are those reported for other derived titanosaurs [48].

**Bravasaurus arrierosorum** gen. et sp. nov.

**Etymology.** *Bravasaurus*, referred to the Laguna Brava, a lake that gives name to the Laguna Brava Provincial Park, and *arrierosorum*, refers to the people who crossed the Andes carrying cattle during the 19th century.

**Holotype.** CRILAR-Pv 612, right quadrate and quadrototjugal, four cervical, five dorsal, and three caudal vertebrae, few dorsal ribs, three haemal arches, left humerus, fragmentary ulna, metacarpal IV, partial left ilium with sacral ribs, right pubis, partial ischium, left femur, and both fibulae.

**Paratype.** CRILAR-Pv 613, isolated tooth, right ilium, right femur, and dorsal ribs.

**Horizon and type locality.** Sandstone levels 34 m above the base of the Ciénaga del Río Huaco Formation (Campanian-Maastrichtian) at QSD, La Rioja, NW Argentina (Geological Setting in Supplementary Information).

**Diagnosis.** A small-sized titanosaurian sauropod characterised by the following association of features (autapomorphies marked with an asterisk): (1) quadrate with articular surface entirely divided by medial sulcus; (2) sprl forms conspicuous step between neural spine and prezygapophyses, in middle cervical vertebrae; (3) strongly depressed centra (up to twice as wide as tall) in posterior dorsal vertebrae; (4) robust dorsal edge of pneumatic foramen in dorsal centra, forming prominent shelf that extends laterally, beyond the level of the ventral margin of the centrum; (5) posterior dorsal vertebrae with a rough posl, ventrally interrupted by middle spinopostzygapophyseal laminae (m.spol) that contact the postzygapophyses; (6) posterior dorsal vertebrae with small ventral spinopostzygapophyseal fossa (v.spol) delimited dorsally by the m.spol and ventrally by the interpostzygapophyseal lamina (tpol); (7) humerus with narrow midshaft, with midshaft/proximal width ratio of 0.36; (8) deltopectoral crest of the humerus expanded distally; (9) slender fibula (Robustness Index [RI] = 0.15); (10) distal condyle of the fibula transversely expanded, more than twice the midshaft breadth.

**Description and comparisons of Bravasaurus.** The holotype of *Bravasaurus* (Figs. 3 and 4), as well as the referred specimen, indicates a small-sized titanosaurian, much smaller than *Punatitan* (Fig. 1c, d) and other medium-sized sauropods, such as *Trigonosaurus*, *Overosaurus*, and *Bonitasaura*. Considering that both specimens could be adults (see below), they would be similar to *Newquensaurus* or *Mygarrasaurus* [50]. Cranial elements include partial right quadrate and quadrototjugal (Fig. 3a, b). The quadrate is anteroventrally directed and bears part of the quadrate fossa. The articular surface for the mandible is transversely elongated. It shows two condyles that separate from each other by a longitudinal sulcus (Fig. 3b). The medial condyle is round, whereas the lateral is anteroposteriorly elongated. *Diplodocus* [51] also has a sulcus but restricted to the posterior region of the articular surface. Among titanosaurians, the articular surface of the quadrate has a kidney shape in *Nemegtosaurus* and *Quaesitosaurus*, with the sulcus restricted to its anterior portion. In *Bonitasaura* [53] and *Rapetosaurus* [54], the articular surface is not divided. The anterior process of the quadrototjugal projects ventrally, whereas the posterolateral process barely extends ventrally, similar to *Nemegtosaurus*, and much less developed than in *Tapuiasaurus* [55] and *Sarmientosaurus* [4]. Unlike in these latter taxa, the posterolateral process reaches the articular condyle of the quadrate, which can only be seen behind (and not below) the quadrototjugal in lateral view (Fig. 3a).

The holotype of *Bravasaurus* preserves cervical, dorsal, and caudal vertebrae. The neural arches of all elements are completely fused to their respective centra, which may indicate that it had reached somatic maturity before death [56–58].

We recovered four anterior-middle cervical vertebrae less than half a meter away from the cranial material. Three of them are articulated and associated with ribs. They are opisthocoelous, with sub-cylindrical and relatively elongated centra (Fig. 3c). The neural arches have low neural spines, as observed in *Rinconosaurus* [59] and *Uberabatitan* [29]. The diaphyses have posterior extensions, and the prezygapophyses are placed beyond the articular condyle of the centrum, as seen in the latter taxa. In *Bravasaurus* the postzygapophyseal lamina (pdl) splits into a diaphyseal and a zygapophyseal segment, which become diaphyseal with each other. Previous studies identified this feature as exclusive of *Uberabatitan* [13,29]. In derived titanosaurians, the neural spines contact the prezygapophyses via the sprl, which is straight or slightly curved ventrally in lateral view. In the anterior cervical vertebrae of few titanosaurians (e.g. *Saltasaurus* [25] and
Rocasaurus\(^47\)), the sprl curves dorsally, forming a step close to the prezygapophysis. This step disappears beyond the first cervical vertebrae but remains present in middle cervical vertebrae of Bravasaurus (C5?–C6?; Fig. 3c).

The dorsal vertebrae of Bravasaurus have relatively short, opisthocoelous centra (Fig. 3d–g). The well-developed pleurocoels are located just below the dorsal margin of the centrum, which forms a shelf that extends laterally, beyond the limits of the centrum, in middle and posterior dorsal vertebrae. Except for D10, the preserved dorsal centra are strongly dorsoventrally depressed (Fig. 3d, f), as in Opiisthocoelicaudia\(^60\), Alamosaurus\(^61\), Trigonosaurus\(^28\), and the “Series A” from Brazil\(^30\). The neural arches of the dorsal vertebrae are tall, but not as tall as in Punatitan, in which the pedicels are particularly long. The orientation of the preserved neural spines follows the same pattern as in other derived titanosaurians, i.e., vertical in anterior and posterior-most dorsal vertebrae, and inclined (as much as 40°) in middle dorsal vertebrae (e.g., Trigonosaurus\(^28\)). The prsl and posl are robust along their entire length (especially in the posterior dorsal vertebrae).

The anterior dorsal (D2) shows a low, laterally expanded neural arch (Fig. 3d). Although poorly preserved anteriorly, this vertebra exhibits a broad prespinal fossa with a weak prsl. It has rounded, ventrolaterally inclined postzygapophyses that join each other by small laminae (tpol?) that intersect at the height of the dorsal edge of the neural canal. The junction between these laminae and the dorsal edge of the neural canal forms two small fossae, as seen in the posterior cervical vertebrae of Overosaurus\(^24\). The neural spine is relatively low, and the postspinal fossa is particularly deep compared with the other dorsal vertebrae. The posl is weak. On the lateral aspect, the pcdl and the apcdl are the most conspicuous laminae. The diapophysis is eroded, and the parapophysis is located on the centrum above the pleurocoel.

The middle dorsal (D7) shows a slightly higher neural arch than D2, and its neural spine is inclined posteriorly, beyond the

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**Fig. 3** Axial elements of *Bravasaurus arrierosorum* gen. et sp. nov. (CRILAR-Pv 612). a, b Quadrate and quadratojugal with interpretative drawing in right lateral a, and ventral b views (anterior to the right). c Middle cervical vertebra in right lateral view. d Anterior dorsal vertebra (D2) in posterior view. e Middle dorsal vertebra (D7) in right lateral view. f–g Posterior dorsal vertebra (D8) in posterior f and left lateral g views. h, i Middle caudal vertebra in left lateral h and ventral i views (anterior towards left). acpl anterior centroparapophyseal lamina, ap anterior projection, dp diapophysis, ift infratemporal fenestra, m.spol middle spinopostzygapophyseal lamina, nc neural canal, ns neural spine, pcdl posterior centrodiapophyseal lamina, pcdf posterior centrodiaaphyseal fossa, pcpl posterior centrodiapophyseal lamina, pl pleurocoel, podl postzygodiapophyseal lamina, posdf postzygapophyseal spinodiapophyseal fossa, posl postspinal lamina, poz postzygapophysis, pp parapophysis, prz prezygapophysis, q quadrato, qj quadratojugal, spdl spinodiapophyseal lamina, tpol interpostzygapophyseal lamina, and v.spof ventral spinopostzygapophyseal fossa. Circled numbers correspond to apomorphies numbered in the text. Measurements in Supplementary Table 2. Scale bars: 10 mm in a, b, and 50 mm in c–i.
depressed, with a ventral longitudinal hollow (e.g., Nor do they possess the ventrolateral ridges (Fig. 3i) present in Aeolosaurus other titanosaurians such as centra, Bravasaurus prezygapophyses, as seen in caudal vertebrae shows signs of distal expansion in the vertical rather than anteriorly directed. None of the preserved orientation of the neural spine in the anterior caudal, which is Punatitan – D8 – D10.

The anterior and middle caudal vertebrae of Bravasaurus are procoelous. The centra are as tall dorsoventrally as they are wide transversely, without any concavities on their ventral surfaces (Fig. 3h, i). The anterior margin of the centra does not appear to be anteroventrally inclined, as occurs in Punatitan, Overosaurus, or Aeolosaurus. The neural arches are on the anterior portion of the centra, as in most titanosaurians, and some other titanosauriforms (e.g., Wintonotitan). The neural spines are laminar and vertically directed, while the prezygopophyses are short and anteriorly projected. Such morphology shows many similarities with Rincosaurus and Muyelensaurus, but even more so with the Brazilian Trigonosaurus and Uberabatitan. As for the centra, Bravasaurus differs from saltasaurines, in which they are depressed, with a ventral longitudinal hollow (e.g., Saltasaurus). Nor do they possess the ventrolateral ridges (Fig. 3i) present in other titanosaurians such as Aeolosaurus, Overosaurus, and Punatitan. Bravasaurus also differs from the latter taxon by the orientation of the neural spine in the anterior caudal, which is vertical rather than anteriorly directed. None of the preserved caudal vertebrae shows signs of distal expansion in the prezygopophyses, as seen in Punatitan.

The morphology of the humerus is compatible with that of many colossosaurian titanosaurians. Its robustness is high (RI = 0.35), as in Opisthocoelicaudia, Diamantinasaurus, and Savannasaurus, much more than in Rincosaurus and Muyelensaurus. The deltopectoral crest is markedly expanded distally (Fig. 4a), as in Saltasaurus, Neuquensaurus, Opisthocoelicaudia, and Dreadnoughtus. All pelvic elements are represented in the holotype, although only the pubis (Fig. 4b) allows comparisons. It is proximodistally elongate and less robust than in Futalognkosaura or Opisthocoelicaudia. The distal end is markedly expanded, as in several derived forms (e.g., Rapetosaurus, Bonitasaura, Muyelensaurus). The ilium of the specimen CRILAR-Pv 613 resembles the ilium of other derived titanosaurians, such as Rapetosaurus and Bonatitan. The femur is straight, with the fourth trochanter placed at the proximal third (Fig. 4c, d), as in Uberabatitan, Patagotitan, Bonitasaura, and Futalognkosaura, whereas in Rincon-saurus, Muyelensaurus, and Diamantinasaurus it is located in the middle third. The humerus-to-femur length ratio in Bravasaurus is 0.75, similar to Opisthocoelicaudia, higher than Neuquensaurus and Saltasaurus, but lower than Patagotitan and Epachthosaurus. The fibula (Fig. 4e, f) markedly contrasts with the rest of the appendicular elements, as it is particularly gracile. Its distal condyle is transversely expanded, as observed in Epachthosaurus.

The known specimens of Bravasaurus indicate a small adult size. We estimate a body mass of 2.89 tons (2.17–3.61 tons, considering 25% error), based on a calibrated equation (see “Methods” section). Estimates of <10 tons are few among titanosaurians. The European Magyarosaurus (750 kg), is interpreted as a case of insular dwarfism, whereas that of the Argentinean Saltasaurus and Neuquensaurus was five and six tons, respectively. Among colossosaurians, estimations for Rincosaurus indicate just four tons and at least some other genera (e.g., Overosaurus, Trigonosaurus, Baurutitan), lacking appendicular bones, are small-sized forms, slightly larger than Bravasaurus, based on their vertebral size.

**Phylogenetic analysis.** The result of our phylogenetic analysis nests Punatitan and Bravasaurus as derived titanosaurians in all most parsimonious trees. The topology of the strict consensus tree is similar to that obtained in previous studies using the same dataset, although some taxa, such as Baurutitan and Trigonosaurus show
noticeable changes in their position (Fig. 5; Supplementary Fig. 4). The former one is placed as the basalmost colossosaurian, and the latter is clustered together with *Uberabatitan*, *Gondwanatitan*, and *Bravasaurus*. Both *Punatitan* and *Bravasaurus* are recovered within Colossosauria. *Punatitan* shows three of the seven ambiguous synapomorphies that diagnose the newly erected clade, and *Bravasaurus* five. Furthermore, the new Riojan species are placed within the clade Rinconsauria, along with several titanosaurians from SW Brazil and Patagonia (Fig. 5). *Punatitan* is nested with the Argentinean *Aeolosaurus*, by sharing the presence of distally expanded prezygapophyses in posteriormost anterior and middle caudal vertebrae. Other features of the caudal vertebrae, such as the dorsal edge of the anterior articular surface of the centrum ahead of the ventral margin, and the neural spines anteriorly oriented in the posteriormost anterior and middle caudal vertebrae, relate the latter taxon with the Brazilian *Aeolosaurus* and *Overosaurus*, as successive sister taxa. *Bravasaurus* is included in a collapsed clade comprising the Brazilian *Trigonosaurus, Uberabatitan,* and *Gondwanatitan*. The clade is supported by a single synapomorphy: height/width ratio smaller than 0.7 in the posterior articular surface of cervical centra.

**QSD nesting site.** We documented three egg-bearing levels in the lower section of Ciénaga del Río Huaco Formation at QSD. The egg clutches and eggshells are included in an interval of floodplain deposits in at least three distinct but closely spaced horizons at 59.2, 62.8 and 63.9 m above the base of the unit (Supplementary Fig. 1). Fossil-bearing rocks are siltstones and sandy siltstones with horizontal lamination and graded and massive bedding that form thin tabular sheets, extending for tens to hundreds of metres. The fossiliferous layer is laterally traced over more than three kilometres, and the egg clutches and eggshells (CRILAR-Pv 620–621) are exposed regularly all along with it. Nineteen egg clutches were spotted, one with up to 15 subspherical eggs, arranged in two superposed rows. The QSD eggs are similar to some Late Cretaceous titanosaurian eggs. Among the remarkable diversity of eggs worldwide, only Auca Mahuevo (Argentina), Dholi Dungri (India), and Totești (Romania) preserve titanosaurian embryos. Therefore, these sites are the most reliable to correlate eggs with their producers. At QSD, the eggs are cracked, slightly compressed and flattened by the sedimentary load (Fig. 6a, b). We estimate an egg size of 130–140 mm, similar to the eggs from Auca Mahuevo and Totești, but slightly smaller than the ones from Dholi.
Dungri (160 mm). The eggshells are mono-layered, measuring 1.67 ± 0.31 mm (n = 30). The thickness is similar to the eggshells from layers 1–3 of Auca Mahuevo. The eggshells from Toteşti and layer 4 of Auca Mahuevo are slightly thicker, measuring 1.7–1.8 mm, whereas in Dholi Dungri they reach 2.26–2.36 mm. The QSD shells are composed of densely packed shell units of calcite crystals, which radiate from nucleation centres (Fig. 6c, d). They flare out at 50°, and their lateral margins become parallel at the inner third of the shell, like in the Auca Mahuevo specimens. Outwards, the units end out in rounded nodes of 0.3–0.4 mm in diameter, forming densely packed ornamentation that is typical of the titanosaurian clade. Multiple straight pore canals run through the eggshell, between the shell units. They have funnel-shaped external apertures that form round depressions between the surface nodes. Among titanosaurian eggshells, those from Dholi Dungri and Auca Mahuevo (layers 1–3) also have straight pore canals, whereas, in those from Toteşti and the layer 4 of Auca Mahuevo, the pore canals ramify in a Y-shaped pattern.

As in Auca Mahuevo and other Cretaceous nesting sites, the QSD specimens are preserved in a floodplain palaeoenvironment. The occurrence of compact accumulations of whole eggs is consistent with the hypothesis of incubation within the substrate, as currently do the megapode birds from Australasia. Along with the egg clutches, hundreds of shells also appear scattered within the egg-bearing levels. Such an arrangement could be a consequence of the local transport of exposed shells during floods, but also the product of local removal during subsequent nesting episodes. Soft sediment deformation and dislocation are frequent, and could also have contributed to their dispersion. These features suggest that each of the three egg-bearing levels could constitute a time-averaged assemblage.

**Discussion**

As far as we know, Punatitan and Bravasaurus represent the first confirmed occurrence of colossosaurian titanosaurians in NW Argentina. For 40 years, Saltasaurus remained as the only well-represented sauropod for this region. Saltasaurus is closely related with the Patagonian Rocasaurus and Neuquensaurus, as well as Yamasaurus, from Ecuador. There is a consensus regarding the close relationship of these taxa, which constitute the Saltasaurinae, a clade of small-sized titanosaurians from the Late Cretaceous that is also supported by our phylogenetic result. The phylogenetic data also suggest that saltasaurines may not have a close relationship with other Late Cretaceous titanosaurians from South America, as previously supported, but recent phylogenetic analyses, including the one here presented, suggest the Brazilian species may represent a distinctive genus, other than Aeolosaurus. Both Riojan species expand the diversity of the clade Rinconisauria, and its geographical distribution.

Based on a combination of direct observations and body mass estimation, Bravasaurus was a small-sized titanosaurian, though not as small as the dwarf Magyarosaurus or Lirainosaurus. Although it had probably reached its maximum size, it is much smaller than Punatitan (Fig. 1c, d). The largest titanosaurians ever known are placed within colossosaurians (e.g., Argentinosaurus, Patagotitan), but others are relatively smaller, such as...
Rinconsaurus, Overosaurus, Triginosaurus, Bauraturitan, and Gondwanatitan. In this context, the available evidence suggests that Bravasaurus (~3 tons) is the smallest colossosaurian yet recorded, followed by the taxa mentioned above. In contrast to Magyarosaurus78, Bravasaurus appears to have inhabited inland territories. By the latest Late Cretaceous, there is an evident reduction in size in saltasaurids and rinconsaurians across South America, which may be related to fluctuations in climate25 and vegetation26 (e.g., grassland), as a result of more temperate conditions and influence of remnant epicontinental seas during the dynamic aperture of the Atlantic.

The new findings from La Rioja reduce the paleobiogeographic gap of Late Cretaceous colossosaurians in South America, which were previously restricted to Patagonia and SW Brazil. Colossosauria is divided into the gigantic Lognkosauria (e.g., Patagotitan, Futalognkosaurus), plus some related forms, and the Rinconsauria. So far, the former clade is mostly limited to Patagonia (although there are few putative non-rinconsaurians in Brazil14), whereas Rinconsauria may contain a few Brazilian forms2,2,6,9,77. Besides, some taxa recovered within Rinconsauria are often included within Aeolosaurini, a group of titanosaurians with unstable interspecific phylogenetic relationships12. Our results suggest that Rinconsauria is much more diverse and widely distributed than previously thought2,6,9,37. The oldest representatives of this clade would be in northern Patagonia, for the earliest Late Cretaceous. By the Campanian–Maastrichtian, the Rinconsauria increased their diversity and spread geographically northward, through La Rioja, to SW Brazil.

Comparison of the QSD eggs with confirmed occurrences of titanosaurian eggs, such as Auca Mahuevo70 and Toteşti72, allow their identification. The spherical shape of the eggs, the monostratified shells and the nodular external ornamentation indicate that the QSD eggs belong to titanosaurian sauropods. More specific features (e.g., egg size, shell thickness, and straight vertical pore canals), associate the QSD specimens with the Auca Mahuevo eggs (layers 1–3). La Rioja Province is already known for its titanosaurian nesting sites in the Los Llanos region, several hundred kilometres southeast of QSD78,79. There, two localities preserve Late Cretaceous nesting sites that show distinct palaeoenvironmental conditions. The eggs from these sites markedly differ in their shell thicknesses but share the same egg diameter, around 170 mm, larger than the 140 mm eggs from QSD. In South America, the only eggs to match that size are those from Auca Mahuevo and Río Negro80, in Patagonia, as well as an isolated record from Baurn81. Eggs similar in diameter were attributed to dwarf titanosaurians from Toteşti72. The QSD eggs are relatively small, so either Bravasaurus or Punatitan may have been the producers. Further specimens are required to evaluate each scenario.

Both the oological and sedimentological data suggest a distinct nesting strategy from other sites of La Rioja. Unlike the sites in Los Llanos, the titanosaurian eggs of QSD appear in successive floodplain deposits, as occurs in Auca Mahuevo and other nesting sites worldwide69. Each of the egg-bearing layers contains multiple egg accumulations that were not necessarily laid contemporaneously. The several episodes interspersed in the sedimentary sequence allow us to infer nesting site philopatry, a behaviour that seems to have been frequent among Cretaceous titanosaurians69,72,78,82,83. This evidence and egg morphological features advocate a nesting strategy similar to that displayed at Auca Mahuevo. The QSD site provides further evidence on the plasticity of Late Cretaceous titanosaurian sauropods regarding their nesting strategies. Although it is still necessary to better understand the nesting conditions in other regions, such as Brazil, it seems increasingly evident that the adaptation to different nesting strategies could have been crucial in the diversification and dispersal of titanosaurians across South America.

Methods
Specimens. All material described in this study is housed at the Palaeovertebrate Collection of CRILAR (La Rioja, Argentina).

Taxa and systematic definitions. For the sake of simplicity, we used generic names when they are monotypic. The only exception corresponds to Aeolosaurus. The data set already included ‘Aeolosaurus’ maximus, a taxon which has been recognised as a member of Aeolosaurini84, although it does not exhibit the diagnostic features of the genus (see Martinielli et al.11 for further discussion) and is not grouped with the Patagonian species in some analyses3,13. Consequently, we refer to it as ‘Aeolosaurus’. We followed the systematic definitions provided by Carballido et al.2 and González Riga et al.8.

Eggshell micro-characterisation. We selected several eggshell fragments from QSD for microscopic imaging. Thin sections were carried out in the Petrology Lab at CRILAR, La Rioja, using the standard protocol for petrographic sectioning. We cut and mounted six eggshell fragments for their observation under a scanning electron microscope, following the protocol described in a previous study85. We used a LEO 1450VP equipment in the Laboratorio de Microscopía Electrónica y Microanalítica (Universidad Nacional de San Luis, San Luis, Argentina).

Body mass. We estimated the body mass of Bravasaurus using a scaling equation adjusted for phylogenetic correlation/covariance27. The equation

\[
\log BM = 2.754 - \log C_{11,1} - 1.097
\]

where BM is body mass, and \(C_{11,1}\) is the sum of circumferences of the humerus and femur. It has been used to estimate the body mass of gigantic (e.g., Patagotitan8), as well as medium-sized titanosaurians (e.g., Rapetosaurus86).

Phylogenetic analysis. We tested the phylogenetic position of Bravasaurus and Punatitan amongst 30 derived titanosaurian terminals using a modified version of the data matrix of Carballido et al.5. This matrix has been used to assess the phylogenetic position of derived titanosaurans and related taxa (e.g., Sarmientosaurus4, Patagotitan8).

Data on several South American titanosaurians was added in order to expand the representation of their diversity. We added scorings for Gondwanatitan and Uberabatitan to increase the information on Brazilian taxa. We also included Aeolosaurus rionegrins80 and the saltasaurian Rocaaurus, from Patagonia to the data set.

We added five characters (four from previous studies and one new) and modified few scorings (Supplementary Tables 4, 5; Supplementary Data 1). This resulted in a data set of 96 taxa and 421 characters (Phylogenetic Analysis in Supplementary Information, and Supplementary Data 2). As in previous studies4, 24 characters were considered as ordered (14, 61, 100, 102, 115, 127, 132, 135, 136, 167, 180, 196, 257, 260, 277, 278, 279, 280, 300, 304, 347, 353, 355).

Statistics and reproducibility. We performed a parsimony analysis of the modified data matrix using TNT v.1.187. We did a heuristic search with 1000 replicates of Wagner trees and two rounds of tree bisection-reconnection branch swapping. Branch support was quantified using decay indices (Bremer support values). They were calculated with TNT v.1.187, and are given in the Supplementary Fig. 4. A TNT file containing raw data for the parsimony analysis is available in the Supplementary Data 2.

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered with ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘http://zoobank.org/’. The LSIDs for this publication are: urn:lsid:zoobank.org:pub:CD87D24-50DA-415A-9EAF-54FB7C26FDD3; urn:lsid:zoobank.org:act:18840DCF-33EF-465D-8F69-0B38BB601BF7; urn:lsid:zoobank.org:act:63885DB4-1432-46BC-B543-DFF1155EC71E; urn:lsid:zoobank.org:act:336215DA-58AB-4B69-8059-C1EFA54D58A; urn:lsid:zoobank.org:act:84B7ECE6-60B4-4324-B983-CB6C9325EA8.

Reporting summary. Further information on research design and fieldwork is available in the Research Report Reporting Summary linked to this article.

Data availability Additional information, including the dataset analysed in this study, is available in the Supplementary Information, and Supplementary Data 1, 2 files. CRILAR-Pv 612-614 and
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