

Braincase Anatomy of the Titanosaurian Sauropod *Lirainosaurus astibiae* from the Late Cretaceous of the Iberian Peninsula

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Source: Acta Palaeontologica Polonica, 56(3) : 521-533

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2010.0043>

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Braincase anatomy of the titanosaurian sauropod *Lirainosaurus astibiae* from the Late Cretaceous of the Iberian Peninsula

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Díez Díaz, V., Pereda Suberbiola, X., and Sanz, J.L. 2011. Braincase anatomy of the titanosaurian sauropod *Lirainosaurus astibiae* from the Late Cretaceous of the Iberian Peninsula. *Acta Palaeontologica Polonica* 56 (3): 521–533.

Lirainosaurus is the only titanosaurian sauropod described to date from the Late Cretaceous of the Iberian Peninsula. The type of *Lirainosaurus astibiae* consists of both cranial and postcranial remains that were found as disarticulated elements in the Laño quarry (Treviño, northern Spain). This taxon was diagnosed originally on the basis of vertebral and appendicular autapomorphic traits. The study of a paratypic skull fragment and a second referred specimen provides information about its braincase morphology. *Lirainosaurus* is regarded as a derived titanosaur on the basis of the complete fusion between the prootic and the exoccipital-opisthotic complex, the position of the cranial foramina, and the shape and orientation of the occipital condyle. The braincase of *L. astibiae* appears to be diagnostic in the presence of a foramen distally on each basal tubera. The absence of median subcondylar foramina in the basioccipital may be an autapomorphic trait or be due to ontogenetic growth. A comparison with other partial skulls known in Europe suggests a high diversity during the Campanian/Maastrichtian, with at least three different titanosaurian species living in the Ibero-Armorican Island.

Key words: Sauropoda, Titanosauria, *Lirainosaurus*, braincase, Upper Cretaceous, Europe.

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Received 5 May 2010, accepted 20 December 2010, available online 30 December 2010.

Introduction

More than 20 sauropod genera are known from substantial portions of both the cranial and postcranial skeleton (Upchurch et al. 2004). Titanosaurs, the predominant sauropods during the Late Cretaceous, are mainly represented by postcranial material; their cranial elements are rather scarce, especially in association with postcranial remains. *Rapetosaurus krausei* from Madagascar is the first described titanosaur with associated cranial and postcranial bones (Curry Rogers and Forster 2001). In recent years, the cranial material of several titanosaurs has been described (Table 1) and offers new information about the titanosaurian skull (Wilson 2005). In the Late Cretaceous of Europe, only two braincases have been described, one of them of *Ampelosaurus atacis* (Le Loeuff 2005) and the other from an indeterminate titanosaur (Le Loeuff et al. 1989), both from southern France. Additional partial skulls found in Europe, including a juvenile specimen from Transylvania (Weishampel et al. 1991), a braincase from Provence (Allain 1998) and several partial skulls from Cuenca in Spain (Barroso-Barcenilla et al. 2009), have not yet been fully described.

Lirainosaurus is the only Iberian titanosaur known to date. This small to medium-sized sauropod (about 8–10 m in length) is the largest-sized component of the Laño vertebrate assemblage (Pereda Suberbiola et al. 2000). Sanz et al. (1999) erected *Lirainosaurus astibiae* from a fragment of skull, isolated teeth and a set of postcranial elements. Here we describe in detail two braincases of *Lirainosaurus astibiae*. One of the skull fragments, which consists of an incomplete braincase, is one of the paratypes of the species (Sanz et al. 1999). Additional material recovered in Laño, including a second braincase, is also referable to *Lirainosaurus*.

The features characterising *Lirainosaurus* and supporting its placement within the Titanosauria and less inclusive clades are identified. Moreover, the affinities of *Lirainosaurus* with other European titanosaurs and the implications of this study are also discussed.

Institutional abbreviations.—FGGUB, Facultatea de Geologie si Geofizica, Universitatea din Bucuresti, Bucarest, Romania; ISI, Indian Statistical Institute, Calcuta, India; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MAU, Museo

Table 1. Titanosaurian braincases. European taxa are emphasized.

Taxon	Catalogue number	Provenance	Age	References
<i>Lirainosaurus astibiae</i>	MCNA 7439, MCNA 13913	Spain	Campanian–Maastrichtian	Sanz et al. 1999
<i>Ampelosaurus atacis</i>	MDE C3-761	France	Campanian–Maastrichtian	Le Loeuff 2005
Titanosauria indet.	Mechin private Collection (cast in MDE)	France	Campanian–Maastrichtian	Le Loeuff et al. 1989
Titanosauria indet.	MNHN collection (uncatalogued)	France	Campanian–Maastrichtian	Allain 1998
<i>Magyarosaurus dacus</i> (?)	FGGUB 1007	Romania	Maastrichtian	Weishampel et al. 1991
<i>Jainosaurus septentrionalis</i>	ISI R 162, GSI K27/497	India	Maastrichtian	Huene and Matley 1933; Chatterjee and Rudra 1996; Wilson et al. 2009
<i>Isisaurus colberti</i>	ISI R 199, ISI R 467	India	Maastrichtian	Berman and Jain 1982; Chatterjee and Rudra 1996; Wilson et al. 2009
<i>Nemegtosaurus mongoliensis</i>	ZPAL MgD-I/9	Mongolia	Campanian–Maastrichtian	Nowiński 1971; Wilson 2005
<i>Quaesitosaurus orientalis</i>	PIN 3906/2	Mongolia	Santonian–Campanian	Kurzanov and Bannikov 1983; Wilson 2005
<i>Mongolosaurus haplodon</i>	AMNH 6710	Mongolia	Aptian–?Albian	Mannion in press
<i>Phuwiangosaurus sirindhornae</i>	SM K11-0006	Thailand	Barremian–Aptian	Suteethorn et al. 2009
<i>Rapetosaurus krausei</i>	UA 8698	Madagascar	Maastrichtian	Curry Rogers and Forster 2004
<i>Malawisaurus dixeyi</i>	Mal-202-1	Malawi	?Aptian	Gomani 2005
<i>Antarctosaurus wichmannianus</i>	MACN 6804	Argentina	Campanian–Maastrichtian	Huene 1929; Powell 2003
<i>Saltasaurus loricatus</i>	PVL 4017-161, PVL 4017-162	Argentina	Campanian–Maastrichtian	Powell 1986, 1992, 2003
<i>Bonatitan reigi</i>	MACN-PV RN 821, MACN-PV RN 1061	Argentina	Campanian–Maastrichtian	Martinelli and Forasiepi 2004
<i>Muyelensaurus pecheni</i>	MRS-PV 207	Argentina	Turonian–Coniancian	Calvo et al. 2007
<i>Pitenkusaurus macayai</i>	MAU-Pv-AG-446/5	Argentina	Campanian	Filippi and Garrido 2008
<i>Narambuenatitan palomoi</i>	MAU-PV-N-4 25	Argentina	Campanian	Filippi et al. 2011
Titanosauria indet.	MPCA-PV 80	Argentina	Campanian–Maastrichtian	Coria and Salgado 2005; Paulina-Carabajal and Salgado 2007
Titanosauria indet.	MUCPv-334	Argentina	Late Cretaceous	Calvo and Kellner 2006
Titanosauria indet.	MGPIFD-GR 118	Argentina	Campanian–Maastrichtian	Paulina-Carabajal and Salgado 2007
Titanosauria indet.	MML-194	Argentina	Campanian–Maastrichtian	García et al. 2008
Titanosauria indet.	MCF-PVPH-765	Argentina	?Turonian	Paulina Carabajal et al. 2008
<i>Tapuiasaurus macedoi</i>	MZSP-PV 807	Brasil	Lower Cretaceous	Zaher et al. 2011

Municipal “Argentino Urquiza”, Rincón de los Sauces, Neuquén, Argentina; MCF, Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina; MCNA, Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; MDE, Musée des Dinosauriens, Espéraza, France; MGPIFD-GR, Museo de Geología y Paleontología del Instituto de Formación Docente Continua de General Roca, Río Negro, Argentina; MML, Museo Municipal de Lamarque, Río Negro, Argentina; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MPCA-PV, Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina; MRS-PV, Museo de Rincón de los Sauces, Neuquén, Argentina; MUCPv, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Argentina; PIN, Russian Academy of Sciences, Moscow, Russia;

PVL, Instituto Miguel Lillo, Tucumán, Argentina; UA, Université d’Antananarivo, Madagascar; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Geological setting

Laño is located in a sand quarry between the villages of Laño and Albaina, in the Condado de Treviño, an enclave of Burgos Province inside the Basque Country (Fig. 1). From a geological point of view, Laño and the adjacent region lie within the southern part of the Basque-Cantabrian Region, in the northern Iberian Peninsula (Astibia et al. 1987; Baceta et al. 1999; Berreteaga 2008). Laño has yielded a diverse conti-

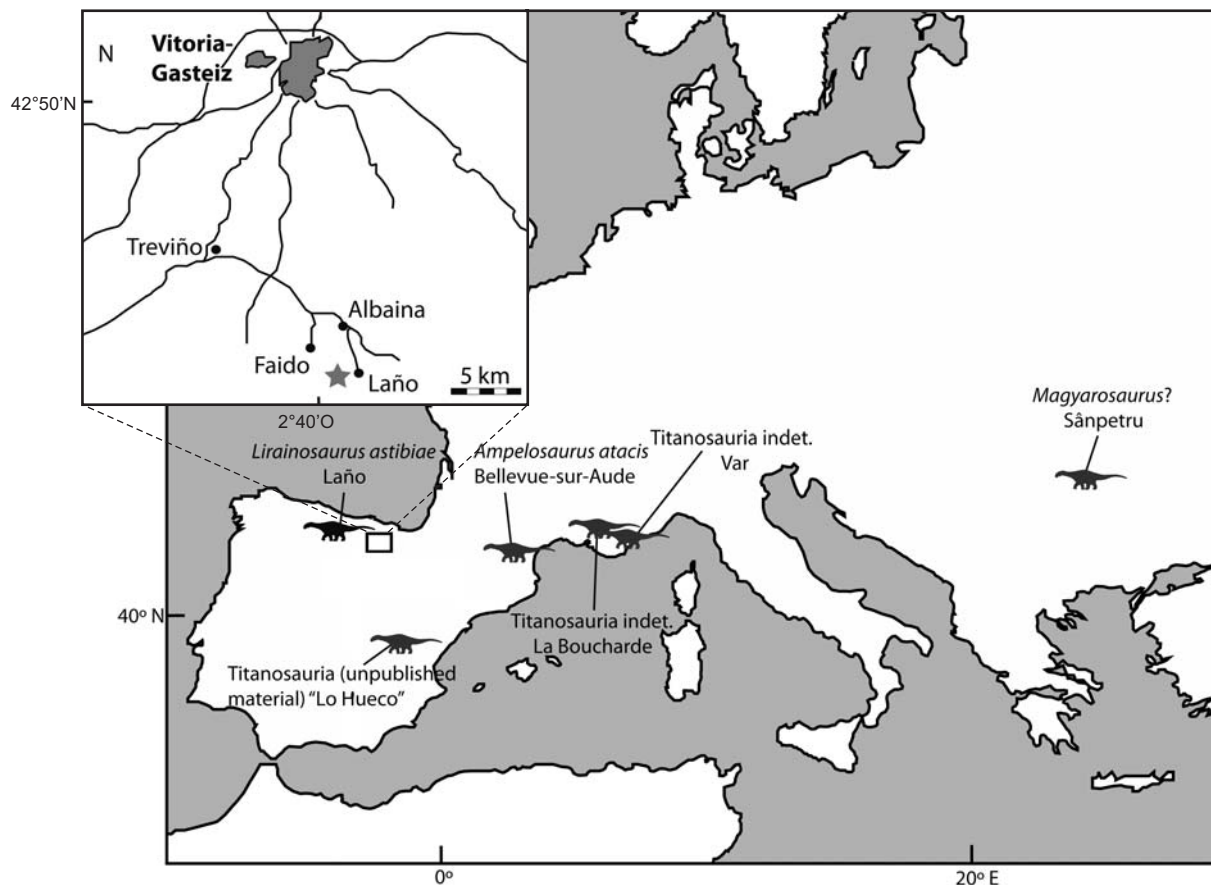


Fig. 1. Titanosaurian record of Europe based on cranial remains, and map showing the location of the Laño quarry (star).

mental vertebrate assemblage of Late Cretaceous (probable late Campanian to early Maastrichtian) age, including remains of bony fish, amphibians, lizards, snakes, turtles, crocodylians, pterosaurs, dinosaurs and mammals (Astibia et al. 1990, 1999; Pereda Suberbiola et al. 2000). The continental fossiliferous beds (L1A, L1B, and L2) of the Laño quarry were deposited in an alluvial system composed primarily of fluvial sands and silts. The sedimentary structures are consistent with channel areas within an extensive braided river (Astibia et al. 1990, 1999).

The fossils of *Lirainosaurus astibiae* come from the three fossiliferous strata of Laño. They correspond to a number of different individuals. As a whole, the remains of *L. astibiae* are quite homogenous and show little osteological variation, indicating that they probably belong to the same species.

Besides Laño, titanosaurian material referred to *Lirainosaurus* has been described from two other Iberian localities (Company et al. 2009; Ortega and Pérez García 2009), but it does not include skull remains.

Systematic palaeontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Sauropoda Marsh, 1878

Titanosauria Bonaparte and Coria, 1993

Lithostrotia Upchurch, Barrett, and Dodson, 2004

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

Genus *Lirainosaurus* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999

Lirainosaurus astibiae Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999

Figs. 2–8.

Type material: Holotype: MCNA 7458, anteriormost caudal vertebra (Sanz et al. 1999: pl. 2). Paratypes: MCNA 7439, incomplete braincase consisting of the basioccipital, the right prootic and exoccipital-ophistotic complex, and fragments of the basisphenoid-parasphenoid (Figs. 2–4). See Sanz et al. (1999: 237, pls. 1, 5, 6) for a complete list of paratypes, which also includes isolated teeth, dorsal and caudal vertebrae, scapula, coracoid, sternal plate, humeri, fragments of ilium and pubis, femora, tibia, fibula and osteoderms (MCNA collection).

Referred specimen: MCNA 13913, incomplete braincase consisting of fragments of the basioccipital, and basisphenoid-parasphenoid (Figs. 5–8).

Type locality: Laño quarry, between the towns of Laño and Albaina (Condado de Treviño), about 25 km south of Vitoria-Gasteiz, Spain.

Type horizon: L1A level; S3U1 unit of Astibia et al. (1987, 1990); upper zone of the B unit of Baceta et al. (1999); unit equivalent to the Sedano

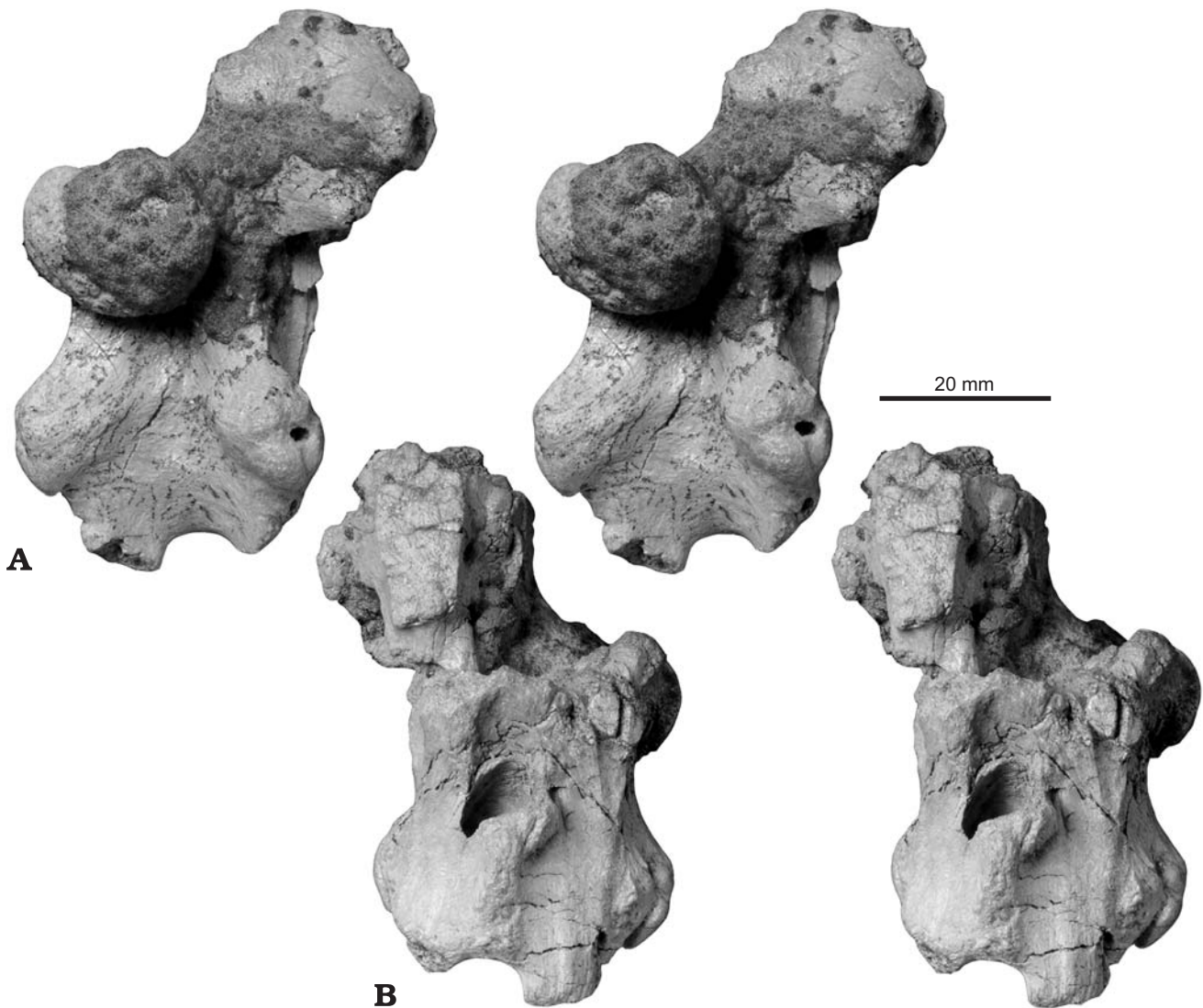


Fig. 2. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), paratypic braincase (MCNA 7439). Stereopairs in posterior (A) and anterior (B) views.

Formation of the North-Castilian Platform (Floquet 1991; Berreteaga 2008); Upper Cretaceous, probable late Campanian to early Maastrichtian.

Revised diagnosis (only skull features).—Presence of a foramen in the distal surface of each basal tubera. The absence of median subcondylar foramina in the basioccipital, below the occipital condyle and between the basal tubera, may be an autapomorphic trait or a feature due to ontogenetic growth. See Sanz et al. (1999) for postcranial autapomorphies of *L. astibiae*.

Description

The elements of the two braincases of *Lirainosaurus astibiae* are partially fused; only a suture is visible between the basioccipital and the basisphenoid, just anterior to the basal tubera. MCNA 7439 lacks the laterosphenoid and orbitosphenoid, and MCNA 13913 lacks the dorsal braincase bones. These braincases probably belonged to both subadult

individuals, as the absence of the laterosphenoid and orbitosphenoid appears to be due to lack of ossification, as there is not a broken surface in the anterior face of the right prootic in MCNA 7439. This absence is typical in subadult sauropods (e.g., immature specimen of *Jainosaurus*; Wilson et al. 2009). The basipterygoid and paroccipital processes are not preserved in the specimens. Both braincases are covered by iron oxides in some areas, as is typical in the Laño fossils (Elorza et al. 1999).

Exoccipital-opisthotic complex.—Only MCNA 7439 has preserved the right exoccipital-opisthotic complex, and only the base of the right paroccipital process is preserved. The contribution of the exoccipital-opisthotic complex to the occipital condyle cannot be observed, as the matrix obscures the surface where the suture between the exoccipital-opisthotic complex and the basioccipital should be. But it can be confirmed that the exoccipital-opisthotic complex forms the lateral margin of the foramen magnum.

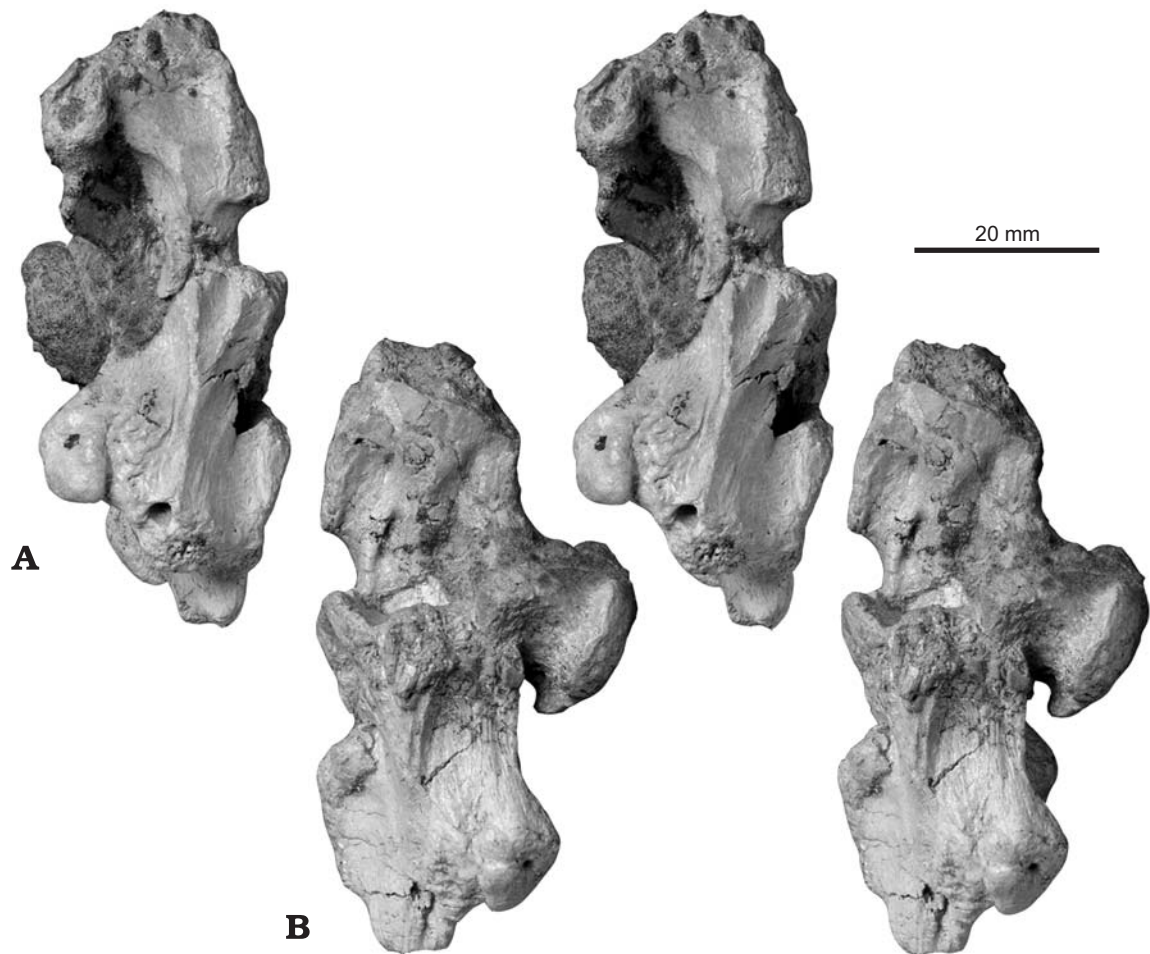


Fig. 3. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), paratypic braincase (MCNA 7439). Stereopairs in right lateral (A) and left lateral (B) views.

In posterior view, the exit for the hypoglossal nerve (XII) could be located in the exoccipital-opisthotic complex near the occipital condyle, though the iron oxides hinder the observation of this area.

Prootic.—Only MCNA 7439 has preserved the right prootic. This element is fused to the anterior surface of the exoccipital-opisthotic complex. Two ridges appear near the base of the ventral margin of the paroccipital process (Figs. 3A, 4C). The posteriormost ridge—probably formed by the exoccipital-opisthotic complex—is sharp and prominent, and the anteriormost or crista prootica is less prominent. The crista prootica extends ventrally to the basipterygoid process, although it is truncated at the height of the occipital condyle. In lateral view, between these two ridges, opens the metotic foramen. This foramen, filled by iron oxides, is ellipsoid. Though the metotic foramen run the glossopharyngeal (IX), vagus (X), and accessory (XI) cranial nerves, as well as the jugular vein (Chatterjee and Zheng 2002, 2005). Anterior to this foramen there is a broken surface where the crista prootica is truncated, showing a small channel. This channel probably belongs to the foramen of the facial nerve (VII). A groove begins ventral to this opening and extends ventrally

to the basipterygoid processes; the crista prootica occurs in its anterior margin. This groove is probably for the branch of the facial nerve (VII). As the laterosphenoid and orbitosphenoid are not preserved, only the posterior margin of the trigeminal nerve (V) is visible, anterior to the crista prootica (Figs. 3A, 4C). This foramen is the largest one of the braincase. Ventral to this opening is a groove, which is anterior and shorter than the one for the foramen of the facial nerve (VII). This groove is probably for the mandibular and/or maxillary branches of the trigeminal nerve (V). In medial view, posterior to the margin of the trigeminal nerve (V), there is a deep groove and, dorsal to it, a small foramen. A similar foramen is present in *Bonattitan reigi* (Martinelli and Forasiepi 2004) and in an indeterminate titanosaur from Patagonia (Paulina Carabajal et al. 2008). Both structures are probably for cranial vascularization.

Basioccipital-basisphenoid complex.—This complex forms the floor of the braincase. Only MCNA 7439 preserves the occipital condyle. The basioccipital probably forms the occipital condyle, which is slightly heart-shaped in posterior view, and its neck. The neck of the occipital condyle is short and wide, and it has a concave dorsal surface. When the

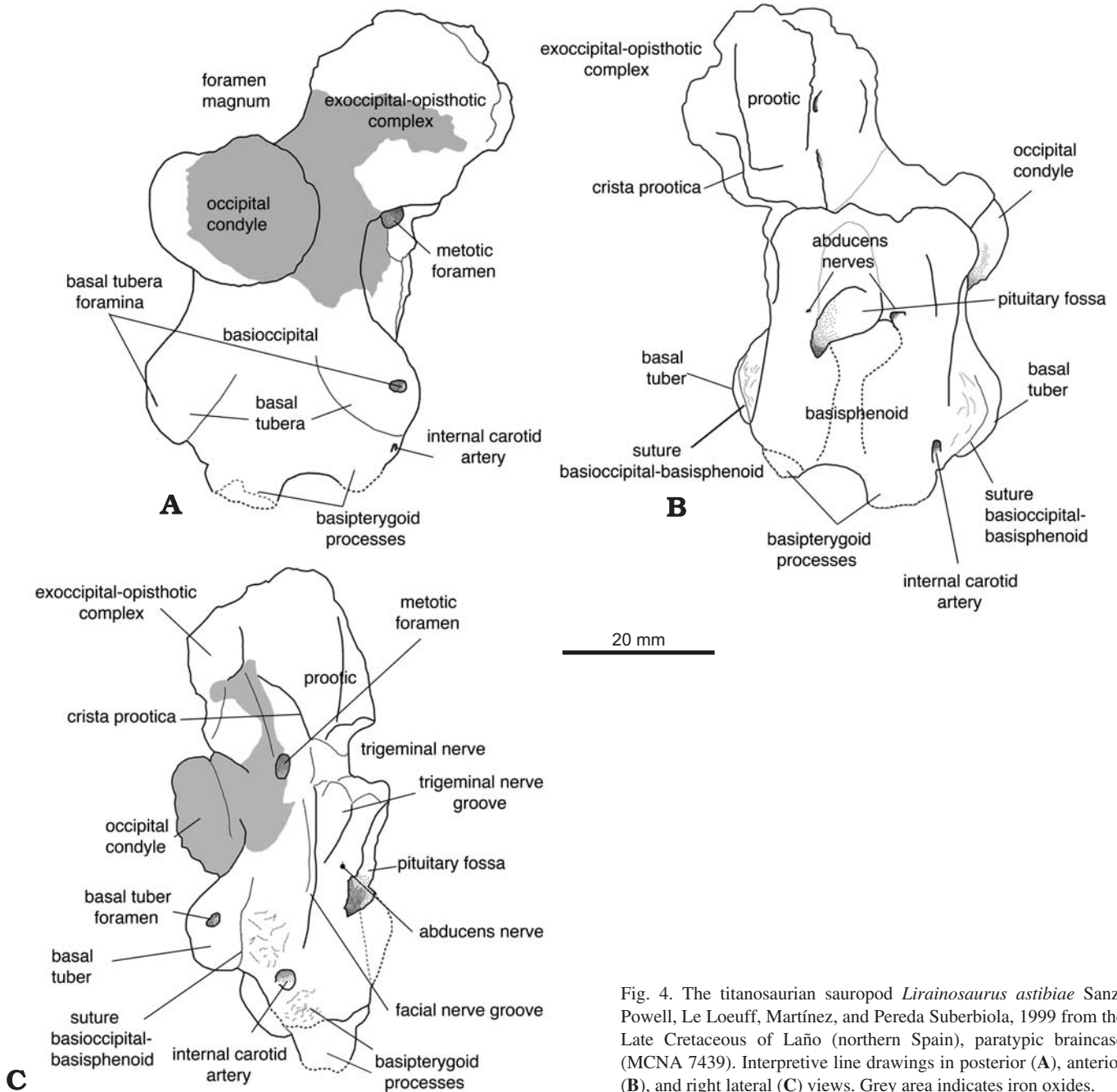


Fig. 4. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), paratypic braincase (MCNA 7439). Interpretive line drawings in posterior (A), anterior (B), and right lateral (C) views. Grey area indicates iron oxides.

basicranium is oriented vertically, the prootic and the base of the basipterygoid processes are aligned in the same vertical plane, the floor of the braincase is horizontal and the occipital condyle projects posteroventrally. It can be inferred that the occipital condyle is wider than the foramen magnum, as is common in other titanosaurs.

The basioccipital shows a median cavity for the pons variolii (Fig. 7A), which is situated in the posterior surface of the floor of the braincase (as in *Jainosaurus septentrionalis* ISI R 162 in Table 1; Chatterjee and Rudra 1996). More anteriorly, the floor of the braincase is pierced by the foramina for the abducens nerve (VI). The surface of the basioccipital below the occipital condyle and between the basal tubera is con-

tinuous and smooth in MCNA 7439, and exhibits a small ridge joining the basal tubera in MCNA 13913 (Figs. 5A, 7C). This surface does not have any median subcondylar foramen, recess, depression or pit. The basioccipital forms the basal tubera, which are rounded, wide and robust and postero-laterally oriented. A foramen pierces the distal surface of each basal tuber, a feature unknown in other titanosaurian basicrania (Figs. 2A, 3, 4A, C, 5A, 6, 7B, C, 8B). Anterior to the suture between the basioccipital and basisphenoid, a rugose zone extends in lateral view, probably for muscle attachment (Curry Rogers and Forster 2004).

In MCNA 13913, the lagena of the osseous inner ear is exposed by fracture, and can be observed in right lateral view

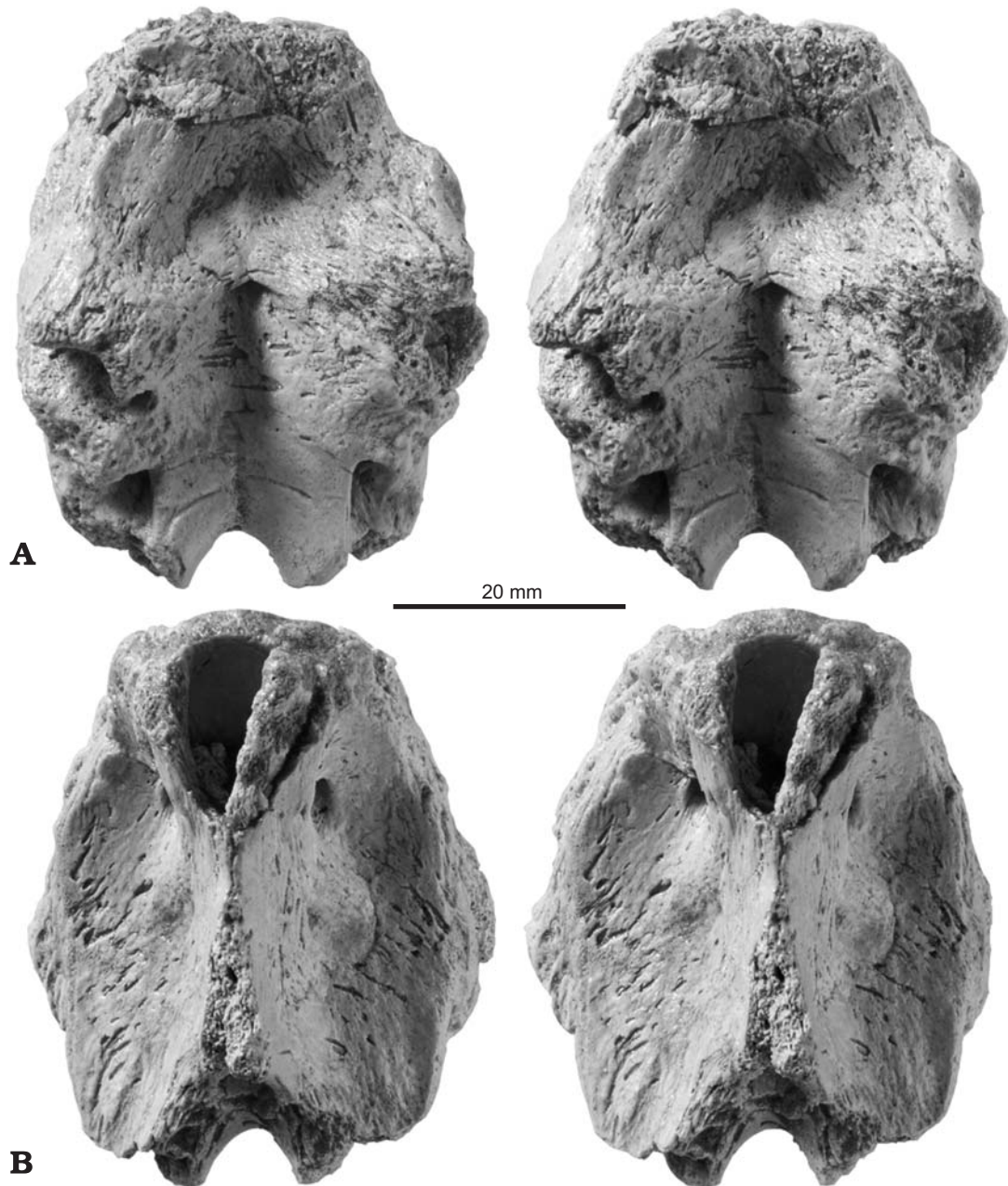


Fig. 5. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), referred braincase (MCNA 13913). Stereopairs in posterior (A) and anterior (B) views.

(Figs. 6, 8B), surrounded by a rugose surface to receive the prootic. Posterior to it, the metotic fissure runs ventrally to the basal tubera.

The basisphenoid forms the basiptyergoid processes, but in both specimens of *Lirainosaurus* these processes are broken at their base. Their cross-section is slightly triangular and flattened anteroposteriorly. The foramina for the internal carotid arteries are near the base of the basiptyergoid processes, at the ventral end of the crista prootica. Each channel runs inside the basisphenoid to open in the floor of the pituitary fossa.

Parasphenoid.—The parasphenoid is fused with the basisphenoid. It forms the anterior wall of the pituitary fossa. In

both specimens of *Lirainosaurus* only the base of the parasphenoid rostrum is preserved, and the pituitary fossa is open dorsally. In anterior view, the dorsum sellae forms the posterior wall of the pituitary fossa, and separates the floor of the braincase and the pituitary fossa (Paulina-Carabajal and Salgado 2007). At both sides of the pituitary fossa the openings for the abducens nerve (VI) can be found (Figs. 2B, 4B, 5B, 8A). Their passages run inside the basisphenoid, without piercing the pituitary fossa, and exit in the floor of the braincase. In MCNA 13913 two small foramina appear anterior to the opening for the abducens nerve (VI), probably for cranial vascularization (Fig. 8B).

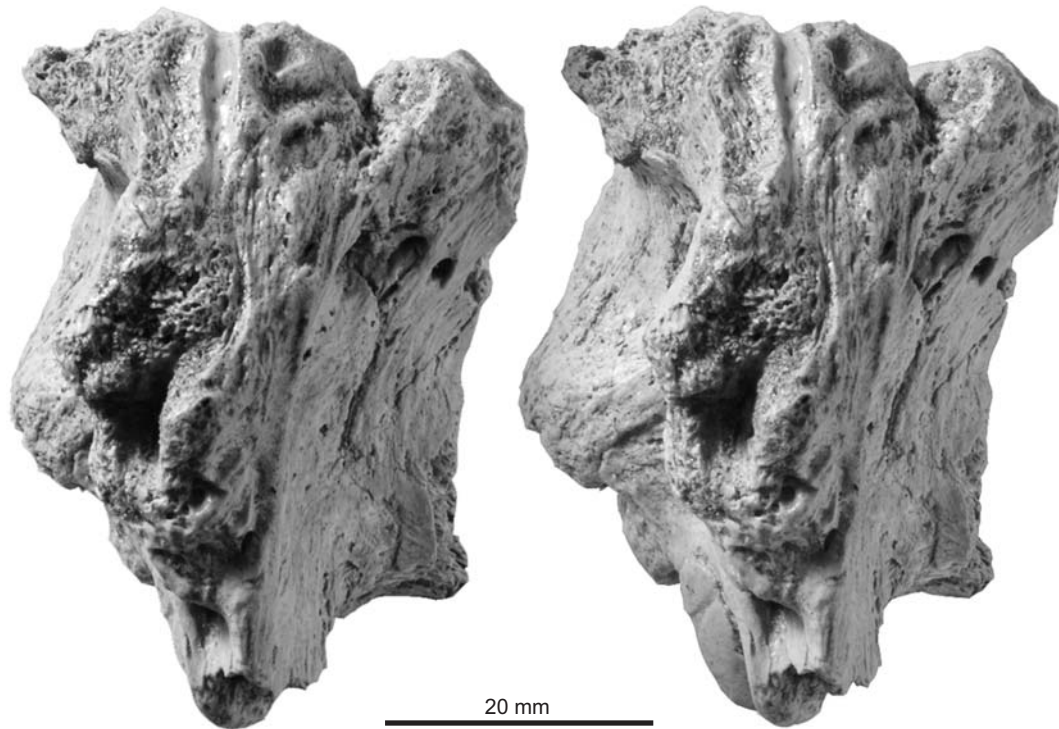


Fig. 6. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), referred braincase (MCNA 13913). Stereopairs in right lateral view.

Discussion

The braincases of *Lirainosaurus* are not completely ossified, and lack the dorsal braincase elements (laterosphenoid and orbitosphenoid), which means they could have belonged to subadult individuals. The occipital condyle is posteroventrally oriented, as occurs in most sauropods (Upchurch et al. 2004). Both specimens of Laño lack a recess in the basisphenoid, which is regarded as a synapomorphy of the Neosauropoda (Wilson 2002).

Lirainosaurus cannot be referred to the Diplodocoidea as it lacks synapomorphies of this clade, e.g., the basal region of the basiptyergoid processes do not form a markedly acute angle to the skull roof (Harris 2006). In addition, the occipital condyle of *Lirainosaurus* is not oriented ventrally (Upchurch 1995) and the basiptyergoid processes are not directed anteriorly, as commonly in diplodocids (Calvo and Salgado 1995). Unlike the Dicraeosauridae, *Lirainosaurus* does not present a “leaf”-like dorsolaterally-directed process on the crista prootica (Salgado and Calvo 1992; Upchurch 1998; Wilson 2002; Upchurch et al. 2004; Harris 2006); the angle between the basiptyergoid processes is approximately 40°, while it is approximately 20° in the Dicraeosauridae (Salgado and Calvo 1992; Upchurch 1995, 1998; Wilson 2002; Upchurch et al. 2004). The area between the bases of the basiptyergoid processes is shallowly concave in *Lirainosaurus*, whereas dicraeosaurids present a long narrow pit extending caudally beneath the rostral part of the braincase (Upchurch 1998; Upchurch et al. 2004; Harris 2006). In *Lirainosaurus*, the basal

tubera breadth is much broader than the occipital condyle, whereas in the Dicraeosauridae it is narrower (Wilson 2002).

The anatomy and position of the foramina of the braincases MCNA 7439 and MCNA 13913 indicate that both belong to the Titanosauria. At least three of the morphological attributes observed in titanosaurian braincases (Paulina Carabajal et al. 2008) are present in *Lirainosaurus*: the complete fusion between the prootic and the exoccipital-opisthotic complex; a single trigeminal foramen that is large and located just below the crista antotica; and an oval metotic foramen that is as large as the exit of cranial nerve V, which is visible in lateral view. In addition, both braincases share several features with other titanosaurian braincases, i.e., the presence of a dorsal concave surface in the occipital condyle, and its posteroventral orientation. The median cavity for the pons variolii is commonly present in titanosaurian braincases, such as in *Jainosaurus septentrionalis* (Chatterjee and Rudra 1996), *Rapetosaurus krausei* (Curry Rogers and Forster 2004) and an indeterminate titanosaur from Patagonia (Paulina-Carabajal and Salgado 2007). MCNA 7439 also shares with other titanosaurs a high ratio (more than 1.2) between the mediolateral width of the paired basal tubera and the mediolateral width of the occipital condyle (Upchurch et al. 2004). Wilson (2005) noted that the braincases of derived titanosaurs, such as *Nemegtosaurus*, *Quaesitosaurus*, and *Jainosaurus septentrionalis* (Wilson et al. 2009), have a novel contact between the quadrate and the basal tubera. This feature cannot be confirmed in the braincases of *Lirainosaurus*.

As in *Antarctosaurus* (Huene 1929), *Saltasaurus* (Powell

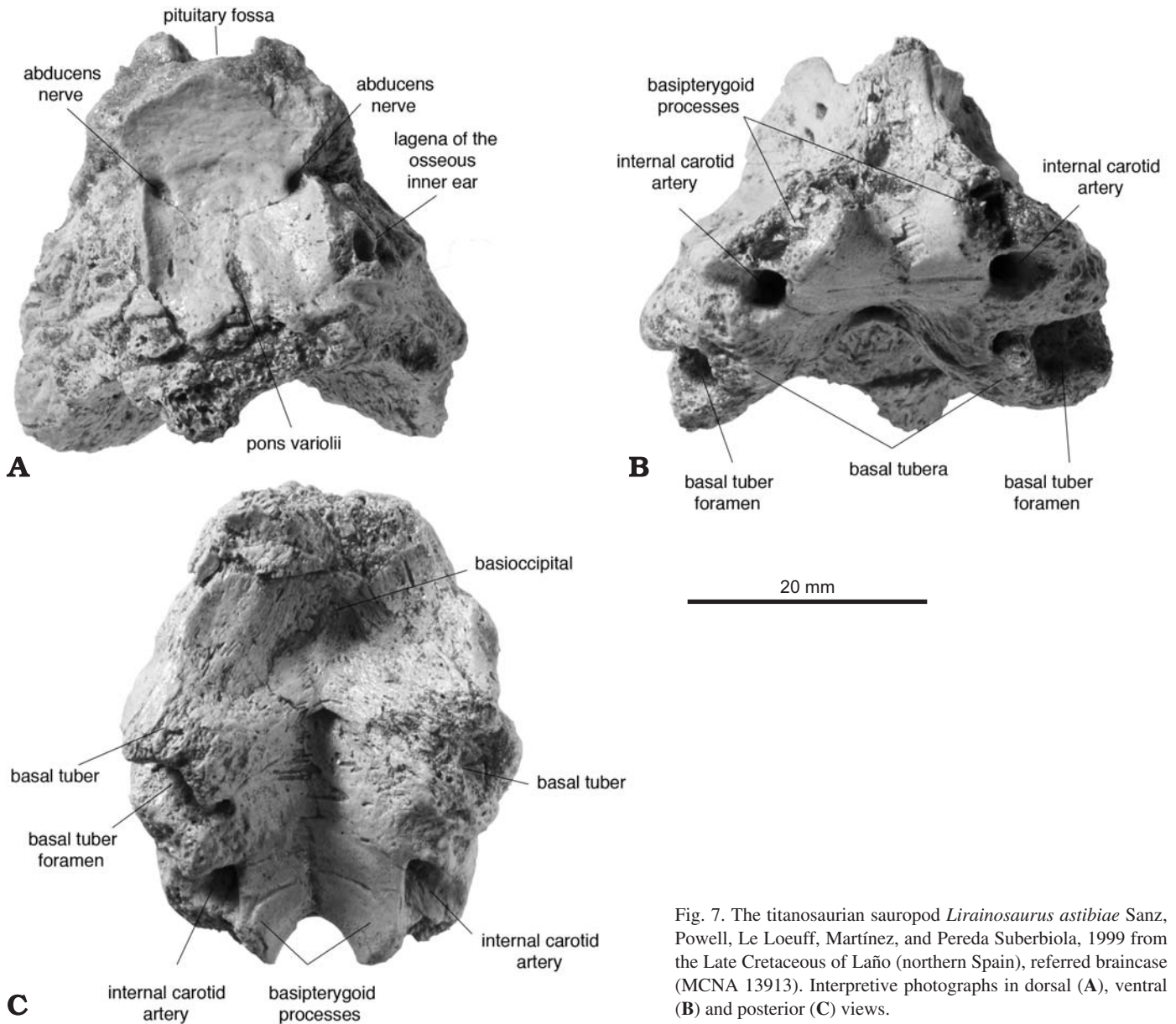


Fig. 7. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), referred braincase (MCNA 13913). Interpretive photographs in dorsal (A), ventral (B) and posterior (C) views.

1992, 2003), *Jainosaurus* (Chatterjee and Rudra 1996; Wilson et al. 2009), *Rapetosaurus* (Curry Rogers and Forster 2004), *Bonattitan* (Martinelli and Forasiepi 2004); *Nemegtosaurus* (Wilson 2005), an indeterminate titanosaur from Patagonia (García et al. 2008), and *Phuwiangosaurus* (Suteethorn et al. 2009), the occipital condyle of *Lirainosaurus* is heart-shaped to hemispherical, the neck of the occipital condyle has a concave dorsal surface, and the positions of the cranial foramina are similar in all specimens. In all of them but *Saltasaurus* the occipital condyle is posteroventrally oriented, and the basal tubera diverge from the midline. The rugose surface of the distal ends of the basal tubera is observed in *Rapetosaurus*, *Phuwiangosaurus* and the Patagonian titanosaur (García et al. 2008). Moreover, the basal tubera of *Lirainosaurus* are robust, as in *Rapetosaurus* (Curry Rogers and Forster 2004) and the Patagonian titanosaur (García et al. 2008), while in the other titanosaurs they are more or less sheet-like. This last condition

is generally observed in titanosauriforms, including the basal forms (Curry Rogers and Forster 2001; Upchurch et al. 2004).

The most striking difference between the braincases of *Lirainosaurus* and the above mentioned titanosaurs is the absence of a basioccipital depression between the foramen magnum and the basal tubera, a feature that is seen in several neosauropods (Wilson 2002), and a median subcondylar foramen. In *Lirainosaurus*, the surface of the basioccipital below the occipital condyle and between the basal tubera does not show any median subcondylar foramen, unlike *Saltasaurus*, *Rapetosaurus*, *Nemegtosaurus*, and *Phuwiangosaurus* (Powell 1992: fig. 1; Powell 2003: pl. 19; Curry Rogers and Forster 2004: figs. 23, 24; Wilson 2005: fig. 11; Suteethorn et al. 2009: fig. 9), but the closure of this foramen could be related with the ontogeny (Ariana Paulina Carabajal, personal communication 2010). Some of the characters discussed above are summarised in Table 2.

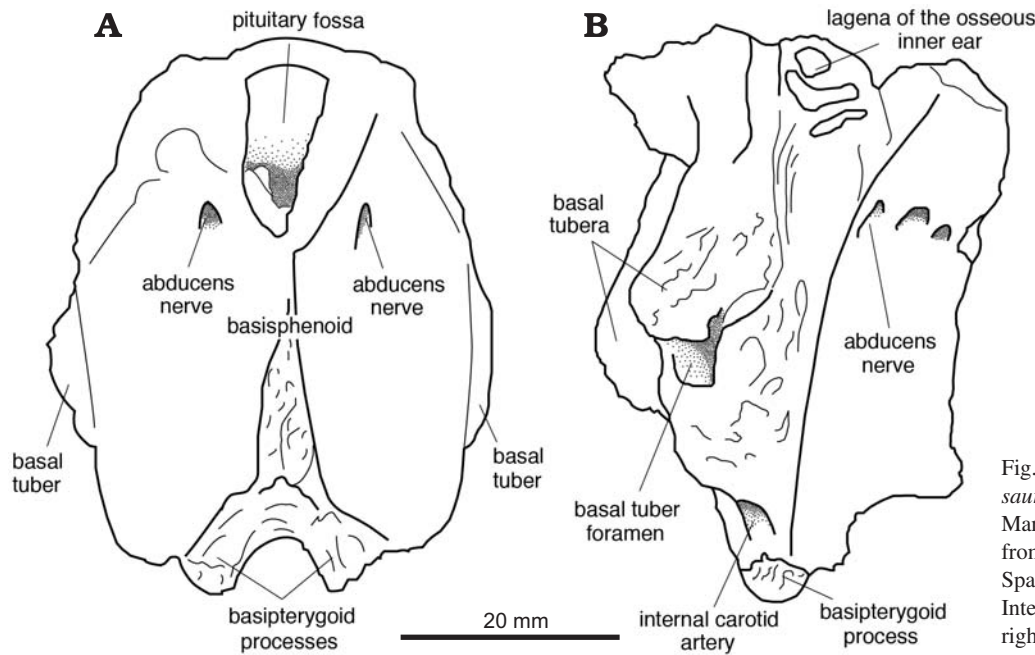


Fig. 8. The titanosaurian sauropod *Lirainosaurus astibiae* Sanz, Powell, Le Loeuff, Martínez, and Pereda Suberbiola, 1999 from the Late Cretaceous of Laño (northern Spain), referred braincase (MCNA 13913). Interpretive drawings in anterior (A) and right lateral (B) views.

Lirainosaurus can also be compared with a few titanosaurian braincases described so far from Europe (see Introduction and Table 1): two braincases from southern France, one belonging to *Ampelosaurus* (Le Loeuff et al. 1989; Le Loeuff 2005), and one juvenile specimen from Romania (Weishampel et al. 1991). The latter, a small braincase associated with a skull roof that has been assigned to *Magyarosaurus dacus* by Weishampel et al. (1991), is in need of revision (Zoltan Csiki, personal communication 2008). Lack of fusion between the floor and the walls of the braincase indicates the immaturity of the individual (Weishampel et al. 1991). The position of the cranial foramina seems similar to that observed in *Lirainosaurus*, but the basal tubera are more rounded in both Laño specimens than in the Transylvanian skull. The occipital condyle of MCNA 7439 resembles that of a partial skull of *Ampelosaurus atacis* from the Campagne-sur-Aude locality (Aude Département) of Languedoc, France in that it is roughly hemispherical and has a dorsal

concavity (Le Loeuff 2005). With regard to the braincase of an indeterminate titanosaur Patrick and Annie Méchin private collection, cast in MDE) from the Var Department of Provence, France (Le Loeuff et al. 1989), the position of the metotic foramen and the foramen for cranial nerve V is similar to the same foramina in both specimens from Laño.

Lirainosaurus exhibits two features that have never been described in other titanosaurian braincases from Europe and elsewhere: the absence of median subcondylar foramina, recesses, depressions or pits in the basioccipital, below the occipital condyle and between the basal tubera; and the presence of a foramen in the distal surface of each basal tubera. The first feature could be due to ontogenetic growth (the braincases are not fully grown but are regarded as from subadult individuals). The significance of the last feature is currently unclear, but could be related to basicranial pneumaticity. It is here regarded as an autapomorphic trait of *L. astibiae*.

The comparative anatomy of the titanosaurian brain-

Table 2. Distribution of various character states among the titanosaurs discussed in the text.

Character	Reference	<i>Lirainosaurus</i>	Other taxa
Basal tubera, anteroposterior depth: approximately half dorsoventral height (0); sheet-like, 20% dorsoventral height (1)	Wilson 2002, #48	(0)	<i>Nemegtosaurus</i> and <i>Saltasaurus</i> (1)
Basal tubera: blunt, rounded projections (0); thin and sheetlike (1)	Upchurch et al. 2004, #48	(0)	<i>Nemegtosaurus</i> , <i>Quaesitosaurus</i> and <i>Saltasaurus</i> (1)
Ratio of rostrocaudal depth: 0.25 (0); dorsoventral height of basal tubercula <0.25 (1)	Harris 2006, #71	(0)	<i>Nemegtosaurus</i> and <i>Saltasaurus</i> (1)
Ratio of mediolateral width of paired basal tubercula:mediolateral width of occipital condyle: <1.0 (0); 1.0-1.2 (1); >1.2 (2)	Harris 2006, #72	(2)	<i>Malawisaurus</i> , <i>Nemegtosaurus</i> , <i>Rapetosaurus</i> and <i>Saltasaurus</i> (2)
Basioccipital depression between foramen magnum and basal tubera: absent (0); present (1)	Wilson 2002, #50	(0)	<i>Saltasaurus</i> (1)
Basisphenoid fossa/foramen between foramen magnum and basal tubercula: absent (0); present (1)	Harris 2006, #73	(0)	<i>Rapetosaurus</i> and <i>Saltasaurus</i> (1)
Foramen in the distal surface of each basal tubera: absent (0); present (1)	this work	(1)	Unknown in other titanosaurs (0)

cases currently known in Europe (some of them yet unpublished) supports the idea of a high diversity during the Late Cretaceous, with at least four or five different species—including *Lirainosaurus astibiae* and *Ampelosaurus atacis*—present in the Campanian–Maastrichtian of the European archipelago (VDD, work currently in progress), as already suggested by Le Loeuff (1993, 1998) on the basis of the postcranial material.

Lirainosaurus astibiae has been included in several phylogenetic analyses, but there is not a consensus about its position within the Titanosauria (see Sanz et al. 1999; Wilson 2002; Upchurch et al. 2004; Díez Díaz et al. 2009, and references therein). Nevertheless, there is a consensus about its membership to the Lithostrotia (Upchurch et al. 2004). According to the phylogenetic analyses made by Sanz et al. (1999) and Calvo et al. (2007), *Lirainosaurus* is a member of the Eutitanosauria (“all titanosaurs closer to *Saltasaurus* than to *Epachthosaurus*”; see Salgado 2003: 20). Some authors had assigned *Lirainosaurus* to the Saltosauridae on the basis of vertebral features, but there is no strong evidence of its membership to this clade (Company et al. 2009).

No phylogenetic analysis based only on cranial features has been published to date, probably because of the small number of titanosaurian braincases discovered until now, and their striking features. *Lirainosaurus* and *Rapetosaurus* share some cranial features—like the rugose surface of the distal ends of the basal tubera, and their robustness—that are not seen in the majority of the titanosaurian braincases known until now. Some differences between *Lirainosaurus* and *Saltasaurus*, like the orientation of the occipital condyle and the morphology of the basal tubera, could indicate that *Lirainosaurus* is not a saltosaurine titanosaur, although we do not know if these features have a phylogenetic significance. Even though these results are preliminary, they are consistent with previous interpretations (e.g., Calvo et al. 2007) regarding *Lirainosaurus* as a non-saltosaurine eutitanosaur.

Conclusion

This work provides the first detailed description of two braincases (one paratype and one referred specimen) of the titanosaurian sauropod *Lirainosaurus astibiae* from the Laño locality (Iberian Peninsula). *Lirainosaurus* exhibits one feature that is unknown in other titanosaurian braincases: the presence of a foramen in the distal surface of each basal tubera. This feature is here regarded as diagnostic of *L. astibiae*. The absence of median subcondylar foramina, recesses, depressions or pits in the basioccipital may be another autapomorphy of *L. astibiae*, although explanation as an ontogenetic growth feature cannot be excluded. Other features observed in the two braincases, mainly the complete fusion between the prootic and the exoccipital-opisthotic complex, the position of the cranial foramina, and the shape and orientation of the occipital condyle, suggests that *Lirainosaurus* is a derived titanosaur.

Acknowledgements

This work is a version of the DEA (Master of Science in Palaeontology) of the senior author. We would like to thank José Carmelo Corral and Jesús Alonso (MCNA, Vitoria-Gasteiz, Spain) for allowing access to the material in their care, Zoltan Csiki (University of Bucharest, Romania) for providing information about the titanosaurian braincase of Pui (Romania), Francisco Ortega (Universidad Nacional de Educación a Distancia, Madrid, Spain) for discussions on sauropod cranial anatomy and Imanol Gaztambide for the photographs. We would also like to thank Jeffrey A. Wilson (University of Michigan, Ann Arbor, USA), Jean Le Loeuff (Musée des Dinosaures, Espéraza, France), Ariana Paulina Carabajal (Museo Carmen Funes, Neuquén, Argentina) and Paul Upchurch (University College of London, UK) for critical reviews, which improved this manuscript. This research was supported by a predoctoral grant BES-2008-006370 associated to the project CGL2007-64061/BTE of the Ministerio de Ciencia e Innovación, Spain. This paper is a contribution of the project CGL2010-18851/BTE3. XPS acknowledges support from the Gobierno Vasco/EJ (GIC07/14-361).

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