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A Spanish saltasauroid titanosaur reveals Europe as a melting pot of endemic and immigrant sauropods in the Late Cretaceous

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Pedro Mocho ^{1,2,3,4} ✉, Fernando Escaso ³, Fátima Marcos-Fernández ^{3,5}, Adrián Páramo ^{3,6}, José Luis Sanz ^{3,7,8}, Daniel Vidal ^{3,9} & Francisco Ortega ³

A new lithostrotian titanosaur, *Qunkasaura pintiquiniestra* gen. et sp. nov., is described based on a single partial skeleton from the late Campanian-early Maastrichtian fossil-site of Lo Hueco (Cuenca, Spain). This new taxon is supported by an exclusive combination of characters that highlights strong convergences with members of the South American Aeolosaurini. *Qunkasaura* allows to reorganise the complex phylogenetic relationships of the increasingly diverse finicretaceous sauropods of Europe. Phylogenetic analyses places *Qunkasaura* within Saltosauridae and possibly Opisthocoelicaudiinae, together with *Abditosaurus*. A new clade is established, Lohuecosauria, including *Saltasaurus*, *Lohuecotitan*, their most recent common ancestor and all its descendants. Two distinct Ibero-Armorican Campanian-Maastrichtian saltasauroid lineages are recognised: (i) Lirainosaurinae that is exclusive from Europe, and (ii) a saltosaurid lineage with possible opisthocoelicaudiine affinities, with a Laurasian distribution. Lirainosaurinae was a relict lineage including possible dwarf forms that evolved in isolation after reaching Europe before the Late Cretaceous through the Apulian route. The occurrence of opisthocoelicaudiines in Europe may be the result of a Late Cretaceous interchange between Europe and Asia. No evidence of insular dwarfism is found in the Ibero-Armorican opisthocoelicaudiines suggesting that they may have been newcomers to the area that arrived before the ‘Maastrichtian Dinosaur Turnover’ in southwestern Europe.

Titanosauria was a successful group of sauropod dinosaurs that experienced an important event of diversification in the Early Cretaceous, with the establishment of several distinct lineages including Lithostrotia^{1,2}. Lithostrotians dominated the Late Cretaceous sauropod fauna and were represented by two main groups, the saltasauroids, and colossosaurs, including from small forms to the largest known land animals^{1–4}. They survived until the Cretaceous-Paleogene boundary, when they became extinct as all other non-avian dinosaurs^{5,6}. In the last two decades, the description of new titanosaurs, as well as, the systematic reevaluation of old taxa, have shed light on the complex phylogeny of the clade^{1,2,4,7–10}. In this context, the

Campanian-Maastrichtian strata of the European Ibero-Armorican domain are known by a rich fossil record of titanosaurs showing a diverse fauna composed by, at least, six taxa^{11–18} whose systematics remains unclear, probably due to the scarcity of partially complete titanosaurian specimens or unquestionable associations of remains to the same species.

The discovery in 2007 of the Lo Hueco fossil-site in Cuenca (Spain) provided an opportunity to shed light on this complex systematic scenario. Lo Hueco is a Campanian-Maastrichtian multi-taxic bonebed from the Villalba de la Sierra Formation that has yielded more than 10,000 fossils of which nearly half are titanosaurian remains, including several partial

¹Instituto Dom Luiz, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa, Portugal. ²Departamento de Geologia, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa, Portugal. ³Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia (UNED), Las Rozas de Madrid, Spain. ⁴The Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, CA, USA. ⁵Facultad de Bellas Artes, Universidad Complutense de Madrid, Madrid, Spain. ⁶Centro de Interpretación Paleontológica de La Rioja, Government of La Rioja, La Rioja, Spain. ⁷Unidad de Paleontología, Universidad Autónoma de Madrid, Madrid, Spain. ⁸Real Academia de Ciencias Exactas, Físicas y Naturales, Madrid, Spain. ⁹Department of Organismal Biology, University of Chicago, Chicago, IL, USA. ✉e-mail: p.mochopaleo@gmail.com

skeletons^{15,19}. Here, it is described a new titanosaur from the Lo Hueco site, based on an articulated and partially associated skeleton that corresponds to one of the most complete specimens found in Europe. Additionally, it is also proposed a new phylogenetic hypothesis including nearly all European titanosaurs from the Campanian-Maastrichtian interval. The description of this new form reveals, for the first time, the presence of at least two distinct saltasauroid lineages in the Ibero-Armorican domain, and supports the establishment of a new saltasauroid clade. This new form is characterised by its peculiar tail morphology, which converges with that of members of the Gondwanan Aeolosaurini clade.

Results

Systematic palaeontology

Sauropoda Marsh 1878

Titanosauria Bonaparte and Coria 1993

Lithostrotia Upchurch et al. 2004

Saltasauroidea Powell 1992

Lohuecosauria new taxon

Etymology

After the Spanish titanosaur *Lohuecotitan pandafilandi*.

Definition

Lohuecosauria is phylogenetically defined as *Saltasaurus loricatus*, *Lohuecotitan pandafilandi*, their most recent common ancestor and all its descendants.

Qunkasaura pintiquiniestra gen. et sp. nov.

Holotype

A partial skeleton referred as HUE-EC-04 was found in articulation to partial association (the disarticulated remains had low dispersion in the field, Fig. 1C–E). The complete set is referred to a single individual being composed by an incomplete posterior cervical neural spine (HUE-2981), ten dorsal vertebrae (some sectors were found in articulation; HUE-2979, HUE-2980 and HUE-2981), several dorsal ribs (HUE-2963, HUE-2966, HUE-2968, HUE-2971, HUE-2974–76), six fused sacral vertebrae (HUE-2957), the first eleven caudal vertebrae (HUE-2957), one middle caudal vertebra (HUE-2959), a partial right ulna (HUE-2967) and fragmentary metacarpal (HUE-2960), an almost complete pelvic girdle (two ilia, two ischia and two pubes; HUE-2957), a femur (HUE-2973, under preparation) and a right fibula (HUE-2977).

Etymology

Qunca (or *Kunca*) refers to the Andalusi city that, after its annexation to Castile in 1177, gave rise to several small villages around it, including that of Fuentes (Cuenca), where the fossil-site of Lo Hueco is located; *saura* is the traditional suffix from the Latinised form of the Greek word for 'lizard'. In this case, it is used in the feminine extending the reference to Antonio Saura, one of the most important painters of the 20th century in Spain, who developed an important part of his activity from Cuenca. The specific name *pintiquiniestra* refers to a character sometimes interpreted as a giantess: the Queen Pintiquiniestra from one of the novels that drove Don Quixote de la Mancha, the character created by Miguel de Cervantes in the 17th century, mad.

Type locality and horizon

Lo Hueco fossil-site (Fuentes, Cuenca, Castilla-La Mancha, central Spain) (Fig. 1), *Margas, arcillas y yesos de Villalba de la Sierra* Formation, late Campanian-early Maastrichtian in age¹⁹.

Diagnosis

Lithostrotian titanosaur with the following autapomorphies (marked with an asterisk) and a unique combination of characters: round and rudimentary epiphyses in posterior cervical vertebrae; concave postzygapophyseal facets in posterior cervical and anterior dorsal vertebrae; pedicels in anterior dorsal vertebrae at centrum mid-length, not reaching the anterior and posterior rims*;

anterior centroparapophyseal (acpl), posterior centroparapophyseal (pcpl), anterior centrodiapophyseal (acdl) and posterior centrodiapophyseal (pcdl) laminae of similar length, resulting in a M-shaped structure in the lateral surface from the last anterior to ninth dorsal neural arches*; intraprezygapophyseal lamina (tprl) anteriorly pointed and projected at midpoint on anterior dorsal vertebrae*; tall posteriormost dorsal neural spines (two times the dorsoventral width of the posterior articular surface of the centrum); posterior dorsal neural spines markedly anteroposteriorly compressed (mediolateral width six times anteroposterior width)*; prespinal lamina (prsl) ventral section gradually becomes anteroposteriorly thicker*; ventral longitudinal groove on first to third sacral centra*; dorsomedial projected hook-shaped dorsal process on sacral plates*; marked anterior inclination of the anterior articular surface on anterior caudal centra; anterior caudal vertebrae prezygapophyses markedly anterodorsally projected; extreme anteriorly displaced postzygapophyses on anterior caudal vertebrae located at the level of the anterior articular facet; anterior caudal neural spines anteriorly projected; maximum dorsoventral height of iliac blade above the pubic peduncle; pubis corresponds to 118% of the ilium*; mediolaterally constricted at midpoint acetabular surface of ischium; flat fibular lateral trochanter; straight fibular shaft.

Descriptions and comparisons

The poorly preserved posterior cervical neural spine is laterally expanded, like the referred posterior cervical vertebra of *Garrigatitan*¹⁷ and some members of Lognkosauria²⁰. The neural spine is markedly deflected posteriorly, with round and rudimentary epiphyses (Supplementary Fig. 1A, B), unlike other European taxa^{13,16,17}. It has pronouncedly concave postzygapophyseal facets. The presence of epiphyses is considered characteristic of *Qunkasaura*, as they are absent in most titanosaurs^{9,20}. Ten articulated-to-associated dorsal vertebrae are preserved (Fig. 2A–E). The anterior and posteriormost centra have a strongly convex anterior articular surface (Fig. 2E) as in most macronarians^{21,22,23}. Some lirainosaurines^{15,24} have lost this strongly convex anterior articular surface in the posterior section of the dorsal series. The ratio of mediolateral width to dorsoventral height of the posterior articular surface in the anterior dorsal centra is greater than 1.3 as in *Abditosaurus*¹⁸ and *Opisthoelicaudia*²⁵, differing from the more subcircular centra of lirainosaurines^{15,26}. The lateral pneumatic fossa of the centrum is eye-shaped, which is set within a fossa as in many somphospondylans²¹ (Fig. 2D), and the anterior one has an acute posterior edge like that of macronarians^{21,27}. Some dorsal vertebrae present sub-vertical struts within the pneumatic fossa as in *Lirainosaurus*²⁶, *Mansourasaurus*⁷, and some dorsal vertebrae of *Opisthoelicaudia*²⁵. A developed ventral keel is only present in the second dorsal vertebra (being incipient in the first one; Fig. 2B). A ventral keel in anterior dorsal centra is absent in *Abditosaurus* and *Ampelosaurus*¹⁸. The ventral surface of the centrum is smoothly transversely concave in the middle dorsal centra (Supplementary Fig. 1I), like the condition of *Abditosaurus*; being transversely convex in the remaining anterior and posterior dorsal centra¹⁸. The ventral surface is also transversely concave in lirainosaurines^{13–15} and *Opisthoelicaudia*²⁵. Cervical and dorsal vertebrae have an internal camellate bone tissue as in titanosauriforms^{27–29}.

The pedicels of the neural arch are placed at midpoint of the anterior and middle dorsal centra not reaching the anterior and posterior articular surfaces of the centrum, an autapomorphy of *Qunkasaura* (Fig. 2C, D). The parapophysis migrates rapidly from an anteroventral position in the first dorsal centrum to a full-placed position in the neural arch of the third vertebra (Fig. 2D). The parapophysis is supported by the acpl and a single pcpl, differing from the double pcpl present in some sauropods such as the saltasauroids *Lohuecotitan*¹⁵, *Saltasaurus*, *Opisthoelicaudia*^{27,29} and *Paludititan*. The diapophysis is ventrally supported by the acdl and pcpl, bordering a subtriangular centrodiapophyseal fossa (cdf). The acpl, pcpl, acdl and pcpl have a similar length and angle resulting in an autapomorphic M-shaped laminar structure well-visible in lateral view from the last anterior to the ninth posterior dorsal vertebra (Fig. 2C). The transverse processes are laterally projected throughout the dorsal series, differing from the dorso-laterally projected processes of *Lirainosaurus* or *Atsinganosaurus*^{14,26}. In the mid-posterior dorsal vertebrae, there is a distinct flat surface near the

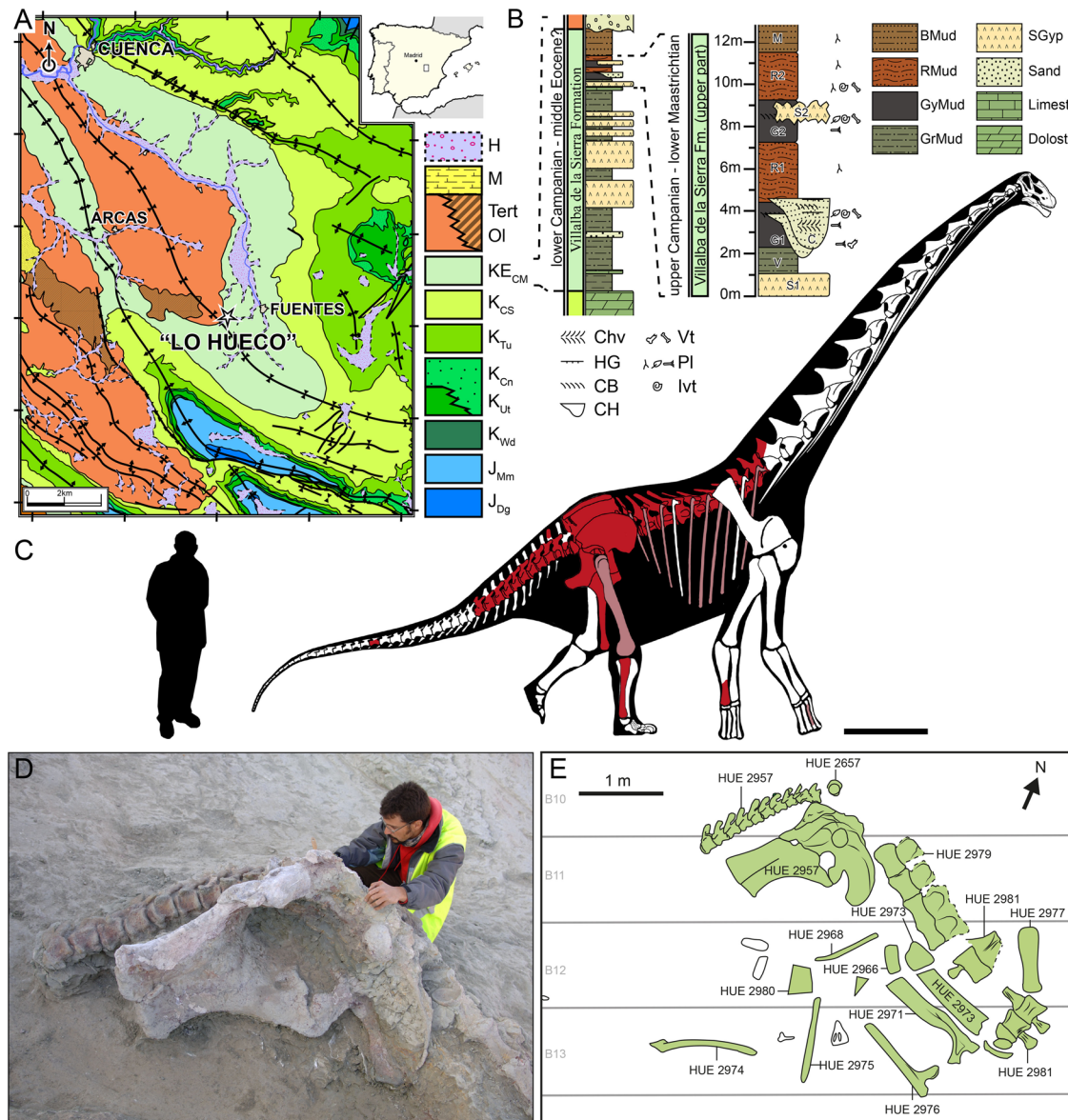


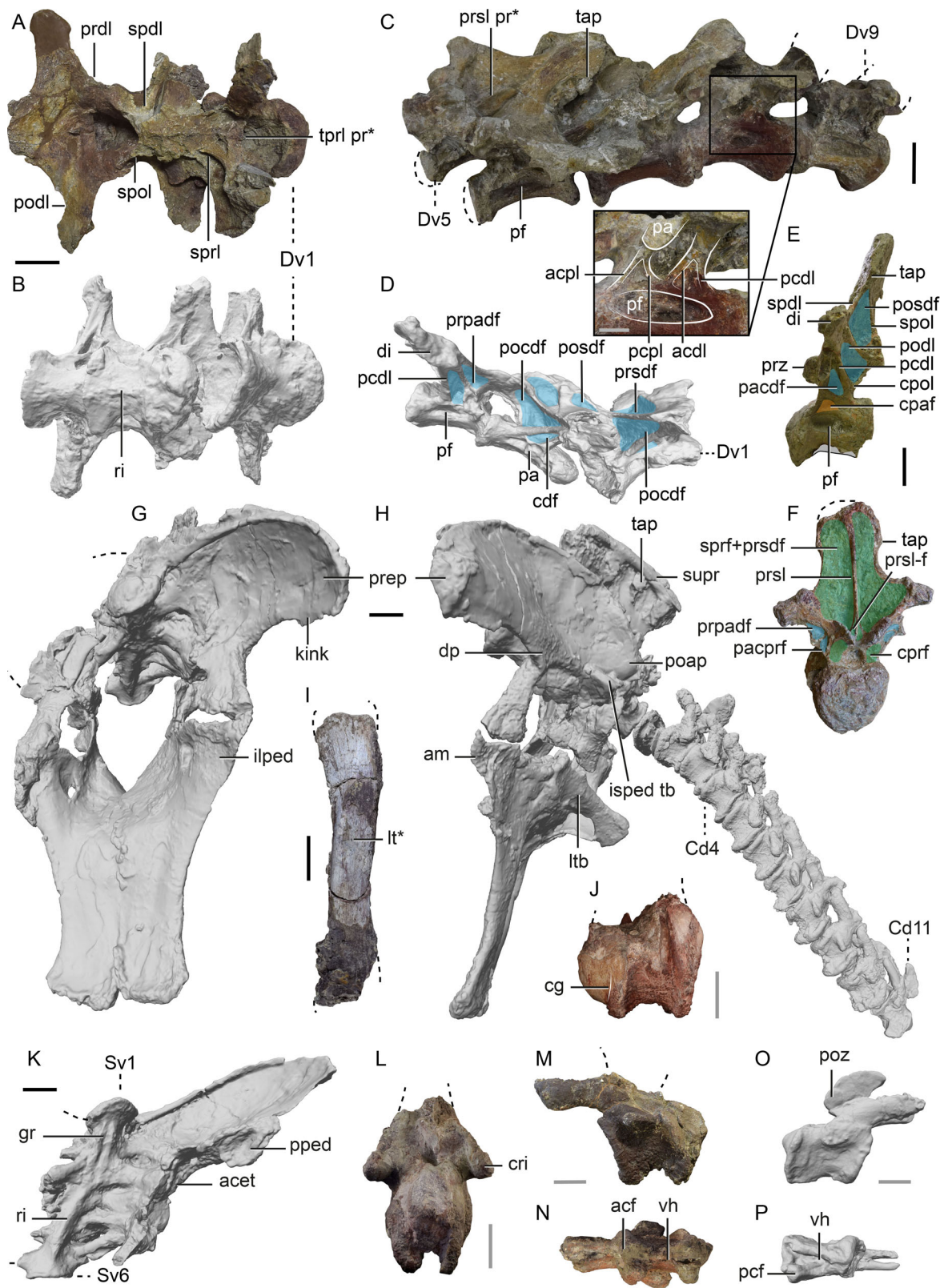
Fig. 1 | Geographic and geological setting of the palaeontological site of Lo Hueco. A geological map of Cuenca Province (Spain); (B) general stratigraphic column of the Villalba de la Sierra Formation and the Lo Hueco fossil site (based on^{19,68}). Schematic skeletal reconstruction in right lateral view, with indication of the recovered elements in red (C). Type specimen of *Qunkasaura pintiquiniestra* gen. et sp. nov. (HUE-EC-04) in the field and; (D) the field map of part of the elements (in light green) that compose HUE-EC-04 (E). Abbreviations: *BMud* brown mudstone,

CB cross-bedding, *CH* channel, *CM* Campanian-Maastrichtian, *Chv* chevron, *Cn* Coniacian, *CS* Campanian-Santonian, *Dg* Dogger, *Dolost* Dolostone, *Fm.* Formation, *GrMud* green mudstone, *GyMud* grey mudstone, *H* Holocene, *HG* hardground, *Ivt* invertebrate fossils (molluscs), *J* Jurassic, *K* Cretaceous, *Limest* Limestone, *M* Miocene, *Mm* Malm, *Oi* Oligocene, *PI* plant fossils, *RMud* red mudstone, *Sand* sandstone/siliciclastic stone, *SGyp* sulphate stone, *Tert* indeterminate Tertiary, *Tu* Turonian, *Ut* Utrillas Fm. (Albian-Cenomanian), *Vt* vertebrate fossils, *Wd* Wealden.

diapophyses and well-visible in anterior view (Fig. 2F) shared by many titanosaurs^{27,29}. The postzygadiapophyseal lamina (podl) disappears in the middle and posterior dorsal vertebrae as in *Lohuecotitan*, *Paludititan*, *Opisthocoeleicaudia* and *Alamosaurus*^{22,24,30} reappearing in the last dorsal vertebrae (Fig. 2E). The anterior face of the middle and posterior neural arches is marked by a shallow and flat centroprezygapophyseal fossa (cprf) as in *Abditosaurus*¹⁸. The trpl has an autapomorphic triangular and anteriorly projected process on the anterior dorsal vertebrae (Fig. 2A, Supplementary Fig. 1C, F). The postzygapophyses are concave in the anterior dorsal vertebrae. The presence of concave postzygapophyseal facets in posterior cervical and anterior dorsal vertebrae (Supplementary Fig. 1B) is also considered as characteristic of *Qunkasaura* unlike *lirinosaurines*^{16,17}.

The neural spine of the anterior to the first posterior dorsal vertebra is markedly inclined posteriorly. In the last posterior vertebrae, the neural spine becomes subvertical, resulting in a dramatic change in the inclination

of the neural spine in the posterior section of the dorsal series in about two positions (Fig. 2C, E). The dorsal neural spines are markedly anteroposteriorly compressed (the mediolateral width is six times the anteroposterior length, an autapomorphy of *Qunkasaura*), unlike in *lirinosaurines*^{13,15,26} and other *saltsaurids*^{31,32} but similar to the condition of some *colossosaurs*² and *Abditosaurus*¹⁸. The spinoprezygapophyseal lamina (sprl) is present in the anterior dorsal neural spines ventrally converging with the prsl (it becomes rudimentary to absent in middle and posterior dorsal vertebrae). The anterior surface of the middle and posterior neural spines is delimited by the prezygadiapophyseal lamina (prdl), diapophysis and spinodiapophyseal lamina (spdpl). They enclose the spinoprezygapophyseal + prezygapophyseal spinodiapophyseal fossae (sprf + prsdf) (Fig. 2F). The prsl is medially restricted and well-developed, and its ventral portion is anteroposteriorly projected (Supplementary Fig. 1H), autapomorphy of *Qunkasaura*. No accessory spdpl is present in middle and



posterior dorsal vertebrae differing from the condition observed in most aeolosaurines³³. The posterior surface is delimited by a dorsoventrally short and single spinopostzygapophyseal lamina (spol). The postspinal lamina (posl) is well-developed and medially restricted in the ventral half of the spine. The spd and spol contact with an anteroposteriorly compressed triangular aliform process. The neural spines are transversely expanded and

have a round dorsal edge. The height of the posteriormost dorsal neural spine is twice the height of the posterior articular surface of the centrum (characteristic of *Qunkasaura*).

The sacrum has six sacral vertebrae (Fig. 2K), as in deeply nested somphospondylans^{2,27,29}. The anterior articular surface of the centrum of the first sacral vertebra is strongly convex. The posterior articular surface of the

Fig. 2 | Skeletal anatomy of *Qunkasaura pintiquirenstra* gen. et sp. nov. (HUE-EC-04). Anterior dorsal vertebrae (Dv1–Dv3, HUE-2981) in dorsal (A, anterior towards right side), ventral (B, anterior towards right side) and right lateral (D) views. Middle to posterior dorsal vertebrae (Dv5–Dv9, HUE-2979) in left lateral view (C). Posterior dorsal vertebra (Dv10, HUE-2980) left lateral (E) and anterior (F) views. Sacrum in articulation with pelvic girdle and caudal series (HUE-2957) in anterior (G), left lateral (H) and ventral (K, anterior towards top and the pubes and ischia were removed) views. Right fibula (HUE-2977) in lateral view (I). First caudal vertebra (HUE-2957) in right lateral view (J); third caudal vertebra (HUE-2957) in posterior view (L); seventh caudal vertebra (HUE-2957) in left lateral (M) and ventral (N, anterior towards left) views; eleventh caudal vertebra (HUE-2957) in right lateral (O) and ventral (P, anterior towards right) views. B, D, G, H, K, O and P correspond to 3D digital models (see Supplementary Note 5). Black dashed line: broken borders. Diapophyseal fossae are in blue, parapophyseal fossae are in orange, and prezygapophyseal fossae are in green. Abbreviations: * diagnostic, *acdl* anterior centrodiapophyseal lamina, *acet* acetabulum, *acf* anterior chevron facet, *acpl* anterior centroparapophyseal lamina, *Cd* caudal vertebra, *cdf* centrodiapophyseal fossa, *cg* cingulum, *cpaf* centroparapophyseal fossa, *cpol* centropostzygapophyseal lamina,

crpf centroprezygapophyseal fossa, *cri* caudal rib, *di* diapophysis, *dp* depression, *Dv* dorsal vertebra, *gr* groove, *ilped* iliac peduncle, *isped tb* tuberosity of the ischial peduncle, *lt* lateral trochanter, *ltb* lateral tuberosity, *pa* parapophysis, *pacdf* parapophyseal centrodiapophyseal fossa, *pacprf* parapophyseal centroprezygapophyseal fossa, *pcdl* posterior centrodiapophyseal lamina, *pcpl* posterior parapophyseal lamina, *pf* pneumatic foramen, *pcf* posterior chevron facet, *poap* posacetabular process, *podf* postzygapophyseal centrodiapophyseal fossa, *podl* postzygodiapophyseal lamina, *posdf* postzygapophyseal spinodiapophyseal fossa, *poz* postzygapophysis, *pped* pubic peduncle, *prep* preacetabular process, *prld* prezygodiapophyseal lamina, *prpadf* prezygapophyseal paradiapophyseal fossa, *prsd* prezygodiapophyseal spinodiapophyseal lamina, *prsl* prespinal lamina, *prsl-f* prespinal lamina fossa, *prsl pr* prespinal lamina process, *prz* prezygapophysis, *ri* ridge, *spdl* spinodiapophyseal lamina, *spol* spinopostzygapophyseal lamina, *sprf* spinoprezygapophyseal fossa, *sprl* spinoprezygapophyseal lamina, *supr* supraspinous rod, *Sv* sacral vertebra, *tap* triangular aliform process, *tprl pr* intraprezygapophyseal lamina process, *vh* ventral hollow. Black scale bar equals 100 mm, grey scale bar equals 50 mm.

last centrum is concave, unlike *Lohuecotitan*. The ventral surface of the fourth to sixth sacral centra have a keel (Fig. 2K), unlike *Atsinganosaurus*¹⁶ and *Garrigatitan*¹⁷, which have a keel in the third-to-fifth sacral vertebrae. In addition, there are two autapomorphic features: a ventral groove from the first to third sacral vertebrae (Fig. 2K), and a dorsomedially projected and hook-shaped process in the dorsal surface of the sacral plates. Sacral vertebrae are camellate unlike *Garrigatitan*¹⁷. The neural spines are completely fused preserving a well-developed supraspinous rod (Fig. 2H), common in titanosaurs³⁴ as occurs in *Lohuecotitan* and *Atsinganosaurus* but is rudimentary or absent in *Garrigatitan*^{15–17}.

Eleven articulated anterior caudal vertebrae and one isolated middle caudal vertebra were recovered (Fig. 2H, J–P, Supplementary Fig. 2). The first caudal vertebra has a biconvex centrum (Fig. 2J) as in the some saltasauroids (e.g. *Alamosaurus* and *Opisthocoelicaudia*^{25,35}) and differing from other Ibero-Armorican forms¹⁵. The remaining caudal vertebrae are markedly procoelous (Fig. 2L–P). The posterior condyle is constricted, and the apex of this convexity is displaced dorsally as in *Lohuecotitan*. In lateral view, the anterior articular surface of the centrum displays a pronounced anterior inclination (Fig. 2M–O) as in aeolosaurines³⁶ and unlike *Lohuecotitan*¹⁵, being considered a possible local autapomorphy of *Qunkasaura*. The ventral surface of the centrum exhibits a hollow bordered by ventrolateral ridges as occur in many titanosaurs^{28,29}. The caudal ribs are projected posterolaterally in dorsal view, surpassing the edges of the posterior articulation of the centrum; and the neural arch is displaced markedly anteriorly as in titanosauriforms²². The anterior caudal vertebrae of *Qunkasaura* preserve other features shared with aeolosaurines and considered as characteristic of this new taxon of Lo Hueco and allow to differentiate it from lirainosaurines: (i) prezygapophyses are markedly anterodorsally projected, reaching 92% of the total centrum length; (ii) postzygapophyses are located at the level of anterior articular surface of the centrum; and (iii) neural spine is anteriorly directed (Fig. 2O).

The ilia, pubes and ischia were found in articulation with the sacrum (Fig. 2G–H). The preacetabular process is anterolaterally projected (not laterally projected as in *Lohuecotitan* and *Garrigatitan*^{15,17}) and twisted in an oblique-to-subvertical plane (never reaching the subhorizontal position as in *Lohuecotitan*¹⁵). The dorsal edge of this process is smoothly round. The ventral edge of the pre-acetabular process bears a rough ventral kink (Fig. 2G) as in many titanosauriforms^{15,32}. Above the base of the pubic peduncle there is a flat to slightly concave triangular surface, distinct from the circular fossa present in *Garrigatitan*. This fossa is well-developed in some lirainosaurines³⁷. The maximum dorsoventral height of the iliac blade is located above the pubic peduncle (autapomorphic of *Qunkasaura*) differing from *Lohuecotitan* and *Garrigatitan*^{15,17}. There is a lateral tuberosity on the lateral side of the ischial peduncle. The pubis has a longitudinal lateral ridge as seen in many deeply nested titanosaurs^{29,32}. The distal end of the pubic blade is coplanar. *Qunkasaura* has a reduced ischium relative to the pubis (ischium to pubis proximodistal length ratio is 0.57) as in

Rapetosaurus, *Opisthocoelicaudia* and *Savannasaurus*^{32,38}. The pubis corresponds to 118% of the proximodistal length of the ilium, differing from many other titanosaurs, and considered an autapomorphy of *Qunkasaura*. The acetabular surface of the ischium is widely concave and mediolaterally constricted at midpoint like rebbachisaurids²⁹, and diagnostic of *Qunkasaura*. The ischiatic shaft has a coplanar position as in macronarians²³. The proximal plate of the pubic peduncle is anteroposteriorly shorter than proximodistally width, as in most titanosauriforms^{22,29,38}. The ridge for attachment of *M. flexor tibialis internus III* is visible in the lateral surface and no associated depression is present (Fig. 2H), like in several titanosauriforms²⁸. The forelimb and hindlimb elements are poorly represented and briefly described in Supplementary Note 1. The right fibula is a relatively robust and straight element (Fig. 2I), differing from *Lirainosaurus* and *Lohuecotitan*^{15,37}. The proximal end preserves a well-developed anteromedially directed crest, anteriorly directed, and not laterally bordered by a groove, unlike *Lohuecotitan*, *Lirainosaurus* and *Abditosaurus*^{15,18,37}. The lateral trochanter is oval as in other Ibero-Armorican forms^{15,18,37}, but the surface is flat, which is considered as characteristic for *Qunkasaura*. For an extended description see Supplementary Note 1.

Phylogenetic analysis

Two phylogenetic analyses were performed using the dataset of Mocho et al.⁹, which is based on Poropat et al.⁹ with equal and implied weights (Supplementary Note 2). The general topology obtained using the implied weight analysis (IWA, analyses II in the Supplementary Note 2) is better resolved (Fig. 3) than in the equal weighting analyses (EWA, analyses I in the Supplementary Note 2). All the analysed European titanosaurs were recovered within Lithostrotia, most within Saltasauroida. *Qunkasaura* is recovered as a saltasaurid saltasauroid, within *Alamosaurus* + (*Abditosaurus* + *Qunkasaura*) clade in the EWA. In the IWA, *Qunkasaura* is placed within Opisthocoelicaudiinae, which includes *Alamosaurus* + (*Opisthocoelicaudia* + (*Abditosaurus* + *Qunkasaura*)) (Supplementary Note 2; Fig. 3). *Abditosaurus* is placed as the sister taxon of *Qunkasaura*, and this relationship is maintained by four shared features (only by the first two in the EWA): (i) the anterior–middle dorsal diapophyses are elongated and dorsoventrally narrow (shared with brachiosaurids; C154); (ii) the anteroposterior width of the dorsal neural spines is approximately constant along the height of the spine (C159); (iii) the zygapophyseal articulation is between horizontal and less than 40° to the horizontal in anterior–middle dorsal neural arches (C337); and (iv) anteroposterior length of the centra shortens from anterior to posterior dorsal vertebrae (this is markedly abrupt in the last dorsal centra of *Qunkasaura*; C466). The relationship of *Qunkasaura* + *Abditosaurus* with *Opisthocoelicaudia* is supported by five synapomorphies in the IWA (Supplementary Note 2). Lirainosaurinae is recovered as monophyletic (supported here by six synapomorphies in the IWA) with a new configuration when compared

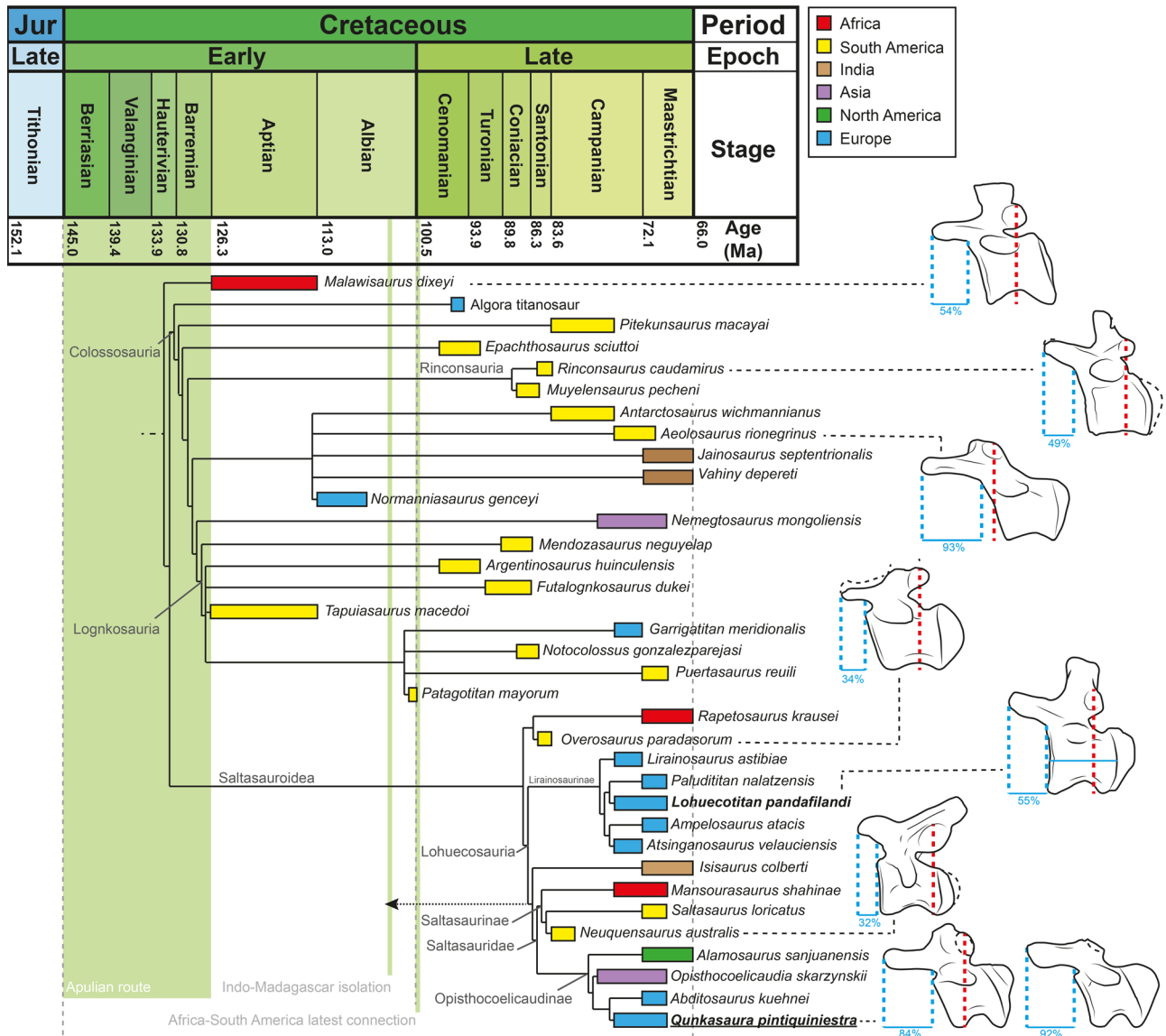


Fig. 3 | Phylogenetic relationships of *Qunkasaura pintiquirestra*. Time-calibrated phylogenetic tree of *Qunkasaura pintiquirestra* gen. et sp. nov. and other lithostrotian titanosaurs, and phylogenetic distribution of some distinct morphologies for anterior caudal vertebrae within Lithostrotia. Topology corresponds to a strict consensus without pruning ‘wild taxa’ from trees obtained with IWA and based on Mocho et al.³⁹ dataset. The box next to each taxon demarcates its temporal range (including stratigraphic uncertainty). Drawings of anterior caudal vertebrae from

*Malawisaurus dixeyi*⁶⁹, *Rinconsaurus caudamirus*⁷⁰, *Aeolosaur rionegrinus*³⁰, *Overosaurus paradasorum*⁴¹, *Lohuecotitan pandafilandi*, *Neuquensaurus australis*³¹ and *Qunkasaura pintiquirestra*. Green shading represents: (i) period when the Apulian route connected northeast Africa and southwest Europe; (ii) separation between South America and Africa, and (iii) isolation of Indo-Madagascar^{49,51,52}.

to previous studies^{4,16,17} including only European forms: *Liranosaurus* + ((*Lohuecotitan* + *Paludititan*) + (*Atsinganosaurus* + *Ampelosaurus*)). The remaining European titanosaurs included in our phylogenetic analyses (*Algora titanosaur*⁴⁰, *Normanniasaurus* and *Garrigatitan*) are retrieved as colossosaurians. However, these positions should be taken with caution because of the incompleteness of these taxa. The detailed description and comparison with the established European taxa, the presence of a set of exclusive features (including many autapomorphies), and the results of the phylogenetic analyses support the validity of *Qunkasaura* (see Supplementary Notes 2–4). A third analysis using the dataset of Silva Junior et al.³³ was performed to analyse the phylogenetic relationships of *Qunkasaura* with aeolosaurines and closely related forms. Herein, *Qunkasaura* was recovered as a sister taxon of *Abditosaurus*, with which it integrates the sister lineage of Saltosauridae. Saltosauridae is more poorly resolved than in the IWA based on the dataset of Mocho et al.³⁹, with a polytomy including *Opisthocoelicaudia*,

Mansourasaurus, Lirainosaurinae and Saltosaurinae. *Qunkasaura* is found to not be related with Aeolosaurini (analyses III in the Supplementary Note 2).

Discussion

The anterior section of the tail in *Qunkasaura* has several features that are considered characteristic of aeolosaurines (Supplementary Note 4). One of these features is the inclination of the anterior articular surface of the centrum³⁶. Along the second half of the anterior series, particularly from the fifth-to-eleventh element of the series, this anterior inclination becomes especially notable (less than 75° from horizontal) in *Qunkasaura*. This noteworthy condition, unique in *Qunkasaura* among saltasaurioids, is shared by some aeolosaurines and closely related forms^{10,30,41–44}. Additionally, the orientation of the neural spine in the anterior and middle caudal vertebrae is also an important feature, being used in several morphological datasets^{2,27}. An anterior inclination is generally common in many

titanosaurs (reaching no more than 80° from the horizontal plane) but some taxa can reach an extreme anterior deflection, including *Qunkasaura* and the members of *Aeolosaurini* and some related taxa^{10,30}. The eleventh caudal vertebra of *Qunkasaura* preserves one of the more extreme anterior deflections of a caudal neural spine recorded for a titanosaur. Another relevant feature is the position of the postzygapophysis in the anterior half of the centrum. This feature, which may be partially related to the anterior inclination of the anterior articular surface of the centrum, is present in *Aeolosaurus* and closely related taxa^{30,43,44}. Non-aeolosaurine lithostrotians preserve postzygapophyses located at the level of the midpoint of the anteroposterior width of the centrum or posteriorly such as saltasaurines, lognkosaurs and lirainosaurines^{2,15,31}. The saltosaurid *Qunkasaura* exhibits an extreme anterior displacement of the postzygapophyses, which are located at the level of the anterior articular surface, corresponding to one of the most extreme examples observed in lithostrotians. The significant development of the prezygapophyseal processes is another common feature of several aeolosaurines such as *Aeolosaurus*^{30,43,44} (i.e. the anteroposterior length of the prezygapophyseal processes is 113% and 93% of the anteroposterior centrum length in *Aeolosaurus colhuehuapensis* and *Aeolosaurus rionegrinus*, respectively). *Qunkasaura* seems to reach the maximum development of the prezygapophyseal process around the seventh caudal vertebra (92% of the anteroposterior centrum length). The acquisition of anterior caudal vertebrae with extreme anteriorly inclined anterior articular surface of the centrum, anteriorly displaced postzygapophyses, anteriorly elongated prezygapophyseal processes, and anteriorly projected neural spines characterise the peculiar morphology of aeolosaurine tail and closely related taxa. However, the phylogenetic results obtained here suggest that this morphology was achieved independently by *Qunkasaura* (Fig. 3).

The Ibero-Armorican domain corresponds to a large landmass of the European archipelago during the Campanian-Maastrichtian. The diversity of primary consumers in their terrestrial ecosystems is composed of small to large sauropods (including some putative dwarf forms⁴⁵) and ornithopods, but a full understanding of their complex structure remains to be clarified. Knowledge of the systematics of some Late Cretaceous titanosaurs from Ibero-Armorica is complex. Apart from *Lohuecotitan*, *Abditosaurus*, and now, *Qunkasaura*, the Ibero-Armorican titanosaurs are mainly represented by holotypes restricted to a single bone or a small set of associated bones plus referred material from the same fossil site where more than one titanosaur may be represented, which may result in chimaeric taxa.

Our phylogenetic analyses revealed that there were different lineages of lithostrotians in the Ibero-Armorican domain during the Late Cretaceous, recently suggested by some authors^{16,18,46}. Colossosaurian titanosaurs would be present in Europe since the late Early Cretaceous, with the presence of the Albian *Normanniasaurus* from France (Fig. 3). The Cenomanian titanosaur from the Algora (Spain) fossil site is placed here as an early branching colossosaur (unlike⁴⁰; Fig. 3). *Garrigatitan* is other European titanosaur that is placed here as a deeply nested lognkosaur, within Colossosauria, closely related to South American titanosaurs (Fig. 3). Our IWA suggests the presence of more than one distinct colossosaurian lineage in Europe, including lognkosaurs, some of which were already present in the late Early Cretaceous. The close relationship of the putative European colossosaurs to the Gondwanan taxa, especially South America forms, suggests that these lineages may have reached Europe via Africa, prior to the Cenomanian, possibly using the Apulian Route^{47–50}. The holotype of *Normanniasaurus* is very incomplete, but the detailed description of new sauropod material recently discovered in the Algora site might add new information about the phylogenetic affinities of these Cenomanian forms. The position of *Garrigatitan* should also be undertaken with caution; not only because the taxon is incomplete, but also, part of the tentatively referred material cannot be assigned confidently to the taxon (restricting the scoring of this taxon to the holotype and referred material or just to the holotype, should be an option to consider in future analyses).

Two distinct saltasauroid lineages have been identified during the Campanian-Maastrichtian in Europe, one corresponding to the Lirainosaurinae clade and a second one setting within Saltosauridae, and possibly within Opisthocoelicaudiinae (following IWA, Fig. 3). The

'mid'-Cretaceous fossil record of saltasauroids is poor, which limits our understanding of the paleobiogeographic relationships and timing of dispersal of the main lineages. Our phylogenetic analyses suggest a possible Gondwanan origin for the saltasauroids and, particularly, for the ancestors of the clade gathering Lirainosaurinae and Saltosauridae, which is named here as Lohuecosauria (Fig. 3). Lohuecosauria is supported by the following ten synapomorphies (following IWA): (i) dorsoventral height divided by posterior centrum height of the posteriormost cervical and anteriormost dorsal neural spines is 1.0 or greater (C19); (ii) the dorsoventral height divided by the centrum height of anteriormost caudal neural spines is 1.2 or greater (C32); (iii) stout ulna, ratio of the maximum mediolateral width of the proximal end to length ratio is 0.4 or greater (C50); (iv) the posterior surface of the basal tubera is not bordered laterally and ventrally by a raised and thickened lip (C100); (v) quadrangular coracoid (C218); (vi) strong bulge or tuberosity (site for *M. latissimus dorsi*) close to the lateral margin of the humeral posterior surface (C226); (vii) linea intermuscularis cranialis marked in the femoral anterior face (C257); (viii) the convex posterior articular surface in middle caudal centra is not dorsally displaced (C351); (ix) ratio of the maximum mediolateral width of the distal end to the proximodistal length is 0.30 or greater in the humerus (C370); (x) proximal end of the metatarsal V not expanded relatively to the shaft (C395). This clade is composed of Campanian and Maastrichtian taxa from Europe, Africa, South America, Asia (including India) and North America, and its origin may be in the Early Cretaceous, when the main lohuecosaurian lineages become established. Lohuecosaurians dispersal between Gondwana and Europe likely occurred during the establishment of the Apulian route (connecting Europe and Africa during the Early Cretaceous)^{47–50}. The lineage from which *Isisaurus* from India and, also, the non-lohuecosaurian saltasauroid *Rapetosaurus* from Madagascar should have dispersed into these areas before the Indo-Madagascar isolation (~105–108 Ma^{151,52}). The fossil record of lirainosaurines seems to be restricted to Europe, being recorded in the Ibero-Armorican and Hațeg realms, with medium- and small-sized forms. These small taxa, such as *Magyarosaurus*, *Paludititan* and *Lirainosaurus*, have been interpreted as a result of island dwarfism^{3,45,53,54}. The possible absence of this group outside Europe suggests Lirainosaurinae was endemic from this domain^{16,17}, that may have evolved in isolation, during the Late Cretaceous, possibly since the late Early Cretaceous. This is consistent with our current understanding about the Late Cretaceous faunas of Europe, which are characterised by the presence of numerous unique taxa, and the absence of several lineages from other paleobiogeographic areas^{55–58}. Some authors suggested a closer relationship of some Late Cretaceous taxa of Mongolia and Egypt to some of European lirainosaurines¹⁷, suggesting for a more complex paleogeographic scenario. However, we do not found evidence for the presence of Campanian-Maastrichtian titanosaurs with African affinities in Europe. Lirainosaurinae is recovered herein outside Saltosauridae.

The presence of a different saltasauroid lineage in the Ibero-Armorica during the Campanian-Maastrichtian is supported, related to Saltosauridae, and possibly corresponding to Opisthocoelicaudiinae (following IWA, Fig. 3). This lineage is composed by *Alamosaurus* as the sister taxa of a Eurasian lineage, composed by *Qunkasaura* + *Abditosaurus* and perhaps *Opisthocoelicaudia*. Opisthocoelicaudiines are restricted to Laurasia (i.e. Laramidia, Europe and Asia) and their origin may be in the late Early Cretaceous. The dispersal of opisthocoelicaudiines through North America, may have occurred during the Cretaceous faunal exchanges between North America and Asia through the Bering land bridge in Early and Late Cretaceous⁴⁹. Finally, the close relationship of *Opisthocoelicaudia* and *Qunkasaura* + *Abditosaurus* indicates a biotic interchange between Europe and Asia. This Asian-American influence in the lithostrotian faunas of the Ibero-Armorican island during the Late Cretaceous has also been observed in other European groups of vertebrates, especially in the eastern of the continent⁵⁷. This exchange may have occurred sometime during the Late Cretaceous, before the establishment of the Turgai Strait during the Turonian-Santonian, as a geographical barrier between Europe and Asia⁵⁸. However, island hopping across the Tethys Ocean have been considered to

describe exchange between the European and Asian bioprovinces to explain the appearance of groups with Asian-American affinities in the Campanian-Maastrichtian of Europe^{59–61}. Evidence of saltasaurids possibly related with opisthocoelicaudiines in Lo Hueco (late Campanian-early Maastrichtian) and Orcau-1 (early Maastrichtian) fossil sites, indicate that this lineage of medium to large lithostrotians was present in Ibero-Armorica before the proposed faunal event called ‘Maastrichtian Dinosaur Turnover’^{18,62–64}.

The evolution of European sauropod faunas during the Late Cretaceous and their paleobiogeographic relationships are relatively complex and still uncertain. The new described taxon and the phylogenetic analyses performed here suggest a different evolutionary history for titanosaurs in this area, which were represented by a variety of saltasaurids, including members of Lirainosaurinae and Opisthocoelicaudiinae, as well as a possible member of Colossosauria. This fauna corresponds to a complex mosaic of small (*Lirainosaurus* and *Atsinganosaurus*) and medium to large lirainosaurines (*Lohuecotitan* and *Ampelosaurus*) and medium to large opisthocoelicaudiines (*Qunkasaura* and *Abditosaurus*), and putative small colossosaurs (*Garrigatitan*). Except for *Garrigatitan*, which is represented by markedly incomplete remains, no titanosaurs from the European Campanian-Maastrichtian show clear affinities with coeval Gondwanan taxa. With the Indo-Madagascar isolation and the latest connection between South America and Africa at the end of the Early Cretaceous and the timing of an effective Apulian route, it is possible that the Ibero-Armorican lithostrotians with colossaurian affinities (*Normanniasaurus*, the Algora titanosaur and *Garrigatitan*) and early branching lirainosaurines migrated to Europe through the Apulian route in the late Early Cretaceous, with the Late Cretaceous taxa comprising members of relict lineages, and possibly reminiscent of late Early Cretaceous faunas⁵⁸. These lineages evolved isolated until the end of the Cretaceous; becoming the lirainosaurines a particularly diverse group with at least five distinct taxa. Currently, no shared lirainosaurine species have been identified between Iberia, Armorica and Hațeg realms, which may be due to strong local endemism established along the Late Cretaceous⁵⁸ and references herein). However, it is important to note that some of these taxa (e.g. *Ampelosaurus*) still need a detailed reassessment of all referred material. The presence of small taxa (e.g. *Lirainosaurus*, *Paludititan*) referred to these possible relict lineages suggests the development of some processes of insular dwarfism, as has been noted by several authors for the Late Cretaceous of Europe^{3,18}. On the other hand, the absence of small opisthocoelicaudiines may indicate that this lineage was a Late Cretaceous newcomer in Europe that did not develop small body forms in this insular environment.

Methods

Phylogenetic analysis

For the phylogenetic analysis of *Qunkasaura pintiuginiestra* we use the dataset of Mocho et al.³⁹. The scoring of some taxa was updated based on the more recent information and the inclusion of some relevant taxa (see all changes in Supplementary Note 2). Following the iterations of this data matrix by Poropat et al.⁹, the characters 11, 14, 15, 27, 40, 51, 104, 122, 147, 148, 195, 205, 259, 297, 426, 435, 472, and 510 were treated as ordered multistate characters, and eight unstable and highly incomplete taxa were excluded a priori (*Astrophocaudia*, *Australodocus*, *Brontomerus*, *Fukuititan*, *Fusuisaurus*, *Liubangosaurus*, *Malargosaurus* and *Mongolosaurus*). This pruned dataset was analysed using the ‘Stabilize Consensus’ option in the ‘New Technology Search’ in TNT v.1.5⁶⁵, to find the most parsimonious trees (MPTs), using sectorial searches, drift, and tree fusing, with the consensus stabilised five times. We then used the resulting trees as the starting topologies for a ‘Traditional Search’, using tree bisection–reconnection. We performed two versions of this analysis: in the first we used equal weighting of characters (Analysis I in Supplementary Note 2) and in the second we used extended implied weighting (Analysis II in Supplementary Note 2). We applied k-value of nine, following the analyses performed by Poropat et al.⁹, which are based on the recommendations of Goloboff⁶⁶ and Tschopp and Upchurch⁶⁷. To analyse the phylogenetic relationships of *Qunkasaura pintiuginiestra* with Aeolosaurini, we scored it to the dataset of Silva Junior

et al.³³ following the protocols established by these authors (Analysis III in Supplementary Note 2). The datasets (TNT files) are included in Supplementary Data 1 and 2.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in 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:6F3D865C-6402-4302-AB4F-F05FED7698BC; urn:lsid:zoobank.org:act:A1ACFB64-62CC-4621-B793-A74C6360C914; urn:lsid:zoobank.org:act:EA323E61-D86C-4E8C-A7F7-FB76B554B01F.

Data availability

All data supporting the findings of this study are available within the paper and its Supplementary Information and Data. The digital models of the specimens are available under request in Morphosource: <https://www.morphosource.org/concern/media/000636805?locale=en>; <https://www.morphosource.org/concern/media/000636799?locale=en>; <https://www.morphosource.org/concern/media/000636793?locale=en>.

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Author contributions

P.M., A.P., D.V. and F.O. designed the project. P.M., F.E., F.M.-F., A.P., J.L.S., D.V. and F.O. performed the research. P.M., A.P., D.V. and F.O. analysed the data. P.M. wrote the manuscript. P.M., F.E., F.M.-F., A.P., J.L.S., D.V. and F.O. author reviewed drafts of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Pedro Mocho.

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