A titanosaurian sauropod with Gondwanan affinities in the latest Cretaceous of Europe

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ABSTRACT

The origin of the last sauropod dinosaur communities in Europe and their evolution during the final 15 million years of the Cretaceous has become a complex phylogenetic and palaeobiogeographic puzzle characterized by the controversy on the alleged coexistence of immigrant, Gondwana-related taxa alongside relictual and insular clades. In this context, we describe a new titanosaurian sauropod dinosaur, *Abditosaurus kuehnei* gen. et sp. nov., from the Upper Cretaceous (Maastrichtian) Tremp Group of Catalonia (Spain). Phylogenetic analyses recover *Abditosaurus* separately from other European titanosaurs, within a clade of otherwise South American and African saltasaurines. The affinity of the new taxon with southern landmasses is reinforced by spatiotemporal co-occurrence with Gondwanan titanosaurian oospecies in southern Europe. The large size and the lack of osteohistological features potentially related to insular dwarfism or size reduction support the idea that *Abditosaurus* belongs to an immigrant lineage, unequivocally distinct from some of the the island dwarfs of the European archipelago. The arrival of the *Abditosaurus* lineage to the Ibero-Armorican island is hypothesized to have occurred during the earliest Maastrichtian (70.6 Ma), probably as a result of a global and regional sea-level drop that reactivated ancient dispersal routes between Africa and Europe. The arrival of large-bodied titanosaurs to the European archipelago produced dramatic changes in its insular ecosystems and important evolutionary changes in its dinosaur faunas, especially with respect to the ‘island rule’ effect.

INTRODUCTION

At the very end of the Cretaceous, Europe was an extensive island archipelago in which titanosaurian sauropods were integral components of terrestrial ecosystems. In the large Ibero-Armorican Island (which included the current areas of south-western France, Spain, and Portugal), the evolution of sauropod communities was shaped by the “Maastrichtian Dinosaur Turnover”, a major faunal change in which the late Campanian–early Maastrichtian (LC–EM) pre-turnover dinosaur communities were replaced by early–late Maastrichtian post-turnover assemblages[1–3]. The pre-turnover titanosaur assemblage included small-sized species such as *Lirainosaurus astibiae*, *Atsinganosaurus velauciensis*, and *Garrigatitan meridionalis*[4–6], and moderate-sized species such as *Ampelosaurus atacis* and *Lohuecotitan pandafilandi* [7,8], some of which have been interpreted to have lowered metabolic rates[6,9–11]. Reduction of body size and shifts in growth rate relative to their contemporaneous sister taxa from continental landmasses may have resulted from selective pressures under insular, limited-resource environments – an evolutionary process known as insular dwarfism[12,13]. In contrast, the post-turnover forms are apparently larger in size but still taxonomically undescribed[14,15], and their first appearance on the island co-occurs with a specific group of oospecies of Gondwanan affinity. Recent phylogenetic analyses distinguish two distinct clades: a relictual core of endemic titanosaurs, and a clade of immigrants with African affinities[11]. This partially supports a previously-postulated biotic interchange, including sauropod faunas, between the archipelago – mostly and particularly with the Ibero-Armorican Island[16] – and the neighbouring landmasses during the latest Cretaceous[17–21].

Here we present a new titanosaurian sauropod dinosaur from the Late Cretaceous (Maastrichtian) of Catalonia that represents the most complete, semi-articulated titanosaur skeleton thus far discovered in Europe. Phylogenetic analyses of this informative taxon provide an opportunity to test hypotheses of phylogenetic relationships among European titanosaurs and shed light on palaeobiogeographic events between the southern islands of the European archipelago and the northern regions of the African landmass. Further, the new taxon is substantially larger-bodied than any species within the late Campanian–early Maastrichtian titanosaur assemblage, probably indicating an eventual decrease of the alleged insular dwarfism or the so-called 'island rule' effect in Ibero-Armorican sauropod faunas.

RESULTS

Nomenclatural acts

Systematic palaeontology

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

SAUROPODA Marsh, 1878

TITANOSAURIA Bonaparte and Coria, 1993

SALTASAURIDAE Bonaparte and Powell, 1980

SALTASAURINAE Bonaparte and Powell, 1980

Abditosaurus kuehnei, gen. et sp. nov.

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Etymology – '*Abditus*', Latin, concealed, because the skeleton was concealed from science for 60 years; '*sauros*', Greek, lizard. '*kuehnei*' honours Professor Walter Georg Kühne (1911–1991), the discoverer of the specimen.

Holotype – An associated, semi-articulated, partial skeleton consisting of isolated teeth, 12 articulated and partial cervical vertebrae, cervical ribs, seven nearly complete or fragmentary anterior and middle dorsal vertebrae, six complete or almost complete dorsal ribs and fragments of others, three chevrons, the right scapula, posterior end of the left scapular blade, right coracoid, left sternal plate, a sternal rib, proximal half of the left humerus, distal half of the right humerus, partial right radius, fragment of the left ilium, part of the proximal half of the right femur, right tibia, right fibula, and distal half of the left fibula with the adhered calcaneum (see Supplementary Section 2.1 for a list of materials with repository numbers). We consider these elements to represent a single titanosaurian individual because they formed a partially articulated skeleton within an accumulation area of 6 m by 4 m at the same stratigraphic level. No duplicated elements were found (Fig. 1).

Type locality – Orcau-1, approximately 6 km east of Tremp, Pallars Jussà county, Catalonia, Spain (Fig. 1; coordinates: 42º 9' 34.1424" N, 0º 58' 22.631" E). The locality (formerly known as "Barranco de Orcau" or "Orcau") was discovered in 1954 by Walter Georg Kühne during fieldwork in the Suterranya-Orcau area (see Supplementary Section 2.1).

Horizon – Lower portion of the Tremp Group, basalmost strata of the Conques Formation[3]. Other fossils identified at the Orcau-1 locality include shed crocodylomorph teeth (MCD-6752), plant remains, and *Lychnus* gastropod casts. Two isolated, shed dromaeosaurid teeth (MCD-6994, MCD-6740) and scattered eggshells (*Fusioolithus baghensis*; IPS59133[22]) were found in a stratigraphic level immediately above the sauropod skeleton.

Age and distribution – ca. 70.5 Ma, early Maastrichtian (C31r), Late Cretaceous[3].

Diagnosis – *Abditosaurus kuehnei* is diagnosed by a unique combination of characters not seen in other titanosaurs as well as 14 autapomorphies (marked with an asterisk): anterior dorsal vertebrae with anterior centrodiapophyseal lamina (acdl) not reaching centrum but intersecting centroprezygapophyseal lamina (cprl)*; anterior and first middle dorsal vertebrae with diapophyses ventral to postzygapophyses*, absence of centroprezygapophyseal lamina (cprl)*, and long axes of zygapophyses at low angle relative to horizontal plane (the latter character shared with *Argentinosaurus*[23]); middle dorsal vertebrae with oblique, posterodorsally oriented accessory lamina dividing parapophyseal centrodiapophyseal fossa (pacdf)*, secondary prezygodiapophyseal lamina (prdl) dividing prezygapophyseal paradiapophyseal fossa (prpadf)*, posterior centrodiapophyseal lamina (pcdl) dorsally penetrated by large pneumatic foramen (shared with *Rapetosaurus*[24], *Lohuecotitan*[8], and *Saltasaurus*[25]), abundant pneumatic foramina in spinopostzygapophyseal (spof)*, centropostzygapophyseal (cpof)*, and postzygapophyseal centrodiapophyseal (pocdf)* fossae, pneumatized centropostzygapophyseal lamina (cpol) (shared with *Rapetosaurus*[24]), and absence of postspinal laminae (posl) (shared with *Overosaurus*[26], *Muyelensaurus*[27], and *Isisaurus*[28]); anterior dorsal ribs without pneumatic foramina on anterolateral and

posteromedial surfaces*; second dorsal ribs with anteroposterior thickening or bulge on posterior margin of distal end*; scapula with co-occurrence of posteroventral process or tubercle on medial margin of acromial plate, subtle process on anteroventral corner, and very prominent bulge on dorsomedial margin of blade, and two oval lateral fossae on posterior end of blade*; coracoid with elliptical foramen that twists its orientation from lateral through to medial surface*; sternal plate without anteroventral ridge on ventral surface (shared with *Mnyamawamtuka*[29]); presence of sternal ribs; humerus with a medially projected deltopectoral crest (shared with *Gondwanatitan*[30]*, Nullotitan*[31]*,* and *Jainosaurus*[32]) and articular surface of radial condyle facing anterodistally (shared with *Saltasaurus*[33] and *Paralititan*[34]); radius with oblique ridge on posterodistal surface*; tibia with anteriorly projected cnemial crest (shared with *Gondwanatitan*[30]) and small prominent bulge at posterior margin of proximal end (shared with *Neuquensaurus*[35]); fibula with distal end beveled posteriorly 20º with respect to long axis of shaft*; presence of ossified calcaneum (shared with *Neuquensaurus*[36] and presumably with *Elaltitan*[37]).

Osteological description and comparisons – The **cervical** vertebrae (Fig. 2a) have opisthocoelous, internally pneumatized centra with ventral surfaces lacking a ventral keel or ventrolateral ridges, thus differing from all or some of the cervical centra of most titanosaurs such as *Lohuecotitan*[8], *Rapetosaurus*[24], *Saltasaurus*[25], and *Overosaurus*[26], which bear some of these structures. Unlike most titanosaurs, the posterior cervical centra bear large, oval, and deep pleurocoels. The parapophyses extend half the anteroposterior length of the centrum, project laterally, and are located on the anterior margin of the centrum, as in most titanosaurs. The neural spine is estimated to be short. **Cervical ribs** are fused in nine of the 12

144 cervical vertebrae and project far laterally from the centrum (Fig. 2a). The anterior
145 process has a projection that curves medially, resembling a characteristic ‘batwing’
146 shape, and extends to the level of the anterior margin of the condyle. The posterior
147 process is elongate and thins distally, overlapping 2.5 more posterior centra. The
148 **dorsal vertebrae** are described with the neural canal oriented horizontally. They are
149 strongly opisthocoelous, have camellate internal tissue, and become shorter from the
150 anterior to the middle vertebrae (Fig. 2b and c). All centra lack a ventral keel, and the
151 lateral pleurocoels are oval and undivided. In the anterior and first middle dorsal
152 vertebrae, the transverse processes are low (with the ventral edge approximately
153 level with the dorsal edge of the posterior cotyle) and laterally directed, as in
154 *Lohuecotitan*[8] and other titanosaurs[23,24,28]. In the anterior dorsal vertebrae, the
155 anterior centrodiapophyseal lamina does not reach the centrum because it intersects
156 the centroprezygapophyseal lamina. The neural spine is large and triangular,
157 moderately tall, and angled posterodorsally (Fig. 2b), like those of the middle dorsal
158 vertebrae of most European titanosaurs and others. The surfaces of the
159 spinopostzygapophyseal, centropostzygapophyseal, and postzygapophyseal
160 centrodiapophyseal fossae are autapomorphically pneumatized by scattered
161 foramina. The intrapostzygapophyseal and postspinal laminae are absent, as in
162 *Overosaurus*[26]. The long axes of the zygapophyses are at a low angle relative to the
163 horizontal plane, as in *Argentinosaurus*[23], and the diapophyses are laterally directed
164 and located at level with the prezygapophyses. *Abditosaurus* is unique in having the
165 diapophyses ventral to the postzygapophyses in the anterior and first middle dorsal
166 vertebrae (first, second, and third dorsals) (Fig. 2b). A secondary
167 prezygodiapophyseal lamina in the first middle dorsal and a parapophyseal
168 centrodiapophyseal fossae internally divided by an oblique, posterodorsally-oriented

accessory lamina in the middle dorsals are two autapomorphies of *Abditosaurus*. Unlike in other Ibero-Armorican species and many other titanosaurs, the centroprezygapophyseal lamina is absent. The posterior centrodiapophyseal lamina bears a dorsal and elliptical pneumatic foramen (Fig. 2b,c), a character shared with *Lohuecotitan*[8], *Rapetosaurus* [24], and *Saltasaurus*[25]. The capitulum and tuberculum of the **dorsal ribs** (Fig. 2d) are oriented at a right angle and united by a thin capitulotubercular web that shows camellate texture. The web lacks pneumatic foramina, unlike most titanosauriforms[38], a feature that we regard as a local autapomorphy of *Abditosaurus*. The rib head bears a proximodistally elongate and narrow ridge (outstandingly pronounced in the third rib) that extends distally from the tuberculum onto the rib shaft. The rib shaft has a plank-like, asymmetric, D-shaped cross-section. The second through fourth ribs show a distal spoon-like expansion. In the third dorsal rib, this expansion produces a distal peduncle where the rib articulates with the sternal plates. Autapomorphically, the posterior surface of the distal end of the second ribs bears a striated anteroposterior thickening or bulge. Caudal **chevrons** (Fig. 2e) are dorsally open and 'Y-shaped' with rounded to oval articular facets. The middle chevron has two dorsal articular subfacets, but unlike *Lohuecotitan*[8] they lack a distinct groove between them.

The **scapula** is described with the scapular blade oriented horizontally. The acromion and acromial ridge are oriented perpendicular to the long axis of the blade and dorsally expanded to twice the dorsoventral breadth of the posterior end (Fig. 2f). The scapular blade has a nearly 'D'-shaped cross section at its anterior end and lacks a ventral ridge on the medial surface, unlike *Atsinganosaurus*[11], *Lirainosaurus*[39], *Ampelosaurus*[40], *Mansourasaurus*[16], and *Opisthocoelicaudia*[41]. Posteriorly, the posterodorsal expansion is more pronounced than the posteroventral expansion, as

194 in several titanosaurs but differing from *Lirainosaurus*[39] and *Ampelosaurus*[40], among
195 others. The posterior end of the scapular blade bears two autapomorphic lateral
196 fossae or depressions. The co-occurrence of a posteroventral process on the medial
197 margin of the acromial plate, a subtle process on the anteroventral corner, and a very
198 prominent bulge on the dorsomedial margin of the scapular blade is unique to
199 *Abditosaurus*. The scapula contributes more to the glenoid than does the coracoid,
200 differing from *Lirainosaurus* (coracoid contributes more than scapula[39]) and
201 *Opisthocoelicaudia* (scapula and coracoid contributes subequally[41]), but similar to
202 *Mansourasaurus*[16]. The **coracoid** is described with the glenoid surface oriented
203 posteroventrally (Fig. 2g). It is longer than tall and has a quadrangular outline, a
204 character shared with several titanosaurs, and as in many of these sauropods it lacks
205 a ridge originating near the midpoint of the anterodorsal border of the lateral surface.
206 The coracoid foramen is far from the scapular articulation, as in several titanosaurs,
207 but differing from *Atsinganosaurus*[11], *Lirainosaurus*[39], *Ampelosaurus*[40], and some
208 other derived titanosaurs[16,24,42]. The foramen is elliptical and autapomorphically twists
209 its orientation from the lateral through to the medial surface. In articulation with the
210 scapula, the dorsal margin of the coracoid is situated below the level of that of the
211 scapular acromial plate. The **sternal plate** (Fig. 2h) is semilunar, with a strongly
212 concave lateral surface, as in other titanosaurs[43,44]. Unlike most titanosaurs[6],
213 however, it lacks an anteroventral ridge on the ventral surface (as in
214 *Mnyamawamtuka*[29]). The ratio of the length of the sternal plate to that of the humerus
215 is 0.68 in *Abditosaurus*, which falls very close to the value seen in saltasaurids
216 (>0.7)[44]. The **sternal rib** (Fig. 2i) is elongate and rod-like and challenges the
217 assumption that the loss of ossified sternal ribs might be a synapomorphy of
218 Titanosauriformes[45]. The presence of this element in *Abditosaurus* is considered a

219 local autapomorphy within the clade. The ossification of at least one sternal rib in the
220 new form might be related to the very advanced ontogenetic age of the holotypic
221 individual.
222 The **humerus** (Fig. 2j and k) is robust and remarkably different from the more gracile
223 humeri of Ibero-Armorican and many other titanosaurs. The mediolateral
224 development of the proximal end is similar to those described in *Saltasaurus*[33],
225 *Neuquensaurus australis*[35], and *Opisthocoelicaudia*[41]. The deltopectoral crest is
226 robust and strongly expanded mediolaterally to reach the central axis of the shaft, as
227 in several titanosaurs, but differs from the unexpanded or moderately expanded
228 crests of all other Ibero-Armorican taxa and many other titanosaurs. It projects
229 unambiguously medially, similar to *Gondwanatitan*[30], *Nullotitan*[31], and *Jainosaurus*[32].
230 Unlike other Ibero-Armorican titanosaurs, the *Abditosaurus* humerus exhibits a
231 distally expanded deltopectoral crest, a synapomorphy of Saltasauridae[44,46] shared
232 with *Opisthocoelicaudia*[41], *Saltasaurus*[47], *N. australis*[48], and *Alamosaurus*[49]. The
233 distal condyles are clearly divided as in saltasaurids[44,46], and the articular surface of
234 the radial condyle faces anterodistally, as in *Paralititan*[34] and *Saltasaurus*[47]. The
235 **radius** (Fig. 2l) has a mediolaterally expanded distal end that is beveled
236 posterolaterally more than 20º relative to the long axis of the shaft and a well-defined
237 interosseus ridge, as in other lithostrotian titanosaurs[44]. The interosseous ridge
238 extends proximodistally and is laterally emarginated, as in *Opisthocoelicaudia*[41].
239 Unlike the rounded shape of *Rapetosaurus*[24] or *Dreadnoughtus*[50], the distal surface
240 is elliptical and anteroposteriorly asymmetrical, as in *N. australis*[48].
241 Autapomorphically, *Abditosaurus* presents a small, oblique ridge on the posterodistal
242 surface of the radius.

The **ilium** has a preacetabular process that projects anterolaterally, as in *Garrigatitan*[6] and *Lohuecotitan*[8] but differing from *Lirainosaurus*[39]. Internally, it is pneumatized, as in most Ibero-Armorican titanosaurs[6,8,11,39], *Alamosaurus*[51], *Saltasaurus*, and *Neuquensaurus*[52], among others. The **femur** exhibits a prominent, proximally located, lateral bulge as well as a posterior accessory ridge. The eccentricity index of the shaft is >185%, as in most titanosaurs[53]. The **tibia** (Fig. 2m) is gracile, and its proximal end is less mediolaterally compressed than in *Atsinganosaurus*[11] and *Lirainosaurus*[39], but also contrasting with the rounded shape of *Lohuecotitan*[8] and *Ampelosaurus*[40]. A small but prominent bulge at the posterior margin of the proximal end is also observed in *Neuquensaurus*[35], and the cnemial crest projects anteriorly, as in *Gondwanatitan*[30]. The distal end is longer mediolaterally than anteroposteriorly, as typical for titanosaurs[43,54]. The anteromedial ridge is more pronounced than in *Lirainosaurus*[39], *Atsinganosaurus*[11], and *Lohuecotitan*[8]. The sigmoid shape of the **fibula** (Fig. 2n) is a character shared with most Campanian–Maastrichtian titanosaurs, and the presence of a prominent lateral trochanter is a synapomorphy of Saltasaurinae[48]. The fibula of *Abditosaurus* is unique in having its distal end beveled posteriorly 20º with respect to the long axis. The distal articular surface is triangular, as in *Rapetosaurus*[24], *Lirainosaurus*[39], *Alamosaurus*[55], and *Laplatasaurus*[56]. The **calcaneum** (Fig. 2o) is a small, convex, and oval element, as in *Euhelopus*[57] and the purported calcaneum reported in *Elaltitan*[37]. The ossification of the calcaneum (and a sternal rib) in the *Abditosaurus* holotype is exceedingly rare in Titanosauria, and therefore their presence in this senescent individual might indicate that the preservation of these elements is related to its advanced ontogenetic stage.

DISCUSSION

Phylogenetic and palaeobiogeographic analyses

We assessed the phylogenetic affinities of *Abditosaurus kuehnei* using both parsimony and Bayesian methods with the dataset of Gorscak and O'Connor[29] (see Methods and Supplementary Section 1.6). In both analyses, *Abditosaurus kuehnei* is recovered as a saltasaurid lithostrotian titanosaur on the basis of the following synapomorphies: coracoid with rectangular anteroventral margin; humerus with strong posterolateral bulge around level of deltopectoral crest apex; humeral deltopectoral crest expanded distally; humeral distal condyles divided; and radius with distal end beveled ca. 20º proximolaterally relative to shaft[43]. More specifically, *Abditosaurus* is positioned within a clade of Late Cretaceous saltasaurines from South America and Africa (Fig. 3). Within this otherwise South American–African clade, *Abditosaurus* and *Paralititan* are sister taxa, and the *Abditosaurus* + *Paralititan* clade is the sister taxon of *Maxakalisaurus*. The (*Abditosaurus* + *Paralititan*) + *Maxakalisaurus* clade is the sister taxon of the South American saltasaurins (*Saltasaurus* + *Neuquensaurus*). The South American–African clade as a whole (that is, [*Paralititan* + *Abditosaurus*] + *Maxakalisaurus* and *Saltasaurus* + *Neuquensaurus*) is supported by two synapomorphies (anterior and middle caudal centra wider than tall; divided humeral distal condyles) and is sister to Opisthocoelicaudiinae[59], a Pan-American, African, and Eurasian clade that comprises most of the rest of the Ibero-Armorican taxa as well as the North American *Alamosaurus*, the South American *Dreadnoughtus*, and the Asian *Opisthocoelicaudia*, among others.

The phylogenetic and palaeobiogeographic analyses (Fig. 3) indicate that *Abditosaurus* is a derived member of a distinct immigrant clade of otherwise South

American and African saltasaurine titanosaurs that reached Europe via a dispersal event from Africa during the post-Cenomanian, very probably during the early Maastrichtian. Further, the direct association of the *Abditosaurus* skeleton with *Fusioolithus baghensis*, an oospecies with in-ovo titanosaur embryos[60] and an otherwise Gondwanan (South America, India, Africa) distribution (see Supplementary Section 2.4), reinforces the southern origin of the clade. The dispersal event from Africa is hypothesized to have occurred during the KMa2 regressive event (70.6 Ma, early Maastrichtian), a eustatic event[61] that affected the central Tethyan margin and northern Africa. With the subaerial exposure of various carbonate platforms, the Europe–Africa connection was reestablished, and Early Cretaceous migratory routes[62-64] were probably reactivated, facilitating the dispersal of titanosaurian taxa (Fig. 4; Supplementary Section 2.6).

Implications for titanosaur evolution in the European archipelago

Abditosaurus was a large titanosaur by Ibero-Armorican standards, representing a very mature, senescent, individual estimated to be 17.5 m in length with a body mass of 14,053 kg (see Supplementary Table 1). Overall, it was substantially larger than any titanosaur species described from the region, being more than 70% larger than the largest known adult *Atsinganosaurus* and *Garrigatitan*, more than twice the size of the largest individuals attributed to *Lirainosaurus* or *Lohuecotitan*, and 20% larger than the largest individual attributed to *Ampelosaurus* (Supplementary Table 1). The anatomical and osteohistological characters of the senescent *Abditosaurus* do not indicate a reduction in growth rate nor a reduction in body size (see Supplementary Section 2.3), two common traits found in *Lirainosaurus*[9], *Ampelosaurus*[10], *Atsinganosaurus*[11], and *Magyarosaurus*[66]. Indeed, the

318 *Abditosaurus* appendicular bones lack modified laminar bone, a bone tissue
319 potentially related to a reduction in metabolic rate and body size[10] and interpreted as
320 evidence for possible insular dwarfism in sauropods[9-11,20]. Therefore, there is no
321 evidence for metabolic adaptations to insular settings in *Abditosaurus*, as are
322 present in other European titanosaurs[13,66]. Our results suggest that *Abditosaurus*
323 must be regarded as a member of a distinct immigrant clade of large titanosaurs that
324 reached Ibero–Armorica during the early Maastrichtian, and as a representative of
325 the post-turnover titanosaurian fauna of this island.
326 The scenario during the middle of the early Maastrichtian (lower part of C31r) of
327 large-bodied, post-turnover titanosaurs in the Ibero-Armorican island replacing small
328 late Campanian–early Maastrichtian forms might be mirrored in other islands of the
329 European archipelago, such as in the eastern Hațeg Island (in modern-day
330 Romania), where large taxa seem to appear later than dwarfed forms (e.g.,
331 *Magyarosaurus*[67]), probably also by the middle of the early Maastrichtian (lower part
332 of C31r[68]). Accordingly, these new titanosaur faunas are expected to be associated
333 with fusioolithid oospecies in post-early Maastrichtian deposits. Hence, this proposed
334 titanosaurian faunal replacement might represent the decrease of the 'island rule'
335 effect on sauropod communities throughout Europe.
336
337 **METHODS**
338 **Osteohistological analyses** - Histological samples were taken from the humerus,
339 femur, and tibia, prepared as thin sections, and studied using a petrographic
340 microscope. **Body mass and length estimates** - We compiled a dataset of limb
341 bone measurements for the Ibero-Armorican titanosaur species (Supplementary
342 Table 1) for use in body mass (BM) and body length (BL) estimations with the

formulas of Campione and Evans[69] based on femoral and humeral circumferences, which were estimated following the allometric equation of González Riga et al.[70] when necessary, and Seebacher[71]. **Photogrammetric models** – 3-D models of fossil specimens were produced following photogrammetric protocols [72-74] and using Agisoft Photoscan Pro (v. 1.2.4, www.agisoft.com), to perform scaling and alignment. **Phylogenetic and palaeobiogeographic analyses** – We performed maximum parsimony and Bayesian analyses. Maximum parsimony analyses used the dataset of Gorscak and O'Connor[29], which included the original 55 taxa plus *Abditosaurus* scored for 272 independent characters that were treated as unordered in all the analyses. Both equal weights and extended implied weighting analyses with different concavity constants were explored. The Bayesian dataset[29], which also included the original 55 taxa plus *Abditosaurus*, was coded for a total of 272 variable characters plus 260 autapomorphic, invariable characters. A non-clock analysis was carried out using MrBayes 3.2.6[75], running in the CIPRES Science Gateway, using a model of variable rates of character state change, sampled from a lognormal-distribution, setting an exponential hyperprior of 1.0 for the rate of variation among characters. Four independent runs of the Markov chain Monte Carlo (MCMC) ran for 10 million generations with one hot and three cold chains. The chains sampled tree-space every 1,000 generations and the first 25% of the posterior distribution was discarded to eliminate the initial climbing phase. Convergence of independent runs was assessed in Tracer 1.7 using effective sample size (ESS) for each parameter greater than 200. We also performed a tip-dating Bayesian phylogenetic analysis to estimate divergence dates and branch lengths based on the additional data in the form of stratigraphic information. The assumed tree model for this set of analyses was the birth-death-skyline-serial-sampling[76]. A relaxed clock was assumed under a

lognormal distribution of sampled rates. Rates of character change were tested under variable (with an assumed gamma-distribution) assumptions. Four independent runs of the MCMC persisted for 50 million generations with sampling of tree-space occurring every 1,000 generations and the first 25% of the sample was discarded. Stratigraphic ranges of each taxon (see Supplementary Section 1.6 and Table 2) were sampled under a uniform distribution to account for stratigraphic uncertainty. Again, convergence of independent runs was assessed in Tracer 1.7 using effective sample size (ESS) for each parameter greater than 200. A palaeobiogeographic analysis following the methodology of Sallam et al.[16] was conducted using the R script BioGeoBEARS[77] over the tip dating maximum clade credibility tree. Three models (DEC, DIVALIKE, and BAYAREALIKE) and alternative models with the additional + J parameter to facilitate long-distance dispersal events alongside the assumptions of each model where evaluated. All figures were created by the authors using Adobe Illustrator CC 2015 2.1.

Data availability –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 authors declare that all other data supporting the findings of this study are available within the paper and its Supplementary Information.

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Author contributions

B.V. devised and directed the project and supervised the fieldwork; B.V., A.S., A.G., N.L.R., and J.I.C. collected the fossils and taphonomic data in the field; B.V, A.S., and A.G. supervised fossil preparation; B.V. described and measured the fossils, and collected historical information; M.M.A. and B.V. performed phylogenetic and biogeographic analyses; A.G.-D., A.S., and B.V. conducted histological analyses; N.L.R. performed the photogrammetry and 3D modelling; B.V. wrote the paper with substantial inputs of A.S., M.M.A., A.G-D., and N.L.R. B.V., A.S., and M.M.A. designed the figures. B.V., A.S., M.M.A., N.L.R., A.G-D., A.G., and J.I.C. reviewed and edited the original draft.

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FIGURE CAPTIONS

Figure 1. Type locality of *Abditosaurus kuehnei* gen. et sp. nov. a, location of the Orcau-1 locality in the southern Pyrenees (Catalonia, Spain). **b**, the discoverer, Professor Walter Georg Kühne (1911–1991), during a lecture at the Palaeontological Society of Berlin in 1959 (courtesy of Urs and Anna Klebe). **c**, site map showing the skeletal disposition of the *in situ* skeletal elements recovered, mapped, and/or collected during excavations since 1954. The position of the remains discovered in the early excavations is based on sketches from Kühne's notebook (see Supplementary Section 2.1). **D**, schematic skeletal reconstruction in right lateral view, with indication of the recovered elements (silhouette courtesy of Bernardo González Riga). ?, indeterminate "flat bone"; ca, calcaneum; ch, chevron; co, coracoid; cr, cervical rib; CV, cervical vertebra; dr, dorsal rib; DV, dorsal vertebra; f,

445 femur; fi, fibula; h, humerus; il, ilium; r, radius; sc, scapula; sp, sternal plate; sr,
446 sternal rib; t, tooth; ti, tibia.
447
448 **Figure 2. Skeletal anatomy of *Abditosaurus kuehnei* gen. et sp. nov. a**, anterior
449 dorsal and cervical vertebrae (MCD-9882) in ventral view; **b**, third dorsal vertebra
450 (MCD-6718) in posterior view; **c**, fourth and fifth dorsal vertebrae (MCD-6729, MCD-
451 6730) in right ventrolateral view; **d**, second left dorsal rib (MCD-6720) in anterolateral
452 view; **e**, anterior chevron (MNCN-62760) in caudal view; **f**, right scapula (from a cast
453 of MCD-6724) in medial view; **g**, right coracoid (MCD-6742) in lateral view; **h**, left
454 sternal plate (MCD-6716) in ventral view; **i**, sternal rib (MCD-6747) in longitudinal
455 view; **j**, left humerus (MNCN-79834) in anterior view; **k**, right humerus (MCD-6988) in
456 anterior view; **l**, right radius (MCD-6748) in posterior view; **m**, right tibia
457 (MNCN79837-79838-79848) in lateral view; **n**, right fibula (MCD-6723) in lateral
458 view; **o**, left fibula and adhered calcaneum (MNCN-79847) in medial view. acdl,
459 anterior centrodiapophyseal lamina; acpl, anterior centroparapophyseal lamina; al,
460 accessory lamina; ap, acromial plate; aspa, articular surface for ascending process
461 of astragalus; avp, anteroventral process; b, bulge; ca, calcaneum; cap, capitulum;
462 cc, cnemial crest; cdf, centrodiapophyseal fossa; cf, coracoid foramen (twisted
463 mediolaterally); cfo, cnemial fossa; cpof, centropostzygapophyseal fossa
464 (pneumatized); cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal
465 lamina; cr, cervical rib; CV, cervical vertebra; d, diapophysis; de, distal end
466 (bevelled); dp, dorsal process; dpc, deltopectoral crest; dr, dorsal rib; DV, dorsal
467 vertebra; gl, glenoid; ior, interosseous ridge; lt, lateral trochanter; pa, parapophysis;
468 pacdf, parapophyseal centrodiapophyseal fossa; pc, pleurocoel; pcdl, posterior
469 centrodiapophyseal lamina; pdr, posterodistal ridge; pf, pneumatic foramen; po,

postzygapophysis; pocdf, postzygapophyseal centrodiapophyseal fossa (pneumatized); podl, postzygodiapophyseal lamina; posdf, postzygapophyseal spinodiapophyseal fossa; prcdf, prezygocentrodiapophyseal fossa; pvp, posteroventral process; r, ridge; rac, radial condyle; scb, scapular blade; spdl, spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; tu, tuberculum; ulc, ulnar condyle. * indicates autapomorphic character. Yellow shading in b indicates a dorsal rib fragment; blue shading in a-c indicates neural arch fossae. Scale bars equal 10 cm.

Figure 3. Time-calibrated phylogenetic analysis and palaeobiogeographic context of *Abditosaurus kuehnei* gen. et sp. nov. and other saltasaurid titanosaurian sauropods. Plot based on the Maximum Clade Credibility Tree inferred by the tip-dated Bayesian analysis; palaeobiogeographic analysis using the BAYAREALIKE model under starting distribution multipliers**.** Letters in coloured squares at the nodes indicate relative support for ancestral range reconstruction. Light blue bars represent the 95% highest posterior density for the timing of divergence date at each node. The colour-coded bars for each terminal taxon indicate palaeogeographic range and the 95% highest posterior density of the recorded stratigraphic range of that taxon. Green line indicates the timing of the final breakup and separation between South America and Africa (see Supplementary Section 2.6 for references). Global Polarity Time Scale (GPTS) after Ogg and Hinnov[58]. A, Asia; E, Europe; F, Africa; N, North America; S, South America.

Figure 4. Chronostratigraphy and hypothesized dispersal route for *Abditosaurus kuehnei* gen. et sp. nov. and other latest Cretaceous Ibero-Armorican titanosaurs. a, chronostratigraphic range and positions of the Ibero-Armorican titanosaurs and their holotype localities, respectively, correlated to the global sea-level curve, with indication of the timing of the hypothesized dispersal event from Africa to Europe during the KMa2 regressive event. **b**, palaeogeography of the western Tethys Seaway in the early Maastrichtian, with hypothesized migratory pathway (yellow arrow) through the 'Apulian' route to the Ibero-Armorican island. Green and yellow boxes represent the chronostratigraphic ranges of the pre- and post-turnover oospecies, respectively. Schemes in circles represent radial thin-sections of *Megaloolithus siruguei* (green circle) and *F. baghensis* (yellow circle) eggshells, taken from Vianey-Liaud et al.[65]. Brackets represent the 95% highest posterior density of the recorded stratigraphic range for each taxon. Ab, *Abditosaurus kuehnei* gen. et sp. nov.; Am, *Ampelosaurus atacis*; At, *Atsinganosaurus velauciensis*; Li, *Lirainosaurus astibiae*; Lo, *Lohuecotitan pandafilandi*. HI, Haţeg Island; IB-ARM, Ibero-Armorican Island; NW AFR, north-western Africa. Global Polarity Time Scale (GPTS) after Ogg and Hinnov[58]. Global sea-level curve and eustatic events after Haq[61]; sea-level (in m) on top, highstand (left), lowstand (right). Palaeogeographic map based on R. Blakey. Titanosaur silhouette modified from illustrations of O. Sanisidro.

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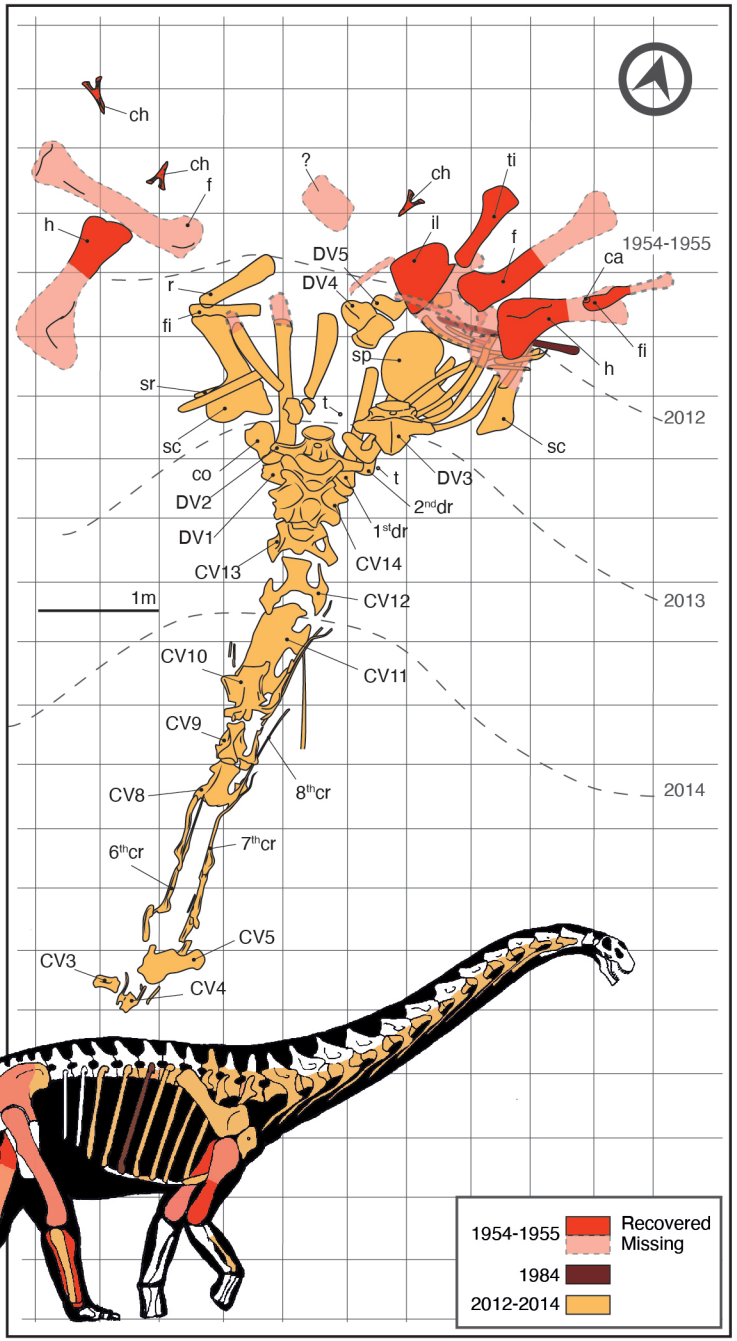
a
2°
3°
ANDORRA
FRANCE
42°
SPAIN
Barcelona
41°
100 km


b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1984
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a
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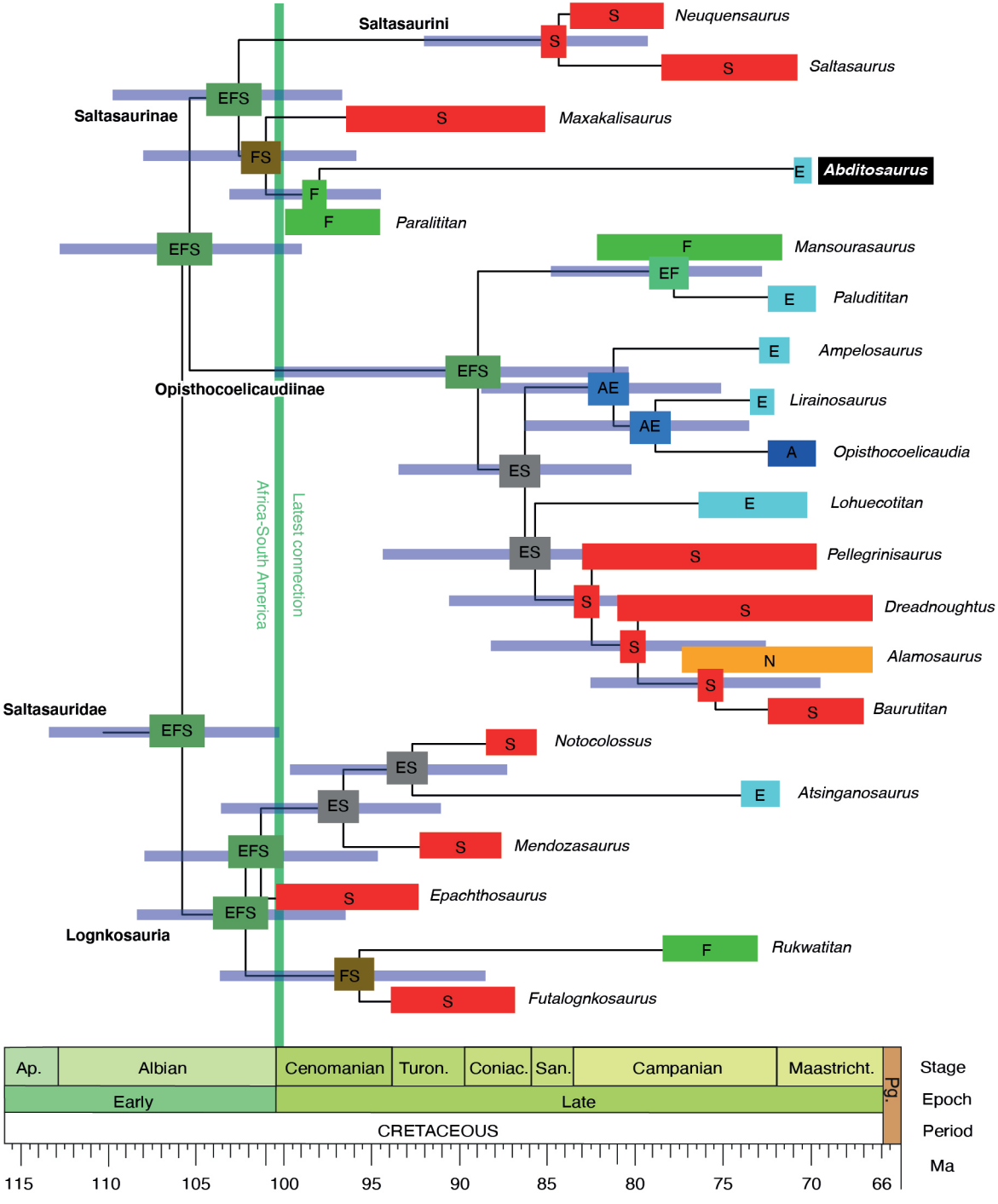
Saltasaurini
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Paralititan
Mansourasaurus
Paludititan
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Lirainosaurus
Opisthocoelicaudia
Lohuecotitan
Pellegrinisaurus
Dreadnoughtus
Alamosaurus
Baurutitan
Saltasauridae
Notocolossus
Atsinganosaurus
Mendozasaurus
Epachthosaurus
Lognkosauria
Rukwatitan
Futalognkosaurus
Africa-South America
Latest connection
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F
N
A
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Ap.
Albian
Cenomanian
Turon.
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Campanian
Maastricht.
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Early
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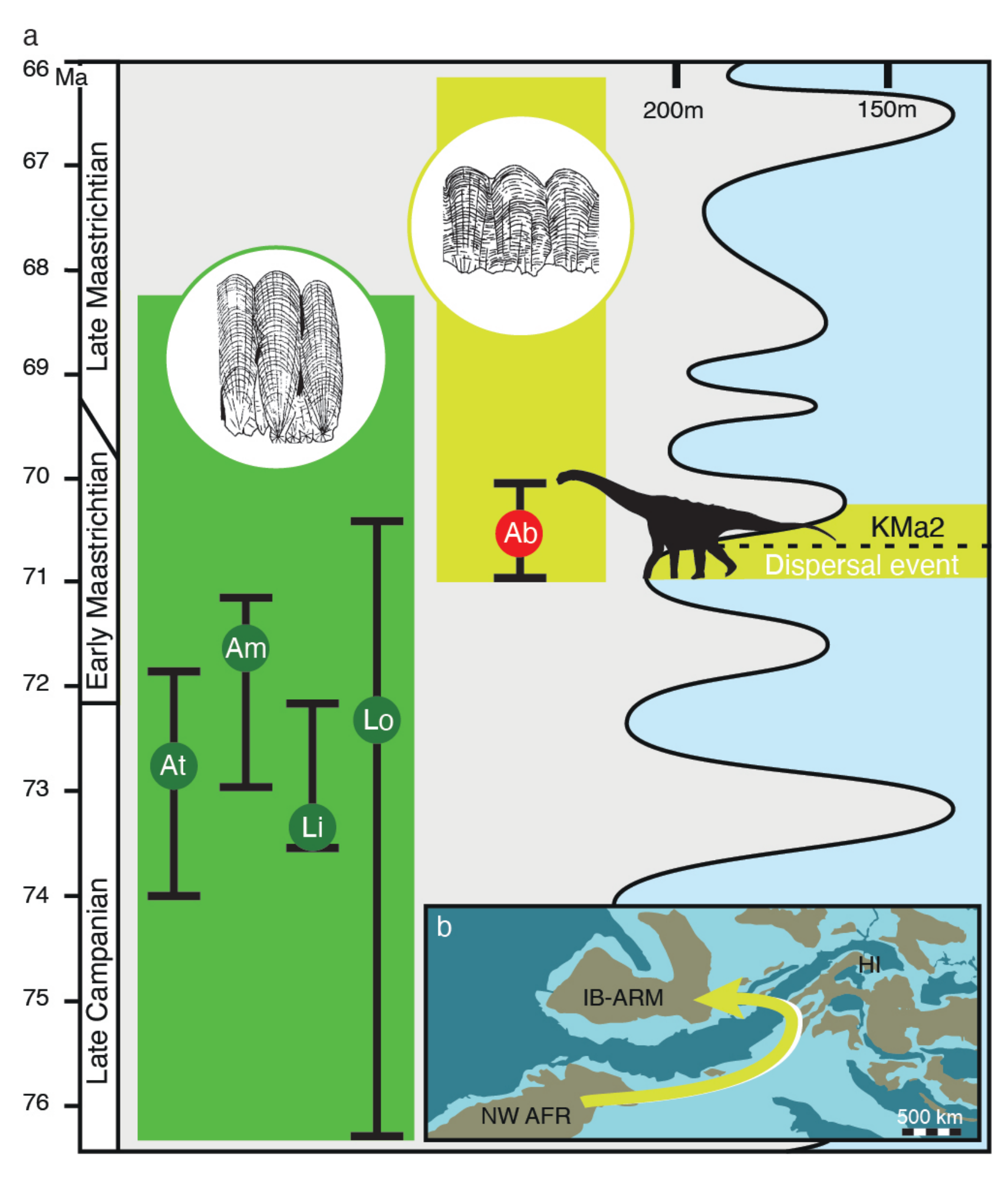
a
66 Ma
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Late Maastrichtian
Early Maastrichtian
Late Campanian
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150m
Ab
KMa2
Dispersal event
At
Am
Li
Lo
b
HI
IB-ARM
NW AFR
500 km