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Extinction of herbivorous dinosaurs linked to Early Jurassic global warming event

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Sauropods, the giant long-necked dinosaurs, became the dominant group of large herbivores in terrestrial ecosystems after multiple related lineages became extinct towards the end of the Early Jurassic (190–174 Ma). The causes and precise timing of this key faunal change, as well as the origin of eusauropods (true sauropods), have remained ambiguous mainly due to the scarce dinosaurian fossil record of this time. The terrestrial sedimentary successions of the Cañadón Asfalto Basin in central Patagonia (Argentina) document this critical interval of dinosaur evolution. Here, we report a new dinosaur with a nearly complete skull that is the oldest eusauropod known to date and provide high-precision U–Pb geochronology that constrains in time the rise of eusauropods in Patagonia. We show that eusauropod dominance was established after a massive magmatic event impacting southern Gondwana (180–184 Ma) and coincided with severe perturbations to the climate and a drastic decrease in the floral diversity characterized by the rise of conifers with small scaly leaves. Floral and faunal records from other regions suggest these were global changes that impacted the terrestrial ecosystems during the Toarcian warming event and formed part of a second-order mass extinction event.

1. Introduction

Dinosaur faunas underwent remarkable evolutionary changes during the Mesozoic, but the discontinuous nature of the terrestrial fossil record and a lack of reliable age constraints have hampered their correlation to environmental changes or to major events in floral evolution [1]. Sauropodomorpha is the first major dinosaurian group that radiated into multiple herbivorous lineages recorded throughout the world [1–3]. The first 40 Myr of sauropodomorph evolution (Late Triassic–Early Jurassic) are characterized by the coexistence of diverse lineages with great disparity in body size, feeding biomechanics and locomotion types [1,3–5], ranging from small (less than 10 kg) bipedal taxa to the large (greater than 5 tons) quadrupedal early sauropods [5–8]. By the Middle Jurassic (*ca* 170 Ma) eusauropod dinosaurs were the only surviving sauropodomorph lineage, with the possible exception of *Yunnanosaurus youngi* [9]. Eusauropods are characterized not only by their large body size but also by their deep skulls, robust mandibles and large spoon-shaped teeth with thick and rugose enamel [1,2,4,8]. Eusauropods then became one of the most conspicuous terrestrial vertebrates of the Mesozoic: abundantly recorded in all continents during the next 100 Myr, with a characteristic and evolutionary stable body plan, and reaching larger body sizes than any other land animal [6,10,11].

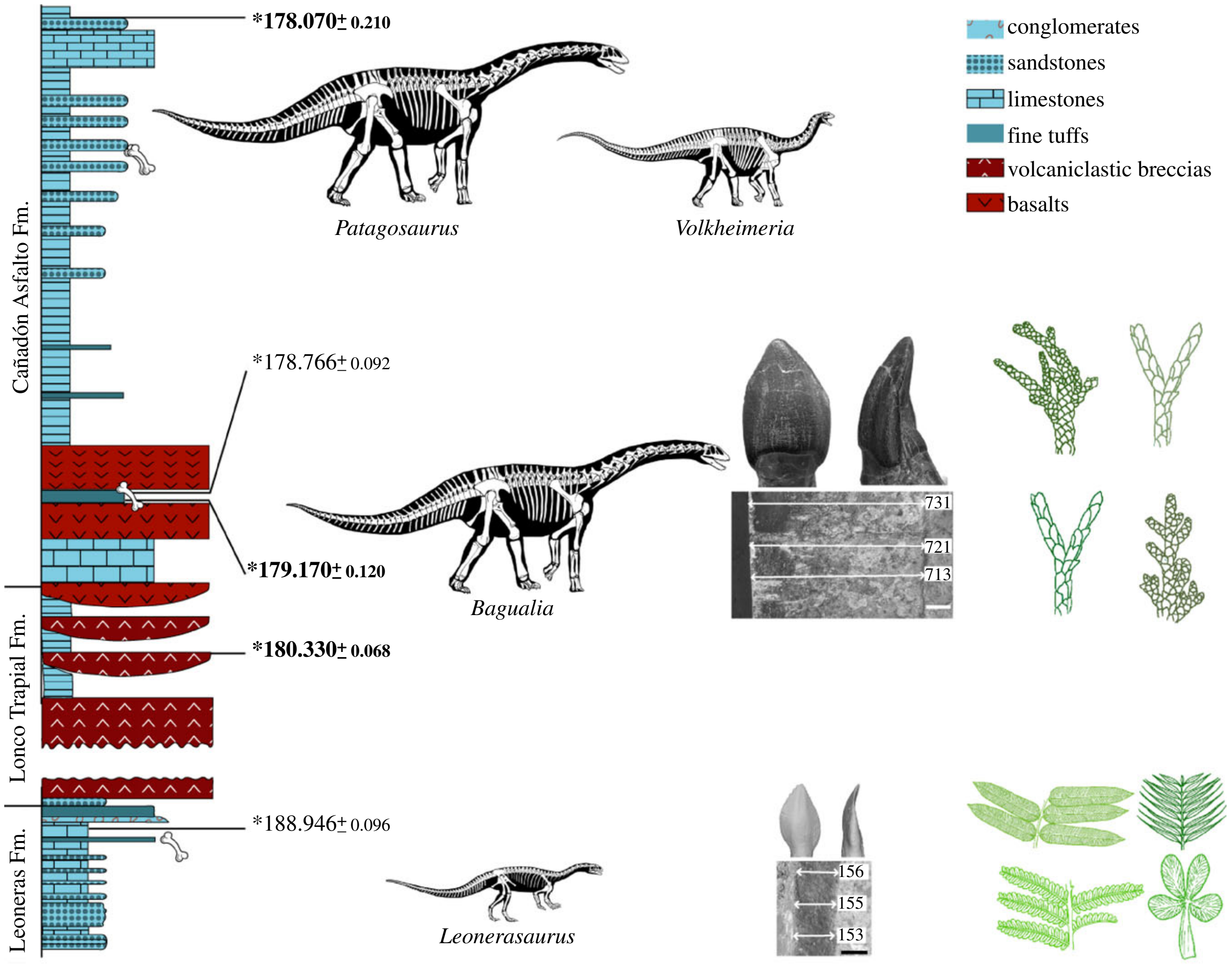

Figure 1. Integrated stratigraphic column of the late Early Jurassic beds of the Cañadón Asfalto Basin [12,13], showing the radioisotopic dates (new dates in bold font) and the distribution of sauropodomorph taxa. Details of sauropodomorph teeth show crowns in labial and distal view and the section of enamel (thickness shown in µm): for the Toarcian *Bagualia alba* and for the pre-Toarcian non-sauropod *Mussaurus patagonicus*. Representatives of the recorded flora are also shown: for the mid-Toarcian the conifers Araucariaceae, Cheirolepidiaceae and Cupressaceae with small scaly leaves and for the pre-Toarcian the diverse assemblage of large dipteridacean ferns, seed ferns and cycads. (Online version in colour.)

Understanding the precise timing and ecological context of the origins of eusauropod dominance in terrestrial ecosystems has been difficult due to the scarcity of sedimentary sequences with relevant fossils throughout this evolutionary transition, which is thought to have happened between the late Early Jurassic and the early Middle Jurassic (180–170 Ma). Although correlations have been proposed between global diversity of sauropods and certain conifer families [1], the depositional settings where they co-occur are limited and mostly restricted to the Late Jurassic, well after the origin of the two groups. Few sedimentary sequences have provided specimens relevant to the origins of eusauropod dominance and nearly all of them lack radioisotopic dates and precise chronostratigraphic control [12–15]. The Cañadón Asfalto Basin in Patagonia accumulated Jurassic sequences that are now well constrained in time with radioisotopic dates [16,17] and has yielded new fossils from terrestrial ecosystems spanning this critical interval of dinosaur evolution. Here, we describe a new species that is interpreted as the oldest eusauropod known to date with a nearly complete skull, whose depositional age is constrained at high precision by the U–Pb technique and marks the onset of the eusauropod-dominated faunas in this basin (figure 1).

2. Results

(a) Systematic palaeontology

Dinosauria Owen, 1842; Sauropoda Marsh, 1878; Eusauropoda Upchurch, 1995

Bagualia alba gen. et sp. nov.

Etymology: bagual, wild horse (Spanish), for the type locality; alba, dawn (Spanish) in allusion to its early age.

Holotype: MPEF-PV 3301, posterior half of skull articulated with seven cervical vertebrae (Museo Paleontológico Egidio Feruglio, Trelew, Argentina).

Locality and Horizon: Bagual Canyon, 5 km south of Cerro Cóndor, Chubut, Argentina. Lower levels of the Cañadón Asfalto Formation dated at 179.17 ± 0.12 Ma (see below and electronic supplementary material), Early Jurassic, Toarcian.

Referred specimens: MPEF-PV 3305–3348 representing remains of at least three individuals (based on repeated elements) found at the same site. The specimens are similar sized (repeated humeri varying up to 15% in length) and include craniomandibular remains (premaxilla, maxilla, nasal, dentary, surangular), multiple isolated teeth, cervical, dorsal, and caudal vertebrae, and limb elements (see electronic supplementary material).

Diagnosis: basal eusauropod diagnosed by the following characters (autapomorphies indicated with *): pointed process on the anteroventral end of the premaxilla and anterodorsal end of the dentary*; anterior margin of the premaxilla without a marked step*; orbital margin of the frontal with a close V-shape pointed medially*, resulting in a short contribution to the orbit; supratemporal fenestra about as anteroposteriorly long as lateromedially wide*; strongly marked proatlantal facets on the laterodorsal margin of the foramen magnum; concave ventral margin of the distal portion of the cultriform process*; axis with the anterior process in the dorsal part of neural spine (convergent in *Jobaria* and *Europasaurus*); accessory lamina below the PCDL in middle cervical vertebrae*; EPRL present in middle cervical vertebrae. See electronic supplementary material for further details on diagnostic features.

Description: The holotype of *Bagualia alba* consists of a posterior half of a skull and the first seven cervical vertebrae, found articulated in a bonebed along with multiple cranial and postcranial elements of the new species (see electronic supplementary material). *Bagualia* has multiple features reported only in eusauropods (figure 2), such as a high and short rostrum with a deep premaxilla and large external nares with a retracted posterior margin. The temporal region also shows derived features of this group, such as a frontal that is wider than long and does not participate in the supratemporal fenestra (which lacks a surrounding fossa and is visible in lateral view). The infratemporal region is deep, and the postorbital descending process is markedly elongated (figure 2). The basicranium is dorsoventrally deep and the basal tubera are placed ventral to the occipital condyle but dorsal to the basipterygoid processes. The preotic pendant is well developed and forms a wing-like crest. The cultriform process of the parabasisphenoid is anterodorsally oriented at its base (although it has been taphonomically deformed along its distal half; figure 2). The supraoccipital is approximately twice as deep as the foramen magnum and the paroccipital processes are similarly deep and ventrally projected.

The lower jaw also shows features that are characteristic of eusauropods. The dentary has a symphyseal region that is broad, U-shaped and dorsoventrally deep. There are 16 alveoli in the dentary and each of these have a well-developed lateral plate on the buccal margin. The tooth crowns are apicobasally high and mesiodistally broad, so that they overlap with each other. As in most early eusauropods, the teeth have a D-shaped cross section, apical denticles, and buccal and lingual grooves (figure 2). The enamel layer of the teeth is over 700 µm thick and heavily wrinkled on its outer surface (figures 1 and 2). Many teeth have an extensive V-shaped wear facets (figure 2). CT scanning of the premaxilla revealed the presence of up to three replacement teeth per position, suggesting high dental replacement rates. The holotype of *Bagualia* includes an articulated cervical series, including the atlas, axis and the following five postaxial cervical vertebrae. The postaxial cervicals are opisthocoelous, elongated (postaxial centrum elongation index = 3.0–4.6) and with well-developed lamination (figure 2). The cervical centra bear ample pleurocoels that are undivided and broadly open laterally. The pleurocoels are anteriorly deep and gradually become shallow toward their posterior end. See electronic supplementary material for further anatomical details.

(b) Phylogenetic analysis

A parsimony phylogenetic analysis robustly places *Bagualia* well nested within Eusauropoda (see electronic supplementary material), along with other taxa recorded worldwide during the Middle and Late Jurassic. The age of *Bagualia* provides the first precise minimum constraint for the radiation time of multiple eusauropod lineages, pushing back their radiation at least into the mid-Toarcian and well before the Middle Jurassic (figure 3). Although Toarcian sauropodomorphs are scarce and many lack precise ages (figure 3), eusauropods (or the slightly more inclusive group Gravisauria) seem to be the exclusive components of the large herbivore guilds in the Toarcian–Aealenian of northern Africa [8,14], Europe [18] and China [12,15]. Other regions that have important sauropodomorph remains from the earliest Jurassic (southern Africa, North America) unfortunately lack sauropodomorph records in the Toarcian. Despite these uncertainties, the calibrated phylogenetic trees clearly indicate the extinction of multiple lineages of early sauropodomorphs before the Toarcian (figure 3), as pre-Toarcian faunal assemblages invariably have diverse lineages of non-eusauropods [3,8,12–13,19–21].

(c) Radioisotopic geochronology

This global pattern of extinction/diversification in sauropodomorphs is uniquely represented in the Cañadón Asfalto Basin. Recent U–Pb zircon geochronology of interbedded tuffs [16] has established a high-resolution chronostratigraphic framework for the fossiliferous rock formations of the basin. Three new U–Pb zircon dates by the CA-ID-TIMS method presented here (see electronic supplementary material) provide more direct age constraints on the *Bagualia* bone bed and further refine the age of peak volcanism of the Jurassic throughout the Cañadón Asfalto Basin. The *Bagualia* fossil site (179.17 ± 0.12 Ma; mid-Toarcian) is positioned close to the base of the Cañadón Asfalto Formation (figure 1). Overlying fossiliferous horizons with dinosaur remains are dominated by eusauropods, such as *Patagosaurus*. Another new U–Pb zircon date of 178.07 ± 0.21 Ma from the upper Cañadón Asfalto Formation in a nearby section reinforces the above date and places a stratigraphically younger age constraint on the fossiliferous interval.

The Cañadón Asfalto Formation is directly underlain by extensive volcanic and pyroclastic rocks of the Lonco Trapial Formation (part of the Chon Aike Igneous Province of Patagonia) with a previously determined age bracket of 188.9–178.8 Ma (Pliensbachian–Toarcian [16,17]) based on tuff ages from the stratigraphically adjacent formations. Our new U–Pb zircon date of 180.330 ± 0.068 Ma from the massive pyroclastic interval of the Lonco Trapial Formation is congruent with previous geochronology [16] and provides a direct age constraint on its peak volcanic activity. This indicates an overall age overlap with the Karoo–Ferrar large igneous province of South Africa–Antarctica [22,23] and raises the possibility of an extensive magmatic province dominating southern Gondwana. The Karoo–Ferrar province has been proposed as the initial trigger of major carbon cycle perturbations [22–25], global warming and rise of atmospheric CO_2 [25] recorded at this time together with marine mass extinctions associated with the early Toarcian oceanic anoxic event (T-OAE).

Underlying the volcanic Lonco Trapial Formation, the fluvial-lacustrine Las Leoneras Formation yielded *Leonerasaurus taquetrensis* [26], one of the youngest documented non-eusauropod sauropodomorphs, from a level previously

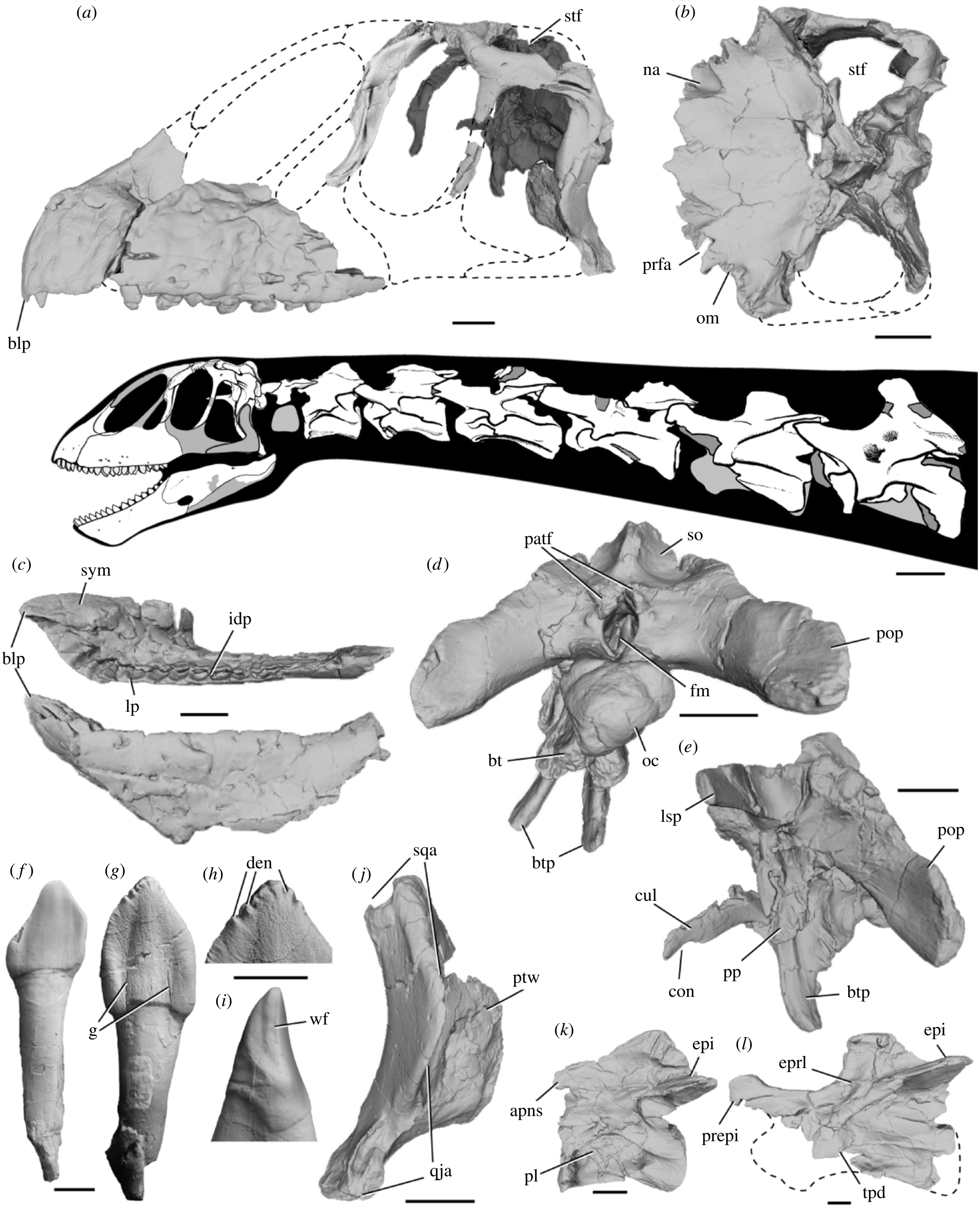

Figure 2. The skull and neck reconstruction of *Bagualia alba*. (*a*) Lateral aspect of the reconstructed skull (combining MPEF-PV 3301, 3305, 3341a, some elements inverted). (*b*) Posterior region of the skull in dorsal view (MPEF-PV 3301). (*c*) Right dentary (MPEF-PV 3302-3) in dorsal and lateral views. (*d* and *e*) Braincase (MPEF-PV 3301) in posterior and left lateral views. (*f* and *g*) Worn (MPEF-PV 11036) and non-functional (MPEF-PV 3176) teeth in lingual view. (*h* and *i*) Details of denticles of MPEF-PV 3176 in lingual view, and wear facet of MPEF-PV 11036 in distal view. (*j*) Right quadrate in lateral view. (*k*) Axis in lateral view. (*l*) Sixth cervical vertebra in lateral view. Scale bars, 3 cm for bones; 1 cm for teeth; 10 cm for the reconstructed skull and neck. Grey colour represents missing elements, white colour represents preserved parts. apns, anterior process of neural spine; blp, beak like process; bt, basal tuber; btp, basipterygoid process; con, concavity; cul, cultriform process; den, denticles; epi, epipophysis; eprl, epipophyseal–prezygapophyseal lamina; fm, foramen magnum; g, groove; idp, interdental plate; lp, lateral plate; lsp, laterosphenoid; oc, occipital condyle; na, articular facet for nasal; om, orbital margin; patf, proatlantal facet; pl, pleurocoel; pop, paroccipital process; pp, preotic pendant; prepi, pre-epipophysis; prfa, articular facet for prefrontal; ptw, pterygoid wing; qja, articular facet for quadratojugal; so, supraoccipital; sqa, articular facet for squamosal; stf, supratemporal fenestra; sym, symphysis; tpd, triangular process of diapophysis; wf, wear facet.

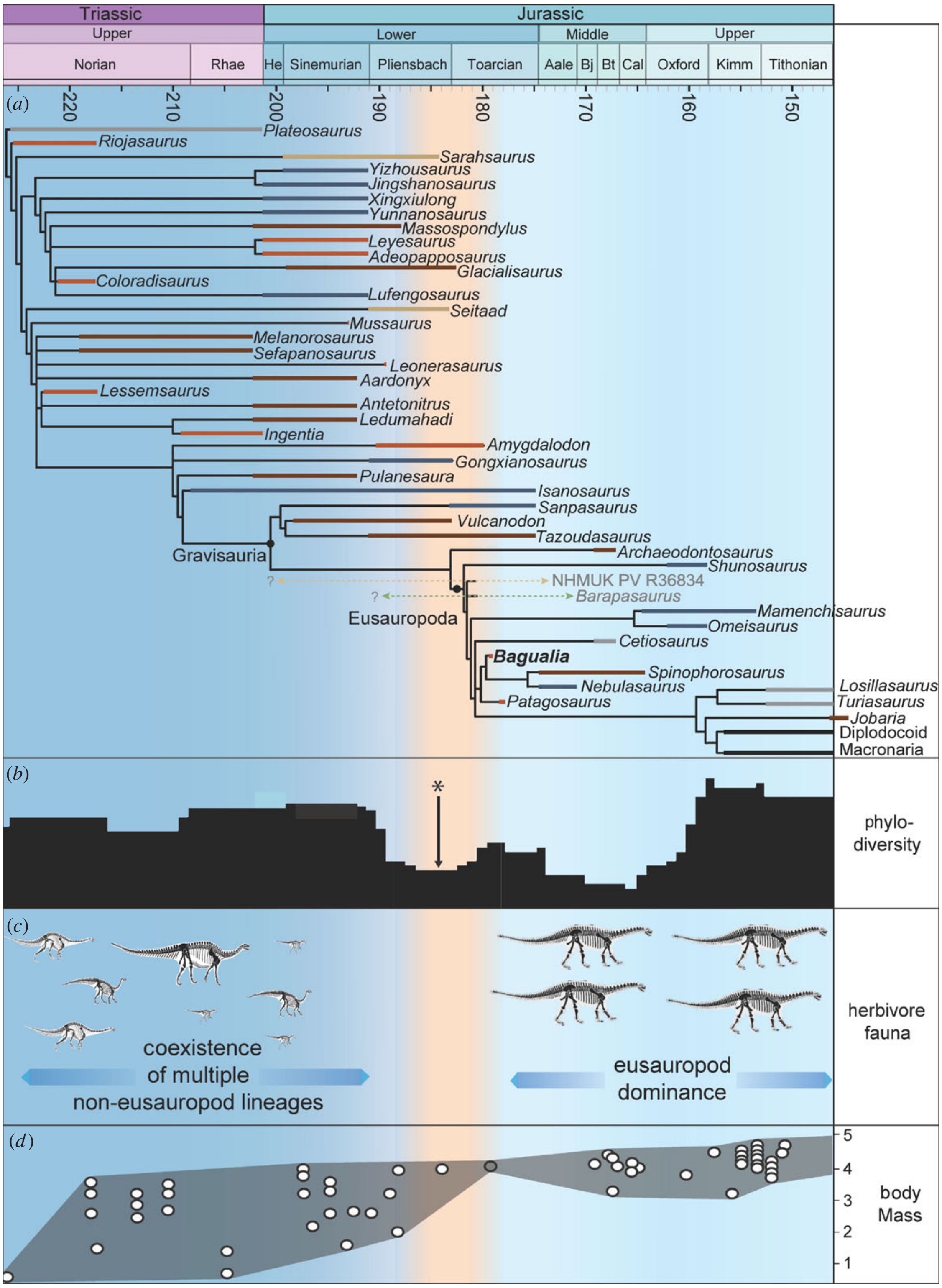

Figure 3. Evolutionary scenario of sauropodomorph faunal turnover, highlighting the Gondwanan volcanic event (red shaded time slice). (*a*) Calibrated phylogeny of Sauropodomorpha (Late Trassic–Late Jurassic). Coloured bars represent temporal uncertainty of terminal taxa (orange = South America, brown = Africa, blue = Asia, grey = Europe, light brown = North America, green = India). Dashed arrows highlight the age uncertainty in previously known early eusauropods. (*b*) Phylogenetic sauropodomorph diversity (arrow marks the extinction of non-sauropods). (*c*) Sauropodomorph faunal change across the Pliensbachian–Toarcian crisis. (*d*) Sauropodomorph body mass estimates in log kg scale. Circles represent mean estimates (data from [5–7]; see electronic supplementary material for numeric values and estimated errors). (Online version in colour.)

dated at 188.946 ± 0.096 Ma [14]. The geochronology now correlates the faunal turnover in Patagonia to the time interval of the Pliensbachian–Toarcian volcanic event (figure 1). All other pre-Pliensbachian faunas from South America include diverse lineages of sauropodomorphs (e.g. *Mussaurus*, *Adeopapposaurus*, *Leyesaurus*) that resemble *Leonerasaurus* in being gracile and small (less than 2 tons) non-sauropods having small leaf-shaped teeth with thin enamel (less than 200 µm).

3. Discussion

The sedimentary successions of the Cañadón Asfalto Basin record a major change in herbivorous dinosaur fauna, as well as major floral and environmental changes concomitant with the Toarcian palaeoenvironmental crises. Before the Pliensbachian–Toarcian volcanism, the plant assemblages [27,28] consisted of a diverse assemblage of sphenophytes, dipteridacean ferns with fronds of 2 m in diameter, conifers, seed ferns, Bennetitales and cycads (figure 1) indicative of humid conditions. By contrast, the less diverse fossil pollen and flora postdating the volcanic event are indicative of seasonally dry and warm conditions, and are largely dominated by the conifers Araucariaceae, Cheirolepidiaceae and Cupressaceae [17,18,29], all of which have small scaly leaves (figure 1). Similar changes in plant assemblages have been recently noted from the Northern Hemisphere coeval with the T-OAE [30,31], including a decrease in taxonomic diversity, increase in abundance of thermophilic groups and progressive dominance of the above-mentioned conifer clades.

Bagualia and other sauropods recorded after the T-OAE time invariably display characters that may have been critical for their success after this environmental change. Their elongated neck provided maximal feeding envelopes and browsing heights [1,32] and their large (greater than 5 tons) body size [2,3,10] has been related to an expansion of gut capacity and fibre digestibility [1,33]. Their deep and robust skulls and mandibles indicate high bite force [3,4] and their long jaw gape and large and broad teeth with thick enamel (greater than 700 μm) and extensive shearing wear facets [2] have been interpreted as adaptations to obligate high-fibre herbivory and bulk feeding on tough, fibrous plant material [1,3,4,10].

The post-T-OAE environment in Patagonia with reduced plant leaf-size and large conifers with coriaceous leaves as the dominant trees likely acted as a strongly selective regime favouring the survival and success of eusauropods. Conversely, the disappearance of many elements of the diverse pre-Toarcian flora could have influenced the extinction of the diverse lineages of smaller non-sauropods, which lacked adaptations to high-fibre herbivory as their gracile skulls and mandibles were less mechanically efficient [3,4] and their teeth were small, with thin enamel (less than 200 μm) and lacked tooth–tooth occlusion.

The apparent temporal and spatial links between the establishment of conifer dominated flora and the emergence of eusauropods in the Cañadón Asfalto Basin in the aftermath of the Toarcian crisis might represent the first documented evidence of plant–herbivore interactions in dinosaur evolution [1]. Furthermore, these linkages are functionally explained by feeding adaptations in sauropods that led to consider conifers such as Araucariaceae and Cheirolepidiaceae as some of the most likely and nutritious food sources for large bodied sauropods [33,34]. Current knowledge on the global distribution and diversity of these conifer and dinosaurian groups suggests that changes recorded in the Cañadón Asfalto Basin may represent a global event that reflects the response of terrestrial ecosystems to the warming of the climate and related environmental changes amid the Toarcian crisis and driven by the Pliensbachian–Toarcian magmatic event of the Southern Hemisphere.

Ethics. The study did not involve humans or live animals and does not require associated ethics approval.

Data accessibility. The specimens described here are housed at the collections of the Museo Paleontológico Egidio Feruglio (Trelew, Argentina). The data supporting the anatomical and phylogenetic study are available in the electronic supplementary material and Dataset S1. The U–Pb age data of this paper are available in the electronic supplementary material and Dataset S2. Both datasets have are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x0k6djhh7 [35].

Authors' contributions. Conceptualization (D.P.), formal analysis (K.G., D.P., J.R.), funding acquisition (D.P., O.W.M.R.), investigation (D.P., K.G., J.L.C., J.R., O.W.M.R., I.H.E., N.R.C.), methodology (D.P., K.G., J.R.), visualization (J.L.C., K.G., D.P.), writing original draft (D.P.), review and editing (O.W.M.R., J.R., K.G., J.L.C., I.H.E., N.R.C.).

Competing interests. We declare we have no competing interests.

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