

Did large foraging migrations favor the enormous body size of giant sauropods? The case of *Turiasaurus*

¿Podieron las grandes migraciones en busca de recursos haber favorecido las enormes tallas alcanzadas por los saurópodos gigantes? El caso de *Turiasaurus*

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Abstract: We propose that the huge sizes attained by many sauropod dinosaurs can be explained in the context of a climate characterized by pronounced seasonal changes. Under these conditions, the large herbivores would have become migratory, forced to move great distances during the drier times of year, in which case large body size becomes an adaptive advantage, since large home ranges and the ability to travel great distances increase with size. In this way, the need for a large foraging radius is a potent source of selection for larger size, and the capacity for sauropods to migrate and explore new territory was significantly higher than in extant herbivores. Examples discussed are *Turiasaurus riodevensis* and *Camarasaurus lentus*; some of their anatomical structures, such as vertebral neural extensions and crests associated with nasal cavities, can also be explained under this scenario, as adaptations to drought conditions.

Resumen: En este trabajo se propone que las enormes dimensiones alcanzadas por muchos dinosaurios saurópodos pueden ser explicadas en un contexto climático caracterizado por cambios estacionales pronunciados. Bajo estas condiciones, estos grandes herbívoros debieron adoptar un comportamiento migratorio, forzados a recorrer grandes distancias durante los momentos de sequía pronunciada. En este contexto, alcanzar grandes tamaños constituye una ventaja adaptativa, dado que la amplitud del área vital, así como la capacidad para recorrer grandes distancias se incrementan en función de la talla. Como consecuencia, la necesidad de incrementar el radio de captación de recursos deviene una potente presión de selección hacia tallas cada vez más grandes. Los enormes tamaños alcanzados por muchos saurópodos sugieren que su capacidad para migrar y explorar nuevos territorios fue mucho mayor que la de los herbívoros actuales, siendo capaces de atravesar grandes distancias en pocos días, a la búsqueda de nuevos recursos.

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INTRODUCTION

Deciphering the huge dimensions of sauropod dinosaurs have long constituted a complex problem, especially since the largest land mammal, the giant rhinoceros *Paraceratherium*, which reached more than 6 m in height, would have been a mid-sized dinosaur in the Mesozoic (Hutchinson, 2021). Evolution towards gigantism in sauropodomorphs started after the end-Triassic mass extinction, in the Early Jurassic, when this group significantly expanded its geographic range to lower latitudes (Dunne *et al.*, 2023). Previously, sauropodomorphs were mostly restricted to higher latitudes, favoring cooler conditions with higher seasonality in surface temperatures. We can find in this early expansion of the sauropodomorph geographic and biotic range a first argument for initial enlargement

of body size. Later in the Jurassic, this spatial pattern seems to have been reversed, sauropods being largely restricted to lower latitudes, their presence at higher latitudes being very rare, in contrast with ornithischians and theropods (Mannion *et al.*, 2012; Dunne, 2022). It seems, therefore, that sauropods were unable to extend to extreme palaeolatitudes because cold temperatures were a constraint (Chiarenza *et al.*, 2022; Dunne *et al.*, 2023). In contrast, the Gondwanan land masses, particularly Africa and South America, probably provided the best conditions for sauropods during the Cretaceous, where we find the largest known titanosaur sauropods (*e.g.*, *Patagotitan* and *Argentinosaurus*; Carballido *et al.*, 2017).

Actually, sauropods reached their largest body mass (more than 40–50 tonnes) during the warmest phases of the Jurassic and the Cretaceous, for instance during the Albian–Cenomanian hot house (Carballido *et al.*, 2017) and the Cenomanian–Turonian Thermal Maximum (Heimhofer *et al.*, 2018). The largest known titanosaur sauropods like *Patagotitan* and *Argentinosaurus* appeared in Gondwana during a time of warm global climates, and this may have happened independently in different sauropod lineages (Carballido *et al.*, 2017). Why these dinosaurs reached such sizes has been the subject of intensive debate, with several possible explanations, concerning sauropod bauplan, biology, resource availability, the high net primary productivity, or even gene pool (e.g., Burness *et al.* 2001; Sander & Clauss, 2008; Sander *et al.*, 2011; Fricke *et al.*, 2011). However, no relationship has been found between body size and estimated genome size in extinct dinosaurs (Organ *et al.*, 2009), which suggests that neutral forces did not dominate the evolution of genome size in this group.

It has also been argued that predator release might have played a role (Curry Rogers & Wilson, 2005; Klein *et al.*, 2011), but it remains to be explained why predators reached also comparative larger sizes (Canale *et al.*, 2023), such as the carcharodontosaurids *Tyrannotitan* (13–14 m), *Giganotosaurus* (12–13 m) or *Mapusaurus* (11–12 m; Paul, 2016). Other authors proposed that sauropod gigantism could be the result of the complex interplay of a historically contingent combination of plesiomorphic and derived traits and characters (Sander *et al.*, 2011; Sander, 2013).

In any case, the evolutionary trade-offs with gigantism appear to be highly environment-specific (Hutchinson, 2021); a variety of evidence points to climate evolution during the Jurassic and the Cretaceous and associated changes in floras and environments as the most feasible explanation (Chiarenza *et al.*, 2022; Dunne *et al.*, 2023). For instance, during the Late Jurassic and Early Cretaceous palaeobotanical evidence points to the spread of savanna-like environments which may have favored the proliferation of large herbivores (Heimhofer *et al.*, 2018).

GEOLOGICAL AND PALAEOENVIRONMENTAL CONTEXT

Although claimed as a stable period dominated by widespread greenhouse conditions, in fact the Jurassic and Early to mid-Cretaceous was a time that was affected by significant climatic and environmental events. Different proxies, such as ^{13}C and ^{18}O isotopes (Friedrich *et al.*, 2012; Li *et al.*, 2006), palaeosol carbonates (Huang *et al.*, 2012; Pan & Huang, 2014) and palaeobotany (Wang *et al.*, 2014), show that ecosystems through this time were affected by major climatic and environmental events (Tennant *et al.*, 2017; Pol *et al.*, 2020), such as changes in atmospheric CO_2 levels (Wang *et al.*, 2014), short

lived glacial events (Bornemann *et al.*, 2008), cooling events (even within the Cenomanian–Turonian hottest greenhouse interval; Bornemann *et al.*, 2008) and global eustatic changes (Hu *et al.*, 2012). Some of these were short-term events (less than 1 My, on the scale of Milankovitch cycles; Hu *et al.*, 2012). Changes in depositional environments, from marine tropical to continental semi-arid (Mediterranean type), also reflect climate changes. For instance, in the Upper Jurassic–Lower Cretaceous Riodeva section (Teruel, Spain), alternating sequences formed by relative sea-level changes on the order of a few meters to thirty meters. These comprise regressive deposits mainly of continental red-beds containing calcareous palaeosols of the caliche type, and transgressive sediments deposited in incised valleys during regressions (Luque *et al.*, 2005). The calcareous palaeosols also indicate seasonal aridity and a seasonal dry and wet cycle (Santisteban & Santos-Cubedo, 2011; Campos-Soto *et al.*, 2015, 2017).

The Tethys sea would have sustained a low latitude anticyclone that made the Meso-Mediterranean zone drier than its modern equivalent (Krassilov, 2003). A climatic latitudinal zonation with seasonal variations was established. South of the nemoral zone, there was a semideciduous arboreal biome with a prominent xeromorphic element. Climatic conditions were warm-temperate to subtropical, of the Mediterranean type, with a dry summer season (Krassilov, 2003). Therefore, in the Late Jurassic, dinosaur ecosystems occurred in a prevalently seasonal biome. Alternating warming and cooling events might have favored the spread of a strongly seasonal savanna-like biome, at the expense of conifer-dominated forests (Chiarenza *et al.*, 2022).

Under these conditions a certain number of dinosaurs, and especially the larger herbivores, should have been forced to adopt migratory behavior and to move great distances during the drier times of year. The extraordinary record of fossilized ichnites, which in many areas greatly exceeds the record of sites with fossil bone remains, seems to support this scenario. Tracks attributed to sauropods and ceratopsians indicate that these were social animals that travelled long distances in groups, with a behavior similar to that of living large herbivores such as elephants or wildebeests (Malone *et al.*, 2021). Also, during the Early Cretaceous several migratory routes have been suggested between Gondwana and Laurasia, such as the ‘Apulian route’ (Dalla Vecchia, 2002; Canudo *et al.*, 2009) or during the Late Cretaceous (Holwerda *et al.*, 2018) based on tracks and skeletal remains.

Today, migrations of this type are common in Africa and Asia, where thousands of animals travel hundreds of kilometers to escape annual drought. In fact, fossil records show that Asian elephants conducted large-scale migrations during the Holocene, which occurred repeatedly with cyclical climatic variations (Wang *et al.*, 2021). In this way, large body size becomes a great advantage (Bell & Snively, 2008; Fricke *et al.*, 2011).

SIZE AND HOME-RANGE

Smaller reptiles and mammals, such as lizards and rodents, have a very limited home range (Perry & Garland, 2002; Ariano-Sánchez *et al.*, 2020; Saanya *et al.*, 2022). When faced with changes in their environment, these small vertebrates have no other option but evolutionary change. In contrast, megaherbivores such as elephants or giraffes have very large home ranges and can travel great distances in only a few days to reach new areas where the conditions for life are still available (Pennycuik, 1979; Lindstedt *et al.*, 1986; Osborn, 2004; Ofstad *et al.*, 2016; Ngene *et al.*, 2017). This makes these mammals much more resilient, and it is likely that many dinosaurs employed this strategy during the Jurassic and Cretaceous when large areas of the globe were subject to seasonal drought. However, while a giraffe or an elephant can cover many kilometers in a single day, the enormous sizes attained by many sauropods meant that their capacity to migrate and explore new territory was significantly higher (Fig. 1). Home range and the ability to travel long distances increase with size (Pennycuik, 1979; Lindstedt *et al.*, 1986; Tucker *et al.*, 2014; Ofstad *et al.*, 2016; Lyons *et al.*, 2019). Therefore, natural selection would have favored larger animals that could travel ever greater distances once resources had run out in the area in which a species normally lived. The extraordinary size of these herbivorous dinosaurs may be explained by an environment in which seasonal drought forced these enormous quadrupeds to travel great distances each day to meet their needs. The existence of bone beds with large concentrations of skeletons of even tens of individuals from the same species, suggests that on occasion these great migratory herds would not have reached their objective, and died in masse when extreme drought made acquiring new resources impossible (Foley *et al.*, 2008; Knight, 2008; Rogers & Krause, 2014; Smit *et al.*, 2020). Actually, the richest sauropod localities coincided with habitats characterized by semiarid environments (Chiarenza

et al., 2022). Drought is the primary cause of mass death accumulations today and evidence of strong seasonality and semiarid conditions in association with bonebeds indicates that drought may also have been a major killing agent for dinosaurs during the Jurassic and Cretaceous (Rogers, 1990; Gates, 2005).

Large vertebrates are better suited to last out seasonal food shortages than small ones. The need for a large foraging radius may well be a potent source of selection for larger sizes. Species make use of a larger foraging radius to increase the reliability of food supply. For herbivores commuting from a water source, increased foraging radius confers the ability to last longer under drought conditions. Some species seek to improve the predictability of their food supply by maximizing the area over which they forage, and this leads to selection pressure for larger sizes and locomotor adaptations conferring economical cruising (vs impracticable defense of a feeding area). It also calls for a type of social organization that tolerates high densities of individuals and facilitates the transfer of information about food distribution between individuals (Pennycuik, 1979). Thus, sauropods would have taken advantage of developing a large-sized, herd-behavioral framework to afford changing ecological conditions.

MATERIAL AND METHODS

Turiasaurus riodevensis (Fig. 2) is a truly gigantic eusauropod with such a peculiar set of anatomical features that it was made not only a new genus and species, but also a new sauropod clade: the Turiasauria. Fossil turiasaurians have been found in several continents, both from the former Laurasia and Gondwana (Royo-Torres *et al.*, 2006, 2017, 2021; Royo-Torres & Upchurch, 2012; Mateus *et al.*, 2014; Schwarz *et al.*, 2020; Allain *et al.*, 2022; Sharma *et al.*, 2022; Milàn & Mateus, 2024) and estimations of

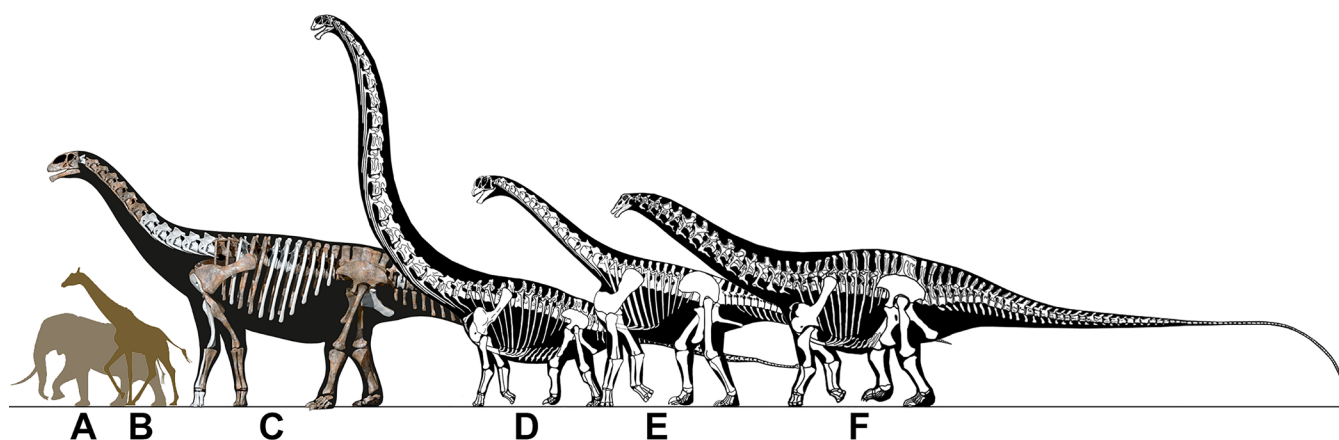


Figure 1. Size comparison of: **A**, *Loxodonta africana*; **B**, *Giraffa camelopardalis* (both modified from O'Connor, 2020); **C**, *Turiasaurus riodevensis* (Fundación Conjunto Paleontológico de Teruel-Dinópolis); **D**, *Mamenchisaurus hochuanensis* (modified from Bivens, 2019); **E**, *Camarasaurus lentus* (after Hartman, 2018); **F**, *Apatosaurus louisae* (modified from Bivens, 2018).

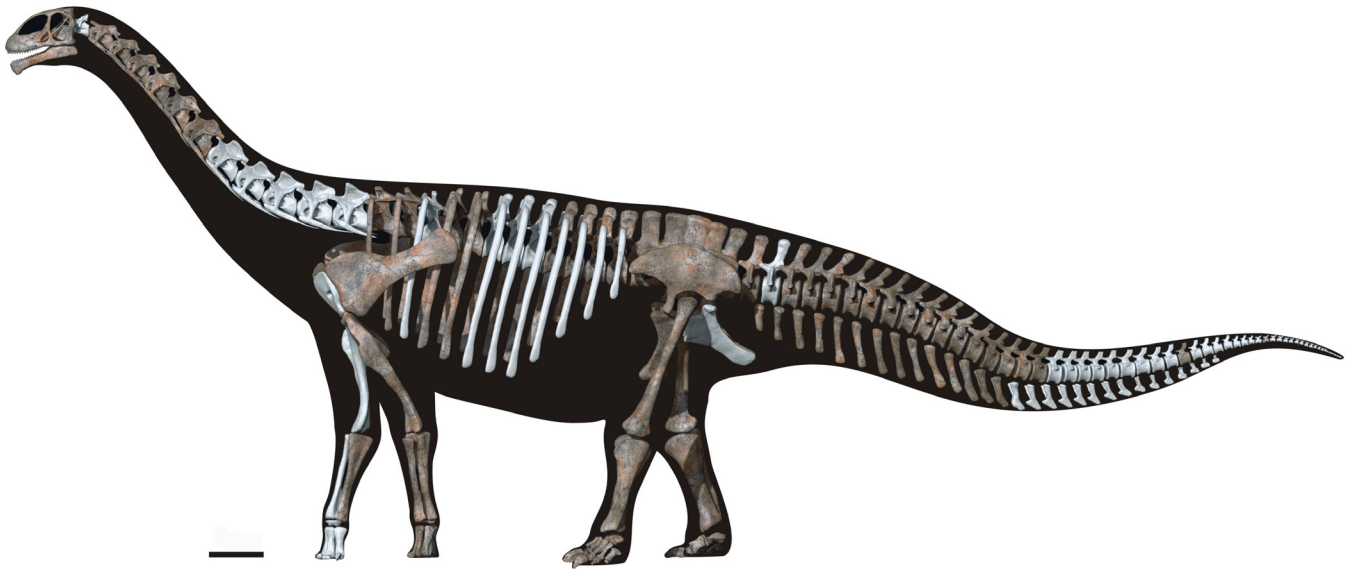


Figure 2. Reconstruction of the skeleton of *Turiasaurus* based on partial skeletons of *Turiasaurus* and the closely related *Losillasaurus* from Riodeva (Teruel, Spain). The length of the humerus (type) is 179 cm. Fundación Conjunto Paleontológico de Teruel-Dinópolis; scale bar = 1 m.

their body mass have been possible because of good representation of their bones.

To estimate the body mass of *Turiasaurus riodevensis* the Anderson *et al.* (1985) method was used, which produces some of the lowest body mass estimates. Being conservative (Royo-Torres *et al.*, 2006), *Turiasaurus riodevensis* ranged between 39.90 and 47.96 metric tonnes. Using the formula obtained by Mazzetta *et al.* (2004), the body mass gives a range from 41.91 to 45.77 tonnes, exceeding 40 metric tonnes. All these data establish *Turiasaurus riodevensis* as one of the largest sauropods yet discovered, and the heaviest European dinosaur. To compare with *Turiasaurus riodevensis*, we also included in our analysis *Camarasaurus lentus*, whose body mass was calculated by Paul (1998), among others.

To calculate the home-range of these sauropods, we use the regression between body mass vs foraging radius established by Pennycuick (1979) for elephants and du Toit (1990) for giraffes, the two largest living terrestrial vertebrates.

RESULTS

Present big terrestrial herbivores, used as comparison, achieve home ranges of 282 km² (giraffe; du Toit, 1990), or some 2,000 km² (elephants; Pennycuick, 1979), although this area increases up to four times in drier environments because of the necessity to look for food, and it is much smaller in forests where food supply is abundant (Osborn, 2004). Assuming that large sauropods could have had similar behavior to large herbivores today, despite not belonging to the same class and with an average body mass of 44,000 kg, an adult *Turiasaurus riodevensis* would have been able to forage in a circle of 144 km radius, equivalent

to a 65,159 km² area, close to the area, for instance, of Ireland (70,000 km²) or Latvia (Fig. 3).

According to the estimates of Paul (1998), an adult *Camarasaurus lentus* weighed 14.2 metric tons, corresponding to nearly 100 km of foraging radius, and an area of 26,365 km² (same area than Rwanda). It has been proposed that *Camarasaurus* migrated in western North America during Late Jurassic–Morrison time, from lowland-river floodplains to upland areas (Sander & Clauss, 2008). Such recorded displacements involved a distance of at least 300 km, and the authors of this study questioned whether these migrations were universal or whether they represent a behavioral response to environmental stress. Were *Camarasaurus* long-distance seasonal travelers or not (some studies consider some large polar dinosaurs capable of migrating up to 2,600 km in 6 months; Bell & Snively, 2008), the longest displacements proposed for the Morrison *Camarasaurus* fit the calculated span of a foraging range of such big individuals. In both examples, *Camarasaurus* and *Turiasaurus*, there is evidence of seasonality, with dry and wet periods.

DISCUSSION

Some of the strange anatomical structures found in the large sauropods might be explained as adaptations for survival in environments with scarce resources and persistent drought over long periods. This is the case, for example, of the moderately long olecranons of some giant sauropods (Bell & Snively, 2008) or the large accumulations of fat observed in some large quadrupeds (Wilkinson & Ruxton, 2013). This accumulation of fat had the disadvantage of inhibiting the dissipation of excess heat, which might have been a serious handicap for organisms that had to adapt to arid environments, where the skin is used as a

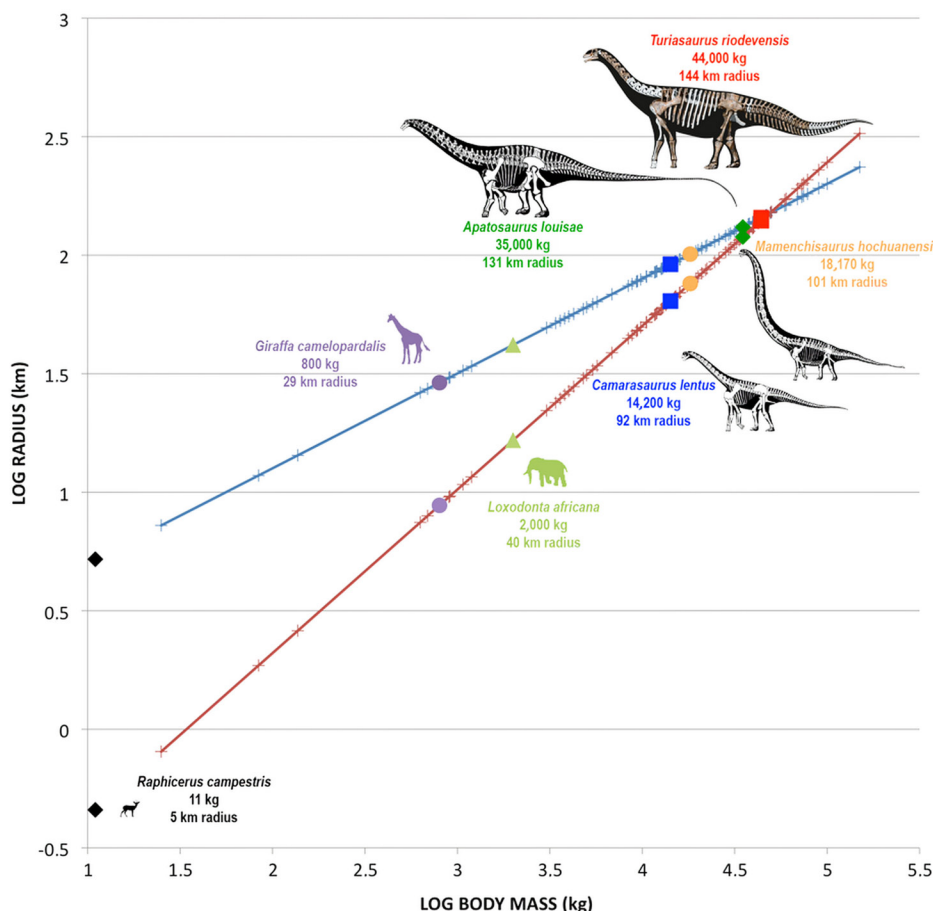


Figure 3. Sauropod home range estimates according to the methodologies of Pennycuick (1979) (blue line), and du Toit (1990) (red line). Dinosaur body mass data from Royo-Torres et al. (2006), Sander et al. (2011) and Paul (2016). Giraffe and steenbok data from du Toit (1990). Elephant data and dinosaur home-range radius estimates according to Pennycuick (1979).

mechanism to dissipate heat and in which a large body volume could be highly counterproductive. It has been suggested that long necks and tails could have shaped sauropod morphology into a higher proportional body surface area (Henderson, 2013). In living camels and zebus, this problem is solved by the accumulation of fat in specific parts of the back, creating humps, which allows them to perspire in other parts of the body. It is very likely that the vertebral extensions in the form of neural spines in many sauropods —usually interpreted in terms of display— were actually structures to support large accumulations of fat on the backs of these animals. Several dinosaurs had elongated neural spines (Bailey, 1997; Rauhut et al., 2005; Ortega et al., 2010; Cerda et al., 2022). According to Bailey (1997), these neural spines formed humps that were adapted to: (i) energy storage, maintenance of gigantothermy, and heat-shielding in unshaded habitats; (ii) long-distance migration from feeding to nesting grounds across terrains of variable productivity; and (iii) lipid conservation for production of large clutches of eggs at the nesting site. Therefore, the complexity and accentuated vascularization of these structures in sauropod dinosaurs suggests they could have acted as energy storage deposits for sustenance during dry seasons and moments of migration. This adaptation could help huge sauropods to survive in poorly shaded palaeoenvironments in which moisture and productivity were seasonally limited, as was the case of semideciduous arboreal biomes with prominent xeromorphic elements.

At the same time, the extended external nares observed in some sauropods such as *Brachiosaurus*, *Camarasaurus* and *Turiasaurus* (Fig. 4) may have served to increase the surface area of the mucous membranes, which would help to reduce the amount of water lost from respiration, humidify air inhaled and cool exhaled air.

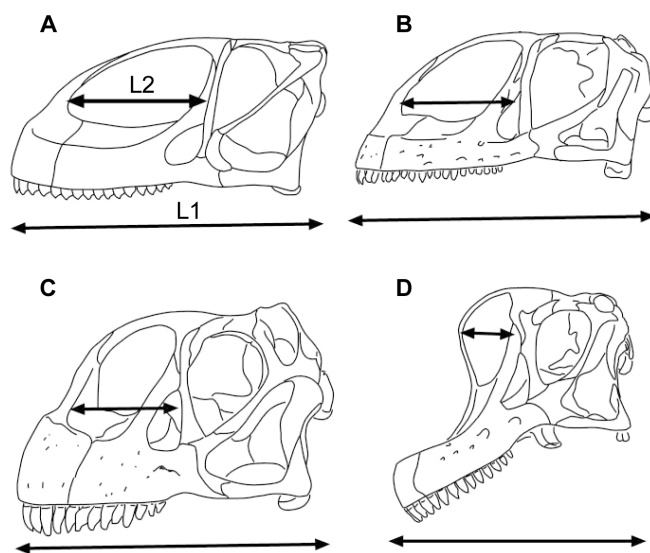


Figure 4. Comparison of external nares. A, *Turiasaurus*; B, *Jobaria*; C, *Camarasaurus*; D, *Brachiosaurus* (after Royo-Torres & Upchurch, 2012). Abbreviations: L1, length of the skull; L2, length of the external nares: not to scale.

CONCLUSIONS

We argue here for the hypothesis that sauropod gigantism was related to the home range of individuals. The most parsimonious explanation to explain their large size could connect to their need to maximize their adaptations to cover wide areas looking for food and water supplies in a time of pronounced seasonality of climates. Large body size could have been a highly adaptive feature, enabling them to migrate through long distances. The enormous sizes attained by many sauropods meant that their capacity to migrate and explore new territories was significantly higher than among extant herbivores (Paul, 2013). However, while sauropods and other non-avian dinosaurs became larger to cover long distances, avian dinosaurs followed an opposite evolutionary trend towards dwarfism, thanks to their endothermic metabolism and development of feathers, which enabled them to fly and cover long distances without the need to increase their body size. In contrast, this adaptation enabled avian dinosaurs to pursue a converse migratory strategy and to reduce their body sizes considerably, a much more efficient strategy which presents fewer mechanical hurdles than its alternative.

Supplementary information. This article has no additional data.

Authors contribution. JA performed the migratory scenario and wrote most of the paper. LA provided the home-range of *Turiasaurus* and *Camarasaurus* and wrote parts of the paper. AS-C provided the geological evidence for Jurassic–Cretaceous seasonality and wrote parts of the paper.

Competing Interest. The authors declare no conflict of interest.

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