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Lowland–upland migration of sauropod dinosaurs during the Late Jurassic epoch

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Sauropod dinosaurs were the largest vertebrates ever to walk the Earth, and as mega-herbivores they were important parts of terrestrial ecosystems. In the Late Jurassic-aged Morrison depositional basin of western North America, these animals occupied lowland river-floodplain settings characterized by a seasonally dry climate[1,2]. Massive herbivores with high nutritional and water needs could periodically experience nutritional and water stress under these conditions, and thus the common occurrence of sauropods in this basin has remained a paradox. Energetic arguments and mammalian analogues have been used to suggest that migration allowed sauropods access to food and water resources over a wide region or during times of drought or both[3,4], but there has been no direct support for these hypotheses. Here we compare oxygen isotope ratios ($\delta^{18}O$) of tooth-enamel carbonate from the sauropod *Camarasaurus* with those of ancient soil, lake and wetland (that is, 'authigenic') carbonates that formed in lowland settings. We demonstrate that certain populations of these animals did in fact undertake seasonal migrations of several hundred kilometres from lowland to upland environments. This ability to describe patterns of sauropod movement will help to elucidate the role that migration played in the ecology and evolution of gigantism of these and associated dinosaurs.

Inferring the behaviour of ancient organisms is difficult, but geochemical information preserved in their fossil remains can provide such an opportunity. This study of sauropod dinosaur behaviour relies on the fact that $\delta^{18}O$ values of surface waters ($\delta^{18}O_{sf}$; for example streams, lakes) vary significantly over any given landscape in response to differences in aridity and elevation among other environmental factors[5,6]. Authigenic carbonates ($CaCO_3$) form in basin soils, lakes and wetlands, and record the oxygen isotopic characteristics of these host isotopic domains when they precipitate. Similarly vertebrate tooth enamel (bioapatite $Ca_5(PO_4, CO_3)_3(OH, CO_3)$) records the oxygen isotope characteristics of the surface water reservoirs that serve as their drinking water[7,8]. If $\delta^{18}O_{sf}$ inferred from 'non-migratory' authigenic carbonates and from dinosaur tooth enamel differ, then it can be concluded that dinosaurs were drinking water that fell outside the basin and thus they travelled outside it.

To use this approach we analysed enamel carbonate from teeth ($n = 32$) of *Camarasaurus* sp. and *Camarasaurus lentus* collected at Thermopolis, Wyoming, and Dinosaur National Monument, Utah (DNM), respectively (Fig. 1a). Palaeosol and lacustrian carbonates were also analysed from DNM ($n = 38$; see Supplementary Information for details on methods and statistics). In addition, we used published $\delta^{18}O$ data obtained from a variety of authigenic carbonates found over the entire Morrison basin including the Thermopolis area[9–12]. Comparisons of isotopic data from co-occurring authigenic carbonates and tooth enamel, from tooth-enamel carbonate and tooth-enamel phosphate, and from single teeth indicate that primary palaeobiological information is preserved in tooth enamel (see Supplementary Information for more details about diagenesis).

To estimate $\delta^{18}O_{sf}$ using dinosaur tooth enamel, it is assumed that they fractionated oxygen isotopes in a manner similar to all water-dependent vertebrates studied so far, including birds, mammals and reptiles[7,8]. To estimate $\delta^{18}O_{sf}$ using authigenic carbonate, it is assumed that oxygen isotope fractionation occurred at 24 °C, a temperature consistent with modelled mean annual temperature for the region[13] (see

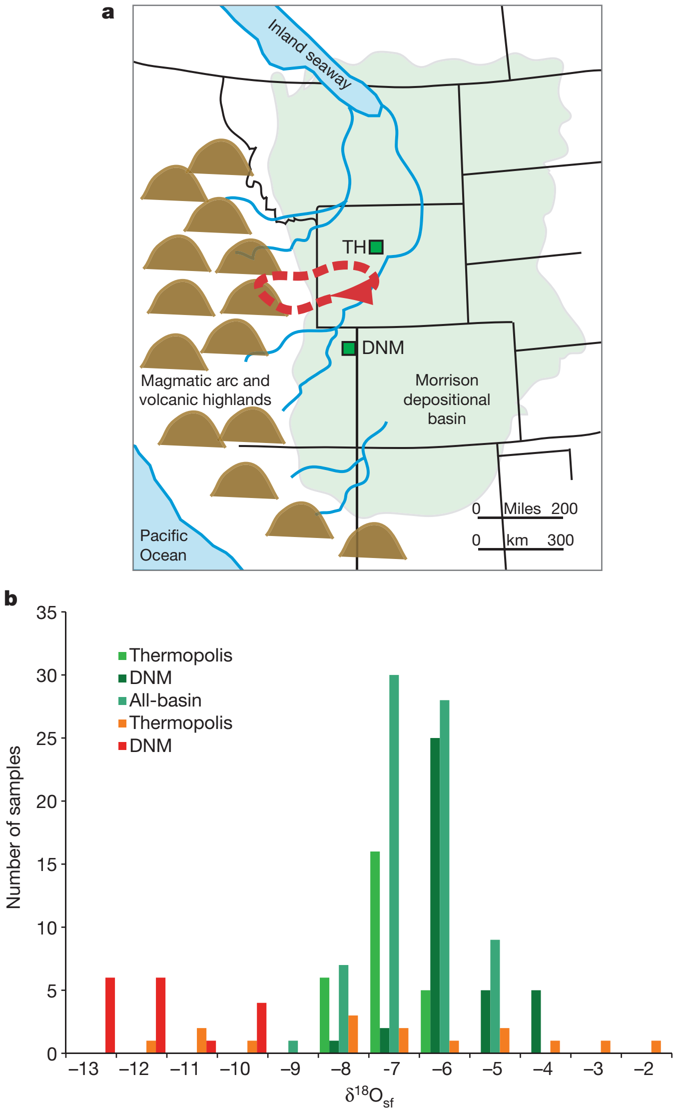

Figure 1 | Fossil localities, inferred oxygen isotope ratios of surface water and possible *Camarasaurus* migration routes. a, Palaeogeography of western North America during late Jurassic/Morrison time (after refs 2, 9), including fossil localities and one hypothetical migration route. **b**, $\delta^{18}O_{sf}$ estimated using tooth enamel (reds) and authigenic carbonates (greens; Thermopolis data from ref. 11; all-basin data from refs 9, 10, 12). See text and Supplementary Information for details.

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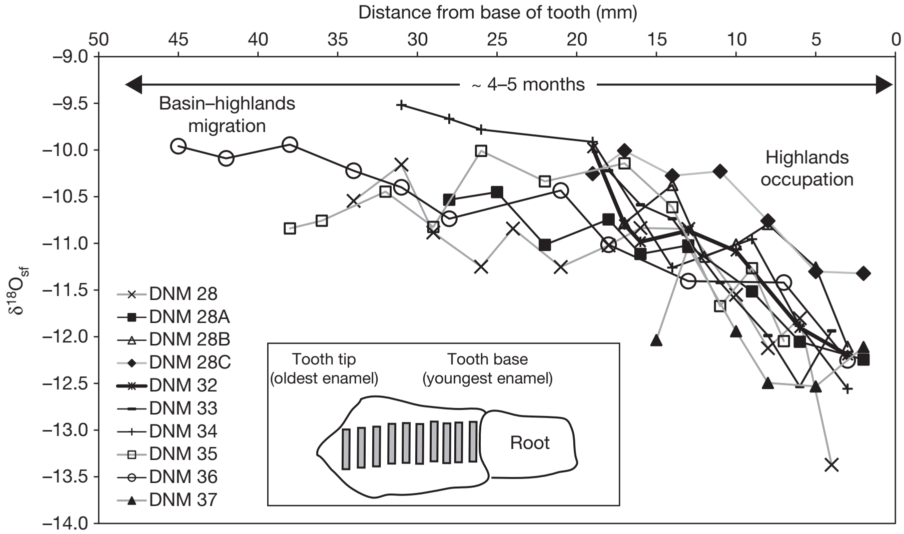

Figure 2 | Oxygen isotope ratios of serial enamel samples compared with position relative to the base of the tooth for ten different teeth from DNM. Teeth form incrementally such that the oldest enamel is at the tip and the youngest enamel is at the base (see inset). Most teeth are characterized by a gradual decrease in oxygen isotope ratios over time. Tooth DNM 36 is unworn and thus preserves the longest temporal record (approximately 4–5 months), whereas records from other worn teeth are truncated to various degrees.

Supplementary Information for details about estimates of $\delta^{18}O_{sf}$). Although $\delta^{18}O_{sf}$ inferred for all authigenic carbonates have relatively high and limited $\delta^{18}O$ values, those inferred for *Camarasaurus* have significantly different means and variances (Supplementary Tables 1–3). Most importantly, they preserve a record of the lowest $\delta^{18}O_{sf}$ of all carbonates analysed from the Morrison basin (Fig. 1b).

$\delta^{18}O_{sf}$ values inferred from *Camarasaurus* that overlap with those from authigenic carbonates are consistent with these animals spending time in the fluvial and wetland environments of the basin. In contrast, lower $\delta^{18}O$ of surface water and precipitation ($\delta^{18}O_{sf} <$ approximately -9‰) implied by a large proportion of *Camarasaurus* teeth indicates that they occupied non-basinal settings. Low $\delta^{18}O_{sf}$ values result from the preferential rainout of ^{18}O from air masses as they rise, cool and lose water while crossing topographic barriers such as volcanic highlands west of the basin (Fig. 1a). Thus, they indicate that animals from both DNM and Thermopolis were drinking water from these high-elevation regions. Although it is possible that ‘extra-basinal’ high-elevation waters could flow into lakes and rivers located in the basin proper, the fact that lake and wetland carbonates do not have low $\delta^{18}O$ indicates that such recharge did not have a major influence on $\delta^{18}O_{sf}$ in the basin (Fig. 1b). Therefore *Camarasaurus* populations in these areas must have directly occupied high-elevation regions for at least part of the year before returning to the basin where they died. To do so, these animals must have migrated approximately 300 km in each direction based on palaeogeographical reconstructions for the Late Jurassic[2,9](Fig. 1a).

Patterns in $\delta^{18}O$ obtained from single teeth provide evidence that this migration was seasonal in nature. Because vertebrate teeth, including those of dinosaurs[14], form incrementally, sequential sampling along the length of a tooth provides a record of $\delta^{18}O_{sf}$ ingested during the time of tooth formation[15–17]. Intra-tooth variations in $\delta^{18}O_{sf}$ inferred from camarasaurid teeth of a single DNM *C. lentus* skull (see Supplementary Information) appear to capture slightly less than half of the sinusoidal cycle that is expected for a single year[15,16], thus indicating that these teeth formed over approximately 4–5 months (Fig. 2). The specific pattern in $\delta^{18}O_{sf}$ implies that this animal moved out of the basin into highland regions over the period of tooth formation, yet the teeth are found in the basin. Such a situation is possible because tooth enamel does not provide an instantaneous record of ingested $\delta^{18}O_{sf}$; rather, there is a temporal lag associated with the turnover of oxygen in the body. This lag is of the order of 2 weeks for small mammals[18], and although the length of time is unknown for sauropod dinosaurs it cannot have been longer than several weeks to a month, otherwise seasonal variations would be obscured altogether. Thus, over 5–6 months, this individual left the basin for the highlands and then returned to the DNM area.

Assuming that *Camarasaurus* migrated in an effort to obtain the food and water they needed to survive, they would have left the basin during the dry season (presumably summer[19]) when plant growth was limited and drought might have been common, and then returned in the wet season (presumably winter[19]). The fact that the DNM *C. lentus* died before preserving a record of basin $\delta^{18}O_{sf}$ in its tooth enamel suggests that it was recently returned, and that it died during the transition from the dry to wet season. The similarity in bulk $\delta^{18}O$ among DNM teeth from other individuals suggests that other *Camarasaurus* from DNM exhibited similar behaviour. Without well-constrained intra-tooth data from Thermopolis is it not possible to describe *Camarasaurus* migrational patterns in as much detail in this area. However, the fact that $\delta^{18}O_{sf}$ inferred from Thermopolis are generally higher than those from DNM (Fig. 1b) could mean that the Thermopolis teeth captured a different part of the seasonal cycle in $\delta^{18}O_{sf}$ and thus might have died during a different time of the year, that Thermopolis teeth grew during different year(s), or that these animals visited a different (possibly lower elevation) part of the western highlands.

Overall, the research presented here provides strong support for the hypothesis that *Camarasaurus* could undertake long seasonal migrations. It does not, however, imply that they must have done so. Ongoing studies of other *Camarasaurus* populations and of other sauropods living in different areas will allow us to determine if migrations were a universal characteristic of these animals, or whether it was a behavioural response to environmental stress. In turn it will be possible to address the role that migration might have played in the evolution of sauropod gigantism.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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