INTRODUCTION

The Upper Jurassic Morrison Formation of the Rocky Mountains and Colorado Plateau is famous for its dinosaur fossils, including large herbivorous sauropods that were the largest terrestrial animals to ever inhabit the Earth (Galli et al., 2018; Sander et al., 2006; Turner & Peterson, 2004). Gastroliths are pebble-to-cobble-sized clasts that are consumed by a variety of extant organisms such as birds to aid in digestion or other functions, and their presence has been observed or inferred in several Mesozoic dinosaur clades (Jennings & Hasiotis, 2006; Kobayashi et al., 1999; Stokes, 1987; Wieland, 1906; Wings, 2007). Gastroliths are readily identified by their rounded shape, durable lithology and smooth, highly polished surface and on occasion they are found in the abdominal cavity of fossil vertebrates (e.g. Kobayashi et al., 1999; Wings, 2007).

Gastroliths composed of red quartzite (among other colours of quartzite and durable rock types such as chert and fine-grained volcanic rocks) are present in the Morrison Formation, and these bear a strong lithological resemblance to Yavapai-Mazatzal (i.e. Baraboo Interval) quartzites that are widely distributed across western and
central Laurentia (Dott, 1983). Baraboo Interval quartzites are noted for their red colour and extreme textural and compositional maturity (i.e. well-rounded and well-sorted with nearly 100% quartz) and occur in Wisconsin (Medaris et al., 2011; Van Wyck & Norman, 2004) and South Dakota/Minnesota (Holm et al., 1998), all of which likely were exposed during the Jurassic (Medaris et al., 2011). Similar Yavapai-Mazatzal quartzites occur in New Mexico and Arizona (e.g. Mako et al., 2015; Spencer et al., 2016). Red quartzite is present, but not common in Mesoproterozoic Belt Series quartzites (Link et al., 2016), which occur in Montana and Idaho, and Neoproterozoic quartzites of the Cordilleran margin that extend from Idaho to California (Yonkee et al., 2014).

We report evidence of long-distance (as much as 1,000 km) movement of dinosaurs, most likely sauropods, using U-Pb geochronology of zircons separated from gastroliths. Detrital zircon age spectra are used as a fingerprint to determine gastrolith provenance. We hypothesize that these gastroliths were ingested by sauropod dinosaurs well beyond the current depositional extent of the Morrison Formation and then transported to the site of deposition within the animals.

1.1 | Background

The Morrison Formation is among the most extensive lithostratigraphic units in Laurentia, occurring from New Mexico northward into Canada (>1.5 million km²; Demko et al., 2004). It was deposited in a foreland basin during the Late Jurassic (155–148 Ma; Kowallis et al., 1998) east of the Cordilleran magmatic arc and incipient Sevier orogenic belt, and west of the Laurentian craton (May et al., 2013). The Morrison Formation forms an eastward-tapering clastic wedge that is as much as 300 m thick at the foot of the Sevier orogenic belt (Galli et al., 2018). It is comprised of variegated mudstones with variable volcanic ash components that range from greenish gray to purple in colour that are interbedded with thin, discontinuous sandstones. Deposition occurred in a broad alluvial plain that included...
fluvial, lacustrine, paludal and eolian environments that may have drained to estuarine environments to the north (Hasiotis, 2004).

Our study area is in the northeastern Bighorn Basin of Wyoming, (Bellahsen et al., 2006; Figure 1). The Middle Jurassic Sundance Formation rests conformably beneath the Morrison Formation (Syzdek et al., 2019); the Lower Cretaceous Cloverly Formation unconformably overlies the Morrison Formation (D’Emic et al., 2019). The Morrison Formation here is about 75 m in thickness and is dominated by mudstone marked with palaeosols.

Morrison Formation gastroliths within aggregated skeletons are reported in one theropod genus (Allosaurus), two or three sauropod genera (Barosaurus, Diplodocus, and possibly Camarasaurus), and no ornithischians (Wings & Sander, 2007). Only 4% of sauropod individuals have been found associated with gastroliths within the Morrison Formation (Wings, 2015). Gastroliths, bone fragments and coprolites occur throughout the Morrison unit at this locality; we restricted our collection to the upper several meters of the unit where these pink quartzite gastroliths were more common. Restricting analysis to pink quartzite gastroliths enabled us to test our Baraboo Interval provenance hypothesis. The horizon sampled is a pink to gray palaeosol formed on silty mudstone with popcorn weathering that is about 5 m in thickness. Within our study area, conglomerate beds are not observed in the Morrison Formation, and the gastroliths occur randomly and scattered within the mudstone, arguing against a debris-flow or lag-deposit origin. Thus, that these stones are gastroliths is viable and admissible and the most likely interpretation of their origin.

2 | METHODOLOGY

We analysed five cobble-sized, red, rounded and polished gastroliths collected from the upper Morrison Formation in the eastern Bighorn Basin of Wyoming (44.690465°, −108.234068°; Figures 2 and 3). We used detrital zircon age spectra as fingerprints for the provenance of these gastroliths. Each gastrolith was crushed and ground individually, and heavy minerals were separated by panning and then further isolated using standard heavy liquid (MI) and magnetic separation techniques. U-Pb geochronology of zircons was conducted by laser ablation–inductively coupled plasma mass spectrometry (LA-ICPMS) at the Arizona LaserChron Center (Gehrels & Pecha, 2014; Gehrels et al., 2006, 2008). The analyses involve ablation of zircon with a Photon Machines Analyte G2 excimer laser equipped with a HelEx ablation cell using a spot diameter of 20 μ. Appendix S1 provides analytical methods and a table of detrital zircon ages.

3 | RESULTS

Each gastrolith that was analysed consists of pink, equigranular, medium-grained quartzite. The heavy mineral suite includes rounded zircon, magnetite and hematite, but lacks tourmaline and rutile reported in the Baraboo Formation heavy mineral suites reported by Medaris et al. (2011). The lack of tourmaline and rutile in our samples may be attributable to our small sample sizes.

The five (n = 36, 68, 66, 41, 29) gastroliths each show bimodal age distributions (Figure 4). Although the n is small for individual samples, K-S analysis indicates that the detrital zircon age spectra for these gastroliths are statistically indistinguishable (Appendix S1). Four of the gastroliths have early Yavapai age peaks (geon 17) with maximum depositional ages of 1,750 Ma. Each gastrolith has a prominent Penokean/Trans-Hudson age peak (geon 18), as well as numerous Archean grains (>geon 25) that have an age peak of ~2.7 Ga. Gastrolith 3, which does not include any geon 17 grains, has a concentration of geon 19 and >geon 30 zircons, which are uncommon zircon ages in Laurentia.
4 | DISCUSSION

4.1 | Late Jurassic palaeogeography

Jurassic strata are rare in the Laurentian midcontinent, suggesting that much of the area between the Appalachian orogenic belt and Morrison Formation depositional basin was exposed in an area of low to moderate relief. Appalachian-derived zircons are present in Early and Middle Jurassic strata to the southwest of our study area in the Colorado Plateau region (Dickinson & Gehrels, 2009). They suggest a transcontinental Jurassic palaeodrainage system transported Appalachian detritus as much as 2,500 km to the Rocky Mountain and Colorado Plateau areas. This palaeodrainage system headed in the Appalachians and had tributaries that drained into the trunk stream from the north and south, which is schematically portrayed in Figure 5. Because of the paucity of Jurassic strata in the Laurentian midcontinent, the exact location of this river system is uncertain. Because derived zircons are not abundant in the Morrison easterly sandstones, this trunk stream may have been sluggish and low-gradient and thus incapable of carrying cobble-sized clasts the >1,000 km from Wisconsin to Wyoming. This trunk stream may have discharged into an estuary of the northward-retreating Sundance Sea (Hasiotis, 2004) or perhaps was an inland delta akin to the Okovango delta of South Africa, which does not flow into any sea (McCarthy, 1993). There, all water is evaporated or transpired. The west-flowing drainage pattern persisted until latest Cretaceous time when the ancestral Mississippi River system developed, transporting Cordilleran detritus to the east and south (Potter-McIntire et al., 2018).

4.2 | Gastrolith provenance

The provenance of Phanerozoic strata in the Bighorn Basin evolved over time (May et al., 2013). The Cambrian Flathead Sandstone reflects local derivation from the underlying Precambrian basement rocks (Malone, Craddock, & Kenderes, 2017), but from Carboniferous through Triassic time, sands originated in the Appalachian highlands several thousand kilometers to the east (Dickinson & Gehrels, 2009; Garber et al., 2018). The local sedimentary provenance evolved
during the deposition of the Sundance and Morrison formations as new source areas emerged in the Sevier orogenic belt to the west and the volcanic arcs beyond (May et al., 2013; Syzdek et al., 2019). Morrison Formation sandstone detrital zircon age spectra combined with palaeocurrent data (May et al. 2013) indicate that detrital sediment of the Morrison Formation was derived largely from the west.

Exotic quartzite pebbles and cobbles in the overlying Cretaceous Cloverly Formation were considered gastroliths by Stokes (1987). Wings (2015) noted gastroliths were rarely found associated with dinosaur skeletons, and Zaleha and Wiesemann (2005) interpreted that the Cloverly stones were derived from Neoproterozoic Brigham Group strata in the Sevier orogenic belt to the southwest and then transported east as debris in hyperconcentrated stream flows. Thick successions of quartzite cobble conglomerate are present in Jurassic-Eocene synorogenic strata to the west of our study area, and these quartzite clasts are indeed derived from the Brigham Group (Malone, Craddock, Link, et al., 2017). The Brigham Group quartzite clasts, however, have detrital zircon age spectra that include concentrations of geon 10 and 11 grains and are thus distinct from the Morrison gastroliths analysed here (Figure 4).

Another candidate for the provenance of the Morrison Formation gastroliths are the quartzites of the Mesoproterozoic Belt-Purcell Supergroup, which are as much as 14 km in thickness and occur in northern Idaho and western Montana (e.g. Link et al., 2016). Detrital zircon age spectra in these rocks are complex and multimodal, and include prominent Yavapai age peaks, but most units contain zircons as young as ~1.45 Ga, and these rocks are rarely red, so a Belt-Purcell provenance for the Morrison gastroliths is unlikely (Figure 4).

Detrital zircon age data are available for three occurrences of Baraboo Interval strata in southern Wisconsin, USA (Van Wyck & Norman, 2004; Figure 4). Their lower Baraboo Formation sample has a zircon age peak of 1.770 Ma, and a broad cluster of ages between 1.75 and 1.9 Ga, and a tail of Palaeoproterozoic and older ages. The upper Baraboo Formation sample has distinct age peaks at 1.85, 1.92 and 2.70 Ga. K-S analysis shows that the age spectra for the Baraboo Formation and the Morrison Formation gastroliths each have comparable Palaeoproterozoic and Archean age peaks (Van Wyck & Norman, 2004)
zircon age spectra, and so it is reasonable to interpret that these quartzites sourced the gastroliths. The ingestion may have occurred from Baraboo outcrops or from stream gravel derived from these outcrops.

The large size of the gastroliths indicates that they pertain to large-bodied animals. In the Morrison Formation, only a few large-bodied dinosaurs have been reported with gastroliths: *Allosaurus*, *Barosaurus*, *Diplodocus* and possibly *Camarasaurus* (Wings, 2007, 2015). Because sauropod skeletons greatly outnumber those of *Allosaurus* throughout the Morrison Formation (Foster, 2003), and because gastroliths are much more common in sauropods than in large-bodied theropods (Wings, 2007, 2015), we hypothesize that sauropods were the animals most likely responsible for transport of these stones.

4.3 | Dinosaur migration

Migration, as defined by Bell and Snively (2008, p. 271) is "a deliberate or instinctive seasonal round-trip movement completed by a single individual between discrete habitats not used at other times of the year and completed at least once annually". Dinosaur migration was initially suggested by von Huene (1928) based on the broad geographic range of some dinosaur species, which has been echoed by other authors for some other clades (e.g. Bell & Snively, 2008). Herd migration is necessary for large animals because large numbers of individuals stress the local food supply (Bell & Snively, 2008). Morrison Formation dinosaurs inhabited lowland river floodplain and lacustrine environments with a monsoonal climate (Parrish et al., 2004), which means that such large animals may have been routinely
stressed for water and nutrition (Engelmann et al., 2004). As much as 300 km of seasonal lowland-upland migration of sauropod dinosaurs in the western areas of the Morrison Formation depositional basin has been inferred using oxygen isotope ratios from tooth enamel (Fricke et al., 2011).

Unlike the regional upland migration of sauropods reported by Fricke et al. (2011), the gastrolith provenance data here suggest a longer-distance migration of as much as 1,000 km. The inferred migration pathway may have been geographically associated with a low energy, low gradient Late Jurassic trunk stream that flowed from the Appalachian Mountains westward to the Morrison Formation depositional basin. This migration trajectory was approximately parallel to the 30-degree palaeolatitude belt and may have occurred in response to the alternately wet and dry monsoonal seasons to find water and food.

5 | CONCLUSIONS

The following conclusions are advanced by this research.

1. The exotic pebble- and cobble-size clasts of red quartzite present in the uppermost Morrison Formation of the Bighorn Basin are interpreted as gastroliths based on their physical characteristics and presence in mudstones rather than conglomeratic beds, ruling out a sedimentary origin.

2. The gastroliths are lithologically indistinguishable from the Baraboo Interval quartzites in the Laurentian midcontinent in terms of texture, colour, composition and detrital zircon age spectra.

3. We hypothesize that these gastroliths were ingested by dinosaurs from occurrences of Baraboo Interval quartzites in the Laurentian midcontinent as much as 1,000 km east of the site of deposition and transported inside the animals from the site of ingestion to the site of deposition. Sauropod dinosaurs are the most likely candidates for the type of dinosaur that ingested the gastroliths based on both the large size of the stones and their absence in other herbivores of the Morrison Formation. Ingestion of these stones downstream (west) of the Baraboo Formation exposures is unlikely but cannot be precluded.

4. Long-distance migration of dinosaurs is suggested, perhaps along a corridor that was associated with a continent-wide drainage system that headed in the central Appalachian Mountains and that drained west to the Morrison depositional basin.

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ORCID

David H. Malone https://orcid.org/0000-0003-2922-7826

REFERENCES


SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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