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Gastroliths and *Deinonychus* teeth associated with a skeleton of *Tenontosaurus* from the Cloverly Formation (Lower Cretaceous), Montana, USA

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A B S T R A C T

Tenontosaurus tilletti was an abundant ornithischian dinosaur from the Lower Cretaceous of North America, commonly regarded as a 'basal' iguanodontian. Here, we describe a remarkably well-preserved specimen, comprising a near-complete skeleton and skull, from the Cloverly Formation, Montana, USA, currently housed at the University of Manchester Museum, UK. Found alongside the specimen were alleged gastroliths, cycad seeds, and teeth of the contemporaneous dromaeosaur *Deinonychus antirrhopus*, all of which were buried in an alleged ash. We assess the credibility of these claims, using X-ray CT scanning and X-ray fluorescence (XRF) respectively, and show that the 'seeds' are non-organic mineral concretions, and that the 'ash' is actually a lime mud with a silica content of approximately 7%. We confirm the identification of the gastroliths and the *Deinonychus* teeth, providing further evidence to support the long-standing assertion, originally made by John Ostrom in 1970, that *Tenontosaurus* was a common food item for *Deinonychus*.

1. Introduction

Tenontosaurus tilletti is a common, moderately-sized graviportal ornithopod from the Lower Cretaceous (upper Aptian-lower Albian) Cloverly Formation of the Bighorn Basin region in northwest Wyoming and south-central Montana, USA (Ostrom 1970). It is known from approximately 80 skeletons of various ontogenetic stages, taphonomic conditions and degrees of completion, including cranial and postcranial elements and teeth (Forster 1990a,b; Maxwell and Ostrom 1995; Horner et al., 2009; Werning 2012). A second slightly stratigraphically older species is currently recognised, *T. dossi* (Winkler et al., 1997), and numerous other remains are known from across the mid-west USA (Cifelli et al., 1997). Alongside *Tenontosaurus*, the Cloverly fauna consists of ankylosaurs, sauropods, ornithomimids, hypsilophodonts, dromaeosaurids, turtles, frogs, crocodiles and triconodont mammals (Ostrom 1969; Forster 1984; Cifelli et al., 1998).

Originally identified by Ostrom (1970) as an iguanodont due to its similarity to *Camptosaurus* and *Iguanodon*, the postcranial skeleton of *T. tilletti* was thoroughly described by Forster (1990a), supplementing the detailed figures and description of a skull (YPM 5456) provided by Ostrom (who only briefly described the postcrania). Phylogenetically, others have found *Tenontosaurus* to be the sister taxon to a group comprising Dryosauridae and Ankylopollexia (Butler et al., 2008; Barrett and Han 2009), whereas earlier studies found it to be the basal-most member of Iguanodontia (Weishampel and Heinrich 1992; Coria and Salgado 1996; Winkler et al., 1997; Sereno 1999; Weishampel et al., 2003). A range of other studies recover *Tenontosaurus* in a variety of positions within an assemblage of hypsilophodont- or iguanodont-grade taxa (Pisani et al., 2002; Varricchio et al., 2007; Boyd et al., 2009), and more recently closely related to rhabdodontids (McDonald 2012). The cranial anatomy of *Tenontosaurus* was subsequently redescribed in detail based on several new specimens and supplemented by 3D CT scan images (Thomas 2015), a study which also found it to be a basal iguanodontian.

Herein, we describe features of a previously unpublished specimen of *T. tilletti* from the Cloverly Formation of Montana, USA, currently housed at the University of Manchester Museum, UK

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(MANCH LL.12275), and comprising a near-complete skeleton and partial skull (Fig. 1). The sub-adult skeleton represents one of the most well-preserved and complete specimens of the species and is currently being prepared to go back on public display. The specimen was originally recorded as being found in association with teeth of *Deinonychus*, as well as some plant fossils (initially identified as cycad seeds) and gastroliths, suggesting rare evidence of a three-tiered trophic interaction system in the uppermost Lower Cretaceous of the USA. It may be that these identifications were initially made by the original collectors, but they have been

Fig. 1. *Tenontosaurus tilletti* skeleton (MANCH LL.12275) fully articulated and mounted in bipedal stance for 1999 Lottery-funded gallery display at Manchester University Museum.

accepted by the university museum which houses the skeleton and have been accessioned and recorded as such on their databases, such that these identifications are now in the academic and public domain. We have tested these identifications herein.

2. History of the specimen

In 1999, one of the most well-preserved and complete specimens (MANCH LL.12275) of *Tenontosaurus tilletti* was acquired for the University of Manchester Museum, UK (by JRN), where it became the centrepiece of the Heritage Lottery-funded refurbished Fossil Gallery (Figs. 1 and SI 1). It was discovered on private land in 1994 by rancher Robert Kelly, at The Kelly Ranch in Wheatland County, Montana (Fig. 2), and is from the Cloverly Formation, upper Aptian-lower Albian, upper Lower Cretaceous. The original description for sale of the mounted and articulated skeleton was that it was 18 feet long, found with gastroliths and cycad seeds in the stomach region, and two *Deinonychus* teeth found associated with cervical vertebrae. It was also described as having arthritis in the hand. In 2004 this original fossil was replaced in the Fossil Gallery at MANCH by a cast of *Tyrannosaurus rex*, and has remained in storage until being studied by one of us (JPT) as part of a Masters' project while at the University of Manchester. A full and systematic description of the material was published on arXiv as a Master's thesis in 2013 (Tennant 2013a,b; SI 2).

The specimen is currently disassembled, with many elements remaining glued to the original steel armature. Some parts contain plaster additions and visual modifications as part of the original 'conservation' process. However, the aesthetic colour wash and varnish which had been applied to the original skeleton has been removed, and while most of the more robust elements remain intact, the more gracile bones, such as the ribs, have been broken or damaged beyond repair. Some elements which were mounted on the original skeleton, such as the characteristic ossified tendons, are now completely missing. The specimen is due to be thoroughly conserved as part of its redisplay at MANCH.

Nonetheless, the completeness and exceptional preservation of this specimen renders it potentially important for future studies of *Tenontosaurus*. An overview of the specimen is provided here, and a full description of MANCH LL.12275 can be found as a thesis published online (Tennant 2013a).

3. Material and methods

Alongside the specimen (MANCH LL.12275) several related items were found by the collector including two teeth (identified as *Deinonychus antirrhopus*) associated with cervical vertebrae, and two spherical structures (identified as cycad seeds) found in the gastric region alongside at least 12 possible gastroliths. These were also granted permanent accession numbers as follows: *Deinonychus*

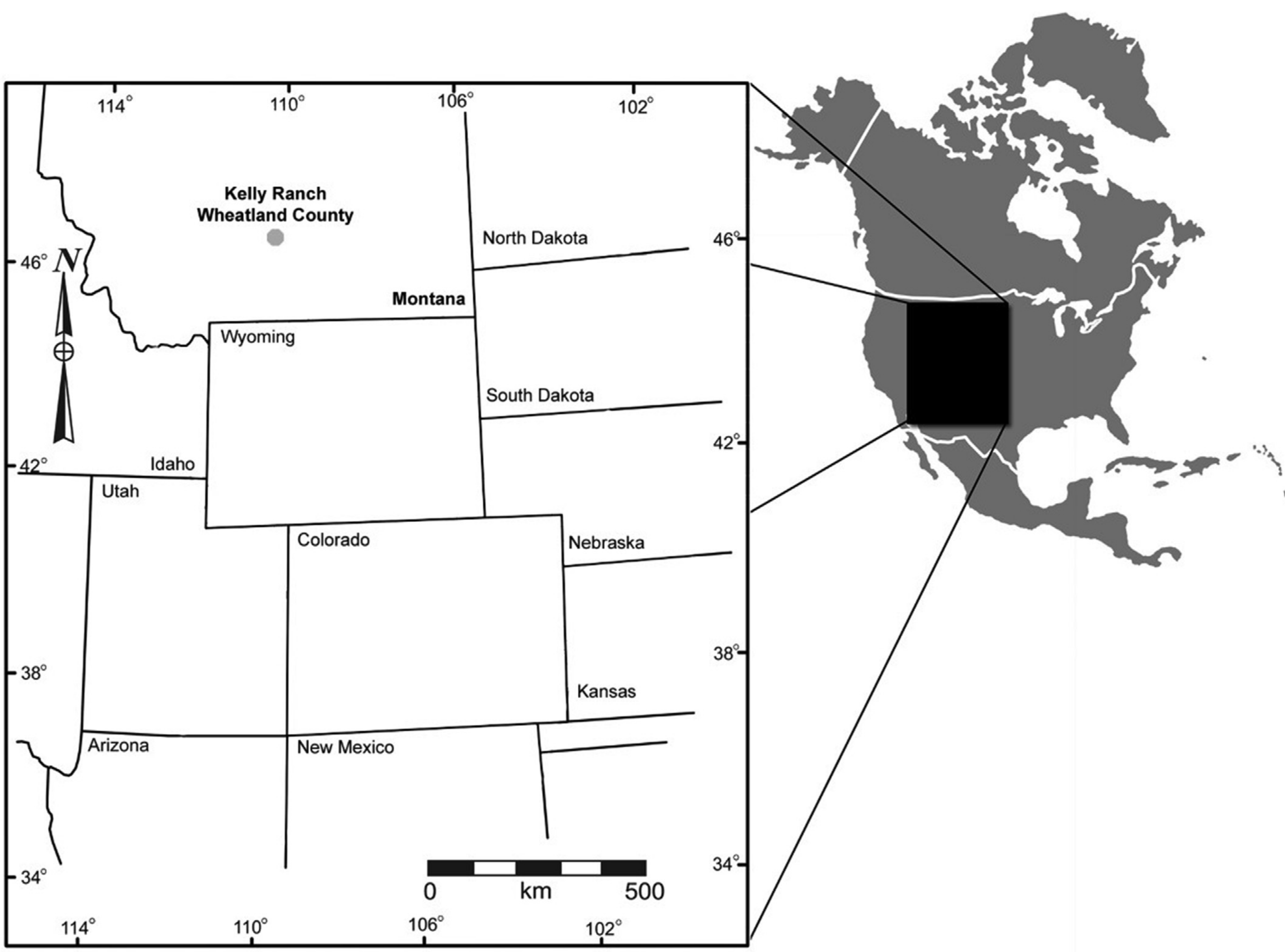

Fig. 2. Locality map showing the position of the Kelly Ranch, Wheatland County, Montana, USA. (Modified from Hartman et al., 2019.)

teeth (MANCH LL. 12277a, b), gastroliths (MANCH LL. 12278a-l), 'seeds' (MANCH LL. 12279a, b). A sample of the sediment in which the skeleton was buried has the accession number MANCH M.9063. (Besides the written documentation, the evidence of these associations comes from a poor resolution photograph that came with the original sale, that shows the skeleton in the ground along with both the alleged seeds and gastroliths within the stomach cavity region (PICT0008 in Image File SI 1, reproduced and enhanced in SI 3).)

The two spherical structures originally purported to be cycad seeds (MANCH LL.12279a, b), which are approximately 25 mm and 35 mm in diameter respectively (Fig. 3), were subjected to X-ray CT scanning carried out using a Nikon Metrology XTH 225 kV instrument at the Henry Moseley X-ray Imaging Facility, The University of Manchester. Each specimen was scanned individually and the field of view maximised. Resulting voxel sizes were 10 um for specimen LL.12279a and 15 um for the larger specimen LL.12279b. Both scans were performed at 200 kV and 90uA, using a tungsten target and a beam filter of 0.5 mm copper. A total of 5013 projection images was taken over 360°, with an exposure time of 500 ms per image. The 3D data was reconstructed using CT Pro 3D reconstructor software (Nikon Metrology). Visualisation images were created using Avizo 2019.1 (Thermo-Fisher). A thin section with coverslip was also cut from the smaller of these specimens (MANCH LL. 12279a.1).

The sediment in which the skeleton was buried, originally interpreted as volcanic ash (MANCH M.9063), was analysed by X-ray fluorescence (XRF) using a PANalytical Axios wavelength-dispersive spectrometer (WDS) fitted with a Rhodium X-ray tube. Major element analysis was performed using the Omnion package optimised for geological samples. Trace element data were obtained using the Protrace trace element package using standard conditions. Loss on ignition (LOI) was determined at 110 °C and 1100 °C. Samples were analysed as pressed powder pellets (12 g sample, 3 g Hoechst wax, C micro powder) (methods following those described in Kundrát et al., 2019). Major element data is provided as weight percentages (wt %) expressed as their oxides, while trace-element concentrations are expressed in parts per million (ppm). A thin section with coverslip was also cut from a sample of this sediment (MANCH M.9063a, b).

Institutional abbreviations are as follows: AMNH – American Museum of Natural History; MANCH – Manchester University Museum; YPM – Yale Peabody Museum; YPM-PU – Yale Peabody Museum Princeton University collection.

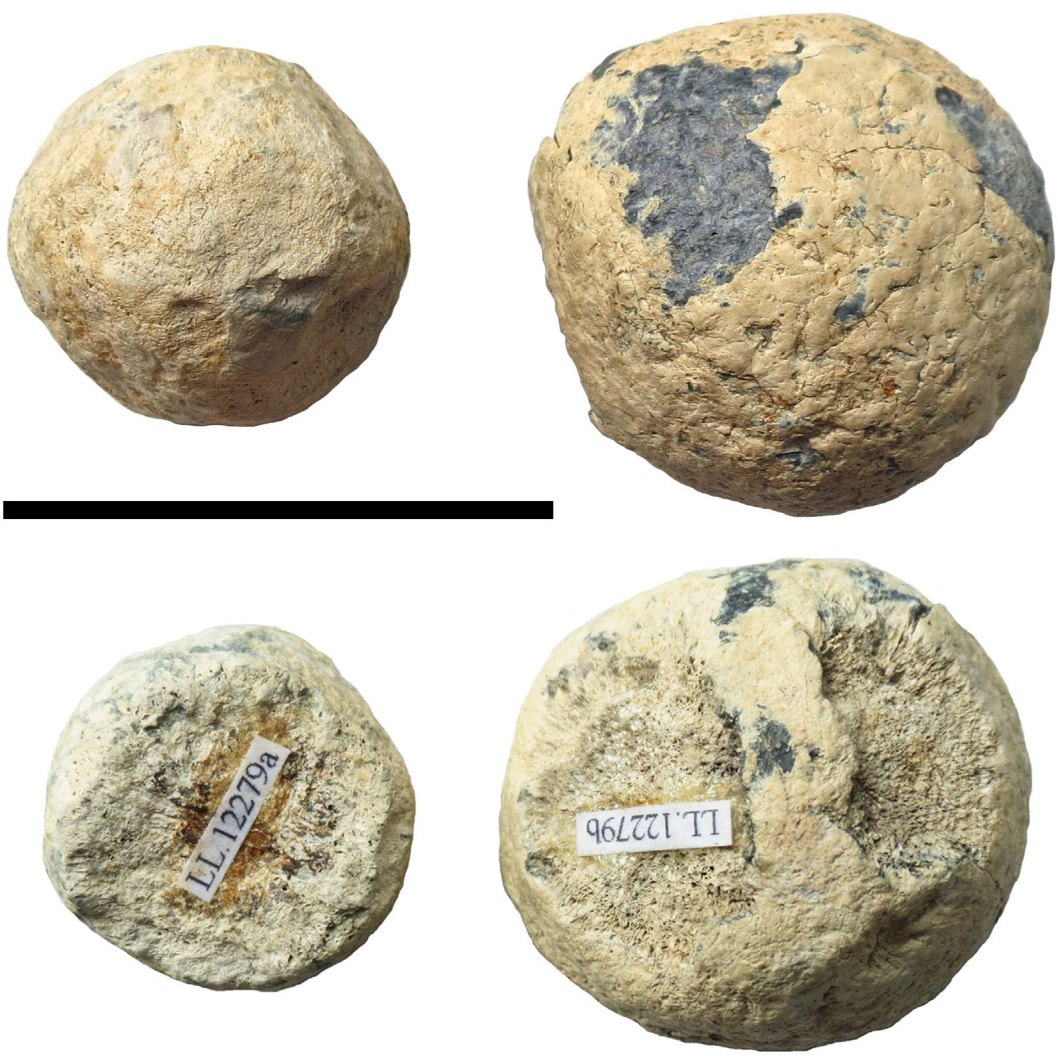

Fig. 3. Spherical structures (MANCH LL. 12279a, b) found associated with MANCH LL.12275, previously identified as cycad seeds, but which we here reinterpret as mineral concretions of goethite/limonite. Scale bar = 3 cm.

4. Systematic palaeontology

Ornithischia (Seeley, 1887)
Neornithischia (Sereno, 1999)
Ornithopoda (Marsh, 1881)
Tenontosaurus tilletti (Ostrom, 1970)

Holotype. AMNH 3040, partial skeleton lacking skull and forelimbs.
Paratypes. YPM-PU 16338, a partial skeleton, and YPM 3456, a well-preserved skull and partial skeleton.
Herein referred specimen. MANCH LL.12275. An almost complete skeleton, comprising semi-complete skull; complete vertebral column (atlas, axis, cervical, dorsal, sacral and caudal series) minus most caudal neural spines; pectoral girdle comprising paired scapulae, coracoids and sternal plates; both forearms (humeri, ulnae and radii) complete; manus near-complete with carpus; pelvic girdle comprising both ischia, ilia and pubes; both hindlimbs (femora, fibulae and tibiae), tarsus and pes complete.
A full systematic description of this specimen can be found in Tennant (2013a), and we only provide a brief overview here.
Skull. The skull is for the most part well-preserved. It is fully articulated, in thanks partly to restorative efforts. Parts of the anterior of the snout have been reconstructed, and the internal anatomy of the braincase and palate cannot be seen without advanced visualisation methods (Thomas 2015). The teeth are all preserved and *in situ*.
Forelimbs and pectoral girdle. Virtually all elements of the forelimbs and pectoral girdle are preserved and undistorted. Several manual elements have been reconstructed and are casts. The near-complete left manus exhibits an abnormal structure that projects caudally approximately 6 mm from the first phalanx of the second digit. There is no analogue to this structure associated with the corresponding phalanx of the right manus, and no similar feature elsewhere on the skeleton. The exceptionally preserved condition of the manus and the lack of an analogous structure elsewhere suggest that this structure may be pathological rather than taphonomic.
Axial skeleton. Almost all elements of the axial skeleton are well-preserved in three dimensions. However, some parts of the individual vertebrae have broken off after time. The ossified tendons, present on the original specimen, are now missing. The delicate ribs are now largely broken and disarticulated.
Hindlimbs and pelvic girdle. Virtually all elements of the hindlimbs and pelvic girdle are preserved and undistorted. Several pedal elements have been reconstructed and are casts.
Geographic locality. The most precise information we have is that it was found on private land at The Kelly Ranch, Township 5 South, Section 29E, Wheatland County, Montana, USA (Fig. 2).
Stratigraphic horizon. Precise stratigraphic information is unknown, but it was collected from the Cloverly Formation, Lower Cretaceous age (upper Aptian-lower Albian). The specimen was found preserved within a sedimentary layer comprising calcitic elements and some detrital material, originally interpreted by the collector as being volcanic ash (MANCH M.9063).

5. Results

5.1. Spherical structures

The resulting CT scans of the spherical structures revealed that the specimens had an irregular amorphous core and an outer radial structure (Fig. 4 and SI 4), confirming that these are not cycad seeds which have a concentric, rather than radial, internal structure. Extinct seed plants belonging to the order Bennettitales were prolific during the Cretaceous. Whilst being superficially similar to cycads (Cycadales), Bennettitales were morphologically quite distinct, and their cones possessed a similar central core and outer radial structure to the preserved spherical structures here

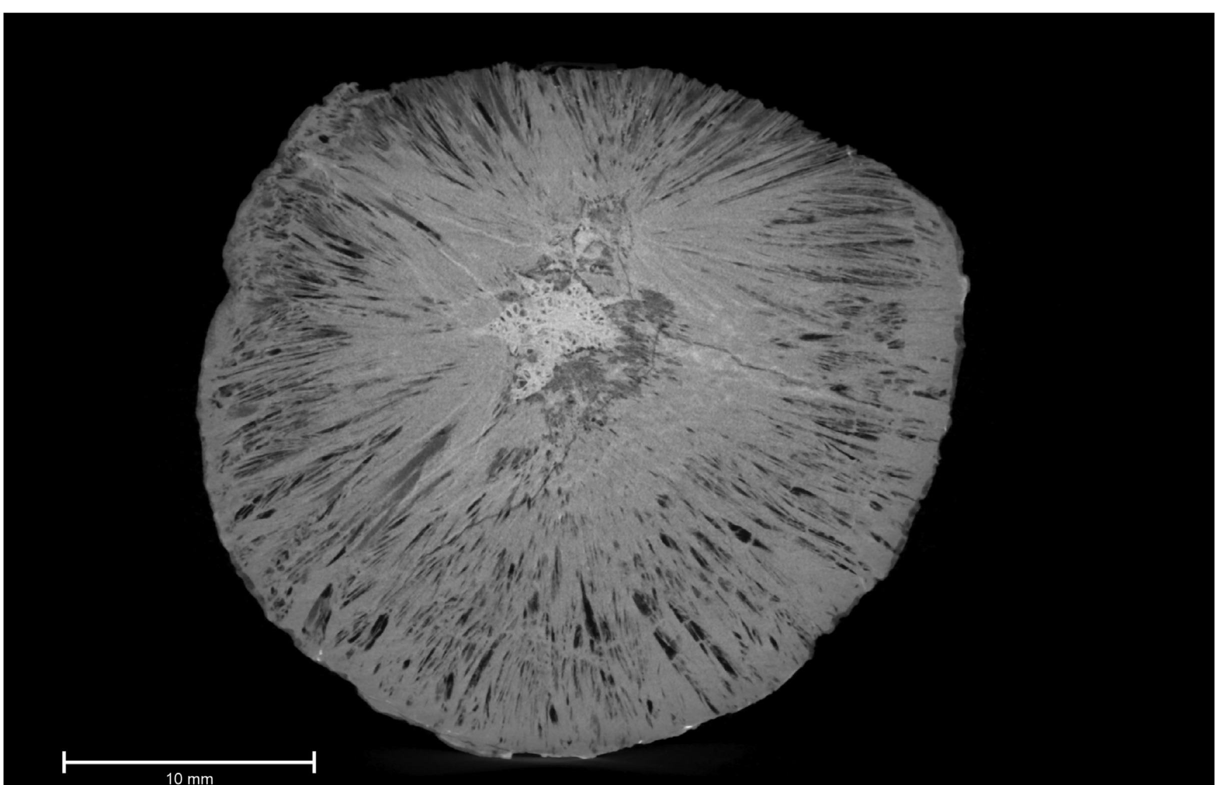

Fig. 4. CT scan cross section of one of the spherical structures (MANCH LL. 12279b) revealing internal radial structure with central core.

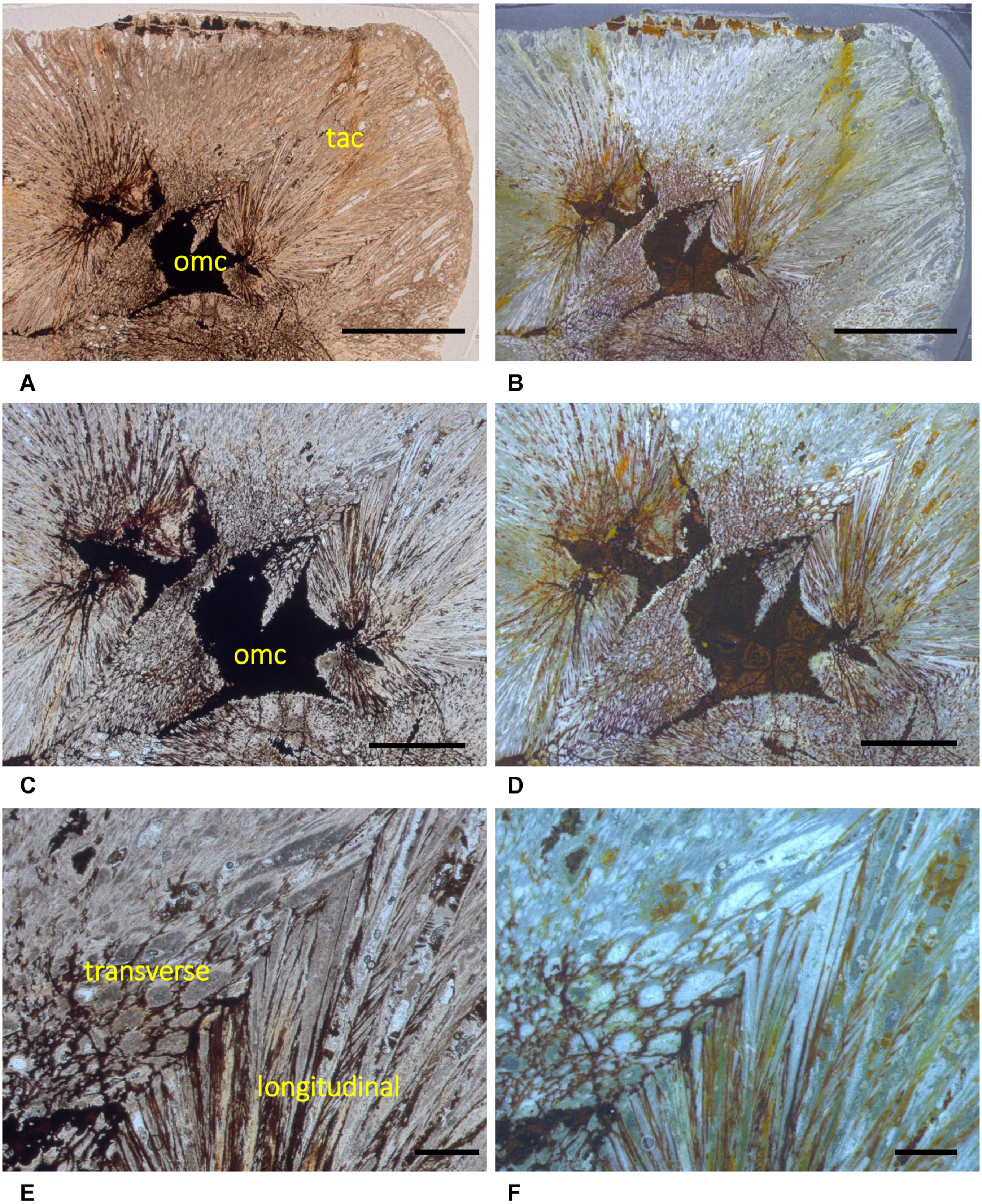

Fig. 5. Thin section of one of the spherical structures (MANCH LL. 12279a.1). A, C, E = transmitted light; B, D, F = oblique incident light. (A, B) Translucent acicular crystals (tac) nucleated on an opaque mineral core (omc). Scale bar = 2 mm. (C, D) Opaque mineral core (omc) composed of iron oxyhydroxides (goethite/limonite); the opaque iron mineral has intergrown with the surrounding translucent acicular crystals imparting a red/yellow colour. Scale bar = 1 mm. (E, F) The acicular crystals are orientated in various ways and have a feathery appearance in longitudinal section. Scale bar = 200 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

examined. Stockey and Rothwell (2003, figs 1A, B) illustrated a cone of *Williamsonia* from the Lower Campanian (Upper Cretaceous) of Vancouver Island, British Columbia, which in both external and internal appearance is comparable to our specimens. Based on these similarities, even after initial CT scanning, a plant origin could not be ruled out for the spherical structures, as agreed by professional palaeobotanists (Paul Kenrick, pers. comm. 2021). To test this hypothesis we examined one of the spherical structures in thin section (Fig. 5) which showed, however, that the structures visible in the X-ray CT images consist of an opaque core composed of iron oxyhydroxides (goethite/limonite), which probably formed during exhumation of the skeleton when conditions changed from reducing to oxidising and any original pyrite or marcasite destabilised. (Pyrite/marcasite commonly nucleates around fragments of decaying organic matter.) Nucleating on this core, and surrounding it, are radiating translucent acicular crystals in various orientations, which have a feathery texture and are probably the highly insoluble baryte. These are likely to have formed in a reaction between the sulphate generated by oxidising iron sulphides and barium ions in the local pore fluids (David Green, pers. comm. 2022, Paul Kenrick, pers. comm. 2021). According to Ostrom (1970), baryte is common in the Cloverly Formation. There are no internal features evident in thin section to indicate that this is a petrifaction of a plant seed or cone. Mineral concretions are, understandably, often mistaken for fruits, seeds or cones because they can take on similar shapes (Carr et al., 2021).

5.2. Gastroliths

The skeleton was also originally found with at least 12 alleged gastroliths (MANCH LL.12278a-l) in its gastric region (Fig. 6). If confirmed this would add support to the hypothesis that the teeth

Fig. 6. Gastroliths (MANCH LL. 12278a-l) found in the gastric region of MANCH LL.12275. Scale bar = 3 cm.

of *Tenontosaurus* were not as effective for chewing and grinding as later branching ornithopods (Stokes 1987), and therefore mechanical assistance was provided through gastrolith consumption (although this does depend on what they were eating; later ornithopods were most probably eating angiosperms instead of gymnosperms). Gastroliths are present in numerous fossil vertebrates and their function has been discussed in detail (Wings 2007). Only three unambiguous records of gastroliths in ornithopods have been reported, specifically for the basal ornithopods *Gasparinisaura* (Cerda 2008), *Haya* (Makovicky et al., 2011) and *Changmiania* (Yang et al., 2020). Some probable gastroliths were also reported in the basal ornithopod, *Notohypsilophodon* (Ibiricu et al., 2014). *Changmiania* is from the Early Cretaceous whereas the other three taxa are from the Late Cretaceous. Thus, the presence of gastroliths in the studied specimen is rare and represents the second oldest occurrence of gastroliths in an ornithopod, and the first to be identified in a more derived ornithopod. There exists the remote possibility that the objects identified as gastroliths could be clasts associated with hyperconcentrated flow deposits (Zaleha and Wiesemann 2005). However, such a flow deposit with large clasts is not consistent with the muddy sediment in which the skeleton is buried, and it is unlikely that such a hyperconcentrated flow would deposit the clasts exclusively within the gastric region of the dinosaur (SI 3). Based on these arguments we can confirm the gastrolith identification.

5.3. Teeth

Two isolated, incomplete *Deinonychus* teeth (MANCH LL.12277a, b) were found associated with cervical vertebrae of MANCH LL. 12275 (Fig. 7). One of these has since gone missing, but based on morphology the remaining tooth is probably a maxillary or dentary tooth, based on comparisons with various *Deinonychus antirrhopus* teeth previously illustrated (for example, see figs 23, 24 in Ostrom 1969). Direct evidence of carnivory with specific prey or carrion preferences, despite numerous popular reconstructions, is exceptionally rare in the dinosaur fossil record (for example, see Charig and Milner 1997; Carpenter 1998; Rogers et al., 2003; Hone et al., 2010; O'Connor et al., 2011; DePalma et al., 2013; Conrad 2018), but even dinosaurs are sometimes found as the food of other animals (Hu et al., 2005; Wilson et al., 2010). Interestingly, *Tenontosaurus* specimens are frequently found associated with remains of *Deinonychus antirrhopus*, a dromaeosaur that some evidence suggests might have been gregarious and hunted in packs (Ostrom 1969, 1970; Forster 1984, 1990; Maxwell and Ostrom 1995; Cifelli et al., 1997), although see Roach and Brinkman (2007). When *Deinonychus* was first described (Ostrom 1969), it contained a note that several specimens had been found in association with a single ornithopod, which was later named as *Tenontosaurus* (Ostrom 1970). Finds from at least 15 different sites also yield remains of both taxa (Maxwell and Ostrom 1995; Brinkman et al., 1998; Roach and Brinkman 2007). It is possible that the common association of these two genera is taphonomic, with post-mortem causes (such as flow deposition), but if this were the case one would expect to find the teeth of other common Cloverly vertebrates (e.g. sauropods, ankylosaurs, crocodilians) readily associated with *Tenontosaurus*, but this does not appear to be the case. The presence of two shed *Deinonychus* teeth with MANCH LL.12275 lends further support for a trophic interaction between both taxa. With such little material (two teeth), we cannot identify whether there was more than one individual of *Deinonychus* present, and this does not provide any additional evidence in confirming whether *Deinonychus* engaged in pack-hunting, or solitary hunting or scavenging, or some combination of all behaviours (Maxwell and Ostrom 1995; Roach and Brinkman 2007). However, this is further evidence to support the original assertion that *Tenontosaurus* was a common food item for *Deinonychus* (Ostrom 1970). As such, this continues to represent one of the best documented examples of a trophic relationship (predator/prey or scavenging) in the dinosaur fossil record.

5.4. Sediment

The major elements suggest that the bulk of the sediment sample (87%) is CaCO3 and it would appear to be a lime mud with a silica content of approximately 7% (SI 5). Any ash would thus be present in only very small proportions and it is not possible to ascribe the trace elements present to a volcanic source, especially without knowing the trace element signature of the uncontaminated carbonate (SI 6).

Thin sections cut from this matrix (MANCH M.9063a, b) also appear to be almost entirely carbonate with lots of calcite, plus some dusty-looking rounded particles that are probably very fine-grained calcite. There are some small patches of a brown, fine-grained matrix with 30% fine, angular fragments of quartz. If these are from a volcanic source, then the ash must have been transported with the quartz representing broken phenocrysts. (In a fresh ash, quartz phenocrysts are usually euhedral or resorbed/rounded, rather than fragmented and angular.) Other phenocryst minerals which you might expect in a silicic ash (plagioclase, K-feldspar, biotite, amphibole) are absent, and there is no evidence that the specimen was vesicular (Margaret Hartley, pers. comm. 2019). In conclusion, it is possible that there is a very small percentage of a volcanic component in the sample, but the evidence is not particularly strong from either the thin sections or the chemical

Fig. 7. One of the *Deinonychus* teeth (MANCH LL. 12277) found associated with the cervical vertebrae of MANCH LL. 12275. Scale bar = 0.5 cm.

data. According to Ostrom (1970) volcanic ash beds are rare in the Cloverly Formation.

6. Conclusions

One of the challenges that palaeontologists are faced with is interpreting the behaviours of organisms preserved only in the fossil record. Studies often rely upon functional morphology to infer behaviour, especially through comparison with modern analogues. However, in rare occurrences, with some examples being more common than others, specimens are sometimes found with direct evidence of interactions, referred to as ‘frozen behaviour’ (Boucot 1990; Radwanski et al., 2009; Boucot and Poinar 2010; Lomax 2021).

MANCH LL.12275 represents one of the most complete and well-preserved specimens of *Tenontosaurus tilletti* currently known. The original documentation indicated that the specimen was found preserved in ash and with associated cycad seeds. Based on our analyses, we cannot confirm the preservation within a distinct ash layer (although there might have been a minor ash component), while the alleged plant seeds are herein identified as non-organic mineral concretions. The association of teeth of *Deinonychus antirrhopus* with the skeleton reinforces evidence for one of the most well-documented trophic relationships in the dinosaur fossil record. The gastroliths within the stomach cavity of the specimen also provides further evidence for the feeding habits of *Tenontosaurus* and is the first case of the use of gastroliths in a more derived ornithopod; it is also one of the geologically oldest examples of gastroliths found within an ornithopod.

Data availability

Data will be made available on request.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2022.105327.