

prosauropods), and no longitudinal crest proximal to the lateral condyle (unlike prosauropods¹⁰).

I. attavipachi can clearly be placed among the Sauropoda because of the above-mentioned derived sauropod characters of its vertebrae and femur, which separate it from the Prosauropoda. Its primitive features are not particularly reminiscent of the Prosauropoda; rather, they seem to illustrate an early stage in the evolution of characters more fully developed in later, more advanced sauropods. Comparisons with other primitive sauropods reveal differences (notably in the femur), but their phylogenetic significance is uncertain. Although there is no consensus about the relationships of the oldest sauropods, recent phylogenies^{15,16,21,22} consistently place *Vulcanodon* in a very basal position; *Gongxianosaurus* also exhibits a number of primitive features reminiscent of prosauropods¹³. Comparisons between *Isanosaurus* and *Vulcanodon* are difficult, because few significant elements are known in both, although their femora are different. The opisthocoelous cervical vertebrae of *Isanosaurus* show that it is more advanced than *Gongxianosaurus*, in which there are no opisthocoelous vertebrae¹³; their femora also appear to be different. Uncertainties about the interrelationships of early sauropods, as expressed by the common use of the paraphyletic family Vulcanodontidae¹⁵, make it difficult to assess the exact phylogenetic and systematic position of *Isanosaurus*. A detailed analysis of early sauropod phylogeny being outside the scope of this paper, we refer *Isanosaurus* to Sauropoda incertae sedis.

The discovery of *I. attavipachi* not only shows that by late Triassic times the Sauropoda had already appeared, but also suggests that they must have had a relatively long and almost completely unknown evolutionary history in the Late Triassic, during which they coexisted with another group of large-bodied, heavily built sauropodomorphs, the melanorosaurid prosauropods. This is not unexpected, as calibrated phylogenies of the Sauropoda^{16,22} all show the history of the group extending well down into the Late Triassic. However, this assumption was theoretical and based mainly on the idea that the Sauropoda are the sister-group of the Prosauropoda. The remains of *I. attavipachi* are the first osteological evidence demonstrating the existence of Triassic sauropods. Previously, the only tentative fossil evidence for Triassic sauropods consisted of footprints^{4,5} (especially *Deuterosauropodopus*²³, from Lesotho), the attribution of which to sauropods is controversial^{4,5,24,25}.

Northeastern Thailand was already linked to China in the Late Triassic²⁶, and the earliest well attested sauropod is thus an Asian form. Even if ichnological evidence from the Late Triassic of southern Africa is inconclusive, *Vulcanodon* definitely indicates that sauropods occurred there at the very beginning of the Jurassic. Convincing sauropod footprints have been reported from the basal Jurassic (Hettangian) of Poland²⁷ and Italy²⁸. All this suggests that by the time of the Triassic–Jurassic boundary, sauropods already had a vast geographical distribution, doubtless made possible by Pangaeon palaeogeographical conditions. □

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Biochemical evidence of cannibalism at a prehistoric Puebloan site in southwestern Colorado

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The existence of cannibalism is one of the most controversial issues in the archaeology of the American Southwest. Disarticulated, cut-marked and heat-altered human remains from non-burial contexts at prehistoric Puebloan (Anasazi) archaeological sites in the Four Corners region of the American Southwest have been interpreted by some scholars as evidence of cannibalism¹. Osteological studies indicate that many of the disarticulated

bodies found at these sites were processed in a manner consistent with food preparation². Opponents of this interpretation point out that non-cannibalistic practices such as secondary interment, corpse mutilation and ritualized witch executions might account for the assemblages³⁻⁷. Osteological evidence alone does not document the actual ingestion of human flesh. Here we show consumption of human flesh did occur as demonstrated in preserved human waste containing identifiable human tissue remains from a site with osteological evidence of cannibalism.

Sometime around AD 1150 a small Puebloan habitation site (5MT10010) located along Cowboy Wash in southwestern Colorado was suddenly abandoned^{8,9}. The site inhabitants' principal residences were three pithouses (Features 3, 13 and 15; Fig. 1). Several lines of evidence indicate that during the abandonment or soon after, the bodies of seven people of both sexes and various ages were disarticulated, defleshed and apparently cooked as if for consumption by other humans⁹⁻¹². Their incomplete remains were left directly on floors and in other non-burial contexts in two of the pithouses (Features 3 and 13; Fig. 2)^{8,9}.

The contexts and types of artefacts left behind in the pithouses and the conditions of their roofs indicate that the pithouses at 5MT10010 were suddenly abandoned^{8,9}. This site was excavated as part of a larger archaeological study of 17 Puebloan sites on the

southern piedmont of Sleeping Ute Mountain. The project involved the excavation of 105 structures, including 36 pithouses or pitstructures dating from AD 450-1280 (refs 9, 10). The abandonment observed in the pithouses at 5MT10010 differed markedly from the pattern seen at the other sites excavated during the project. The typical pattern of structure abandonment involved removal of virtually all artefacts and materials of value. Grinding stones, finely polished tools, ornaments and whole vessels were rarely left behind. Structural wood and stone, especially shaped slabs, were routinely scavenged for re-use. In cases where roofing materials were not stripped, the roof was typically set ablaze after useable artefacts had been removed from the structure.

In contrast, at 5MT10010, household goods, such as cooking pots and serving wares, valuable items, such as ornaments and polished stone tools, and salvageable construction materials, such as shaped stone slabs and wooden posts, were left in place in all the pithouses at abandonment. Many of the vessels, tools, ornaments and shaped stones were found directly on floor and bench surfaces with no sediment underneath, indicating that they were found at or near where they were originally left. Microstratigraphic evidence also indicates that the roofs of all the pithouses decayed gradually in place, rather than being burned or scavenged for re-use as was done with virtually all other southern Piedmont habitation structures^{8,9}.

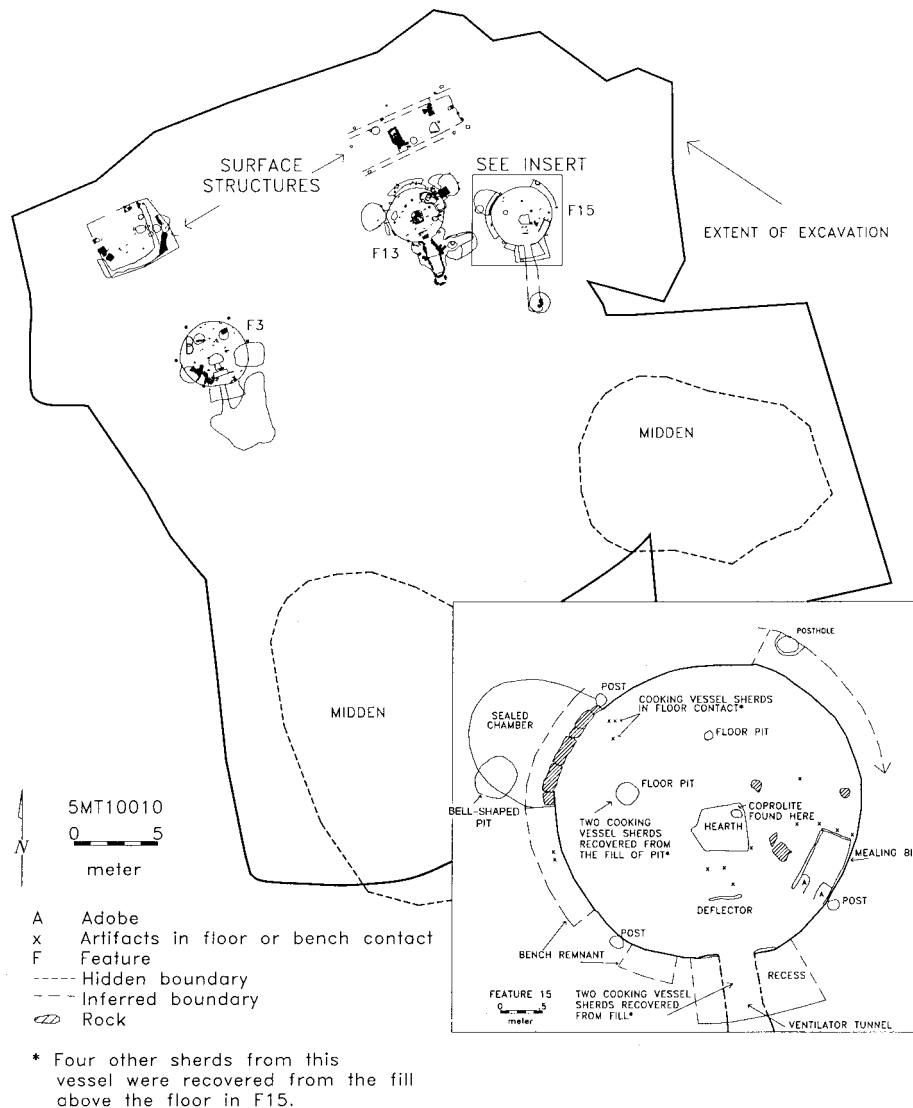


Figure 1 Site map of 5MT10010, showing the three residential pithouses (Features 3, 13 and 15; F3, F13 and F15) with the associated surface structures and trash middens that were in use when the site was abandoned. The inset depicts the interior of Feature 15,

showing where the coprolite was recovered from the hearth and where cooking pot shards were recovered from the structure. The location of four shards recovered from fill above the floor is not indicated.

The disarticulated human remains were found scattered and piled in similar contexts to the valuable artefacts^{8–12}. In Feature 3, over a thousand human bones and fragments were found piled in a side chamber while others were recovered directly from the floor of the structure, with no sediment underneath (Fig. 1). The remains represented a minimum of four adults and one adolescent. In Feature 13, whole bones and fragments were left directly on the floor, piled in a side chamber and stacked on a bench. Scorched tooth and bone fragments were also found in the central hearth and in ash piles on the structure floor. The bones in Feature 13 were from two subadults.

Other things were left in the pithouses during or soon after the site was abandoned^{8,9}. A set of stone tools consistent with use in butchering was scattered around the hearth on the floor of Feature 13. Several of the tools were tested by crossover immunoelectrophoresis for blood residues; two cutting tools tested positive for human blood^{13,14}. Although no human remains were left behind in the third pithouse at the site (Feature 15) near the time of abandonment, fragments of a cooking pot were found scattered throughout the structure. Some of the fragments were in direct contact with the floor (Fig. 1, inset). Finally, an unburned human faecal deposit (coprolite) was found in the ashy fill of the structure hearth (Fig. 1, inset). Its unburned condition demonstrated that it was deposited after the last use of the hearth. This was the only coprolite recovered from the site and may be the only one identified from a structure hearth from anywhere in the American Southwest.

The abandonment of a cooking pot in Feature 15 opened the possibility that biochemical analyses might detect human tissue residues, supporting the hypothesis that human body parts were cooked. An immunological detection assay method (ELISA) has been used to identify animal meat residues in cooking pots from archaeological contexts¹⁵. To test for the cooking of human muscle tissue in ceramic vessels, 11 shards from the Feature 15 cooking vessel were analysed for human myoglobin. Myoglobin is a protein molecule that transports oxygen from the inner surface of the membrane of skeletal and cardiac muscle cells to the energy-generating components within the cells. Five shards from other vessel types, or from vessels that were already broken before the events surrounding the abandonment of 5MT10010 began, were also analysed for human myoglobin. One of these was from the floor of Feature 3, where it was found lying directly under the face of a

disarticulated human adolescent. The other four were from the floor of Feature 13, the same structure where blood residues were detected on cutting tools. Only the shards from the cooking vessel in Feature 15 tested positive for human myoglobin (2.8–48 μg of human myoglobin per shard).

For controls, 29 shards from other archaeological sites were tested using the same procedures: 14 cooking vessel shards from a midden area associated with a contemporaneous Pueblo II/Pueblo III (AD 1075–1175) site (5MT5501) from southwestern Colorado, and 15 shards from an intermittent campsite (5JF321) southwest of Denver that contained a Woodland Ceramic Tradition component (AD 150–1150) with associated shards from a minimum of 6–8 cooking vessels¹⁵. All control shards were negative for human myoglobin (< 1 ng per sample). The presence of human myoglobin only on cooking vessel shards from 5MT10010 is consistent with the hypothesis that human muscle tissue was cooked in that vessel.

The discovery of a coprolite that was deposited near the time of abandonment of the site, during or shortly after butchering and cooking of human remains, provided the potential to yield direct evidence of cannibalism. The coprolite was found in Feature 15 (Fig. 1) and consisted of a single mass of desiccated faecal material, 30 g dry weight, of a size and shape consistent with human origin^{14,16}. The position and condition of the coprolite indicated that it was defecated directly into the cold hearth in Feature 15 (Fig. 1, inset)^{8,9}. Macroscopic analysis of the human coprolite revealed no detectable plant remains, which is extremely unusual for an ancient Puebloan coprolite^{14,16–18}. Microscopic analysis indicated that starch granules and phytoliths were virtually absent. The absence of starch granules is considered a strong indicator that maize in particular was not part of the meal(s) represented in the coprolite¹⁹. The only pollens identified were from *Cheno-Am*, low-spine *Compositae*, and trace amounts from *Poaceae*, all of which could have derived from wind-borne, ambient pollen¹⁶. The absence of plant remains except for these pollen types is consistent with the hypothesis that the depositor of the coprolite had not consumed plant foods 12–36 h before defecation. Although bone fragments and keratinous elements, such as hair, were not detected among the gross contents, the absence of plant material indicated that the meal(s) represented by the coprolite were probably composed entirely of meat^{14,16}.

To test the hypothesis that human flesh was consumed, it was

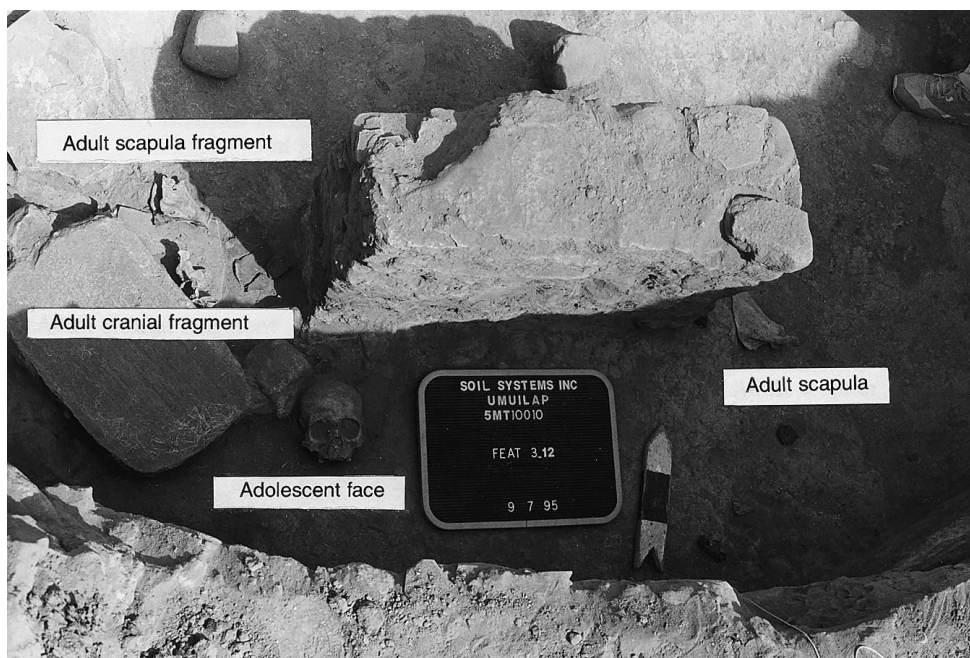


Figure 2 Human bones on the floor of Feature 3, south of the structure hearth.

necessary to identify a human-derived substance in the coprolite², but many human molecules normally occur in human stool material. For example, cells from the intestinal lining are constantly shed during the peristaltic process and blood from intestinal lesions may be present in stool samples. Therefore, it was necessary to identify a human substance that could only be present in the coprolite because it had been consumed by the depositor and could not be derived from his/her own tissues during digestion and elimination. Myoglobin is found only in skeletal and cardiac muscle cells, and not found in cells of the blood, skin, connective tissue, vascular tissue, tissues of the lymphatic system, nor in the smooth muscle cells of the digestive system. Therefore, human myoglobin should only be present in faecal material if it is consumed and passed through the digestive system by the depositor of the faeces. Furthermore, the chemical composition of myoglobin differs among animal taxa, making it possible to identify the type (species) of flesh consumed (J.E.M., unpublished results). Consequently, the ELISA technique can distinguish the presence of taxon-specific meat remains in the faeces of meat consumers. Bovine myoglobin, for example, was detected in samples from modern individuals that had consumed cooked beef within the last 24 h, demonstrating that taxon-specific myoglobin can be detected in faecal material.

Analysis of the coprolite from Feature 15 by ELISA detected human myoglobin (18–62 ng of human myoglobin per g of coprolite). The amount of myoglobin (> 5 s.d. above the average of the negative control) was lower than the amount detected on some of the shards from Feature 15 (7–10 s.d.). Apparently, the majority of the human myoglobin was broken down (degradation and hydrolysis) in the cooking process and in the gastrointestinal system of the consumer, and only a small amount remained in the coprolite that was recognizable to the human myoglobin-specific purified antibody. Human myoglobin was undetectable (< 5 s.d.) in 39 modern human faecal extracts used as controls, including samples from patients with positive blood in the stool sample. Furthermore, 20 prehistoric coprolites were tested as controls and showed no human myoglobin (< 5 ng of human myoglobin per gm of coprolite). The control coprolites were from Salmon Ruin, an open-air Puebloan site with occupation contemporaneous to 5MT10010. Although a possible cannibalism assemblage has been described from Salmon Ruin¹, all of the control coprolites were recovered from a deep

latrine deposit that clearly predates events surrounding the formation of the possible cannibalism assemblage (K. Reinhard, personal communication). To rule out contamination from insects in the coprolite from 5MT10010, internal larval proteins were tested for crossreactivity with human myoglobin; the results of these tests were negative.

Direct evidence for the consumption of human tissue by humans is necessary to demonstrate definitively that human cannibalism occurred at an archaeological site. Previous archaeological and osteological studies have strongly indicated that cannibalistic episodes took place among the ancient Pueblos, but the evidence has been essentially circumstantial. The analysis of the coprolite and associated remains from 5MT10010 at last provides definitive evidence for an episode of cannibalism involving ancient Pueblos. Results of the human myoglobin ELISA analyses of the human coprolite and shards from a ceramic vessel are consistent with the archaeological and osteological evidence of cannibalism at 5MT10010. During or after the sudden abandonment of the site, disarticulated, defleshed and heat-altered human remains were left in non-burial contexts in association with butchering tools with human blood residue, a cooking vessel with human myoglobin residue and a human coprolite containing human myoglobin. These data demonstrate that humans both processed and consumed human flesh at the site.

Cannibalism has occurred in a wide range of societies for a wide variety of reasons, including starvation, ancestor worship and political terrorism^{20–23}. With the presentation of the first direct evidence of cannibalism in the American Southwest in the prehistoric era, we hope that the debate will shift from the question of whether or not cannibalism occurred to questions concerning the social context, causes and consequences of these events. □

Methods

Artefact, coprolite and stool sample processing

We processed the shards, coprolite and control samples in an identical manner. We immersed the shards in artefact buffer (0.02 M Tris, 0.5 M NaCl, 0.5% Triton X-100, pH 7.4), sonicated them for 2 h and centrifuged them to remove particulate matter. We removed Triton X-100 by dilution/concentration three times using ultra-filtration membranes (cut-off at relative molecular mass < 10,000; Amicon). We dissolved the coprolites (100 mg) and control stool samples (500 mg) in artefact buffer and processed them as for the shards. The final volume was one-fifth the starting volume.

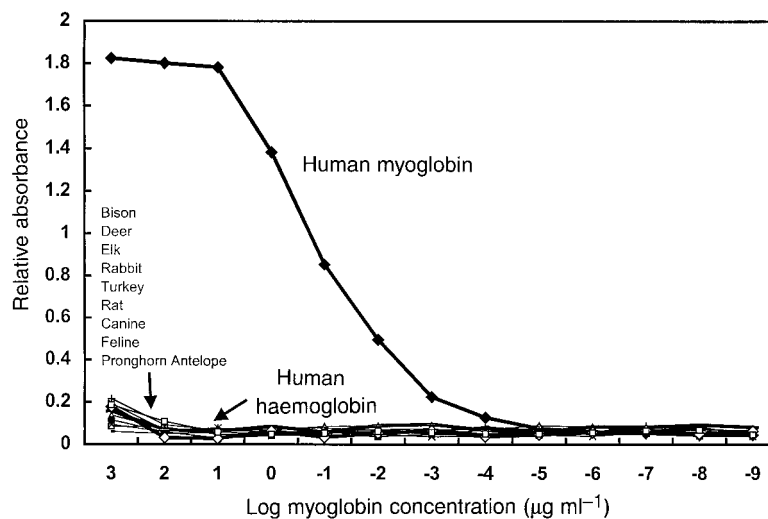


Figure 3 Specificity and sensitivity of the myoglobin assay. Dose–response curves from the ELISA assay demonstrate the specificity of the immuno-purified human myoglobin antibody toward human myoglobin, human haemoglobin and myoglobin from other animal species. The concentrations of myoglobin from each species were determined using a commercial protein assay. The myoglobin samples were assayed by

serial log-dilution for each myoglobin/haemoglobin sample. Each species of myoglobin was purified (> 90% myoglobin) by ion-exchange chromatography after extraction from skeletal muscle tissue. The other myoglobin species tested were bison, deer, elk, rabbit, turkey, rat, canine, feline and pronghorn antelope. Purified human haemoglobin was also tested.

Myoglobin detection assay

We used a sandwich-type ELISA to analyse for human myoglobin on shards, human coprolite samples and human stool samples. We applied a 100 µl aliquot of 1/1000 dilution of the capture antibody (immuno-purified rabbit anti-human myoglobin antibody from the purified immunoglobulin fraction, Sigma) in 0.05 M carbonate buffer, pH 9.6, to the plate overnight at 4 °C. We removed the unbound antibody by washing five times with ELISA wash buffer (0.025 M Tris, 0.14 M NaCl 0.025% Tween, pH 7.4) in an automated ELISA washer.

We diluted the sample and controls 1/100 in ELISA dilution buffer (0.5 M Tris, 0.14 M NaCl, 0.03 M KCl, 0.2% Tween, 0.4% PEG-8000, pH 7.4) and applied 100 µl to the appropriate wells for 1 h at 22 °C. After washing the wells (as above), we applied mouse monoclonal anti-human myoglobin (Sigma; 100 µl diluted 1/4,000 in ELISA dilution buffer) for 1 h at 22 °C. We washed the wells three times and applied the detection antibody (Sigma; 100 µl of sheep anti-mouse IgG conjugated to horse radish peroxidase, diluted 1/10,000 in ELISA dilution buffer) 1 h at 22 °C. We washed the wells three times and added the substrate (TMB/Urea; Sigma) for 5 min. We stopped the reaction with 2 M H₂SO₄ and read the plate at 450 nm on an ELISA reader (Dynex MRX, Chantilly, VA). We assayed each sample or control using six replicates, three times each by two individuals. We averaged the values from each experiment and compared them statistically to the negative controls using the Student's *t*-test. We considered the results as positive when *P* < 0.001 and at least 5 s.d. above the average negative control.

The commercial rabbit anti-human myoglobin antibody reacted minimally with myoglobin from several other species used as possible food sources. To remove these crossreacting antibodies, the rabbit anti-human myoglobin antibodies were immuno-adsorbed with different species of myoglobin (deer, bovine, sheep, antelope, rabbit, turkey, chicken, elk, mouse and rat). The individual myoglobin samples were coupled to Sepharose (Pharmacia) to bind the antibodies specific for the different species of myoglobin. The remaining human-specific antibodies were concentrated and used in the ELISA procedure. The immuno-purified polyclonal rabbit anti-human myoglobin antibodies recognized only human myoglobin in a dose-dependent manner (Fig. 3). The concentration of human myoglobin detected in the coprolite ranged from 18 to 62 ng ml⁻¹. No detectable concentrations of myoglobin were observed with serial dilutions of myoglobin (> 1 mg ml⁻¹) from the other species, including the 'food source' species found in the region (Fig. 3). Crossreactivity with non-human primates was not considered, because no evidence of non-human primates has been found in prehistoric archaeological contexts in the continental United States. Furthermore, the nearest contemporaneous non-human primate populations were located in tropical Mexico.

Artefact and faecal controls

The control shards from 5MT5501 were provided by Jerry Fetterman, Woods Canyon Archaeological Consultants, Inc. The site occupation was contemporaneous to the Cowboy Wash site (5MT10010), but lacked any indication of possible cannibalism. 5MT5501 is located about two miles west of Dolores and 18 miles north of Sleeping Ute Mountain, in southwestern Colorado. The control shards from 5JF321 were provided by the Colorado Archaeological Society from their excavation about ten miles southwest of Denver in the Ken Caryl Valley¹⁵. These shards are of the Woodland Ceramic Tradition. Some control shards from both 5MT5501 and 5JF321 were positive for deer and rabbit myoglobin and/or blood, but control shards from ancient Pueblo or Plains cultures did not contain human myoglobin residue.

Control faecal tests were conducted to determine whether human myoglobin was present in faeces from modern normal individuals (25 samples), modern individuals with blood in their stool samples (ten samples), or modern individuals who had consumed cooked beef within 24 h of defecation of the specimen (four samples). These controls did not show detectable levels of human myoglobin (< 5 s.d. of the average negative control). This result is consistent with the hypothesis that human myoglobin is not derived from the tissues of a defecator, even when the stool sample is positive for blood. In contrast, the control samples from the beef consumers tested positive for bovine myoglobin, demonstrating that orally ingested myoglobin can survive the processes of cooking and digestion, can be detected in human faecal material, and can be identified as to biological taxon of origin. The modern stool samples were collected for clinical testing and the remaining material was considered 'discarded specimen material' from the clinical laboratory. The only personal information available to the authors was the patient's occult blood status.

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Uptake of dissolved organic carbon and trace elements by zebra mussels

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Zebra mussels (*Dreissena polymorpha*) are widespread and abundant in major freshwater ecosystems in North America, even though the phytoplankton food resources in some of these systems seem to be too low to sustain them^{1,2}. Because phytoplankton biomass is greatly depleted in ecosystems with large *D. polymorpha* populations^{3,4} and bacteria do not seem to be an important food source for this species⁵, exploitation of alternative carbon sources may explain the unexpected success of *D. polymorpha* in such environments. Here we examine the possibility that absorption of dissolved organic carbon (DOC) from water^{6–9} could provide a nutritional supplement to zebra mussels. We find that mussels absorb ¹⁴C-labelled DOC produced by cultured diatoms with an efficiency of 0.23%; this indicates that DOC in natural waters could contribute up to 50% of the carbon demand of zebra mussels. We also find that zebra mussels absorb some dissolved metals that have been complexed by the DOM; although absorption of dissolved selenium was unaffected by DOC, absorption of dissolved cadmium, silver and mercury by the mussels increased 32-, 8.7- and 3.6-fold, respectively, in the presence of high-molecular-weight DOC.

