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"STOMACH" CONTENTS OF A HADROSAUR FROM THE DINOSAUR PARK FORMATION (CAMPANIAN, UPPER CRETACEOUS) OF ALBERTA, CANADA

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INTRODUCTION

The dietary preferences of hadrosaurs have long been a topic of research interest (Ostrom, 1964; Farlow, 1987; Weishampel, 1984b). The dental batteries and jaw mechanics of hadrosaurs (Weishampel, 1984a) were well-adapted for reducing ingested plant material to small pieces that could be broken down more efficiently by digestive acids and possibly microbial symbionts. However, cranial characteristics cannot resolve precisely what food was being ingested. Nor can other lines of indirect evidence (Krassilov, 1981). This is of interest for many reasons, including the fact that the diets of hadrosaurs have been cited both as a cause of their extinction (Swain, 1976), and as a significant factor in the evolution of angiosperms (Bakker, 1978; Coe *et al.*, 1987).

The most direct evidence of dietary preferences comes from the gut contents of two "mummified" hadrosaurs (*Edmontosaurus annectens*) collected in Wyoming. The first specimen (AMNH 5060) contained the carbonized contents of the stomach according to C. H. Sternberg (1909), although there has never been any published study identifying the plant material. A second mummified specimen was found in the same region in 1910 (Sternberg, 1985), and was shipped to the Senckenberg Natural History Museum in Frankfurt, Germany. This specimen included an earthy brown concentration of plant fragments within the thoracic cavity. Because of the location and composition of the plant fragments, Kräusel (1922) interpreted the material as probable stomach contents. The concentration was macerated, and was found to be composed mostly of conifer needles (which he identified as *Cunninghamites elegans*), pieces of branches of coniferous and deciduous trees, and seeds and/or fruits. The possibility was considered that the plant material was washed into the body cavity (Abel, 1922; Kräusel, 1922), but Kräusel thought this was a less likely interpretation because of the absence of saprophytic fungi, pollen, and the eggs of water insects. Unfortunately, maceration of the "stomach contents" and removal of most of the skin impressions and sediments from the specimen make it impossible to follow up the original studies (Weishampel and Horner, 1990).

In 1976, the first author looked at an uncollected specimen of a duckbilled dinosaur that had been found in Dinosaur Provincial Park (near Brooks, Alberta, Canada) more than five years before. The thoracic region was almost entirely covered by skin impressions, but it appeared that erosion had destroyed most of the skeleton. A peculiarity of the specimen that was immediately noticed was that the sandstone within the body cavity contained abundant remains of small pieces of twigs and branches, whereas the sandstone external to the skin impressions lacked any significant evidence of plant fossils. Because it seemed possible that the plant remains in the body cavity might represent "stomach" contents, the specimen was excavated in 1980.

RTMP 80.40.1 turned out to be a better specimen than anticipated, and is a virtually complete skeleton of the hadrosaur *Corythosaurus casuarius* that lacks only the pelvis and tail. It is a mature adult with a skull length of 680 mm. Although skin impressions are frequently found associated with dinosaur skeletons in Dinosaur Provincial Park, no specimens recovered to date have as much skin over the thoracic region as RTMP 80.40.1. To determine whether the fossils might represent food ingested by the hadrosaur, macroplant remains and palynomorphs found within the body cavity were examined microscopically.

Abbreviations AMNH, American Museum of Natural History, New York; NMS, Naturmuseum Senckenberg, Frankfurt am Main; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller.

Material RTMP 80.40.1 was recovered from Quarry 150, Dinosaur Provincial Park (Legal Subdivision 13, Section 32, Township 20, Range 11, West of the 4th Meridian). The specimen has been on display at the Museum since, 1985 in the same pose in which it was found. It was collected from low in the Dinosaur Park Formation of the Judith River Group (Campanian, Upper Cretaceous).

DESCRIPTION

RTMP 80.40.1 was found in a typical death pose, with the neck twisted so the back of the skull lies close to the sixth dorsal vertebra. Both arms were stretched out, and the hands were practically touching. The knees were bent so that the feet were folded up beneath the abdomen. Unlike the majority of skeletons found in Dinosaur Park, the bones had retained their three dimensional association with each other, and had neither collapsed nor been crushed into a single plane. The thorax was enclosed in skin impressions, indicating that the carcass had been buried rapidly. No skin impressions were found on the head or limbs.

The medium-grained, fluvial sandstones surrounding the skeleton contained sparsely distributed plant remains, whereas plant fragments are densely concentrated (up to 70 fragments per 25 square centimetres) inside the body cavity. The plant remains are not packed into a concentrated mass as they apparently were in NMS R4036 (Kräusel, 1922), and a sauropod from the Morrison Formation of Utah (Stokes, 1964). They are distributed throughout the body cavity, and fragments are suspended in the sandstone matrix.

Most of the plant remains are in the form of wood or bark fragments ranging from 1.0 to 4.0 centimetres in length and 0.2 to 1.5 cm in width. The fragments are mostly young twigs with primary xylem and pith. The number of growth rings varies between three and nine, with five to seven rings being most common. Wood fragments do not show the presence of sharply broken ends, and the edges of the woody cells appear to be either partially digested or rotted. In addition to the woody fragments, seeds and seed pods seem to be relatively common. Conifers are about twice as common as angiosperms. Finally, small pieces of charcoal were less common, but seem to have been distributed throughout the body cavity. The charcoal particles were on average much smaller than the twig and bark fragments.

Palynomorph recovery is generally poor in fluvial sandstones, so the results of preparing a 42.8 gram sample of the plant rich matrix inside the body cavity were somewhat surprising. The assemblage included more than thirty taxa of spores, pollen, megaspores, fungal spores, acritarchs, dinoflagellate cysts, and possible algae. The dinoflagellates were poorly preserved, Early Cretaceous forms that had clearly been reworked into younger sediments from upstream localities. Although megaspores are fragmentary, the majority of the palynomorphs are well-preserved, and none show any evidence of effects that could be interpreted as the activity of digestive acids or intestinal microbes. The most frequently recovered palynomorphs are bisaccate pollens from gymnosperms. Pollen from angiosperms are also common, but spores from bryophytes and pteridophytes are not.

DISCUSSION

RTMP 80.40.1 was buried rapidly in a stream bed, and the carcass was covered by sand before the skin on the upper surface of the body had a chance to decompose. It cannot be determined whether or not the abdomen had ruptured before the specimen was completely covered by sediments. However, by the time the body cavity became open to the outside environment, most of the internal organs and fascia had decomposed. Plant material in the body cavity may have been present in the alimentary canal, in which case it was distributed throughout the thoracic and abdominal regions by the invading water and sediments. Alternatively, the plant fragments may have come in with the sediments, or they may have originated from both sources.

Most plant fragments were derived from relatively young stems and twigs of gymnosperms and angiosperms. The twigs and the leaves they carried would not have been an unexpected source of food for hadrosaurs. The sizes of the woody fragments are consistent with the idea that they had been chewed up by hadrosaur teeth. The absence of sharp edges might be attributable to partial digestion. Seeds found within the body cavity would have been a good source of nutrition, and their presence in the body cavity supports the hypothesis that the plant material may have been ingested by the hadrosaur. However, the uniformity of size of plant fragments could also have been the result of hydraulic sorting, and the edges may have been smoothed by water transport. Although it seems unlikely that a hadrosaur would ingest charcoal fragments, there is a remote possibility that it was required for some aspect of digestive or metabolic activity.

Miospores are an unlikely source of food for an animal as large as a hadrosaur. However, large quantities could have been ingested along with the leaves, flowers and twigs that formed the bulk of its diet. Palynomorphs are chemically resistant, so the lack of evidence of acid etching is probably not significant. However, Waldman and Hopkins (1970) did notice corrosion of palynomorphs in carnivore coprolites, and attributed it to digestive acids.

The high diversity of palynomorphs cannot be regarded as an indication of a diverse diet, even if the plant remains were stomach contents. Many of the palynomorph taxa may represent spores and pollen that were ingested incidentally with food. Aquatic plant taxa like the rare algae, and even the reworked dinoflagellate cysts, may have been washed into the body cavity after death, or may have been swallowed when the hadrosaur drank water.

Differences in the preservation of plant material in the sediments inside and outside the hadrosaur body could be explained several ways. The presence of skin on most of the upper surface of the body suggests that the carcass was buried before any significant decomposition had taken place. Because the surrounding sediments would have been deposited in a flowing stream, plant fragments would not have had a chance to settle. However, the breakdown of tissue within the carcass by microbes and by the animal's own digestive acids would have continued after burial. If the body cavity ruptured somewhere at this point in time, water, sand, mud and plant remains would have entered the cadaver. Because the carcass was already buried, flow velocity would have been restricted inside the rib cage, and lighter particles would have had an opportunity to settle. In addition, there may have been chemical differences in the microenvironment within the body cavity caused by decomposition within a restricted space. These chemical differences may have favoured the preservation of plant remains within the carcass, whereas those immediately outside the body may have decomposed.

The various scenarios presented here for RTMP 80.40.1 could also be applied to AMNH 5060 and NMS R4036, even though the plant material in the latter was apparently found in a concentrated mass. The evidence for fossilized "stomach" contents in a sauropod (Stokes, 1964) is no stronger. In fact, the presence of bone and tooth fragments in the supposed "fossilized stomach contents" is completely inconsistent with what we know about sauropod diets. Finally, it is worth noting that one other hadrosaur specimen collected recently by the Royal Tyrrell Museum of Palaeontology has abnormal inclusions in the abdominal cavity. RTMP 90.104.1 is a nicely preserved, articulated skeleton of *Brachylophosaurus canadensis*. Inside the rib cage was found the skeleton of a sturgeon, which is the first articulated specimen ever recovered from the Cretaceous rocks of Alberta. Clearly the sturgeon was not ingested by the hadrosaur, although something about the microenvironment within the body cavity significantly improved the chances of the fish to be preserved intact.

CONCLUSIONS

As in previously collected hadrosaurs with possible stomach contents (Sternberg, 1909; Kräusel, 1922), it cannot be determined whether the plant material inside the body cavity of RTMP 80.40.1 represents the last meal of the animal, or was simply washed into the body after death. The fragments mostly represent one to four centimetre long sections of five to seven year old twigs from angiosperms and gymnosperms. These, and the leaves they would have carried, would have been a reasonable food supply for a large hadrosaur. This concept is strengthened by the presence of seeds and seed pods in the body cavity. However, the presence of a diverse palynomorph assemblage and charcoal fragments suggest all or part of the inclusions were introduced by fluvial action. The most conservative conclusion is that the plant remains associated with RTMP 80.40.1 cannot be shown to be "stomach" contents. Although the same level of study has not been done on the abdominal contents of AMNH 5060 and NMS R4036, the authors suspect that the results would also be ambiguous.

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