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Gastroliths in an ornithopod dinosaur

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Gastroliths (stomach stones) are known from many extant and extinct vertebrates, including dinosaurs. Reported here is the first unambiguous record of gastroliths in an ornithopod dinosaur. Clusters of small stones found in the abdominal region of three articulated skeletons of *Gasparinisaura cincosaltensis* were identified as gastroliths on the basis of taphonomic and sedimentologic evidence. The large number of stones found in each individual, their size, and the fact that *Gasparinisaura cincosaltensis* was herbivorous, all suggest that they were ingested as a result of lithophagy rather than accidental swallowing.

Introduction

Gastroliths or geo-gastroliths sensu Wings (2007) are known in many taxa of extant and fossil vertebrates (Whittle and Everhart 2000). Gastroliths have been occasionally reported in non-avian dinosaurs (Wings 2004) but only few cases can withstand rigorous testing. The clusters of stones associated with the prosauropod *Massospondylus* (Bond 1955) and the sauropods *Seismosaurus hallorum* (Gillette 1994), *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus 1999), and *Cedarosaurus weiskopfae* (Sanders et al. 2001), indicate the occurrence of gastroliths in at least some sauropodomorphs. Also, the presence of stones in the abdominal cavities of the maniraptoriform theropods *Sinornithomimus dongi* (Kobayashi et al. 1999; Kobayashi and Lü 2003), *Shenzhousaurus orientalis* (Ji et al. 2003), *Caudipteryx zoui*, and *Caudipteryx dongi* (Ji et al. 1998; Zhou et al. 2000; Zhou and Wang 2000) suggests that these non-avian theropods were lithophagic.

Among ornithischians, unambiguous evidence supporting lithophagy is known from the basal ceratopsian *Psittacosaurus* (Osborn 1923; You and Dodson 2004). Supposed gastroliths reported in several thyreophorans and ornithopods are possibly secondarily transported clasts (Currie 1997; Lucas 2000). Stones associated with remains of the ornithopods *Edmontosaurus* (“*Claosaurus*”) (Brown 1907) and *Iguanodon* (Rivett 1956) appear to lack the taphonomic features that would allow their identification as true gastroliths (Wings 2004).

A partial skeleton of *Gasparinisaura cincosaltensis* Coria and Salgado, 1996 (MUCPv 213), a basal ornithopod from South America collected in 1992, contains a cluster of stones in the abdominal region which are here identified as gastroliths. In addition, two new specimens of *G. cincosaltensis* (MCSPv 111 and MCSPv 112) provide additional evidence of stomach stones in this species. These stones represent the first unambiguous evidence for lithophagy in ornithopod dinosaurs.

Institutional abbreviations.—MCSPv, Vertebrate paleontology collection of the Museo de Cinco Saltos, Río Negro Province, Argentina; MUCPv, Vertebrate paleontology collection of the Museo de la Universidad Nacional del Comahue, Neuquén Province, Argentina.

Material and geologic setting

Three specimens of *Gasparinisaura cincosaltensis,* MUCPv 213, MCSPv 111, and MCSPv 112, were collected near the city of Cinco Saltos (Río Negro Province, Patagonia, Argentina) (Fig. 1), in mudstones and sandstones of the early Campanian Anacleto Formation, in the uppermost portion of the Neuquén Group (Ramos 1981; Dingus et al. 2000). MUCPv 213 (Fig. 2A) consists of a partial skeleton that includes cranial and postcranial elements (see Salgado et al. 1997 for a detailed anatomical description). A portion of the preserved elements (both incomplete humeri articulated with both radii and ulnae, several posterior dorsal ribs from both left and right sides) are included in a compacted, reddish mudstone, whereas the posterior ribs are imbedded in a medium to coarse sandstone. Nine of the left ribs appear to be preserved in their original position. The bone surfaces do not show any significant preburial or diagenetic damage.

MCSPv 111 (Fig. 3A) is the most complete, articulated specimen of *Gasparinisaura cincosaltensis* collected to date, lacking only the skull and most of the tail. The left ventrolateral side of the skeleton is exposed, with the left hind limb in flexion over the abdominal area. Several characters allow the assignment of MCSPv 111 to *G. cincosaltensis* (Coria and Salgado 1996; Salgado et al. 1997): (1) long pubic peduncle of ilium, (2) greater and lesser trochanter of femur fully fused to each other, (3) absence of anterior intercondylar groove in the femur, (4) tibial malleoli approximately at the same level, and (5) metatarsal II transversely compressed and anteroposteriorly developed. The relatively small size of MCSPv 111 (around 43 % of the *G. cincosaltensis* largest individual, MUCPv 213) suggests that it is a juvenile specimen. MCSPv 111 is preserved in friable, medium- to coarse-grained, quartzose sandstone.

Specimen MCSPv 112 (Fig. 3B) was found approximately 0.3 mm from MCSPv 111 (Leonardo Salgado, personal communication 2008). It consists of the skull, several dorsal and caudal vertebrae, and the pelvic girdle in articulation with both hind limbs. Several characters including the ascending process of jugal anteroposteriorly wide, chevrons in midcaudal region roughly triangular, anteroposteriorly expanded, and characters (1), (2), and (3) as in MCSPv 111 allow its assignment to

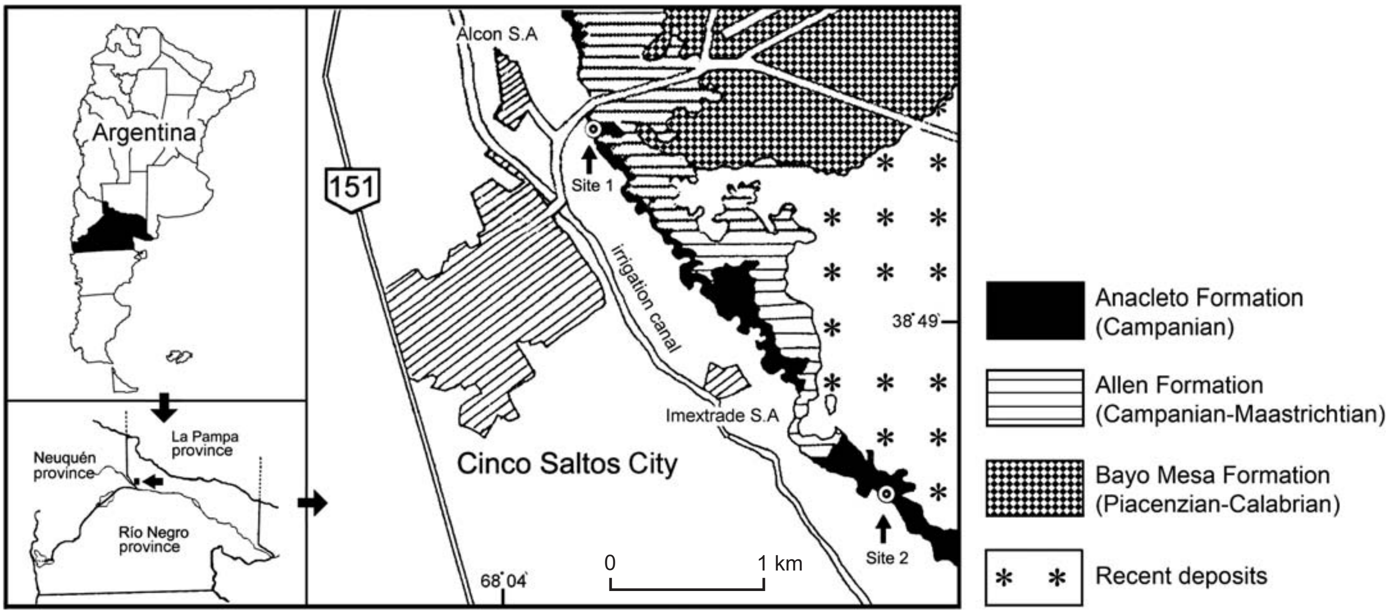

Fig. 1. The surroundings of Cinco Saltos City where MCSPv 111, MCSPV 112 (Site 1) and MUCPv 213 (Site 2) were found (modified from Andreis et al. 1974).

Gasparinisaura cincosaltensis. MCSPv 112 is also a juvenile, even slightly smaller than MCSPv 111.

Near the town of Cinco Saltos, the Anacleto Formation is composed of two lithofacies: (1) cross-stratified sandstones and (2) reddish mudstones (Salgado et al. 1997; Heredia and Salgado 1999). MUCPv 213 was found in the mudstones, and MCSPv 111 and MCSPv 112 in the sandstones. Field observations of both lithofacies showed no accumulations of stones similar to those contained inside the specimens of *Gasparinisaura cincosaltensis*.

Most of the following description is based on specimen MUCPv 213, from which the stones were removed and examined in a scanning electron microscope (Philips SEM 515). The stones found in specimens MCSPv 111 and MCSPv 112 were studied *in situ*.

Description

All three *Gasparinisaura cincosaltensis* individuals were found with stone clusters. In MUCPv 213, a cluster of stones occupies about 70 cm^2 in the rib cage on the left side of its abdominal area. Several stones are flanked by both left and right dorsal ribs, preserving several contacts between bones and the other stones (Fig. 2B, C). There are no stones outside the abdominal region on the lateral side of the rib cage. In total, 180 stones were counted (only stones larger than 4 mm in diameter were considered). The average length of the stones was 7.9 (±2.5) mm and the length of the largest stone was 17 mm (Fig. 2B). The total mass of the stones was 51.1 g.

Most of the stones were of igneous rock (47.22%). Other materials include quartz (27.22%), sandstone (23.89%), and three were composed of metamorphic rock (1.67%). Stones ranged from light brown and light gray to dark brown or nearly black in color. Following the roundness classification proposed by Powers (1953), the stones are mainly sub-rounded with dull surfaces. Sphericity (Blatt et al. 1972) varied from 0.51 to 0.91 with an average of 0.73 (±0.08). The 10 stones analyzed with SEM show smooth surfaces and a lack of pits or grooves as observed in other vertebrate gastroliths (Fig. 2D) (Whittle and Oronato 2000).

A conspicuous, three-dimensional accumulation of stones was exposed during preparation in the abdominal region of MCSPv 111. The cluster is located caudal to the rib cage and anteroventral to the postpubic processes (Fig. 3A). More than 40 rounded and sub-rounded, igneous stones can be seen in the cluster (few stones in contact with bones), all accumulated within an area of approximately 11 cm^2.

In MCSPv 112, two clusters of stones were found. The largest cluster is located anteroventral to the pelvic girdle, underneath the last dorsal vertebra and the first sacral vertebra (Fig. 3B). Many stones of this cluster are in contact with ribs and vertebrae. The smallest accumulation is located in front of the main cluster, near the skull. Both accumulations seem to be part of a major cluster, partially lost by weathering. As in MCSPv 111, the stones were only observed inside the abdominal region.

Discussion

The inorganic nature of gastroliths makes their identification difficult. Stones associated with bones are identifiable as gastroliths if they are clustered in the abdominal area of relatively complete skeletons (Wings 2004: 113). In addition, Wings (2004: 84) proposed a series of detailed taphonomic and sedimentologic criteria for identification of gastroliths. Many of these criteria are met by the rocks associated with the three specimens described here: (1) all the stones were found in situ in the abdominal area of the skeletons, like in MUCPv 213 and MCSPv 112, the stones were inside the rib cage; (2) the specimens are almost complete (MCSPv 111 and MCSPv 112) and

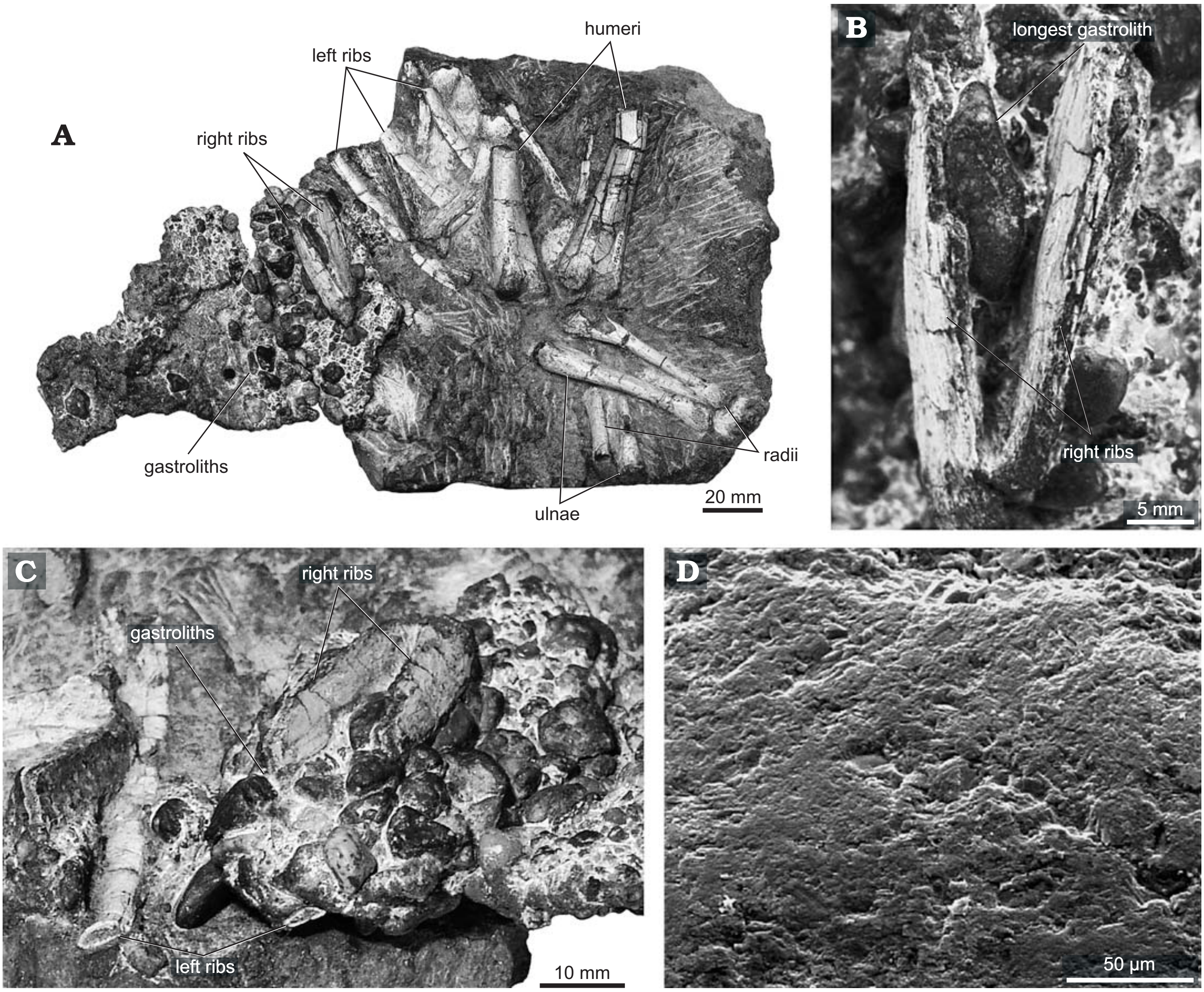

Fig. 2. The ornithopod dinosaur *Gasparinisaura cincosaltensis* Coria and Salgado, 1996, MUCPv 213 from the Late Cretaceous Anacleto Formation of Patagonia. **A**. Forelimb bones and ribs. **B**. The longest gastrolith in contact with two right dorsal ribs. **C**. Cluster of gastroliths associated with the ribs. **D**. Scanning electron microphotograph of a gastrolith from metamorphic rock.

articulated (MUCPv 213, MCSPv 111 and MCSPv 112); (3) there is a direct association between bones and stones; (4) the stones were found in clusters; (5) the matrix that supports each specimen lacks similar stones, isolated or forming clusters; (6) there were no isolated stones forming accumulations in the outcrops where the skeletal remains were collected; (7) there are three individuals of the same species with rocky accumulations in the gut area. Hence, the most parsimonious explanation for the stones is to consider them as true gastroliths (category 1 in the taphonomic classification of gastroliths finds proposed by Wings [2004: 113]).The presence of gastroliths in *Gasparinisaura cincosaltensis* is the first unequivocal evidence for lithophagy in Ornithopoda, thus increasing the number of documented cases of lithophagy among the Dinosauria.

The large number of gastroliths observed in each individual, their size, and the fact that *Gasparinisaura cincosaltensis* was a herbivorous dinosaur (Norman et al. 2004), indicate that the stones were ingested as a result of lithophagic behaviour rather than accidental swallowing. Keeping in mind all possible functions of gastroliths in vertebrates (Wings 2007), the most probable utility of these stones in *Gasparinisaura* seems to have been the trituration of plant materials, perhaps because the food was especially tough and thus needed trituration to make it digestible. This function was certainly linked to the presence of a gizzard, where food is mechanically broken down as in many extant birds (Gionfriddo and Best 1999). However, the existence of a gastric mill in sauropod dinosaurs has recently been denied, since the amount of gastroliths reported in these dinosaurs was too small (0.03% of their body mass) to support a gastric mill as present in extant birds (Wings and Sander 2007). In MUCPv 213, the total mass of gastroliths (51.1 g) amounts to about 0.3% of the body mass which is estimated (based on the femur cir-

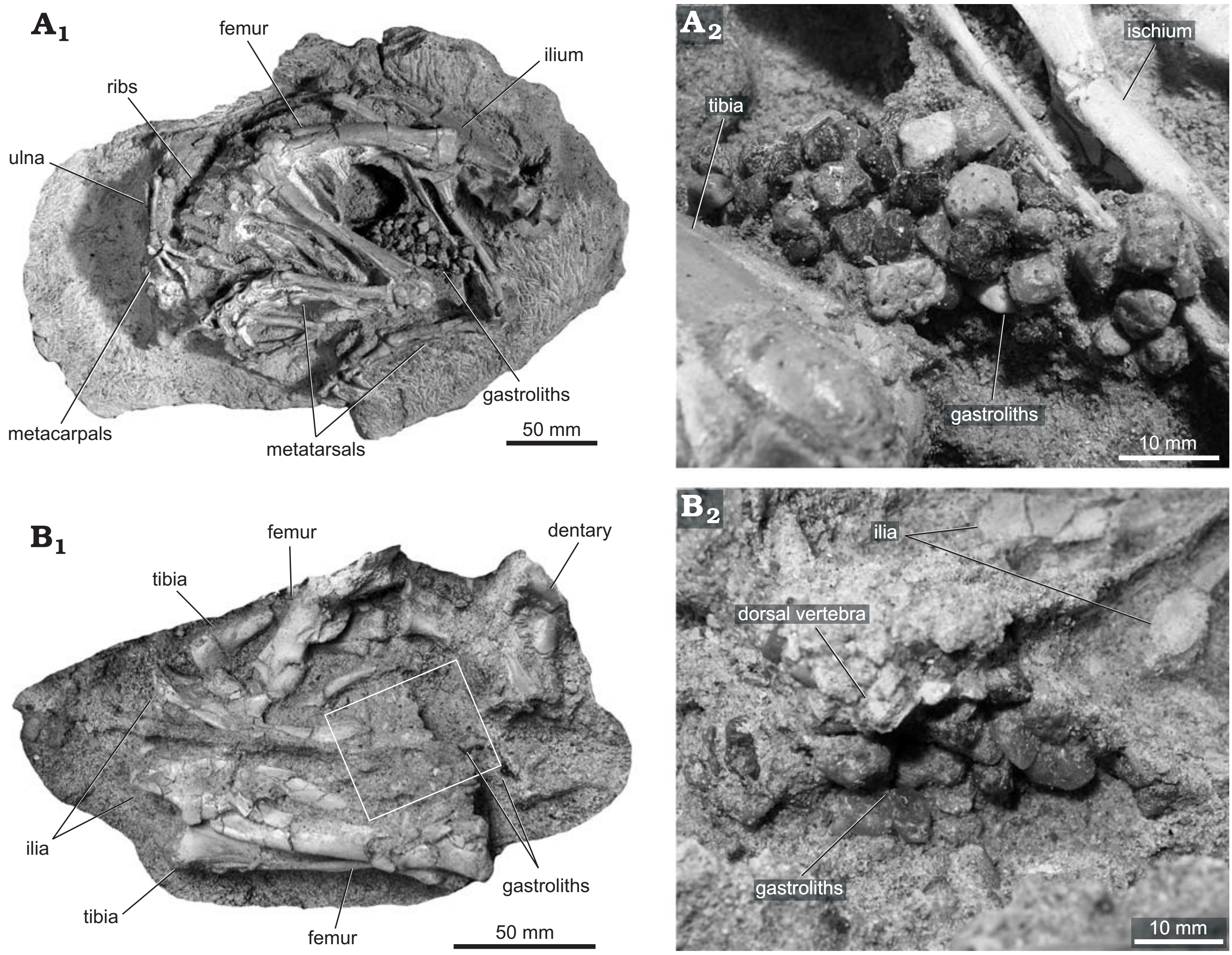

Fig. 3. The ornithopod dinosaur *Gasparinisaura cincosaltensis* Coria and Salgado, 1996 from the Late Cretaceous Anacleto Formation of Patagonia, MCSPv 111 (**A**) and MCSPv 112 (**B**). A_1, nearly complete postcranial skeleton in left lateral view; A_2, cluster of gastroliths in the abdominal cavity; B_1, nearly complete skeleton in dorsal view; B_2, the largest cluster of gastroliths below the last dorsal vertebra.

cumference of 71 mm) as 18 kg (Anderson et al. 1985). Thus the relative mass of gastroliths in MUCPv 213 is much higher than that estimated for sauropod dinosaurs, but similar to that calculated for several extant birds (Wings and Sander 2007). If *Gasparinisaura* utilized gastroliths in the same way as in living birds, the amount of gastroliths would have been sufficient to support a gastric mill.

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