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Prey choice and cannibalistic behaviour in the theropod *Coelophysis*

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Direct evidence of prey choice in carnivorous dinosaurs is rare in the fossil record. The most celebrated example pertains to purported stomach contents in the carnivorous dinosaur *Coelophysis bauri*, which besides revealing prey choice, also points to cannibalistic behaviour as being commonplace (Colbert 1989, 1995). Here, we test this hypothesis by conducting the first comprehensive anatomical and histological examination of the famed *Coelophysis* 'cannibals'. The results unequivocally show that the gut contents derive from early crocodylomorphs rather than juveniles of *Coelophysis*. These findings suggest that this taxon is not cannibalistic and bring into question the commonality of this behaviour among non-avian dinosaurs.

Keywords: *Coelophysis*; prey choice; cannibalism; palaeobiology; Mesozoic; dinosaur

In 1947, crews from the American Museum of Natural History (AMNH) unearthed an enormous bonebed composed of hundreds of skeletons of the early theropod *Coelophysis bauri* from the Upper Triassic (210 Myr old) Chinle Formation near Ghost Ranch in north-central New Mexico, USA. Preparation of two of the more complete *Coelophysis* skeletons revealed aggregations of relatively small, archosaurian reptile bones that appeared to lie within the dinosaurs' body cavities. Colbert (1989, 1995) deduced, without specific justification, that these remains represent juveniles of *Coelophysis* and presented this as unequivocal evidence for dinosaurian cannibalism. Colbert's specimens have stood as the quintessential example of this behaviour in theropods. They are also the basis for one of the most recognized palaeobiological anecdotes presented in museum exhibitions, countless children's books and in popular press (Paul 1988; Colbert 1995; Currie & Padian 1997; Farlow & Brett-Surman 1997; Mayell 2002; Rogers *et al.* 2003).

The famed cannibal-*Coelophysis* hypothesis, although tenable, has never been rigorously examined. Two criteria must be met to unequivocally ascribe cannibalistic behaviour to dinosaurs from 'stomach' contents. The remains must be shown to reside in the abdominal cavity and come from the same taxon. This has not occurred. The stomach contents were never prepared to a degree allowing their location in the body to be definitively ascertained. Furthermore, it is well established that most basal archosaurian reptiles, including early dinosaurian taxa, have similar hindlimb morphology, thus leaving open the possibility that the purported stomach contents come from other animals besides *C. bauri*.

Recent access to the Colbert's *Coelophysis* specimens allowed an unprecedented opportunity to reanalyse the cannibal-*Coelophysis* hypothesis. We further prepared the specimens (AMNH FR 7223 and AMNH FR 7224) and used detailed morphological and bone histological analyses to critically examine whether the aforementioned criteria supporting cannibalism in *Coelophysis* are met.

AMNH FR 7223 (see figure 1*c* and electronic supplementary material) is a nearly complete adult skeleton (femoral length = 209 mm) lying on its right side, with purported gut contents consisting of articulated vertebrae, an articulated leg (femoral length = 130 mm) and various small bone fragments. Other than the articulated leg, none of the purported gut material possesses diagnostic characters, allowing it to be referred to a taxon below the sauropsid level; let alone to a dinosaur such as *Coelophysis*. Furthermore, it seems unlikely that such a large item, an entire hindlimb (62% adult size hindlimb), could have been ingested in its entirety (Gay 2002; see electronic supplementary material). Whether these materials represent gut contents is also questionable. Although the left dorsal ribs cover all the possible stomach remains laterally, the right dorsal ribs are deflected posteriorly and do not underlie the purported gut contents. This indicates that the abdominal cavity may have been ruptured prior to burial and/or the ribs were disarticulated by fluvial processes (Schwartz & Gillette 1994). In any event, all that can be concluded is that the remains of AMNH FR 7223 came to lie upon the supposed stomach contents. Collectively, no evidence exists to unambiguously conclude that 'stomach contents' were preserved in this specimen's abdominal cavity.

The neotype of *C. bauri* (AMNH FR 7224) consists of a nearly complete mediolaterally crushed skeleton (femoral length = 203 mm) lying on its left side (figure 1). The abdominal cavity contains disarticulated skeletal remains concentrated in the posterodorsal region and articulated remains in the anteroventral region (figure 1). The left and right dorsal ribs surround the posterodorsal portion of the abdominal remains; however, both the right and the left ribs of the anterior dorsal vertebrae lie atop of the articulated series of caudal vertebrae in the anteroventral region. Articulated gastralia just anterior to the pubis indicate that the abdominal cavity remained intact prior to and after burial. Thus, we conclude that the posterodorsal remains, but not the anteroventral ones, are unambiguously *contained* in the abdominal cavity. The first criterion for these being cannibalized gut contents is met.

The posterodorsal concentration of bones preserves a three-dimensional structure that appears to delimit the stomach cavity (figure 1). Small bone fragments are

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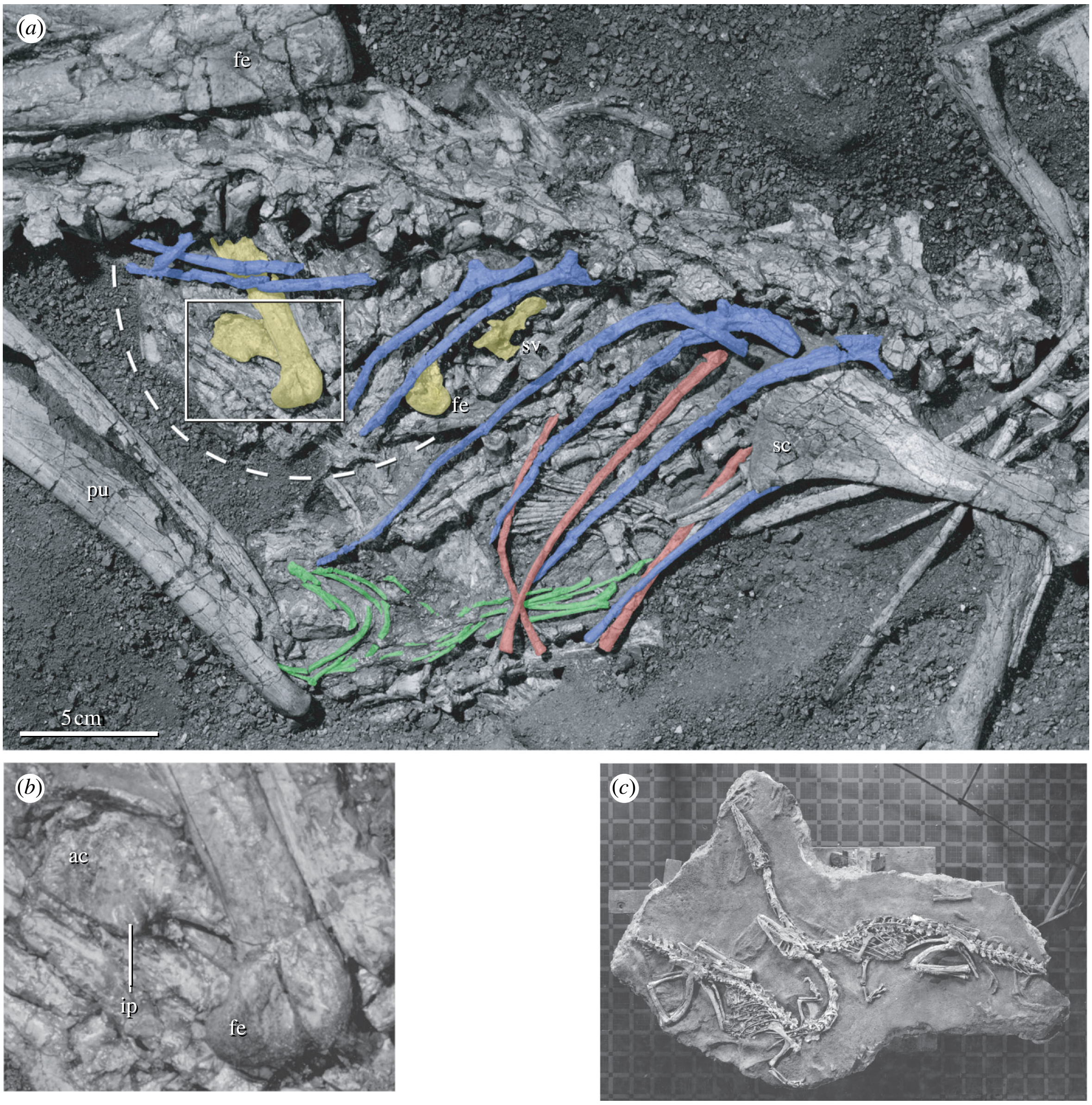

Figure 1. Abdominal region of *Coelophysis bauri* neotype (AMNH FR 7224). (*a*) Detail of abdominal cavity of AMNH FR 7224 showing posterodorsally intact stomach (dotted line) with preserved contents (AMNH FR 30616) highlighted in yellow. Right femur and left ilium, left femur (fe) and sacral vertebra (sv) of stomach content material. Intact gastralia in green, right dorsal ribs in blue and left dorsal ribs in red. Note that both left and right ribs lie above purported stomach remains in anteroventral portion of abdomen, thereby rejecting that material as preserved stomach content. (*b*) Detail of ingested right femur and left ilium in lower left. (*c*) The two purported cannibalistic *C. bauri* specimens prior to exhibition in 1950s. Neotype of *C. bauri*: (*b*) AMNH FR 7224 and (*c*) AMNH FR 7223. Abbreviations: ac, acetabulum; fe, femur; ip, ischial peduncle of ilium; pu, pubis; sc, scapula; sv, sacral vertebra.

concentrated near, and the smaller flat bones are oriented parallel to, the surface of the inferred stomach wall. Previous studies (Colbert 1989, 1995; Gay 2002) specifically highlighted the bones of this region as juvenile *Coelophysis*. We have identified well-preserved remains consisting of left and right proximal ends of femora, a left ilium and a sacral vertebra within the stomach cavity (figure 1). Comparative morphological analysis of this material reveals that these bones lack any synapomorphies of *Coelophysis*, Theropoda or even Dinosauria (figure 2). However, they are consistent with Crocodylomorpha. For instance, the left ilium bears a closed acetabulum; nearly all dinosaurs (including *Coelophysis*) possess an open acetabulum. The sacral vertebra shows no indications of fusion with surrounding vertebrae, has an anteroposteriorly short, dorsally expanded, neural spine, and a sacral rib articulating to the centre of the centrum—all characters consistent with crocodylomorphs, but not with *Coelophysis*. Additionally, the femora lack the typical dinosaurian offset femoral head, anterior trochanter and well-developed articular facet for the antitrochanter (Langer 2004); instead they exhibit proximal condylar folds (C. A. Brochu 1992, Unpublished Master's Thesis; figure 2). A proximal condylar fold is found only in crocodylomorph archosaurs, including *Hesperosuchus agilis* (figure 2), whose presence is well known from the Chinle Formation and the Ghost Ranch *Coelophysis* Quarry. Our results show that although stomach contents were remarkably preserved *in situ* in Ghost Ranch *Coelophysis*, no evidence for cannibalism exists.

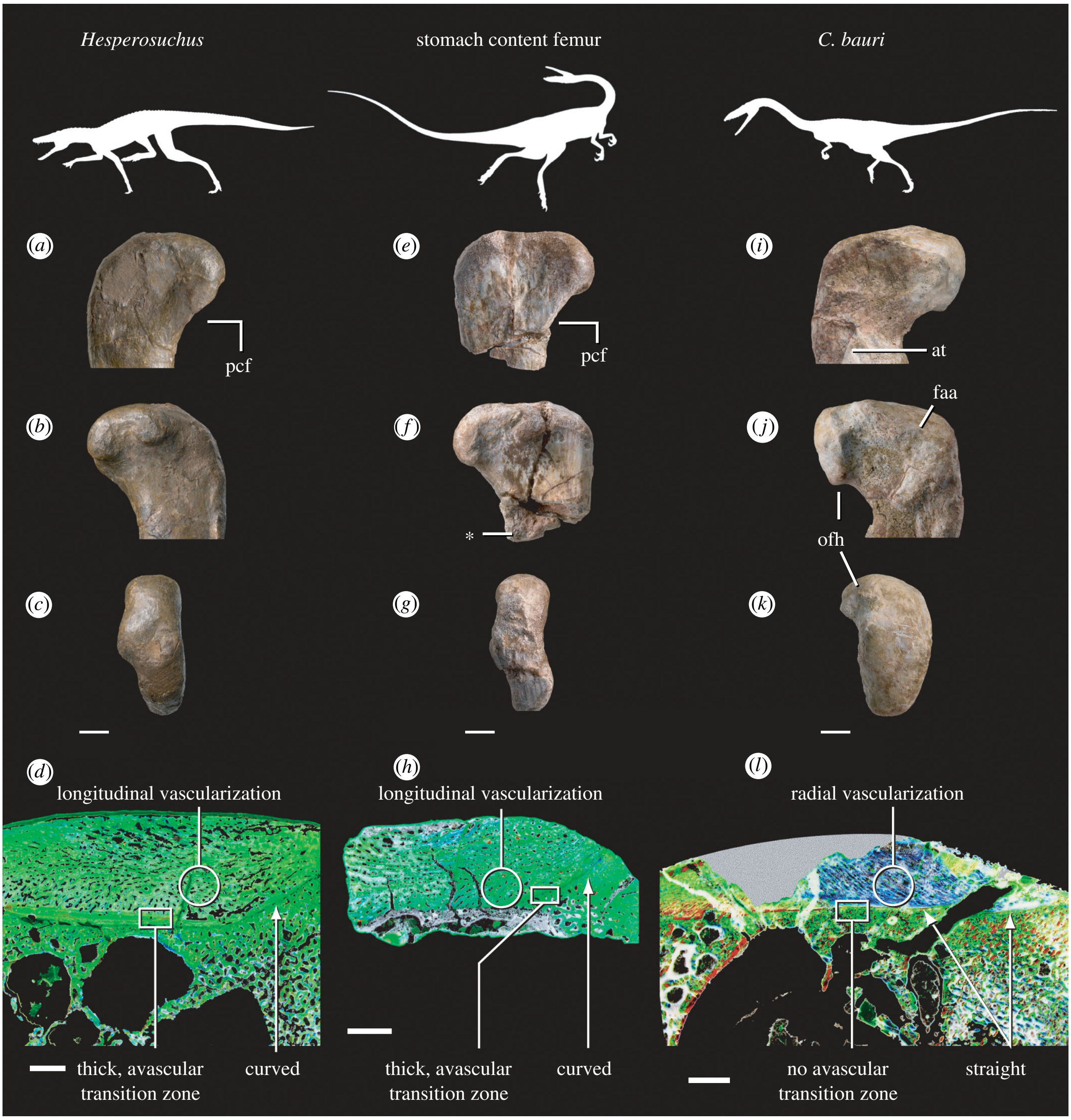

Figure 2. Comparative morphological and histological evidence illustrating Crocodylomorpha affinities of the *Coelophysis bauri* stomach contents. (*a–d*) *Hesperosuchus agilis* (AMNH FR 6758), right proximal femur in (*a*) lateral, (*b*) medial and (*c*) dorsal views, and (*d*) histological section from the medial metaphysis of cf. *Hesperosuchus* (GR 215; see electronic supplementary material). (*e–h*) Right proximal femur of stomach contents (AMNH FR 30616) in (*e*) lateral, (*f*) medial and (*g*) dorsal views, and (*h*) histological section from the medial metaphysis. (*i–l*) *Coelophysis bauri* (AMNH FR 30618), right proximal femur in (*i*) lateral, (*j*) medial and (*k*) dorsal views, and (*l*) histological section from the medial metaphysis from a juvenile *Coelophysis* (AMNH FR 30617). All histological specimens show compacted cancellous bone, indicative of incorporation of what was formerly the ends of the bones into the dense bone shafts later in development. Each was capped by a layer of primary fibrolamellar bone along a mediolateral front, attesting to the deposition of new bone atop of the former metaphyses. The presence of a concave, indistinct transition to the initially avascular primary bone and subsequent primary bone showing longitudinal or locally semi-radiating vascularization patterns indicates that the (*h*) stomach content specimen and (*d*) cf. *Hesperosuchus* possess nearly identical developmental histories. In contrast, (*l*) the transition zone in *Coelophysis* lacks an avascular zone, and is very thin and distinctive, indicating a complete cessation of bone deposition prior to the capping with primary periosteal bone. The transition zone is straight, unlike the concave pattern seen in cf. *Hesperosuchus* and the stomach content. Finally, the vascular canals in *Coelophysis* are relatively long and show pronounced, inclined radiating patterns. The histological patterning and developmental histories are consistent with the stomach contents' referral to Crocodylomorpha from the independent morphological character evidence. Institutional abbreviation: GR, Ruth Hall Museum of Paleontology at Ghost Ranch Conference Centre, Ghost Ranch, New Mexico. Femoral scale bars, 5 mm. Histology scale bars, 1 mm. Asterisk indicates site of histology sample. Abbreviations: at, anterior trochanter; faa, facies articularis antitrochanterica; pcf, proximal condylar fold; ofh, offset femoral head.

As an independent test of our hypothesis that AMNH FR 7224 consumed a crocodylomorph rather than a juvenile *Coelophysis*, we conducted comparative histological analyses between the purported cannibalized stomach contents, *Coelophysis*, and the most common Chinle Formation crocodylomorph—*Hesperosuchus* (see electronic supplementary material for taxonomic assignment). The metaphyses of the femur from the stomach content specimen and cf. *Hesperosuchus* show nearly identical histological patterning and structure and hence, attest to comparable developmental histories (figure 2). In the stomach content specimen and cf. *Hesperosuchus*, the transition zone to the primary bone is not distinct; instead it blends with the compacted cancellous bone. Furthermore, the initial primary bone that was deposited across the zone is avascular. Notably, the transition zones in both also show a pronounced concavity. The rest of the primary bone shows longitudinally or locally semi-radiating vascularization. In stark contrast, the transition zone of the dinosaur *Coelophysis* is very thin, and distinctive—like the structuring seen when lines of arrested growth form. This suggests that bone deposition completely stopped before the capping of primary bone began. The thick avascular zone seen in the stomach content and cf. *Hesperosuchus* is not present in *Coelophysis*. The transition zone is straight, unlike the concave pattern seen in the stomach content and cf. *Hesperosuchus* specimens. Finally, the vascular canals in *Coelophysis* are relatively long and show pronounced, inclined, radiating patterns—those stemming more medially incline laterally and those originating laterally incline medially.

Cannibalistic behaviour is very common among carnivorous animals (Polis 1981), and may be expected in non-avian dinosaurs. Then again, among living dinosaurs (birds) this behaviour is not prevalent, being most common in colonial nesting seabirds (Parsons 1971) and birds of prey (Ingram 1959). This brings into question just how prevalent this behaviour was among non-avian dinosaurs. The phylogenetic distribution of cases supposedly attesting to cannibalism suggests that it was prevalent throughout the Theropoda. This study shows that there is no compelling evidence for this behaviour in the famed *Coelophysis* AMNH 'cannibals'. What about the other cases? Recent reports of coprolites and cololites (internal intestinal casts), said to be preserved below the base of a *Coelophysis* tail (Rinehart *et al.* 2005) and to contain cannibalized manual elements, also cannot be considered as evidence for cannibalism in *Coelophysis* as the purported digested skeletal material is taxonomically uninformative.

Occurrences of cannibalism in other theropods are also problematic. Jacobsen (1998) reported tyrannosaur bite marks on the remains of tyrannosaurs from the Dinosaur Park Formation of Alberta and used these as evidence for cannibalism. However, given that there are at least two species of tyrannosaurs in the formation (*Daspletosaurus* and *Gorgosaurus*; Jacobsen 1998), cannibalism cannot be demonstrated sufficiently. This leaves just bite mark evidence and associated tooth crowns in the large theropod *Majungatholus atopus* (Rogers *et al.* 2003) as the only compelling evidence for cannibalism out of the hundreds of known Mesozoic theropod dinosaurs. On the basis of this evidence, cannibalism is not as prevalent as was once supposed in non-avian dinosaurs.

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