A densely feathered ornithomimid (Dinosauria: Theropoda) from the Upper Cretaceous Dinosaur Park Formation, Alberta, Canada

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**ABSTRACT**

A recently discovered articulated partial skeleton of *Ornithomimus* from the Upper Cretaceous Dinosaur Park Formation of Alberta, Canada is remarkable in the extent and quality of preservation of integumentary structures including feathers. It is the first ornithomimid to preserve a tail bearing extensive plumaceous feathers that are slightly more elongate in comparison to those present on the remainder of the body. However, the underside of the tail and the hind limb distal to the middle of the femur appear devoid of plumage. Overall, the plumage pattern in *Ornithomimus* is similar to that of *Struthio camelus* (ostrich) and other large palaeognaths, indicating a probable function in thermoregulation. The specimen also preserves the body outline around the legs, including a skin contour anterior to the femur, analogous to skin webs in extant birds. Whereas the knee web of birds bridges the knee to the abdomen, in *Ornithomimus* it spans from the mid-femoral shaft to the abdomen, and is herein referred to as an anterior femoral web. This is the first report of such soft tissue structures in non-avian theropods. It may indicate that the resting position of the femur was positioned more anteroventrally in ornithomimids than in most theropods, and in that sense may have been transitional to the situation in modern birds.

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1. Introduction

Feathered non-avian dinosaurs are best known from the Upper Jurassic and Lower Cretaceous of China, where they were first discovered in 1996 (Chen, Dong, & Zhen, 1998; Hu, Hou, Zhang, & Xu, 2009; Ji, Currie, Norell, & Ji, 1998; Li et al., 2012; Norell & Xu, 2005). More recently, these specimens have been augmented by discoveries from the Upper Jurassic of Germany (Chiappe & Göhlich, 2010; Rauhut, Foth, Tischlinger, & Norell, 2012) and the Upper Cretaceous of western North America (Zelenitsky et al., 2012). The latter includes three relatively complete specimens assigned to *Ornithomimus edmontonicus* from the Dinosaur Park and Horseshoe Canyon formations of Alberta, Canada. One juvenile and two adults each reveal feather impressions over parts of their respective bodies. The juvenile preserves feather traces over the neck, body, forelimb and hind limb, whereas the less complete adult retains a halo of feather traces around the neck, back, and upper forelimb. The other and more complete adult has oblique carbonaceous markings on the ulna and radius that are interpreted by Zelenitsky et al. (2012) as attachment traces for the calami of pennaceous feathers; these authors suggest that the forearm of *Ornithomimus* possessed a pennibrachium. Although there are no quill knobs present on TMP 1995.110.0001, this interpretation is compatible with both ulnar quill knobs in modern birds and comparable structures in the non-avian theropod *Velociraptor* (Turner, Makovicky, & Norell, 2007).

However, because feather preservation is discontinuous and varies considerably between each of the specimens considered by Zelenitsky et al. (2012), the full extent and character of plumage adorning *Ornithomimus* remains incompletely resolved. In this paper, a new specimen is described with exceptionally well-preserved integumentary structures consisting primarily of feathers and secondarily of skin traces. In addition to morphological and evolutionary implications, this specimen adds considerable insight concerning the probable function of feathers in ornithomimid dinosaurs. Because ornithomimids were common in the Late Cretaceous of Alberta (Cullen, Ryan, Schröder-Adams, Currie, &
Kobayashi, 2013; Currie, 2005; Longrich, 2008; Makovicky, Kobayashi, & Currie, 2004), this information is broadly relevant to understanding these diverse and remarkable ecosystems.

2. Materials and methods

The new ornithomimid specimen (UALVP 52531) was discovered in 2009 in the northeastern sector of Dinosaur Provincial Park (Fig. 1) from the lowermost portion of the Dinosaur Park Formation (Campanian; Eberth & Hamblin, 1993). The specimen was collected 3.5 m above the boundary between the Oldman and Dinosaur Park formations (Fig. 2), and was reposing on its left side in classic opisthotonic posture (i.e., death pose). Following removal of the jacketed specimen from the field, preparation of UALVP 52531 was conducted using hand-operated pneumatic tools and needles. Preservation of integumentary structures was revealed along planes of matrix fragmentation during initial preparation. Subsequently, detailed work surrounding bone and preserved integument was performed under magnification. Preparation of the skeleton was stopped in order to preserve as much of the integumentary structures as possible. Standard consolidants (cyanoacrylate and Vinac dissolved in acetone) were used to stabilize bone elements during removal of the matrix, but were not applied to integumentary structures in order to preserve delicate carbonaceous traces. Photographs were taken with a Canon 7D digital SLR camera and 50 mm macro lens, processed with Photoshop CS6 software, and were stitched together to produce large images. Line diagrams were created from tracings of original stitched images in Adobe Illustrator CS6 with line drawings using a Wacom Intuos 5 Touch tablet. All straight-line measurements were made with digital calipers and are accurate to ±0.01 mm; non-linear measurements were made with a fabric tape measure to the closest millimeter.

3. Results

3.1. General description and provisional identity of UALVP 52531

UALVP 52531 is preserved lying on its left side, the right side of the animal having been exposed in the field and partially destroyed by erosion. Although the skull and forelimbs were apparently lost to erosion, remaining elements include cervical vertebrae 3–6, the second dorsal to the 17th caudal vertebrae, the majority of the left costal elements, partial left scapula, left ilium, and left hind limb (Fig. 3). Of these remains, approximately 15% are surrounded by integumentary structures, allowing comparisons with previously described feathered Ornithomimus specimens that, together, produce a more complete reconstruction of plumage patterns in Late Cretaceous ornithomimids. The most common integumentary structures are unambiguous feathers comprising filaments that range from 25 to 87 mm in length and 0.2–0.5 mm in width, preserved as dark carbonaceous imprints surrounding specific portions of the skeleton (Fig. 4).

The femur of UALVP 52531 measures 480 mm in length whereas the tibia measures 520 mm, falling within the reported ranges for Ornithomimus edmontonicus (Table 1), but 13% and 12% longer than the same measurements from the complete adult specimen TMP 1995.110.0001 (Zelenitsky et al., 2012). This indicates UALVP 52531...
Fig. 2. Stratigraphic log and position of UALVP 52531 in the lowermost 5 m of the Dinosaur Park Formation.
Fig. 3. UALVP 52531 complete specimen. (a) Full view of articulated partial skeleton in opisthotonic death pose. (b) Line diagram of preserved material, illustrating exposed skeletal elements and inferred feathers, cartilage, body outline and skin. Abbreviations are as follow: ca, caudal vertebrae; cv, cervical vertebrae; f, femur; fl, fibula; mt IV, metatarsal IV; p, pelvic elements (ilium and sacrum); r, ribs; sc, scapula.
represents a large adult. Although the lack of skull and forelimb elements make a conclusive diagnosis difficult, given that most autapomorphies for *Ornithomimus*, involve the quadratojugal and metacarpal elements (Makovicky et al., 2004). However, the distal caudals of *Ornithomimus* are distinguishable from those of *Stuthiomimus* by the presence of a groove on the ventral face of the prezygapophyses (Kobayashi, Makovicky, & Currie, 2006). Preparation of caudals 16 and 17 revealed the presence of such grooves in UALVP 52531, allowing a positive identification of the specimen to *Ornithomimus*.

3.2. Integument of the neck and trunk

Cervical vertebrae in UALVP 53521 are preserved within loosely-consolidated, coarse-grained sandstone that is devoid of integument. However, distinct feathers are preserved along the dorsal vertebral series, where they have been compressed to adhere closely to skeletal elements (Fig. 5). In this case, these structures are preserved in well-consolidated, coarse-grained sandstone with extensive iron oxide cementing. Feathers around dorsal vertebrae 2–7 are compressed into a single layer that is separated from the

<table>
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<tr>
<th>Taxonomic designation</th>
<th>Specimen</th>
<th>Femur length (mm)</th>
<th>Tibia length (mm)</th>
<th>Femur/tibia ratio</th>
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<td>480</td>
<td>520</td>
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<td>TMP 95.110.1</td>
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<td>465</td>
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Fig. 4. Close-up of feather preservation in UALVP 52531. (a) Dense filaments above the dorsal vertebrae. (b, c) Examples of less-densely spaced but clearly branching plumage above the ilium.
Fig. 5. Dorsals 2–8 with ribs and partial left scapula of UALVP 52531. (a) Photograph showing a thin film of compressed integument overlying rib heads. The high iron content of the matrix has limited preparation of plumage in this region. (c) Line diagram illustrating the location of exposed plumage. Integument is densely arranged with anterio-posterior directional arrangement. Abbreviations are as follow: dtp, dorsal transverse processes; r, ribs; sc, scapula. Legend as for Fig. 3.
bone by a thin sheet of sediment <1 mm thick. Feathers are moderately well defined and have similar morphologies to those elsewhere on this specimen (Fig. 4). Integument is preserved over the entirety of the rib cage, although some areas were damaged during preparation. Because parts of ribs were exposed in the field, feathers that may have covered the flanks and belly were lost. However, feathers extend continuously to the eroded surface, indicating that plumage on the flanks extended at least halfway to the belly. This is consistent with observations from the juvenile specimen of Ornithomimus edmontonicus (TMP 2009.110.0001), and confirms that feathers probably extended ventrally to at least the gastralia, and are as densely arranged as those found elsewhere on the body.

3.3. Integument of the appendicular skeleton

Because the forelimbs of UALVP 52531 are absent, comparisons with other specimens from Alberta, in particular TMP 1995.110.0001 and TMP 2009.110.0001, are impossible. However, the preserved portion of the scapula is surrounded by a thin layer (~0.5 mm) of feathers (Fig. 5). Both the right ulna and radius of TMP 2009.110.0001 bear feathers, although none are apparent on the corresponding humerus. Feathers over the right forearm are relatively short, with a maximum length of 27.4 mm. The left forelimb of TMP 2009.110.0001 lies alongside the body and is also feathered, but the unguals are not visible because they are obscured by body plumage.

The sacral neural spines and ilia were the only pelvic elements exposed during preparation, although exposure of the right side of the animal is limited. A well-defined hard yellowish ovoid mass, 37 mm long and 12 mm wide, sheathes the top of the greater trochanter of the left femur and is interpreted as cartilage (Fig. 6). Feathers covering the left ilium are the best preserved on the entire specimen (Fig. 4). Most are preserved as dark brown to black carbonaceous traces within a fine-grained siltstone having a slight reddish iron oxide hue. A thin layer of highly compressed feathers is
also preserved along the dorsal half of the preacetabular process, where they closely adhere to the surface of the bone. Integument on the postacetabular process of the ilium is a well-defined, multiple layered mat with a thickness ranging from 4.5 to 11.9 mm. At their bases, these feathers are dorsoventrally oriented, but curve posterodorsally more distally. A small dorsoventrally oriented patch of feathers is preserved over the acetabulum and part of the femoral head (Fig. 6).

Remarkably, skin and corresponding body outlines are also apparent on this part of UALVP 52531, mainly as a light-colored halo surrounding portions of the skeleton (Fig. 6). Skin and feathers are visible ventral to the preacetabular process of the ilium, originating from the posterior ribs, then sharply curving ventrally to join the femur approximately half way down the shaft. Skin in this location is identified by a thin, slightly undulating, ferruginous layer with feathers preserved on the surface. The total length of this skin outline is approximately 175 mm anteroposteriorly along the curvature of the ventral margin. Feathers are also present posteriorly and on the lateral surface of the proximal half of the femur. The distal half of the femur and the remaining lower leg are devoid of feathers. Instead, portions of the hind limb of UALVP 52531 preserve a distinct gray-white skin outline (Fig. 6). This halo ranges from 12 mm from the skeleton on the anterior face of the metatarsals to 76 mm on the posterior edge of the proximal end of the femur.

3.4. Caudal integument

The matrix in which the caudal series is preserved changes significantly over the length of the tail (Fig. 7). As a consequence, integument preservation varies. The five proximal caudals are preserved within fine-grained mudstone with organic (plant) matter throughout. Here, detail of feather preservation is excellent. Caudals 6–8 are preserved within a mixture of sand and mud that obscures the definition of individual feather filaments. The remaining caudals (9–17) are preserved within sandstone with more extensive iron oxide cementation, which further compromises the quality of feather preservation.

Plumage preserved along the first six caudal vertebrae is of uniform length and begins at the level of the transverse processes. The feathers curve dorsoposteriorly and terminate 69–87 mm from individual caudal transverse processes, progressively shortening in length distally. At the transverse process of the sixth caudal, a well-defined dense clump of feathers folds over those on the neural spine (Fig. 7). This clump extends posterodorsally, terminating in splayed-out feathers that form a fan with the furthest point 112 mm from the transverse process of the ninth caudal. Integument located between caudal vertebrae 11 and 14 are visible only as a mat of filaments overlying one another. No traces of feathers are preserved beyond caudal 14, and no feathers are encountered ventral to the transverse processes of caudals one through nine. From caudal vertebrae 10–13, feather traces are found only up to 21 mm ventrally to the transverse processes.

4. Discussion

UALVP 52531 augments the understanding of integumentary structures in Ornithomimus considerably. It shows that plumage (or ptilosis) was distributed as a relatively uniform, even coating over most of the body, with the exceptions of the caudal ventrum and the hind limbs distal to the mid-femur, which were most likely devoid of feathers. It remains uncertain whether feathers covered the abdomen ventral to the gastralia. Additional specimens of Ornithomimus, in particular TMP 1995.110.0001 (Fig. 8), indicate that the forearm is the only part of the anatomy where the existence of pterylae (defined tracts of feathers) can be confirmed. Here, at least five pterylae tracts exist on the ulna, and at least three on the radius, restricted in both cases to the bone shafts (Fig. 8). The average width of these marks is 1.2 mm (Zelenitsky et al., 2012). The greatest width of individual feather filaments on the body of UALVP 52531 is 0.4 mm laterally (Fig. 4 b and c), and may represent the
equivalent of feather rachi. Given these attain a maximum length of ~87 mm on UALVP 52531, if a similar length to width ratio existed for the forearm feathers arranged in pterylae on TMP 1995.110.0001, then a length of 260 mm can be estimated, making the forearm feathers approximately three times longer than body feathers on *Ornithomimus*. The presence of forearm pterylae in Ornithomimosauria may also have important phylogenetic implications, given they have not yet been reported in Tyrannosauroidea, the well-studied sister group to Maniraptoriformes (i.e., Ornithomimosauria + Maniraptorida) (Holtz, 1994), for which several basal representatives are known to have been feathered (Xu et al., 2004, 2012). This indicates that forearm feather pterylae represent a possible synapomorphic character for Maniraptoriformes.

UALVP 52531 is furthermore the first ornithomimid reported with integumentary structures on the tail, given that no caudal series were reported for either TMP 2008.070.0001 or TMP 2009.110.0001. The elongate caudal feathers of UALVP 52531 are best preserved as a distinct clump ventral to the neural spines (Fig. 7). This indicates that feathers may have draped the tail lateroventrally, thus partially covering the ventral two-thirds of the tail that shows no sign of feather attachment, even in the region of otherwise outstanding preservation. In this model, the tail would have no bare skin exposed when the animal was at rest in a sitting or nesting position. Yet there is no evidence of elongated pennaceous or plumaceous structures associated with the tail of *Ornithomimus*, such as those of the basal oviraptorosaur Caupodipteryx (Ji et al., 1998). On the other hand, the pygostyle of Deinonychus suggests the possible existence of a fan of elongated caudal feathers in this atypical ornithomimosaur (Lee et al., 2014). Neither the pygostyle nor the presence of elongated caudal feathers are phylogenetically conservative characters, given their inconsistent occurrence between and among groups.

With respect to the non-feather integument of UALVP 52531, the preserved skin extending from the posterior ribs to the proximal half of the femur resembles the knee web of birds. Skin webs are located in areas of high skin flexion (Cooper & Harrison, 1994), and likely function as a way to increase mobility by allowing skin to stretch further at joints. The avian knee web is the fold of skin that extends from the ventrolateral portion of the body to the knee, most evident when the limb is extended posteriorly (Lucas & Stettenheim, 1972). However, in *Ornithomimus* the skin web attaches to the leg mid-femur and not more distally at the knee. Given this difference, coupled to the functional importance of skin webs and analogous membranes such as patagia, the structure evident in UALVP 52531 is referred to as the anterior femoral web in order to differentiate it from the avian knee web. This is the first report of this anatomical feature and one of the few reports of skin membrane preservation in dinosaurs (Xu et al., 2015), thus providing evidence of these structures in the basal maniraptoriformes, and increasing the understanding of dermal evolution in non-avian theropods and their close affinity to extant neornithines. The anterior femoral web of UALVP 52531 is preserved with the middle portion stretched dorsally into a tight arch (Fig. 6). This portion of the hind limb is also feathered in UALVP 52531. In the juvenile specimen TMP 2009.110.0001, ptiosis of the pelvic and femoral regions follow closely the contour of the thigh (Zelenitsky et al., 2012), which suggests the presence of the anterior femoral web in a second specimen. Thus, the distal extent of femoral ptiosis in UALVP 52531 is not an artefact of preservation, but rather an indication that feathers extended no further than halfway down the femur in *Ornithomimus*. This contrasts sharply other theropods including Anchiornis (Hu et al., 2009), Microraptor (Li et al., 2012), and Yutyrannus (Xu et al., 2012), which have either short filamentous or large pennaceous feathers on the distal parts of their hind limbs. The anterior femoral web in *Ornithomimus* indicates that neutral position of the femur may have been more anteroventral than most other non-avian theropods, suggesting a possible transitional state to that in modern birds.

Fig. 9. Reconstruction of *Ornithomimus* showing a plumage pattern that is consistent with both UALVP 52531 and previously described feathered specimens from Alberta (Zelenitsky et al., 2012), as well as with modern ratite birds, collectively suggesting a thermoregulatory role in all cases. Artwork: Julius Csotonyi.
Similarities between the body forms of ornithomimids and large-bodied palaeognaths have been recognized for at least a century (Osborn, 1917). With respect to Struthio camelus (ostrich), plumage of the neck is sparse but continuous, whereas feathers are completely absent below the femoral—tibiotarsal joint (Cho, Brown, & Anderson, 1984). In contrast, in birds such as Casuarius casuarius (cassowary) and Dromaius novaehollandiae (emu), plumage extends distally beyond the tibiotarsal—tarsometatarsal joint, but is highly variable on the neck. During periods of physiological heat stress, the maintenance of optimal body temperature is largely modulated by heat loss from feather-free skin surfaces, which range from 12% in Struthio to ~18% in Dromaius and Casuarius (Phillips & Sanborn, 1994). Through combinations of conductive (radiant) and convective (fanning, wind) processes, up to 40% of total heat loss from these animals occurs from regions of exposed skin, noting that they are endemic to warm climates such Australia and Africa. The bare hind limbs and absence of feathers on the ventral surface of the tail of Ornithomimus (UALVP 53521), coupled to a lightly-feathered neck (Zelenitsky et al., 2012), can be interpreted parsimoniously as having served the same thermoregulatory function as in large palaeognaths (Fig. 9).

5. Concluding remarks

In conclusion, while UALVP 52531 is not the first feathered ornithomimid dinosaur from the Late Cretaceous of western North America, the quality and extent of feather preservation in this specimen is unparalleled. As such, it provides a much stronger basis for interpreting the most likely function of feathers in non-avian theropods, and a much-refined perspective of the biology and ecology of ornithomimids.

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References


