

A Mummified Duck-Billed Dinosaur with a Soft-Tissue Cock's Comb

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Summary

Among living vertebrates, soft tissues are responsible for labile appendages (combs, wattles, proboscides) that are critical for activities ranging from locomotion to sexual display [1]. However, soft tissues rarely fossilize, and such soft-tissue appendages are unknown for many extinct taxa, including dinosaurs. Here we report a remarkable “mummified” specimen of the hadrosaurid dinosaur *Edmontosaurus regalis* from the latest Cretaceous Wapiti Formation, Alberta, Canada, that preserves a three-dimensional cranial crest (or “comb”) composed entirely of soft tissue. Previously, crest function has centered on the hypertrophied nasal passages of lambeosaurine hadrosaurids, which acted as resonance chambers during vocalization [2–4]. The fleshy comb in *Edmontosaurus* necessitates an alternative explanation most likely related to either social signaling or sexual selection [5–7]. This discovery provides the first view of bizarre, soft-tissue signaling structures in a dinosaur and provides additional evidence for social behavior. Crest evolution within Hadrosaurinae apparently culminated in the secondary loss of the bony crest at the terminal Cretaceous; however, the new specimen indicates that cranial ornamentation was in fact not lost but substituted in *Edmontosaurus* by a fleshy display structure. It also implies that visual display played a key role in the evolution of hadrosaurine crests and raises the possibility of similar soft-tissue structures among other dinosaurs.

Results

Locality and Age

The newly discovered specimen (UALVP [University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada] 53722) comes from the fluvial deposits of the Wapiti Formation exposed on the Red Willow River 75 km west of the city of Grande Prairie in west-central Alberta. Beds exposed at the site are typical of an active channel belt with recurrent crevasse splay, organic-rich overbank deposits, and minor bentonitic paleosols [8, 9]. Ar/Ar dating of an altered volcanic ash located approximately 2 m above the skeleton provided an age of 72.58 ± 0.09 million years, coeval with the Drumheller Member of the Horseshoe Canyon Formation of southern Alberta [10]. The Wapiti Formation represents a

Late Cretaceous high-latitude ecosystem, with an estimated paleolatitude of 65°N [11].

Description

UALVP 53722 is preserved in a single sandstone boulder in a characteristic “death pose” with the neck and skull tightly retracted over the back. The skeleton, exposed in right lateral view, consists of an articulated skull and four cervical and four dorsal vertebrae; however, parts of the skull, neck, and back are truncated at the edges of the block (Figure 1A). The skull is sheared transversely through the orbits and is missing much of the anterior portion, including the upper and lower jaws. The postorbital is inflated, with a deep fossa along its orbital rim (Figures 2D and 2E). The frontals are missing, but impressions of these elements in the surrounding sediments clearly show they were flat and extended laterally to participate in the dorsal rim of the orbit (Figures 2D and 2E). This combination of characters and latest Campanian age permit unambiguous assignment of UALVP 53722 to *Edmontosaurus regalis* [12]. The braincase is partly exposed, revealing the large, circular opening for the trigeminal nerve (or fifth cranial nerve). Posterior to this opening, the delicate stapes exits the cranial vault via the fenestra ovalis. It is oriented parallel to the skull roof and measures 25 mm long before becoming obscured by matrix medial to the quadrate. Computed tomographic (CT) scans were of insufficient detail to further elucidate its trajectory, and no indication of the external ear was visible on the integument preserved immediately posterior to the quadrate.

Integumentary traces over the neck and back form an unbroken sheet consisting of raised oval cluster areas of polygonal basement scales (sensu Bell [13]; Figure 1D). Cluster areas have been described as typical of *Edmontosaurus annectens* integument ([14]; P.R.B., unpublished data) but are also present on the tail of *Sauroplophus osborni* [13]. Cluster areas are dorsoventrally elongated and composed of large (up to 9 mm width) polygonal scales decreasing in diameter toward the periphery of the cluster. Cluster areas are largest in the midneck region (up to 8 cm in dorsoventral height), becoming smaller both anteriorly, as they approach the back of the skull, and posteriorly (3–4 cm high). The area between clusters consists of up to 2 cm wide bands of 1 mm diameter pebbly scales. Wrinkles between cluster areas show that the pebbly skin was more pliable than other parts of the integument. In contrast, cluster areas of larger scales are smooth and undistorted. In the middorsal region, cluster areas are absent and are replaced by a uniform basement of large (5–6 mm average width) polygonal scales. This transition occurs in line with the third preserved dorsal vertebra. Midline feature scales are altogether absent. Wrinkles in the skin are presumably a result of the head and neck having retracted over the back in death.

Skin is not preserved on the side of the face, but a conspicuous dome of integument sits atop the skull, spanning from the anterior limit of the orbit (where its margins become indistinct) to the posterior edge of the squamosal (Figure 1B). This integumentary crest reaches its maximum height (20 cm) above the quadrate and is 33 cm long anteroposteriorly. The crest is

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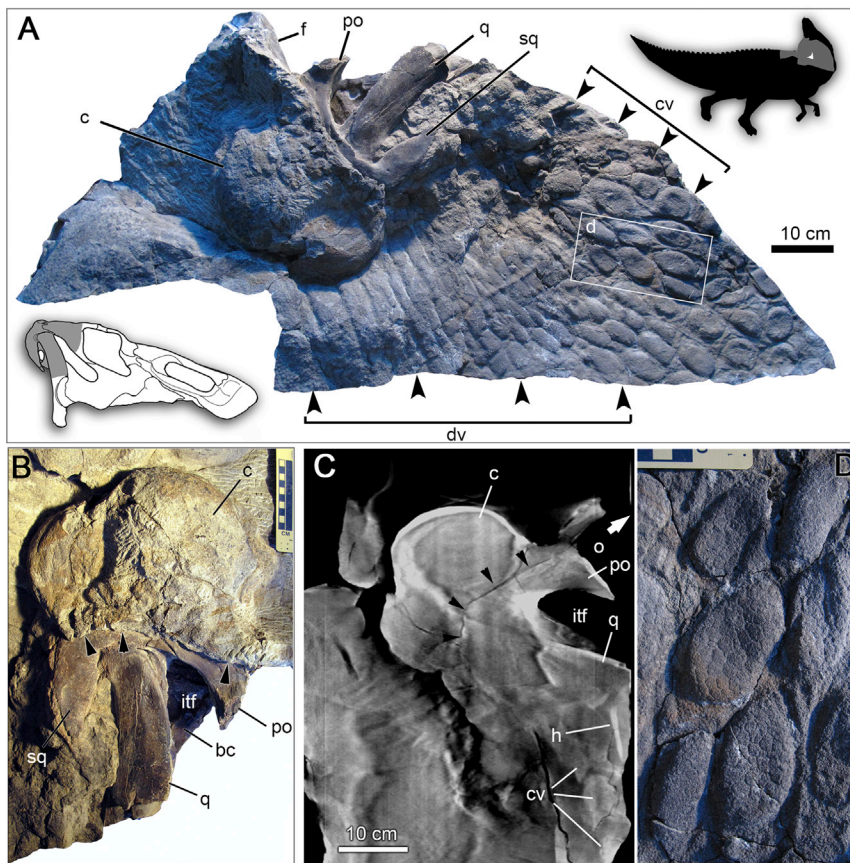


Figure 1. *Edmontosaurus regalis* with Preserved Soft-Tissue Structures

(A) Right lateral aspect of head and neck showing approximate orientation of the block on the body (gray part on inset silhouette) and inset of skull showing preserved elements (gray).

(B) Close-up of partial skull and comb structure. Skin overlapping the side of the skull is indicated by arrowheads. Anterior is to the right.

(C) X-ray of posterior part of skull and neck showing posterodorsal margin of the skull (arrowheads) and interior of comb. Image is rotated 45° anticlockwise relative to (C). Anterior is indicated by arrow.

(D) Close-up of neck scales demarcated in (A).

Scale bar increments in (B) and (D) represent 1 cm. Scale bar in (C) is approximate. bc, braincase; c, comb structure; cv, cervical vertebrae; dv, dorsal vertebrae; f, frontal (impression); h, hyoid; itf, infratemporal fenestra; o, orbit; po, postorbital; q, quadrate; sq, squamosal. Skull illustration is modified from Campione and Evans [12].

three-dimensionally preserved (Figure 2A–2C), spanning nearly the entire width of the skull; however, CT scans revealed no discernible internal structures. Skull bones do not invade the interior of the crest (Figure 1C), but the base of the crest overlaps the lateral edges of the postorbital and squamosal (Figure 1B), leaving no doubt as to its connection with the skull. The integument itself is undulating and partly wrinkled posteriorly, implying that the original structure was soft and supple. Integument on the crest consists of homogenous polygonal basement scales that measure 3–4 mm in diameter.

Discussion

The presence of soft-tissue crests in Hadrosauridae has historically been the subject of speculation [15, 16], and until now, direct evidence of their existence has been entirely lacking. Bony crests are present in many hadrosaurids, but no soft-tissue cranial crests have been previously described for any dinosaur. Soft-tissue crests have been reported in some pterosaurs, but these appear to have been smooth skinned (not scaly), keratinous, and/or bone supported [17, 18]. Phosphatized soft tissue associated with the head of the primitive ornithomimosaur *Pelecanimimus* has also been interpreted as a soft crest [19], although integumentary contours of these remains are imprecise, and the presence/absence of such a crest is equivocal.

We reject the possibility that the *E. regalis* crest is a taphonomic feature on several grounds: (1) the crest is bilaterally symmetrical and (2) is closely adhered to the lateral sides of the skull, and (3) evidence of displaced skin is absent from the remainder of the body. Despite the discovery of several

superbly preserved *Edmontosaurus* “mummies” [14, 20, 21], no evidence of a soft cranial crest has been previously identified. Two considerations may explain this apparent absence: (1) crests were present but were inadvertently lost during collection/preparation of the specimen, or (2) presence of the crest is a trait specific to *E. regalis*. Finally, it is of course possible that facial skin

was never in fact preserved on these specimens. In their eagerness to reveal the skull, paleontologists have historically overlooked possible skin impressions: perhaps the best-preserved specimen (AMNH [American Museum of Natural History, New York City, NY, USA] 5060) may have retained such a crest; however, the skull was exposed before skin impressions were identified on other parts of the body [14]. Another specimen reported by Manning et al. [21] may hold promise but as yet awaits complete preparation and description. Furthermore, all previously reported *Edmontosaurus* “mummies” are assignable to the Maastrichtian species *E. annectens*. The present specimen is identifiable as *E. regalis*, and therefore the presence of a crest may be an autapomorphy of that taxon. Additional species-specific differences between *E. annectens* and *E. regalis* are seen in the architecture of the integument elsewhere on the body; specifically the disposition of raised, oval cluster areas in *E. regalis*. In contrast, cluster areas in *E. annectens* (including anatomically equivalent regions of the neck and back) do not form discrete raised areas and are separated from one another by greater expanses of pebbly basement scales (“ground tubercles” of Osborn [14]). However, with a limited sample size, the possibility that these differences arise—or are in some way exaggerated—from sexual or some other taphonomic effect cannot be entirely discounted.

Interpretation of the evolution of hadrosaurine cranial crests is hampered by widespread inconsistencies between phylogenetic tree topologies [22–25]. At this time, we cannot comment definitively on the evolution of soft-tissue crests in Hadrosauroidae, although three alternative hypotheses may be presented: (1) fleshy crests evolved in the ancestor of

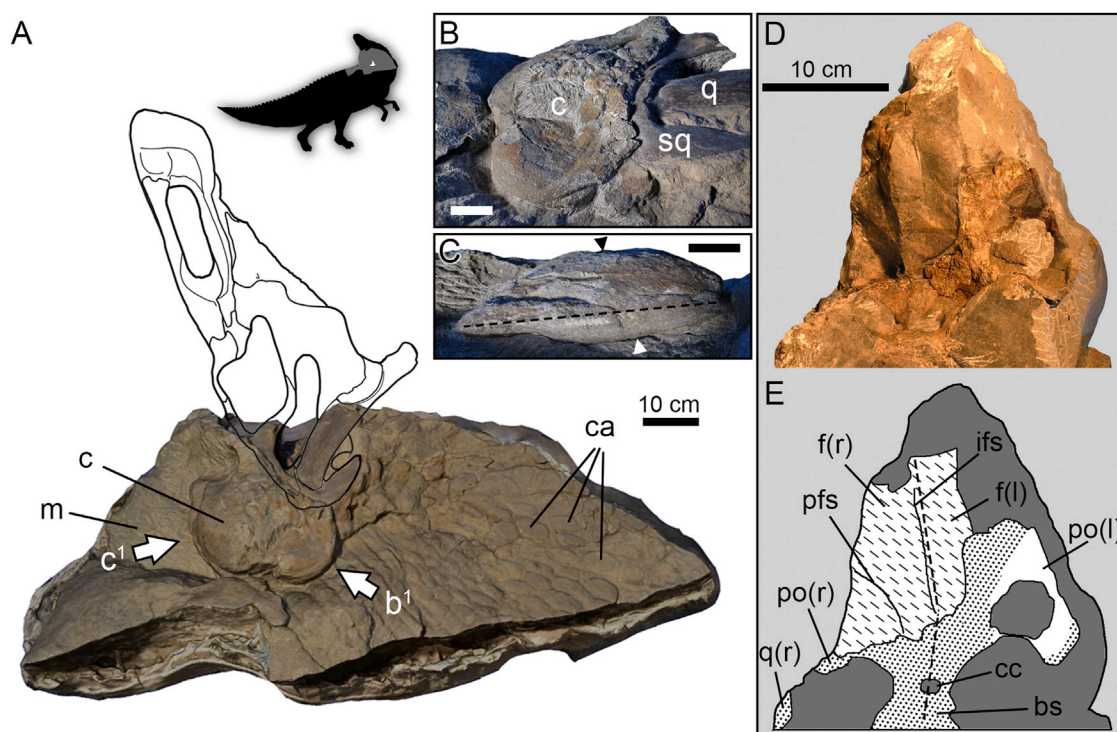


Figure 2. “Mummified” *Edmontosaurus regalis*

(A) Three-dimensional photographic rendering with skull superimposed. Orientation of block is indicated by gray portion on inset silhouette. Depth and three-dimensional “bulk” of the soft-tissue comb and surrounding epidermal structures are clearly visible. (B and C) Posterolateral (B) and anterior (C) views of comb structure. Direction of views in (B) and (C) is shown by white arrows b^1 and c^1 , respectively, in (A). Arrowheads indicate lateral edges of the crest; midline is shown by the dashed line. Scale bars in (B) and (C) represent 4 cm. (D) Anteroventral view of partial skull and braincase sheared in frontal section. Anterior is up. (E) Interpretive illustration of (D). Stippling indicates broken bone surface, and impressions of the skull roof on the surrounding matrix are shown by dashed region. Heavy dashed line indicates the approximate midline of the skull. All other areas of matrix are shown in dark gray. Note that part of the postorbital “pocket” is filled by matrix. bs, basisphenoid; c, comb structure; ca, cluster areas; cc, cerebral cavity; f, frontal; ifs, interfrontal suture; m, matrix, pfs, postorbital-frontal suture; po, postorbital; q, quadrate. Skull illustration is modified from Campione and Evans [12].

hadrosaurids, or earlier, in which case it is plesiomorphic for Hadrosauridae; (2) it evolved in the ancestor of the “flat-headed” clade comprising *Edmontosaurus*, *Kerberosaurus*, and *Kundurosaurus*, or (3) a soft-tissue crest is autapomorphic for *Edmontosaurus* or possibly *E. regalis*. Despite disagreement between phylogenies, it is clear that the absence of a bony crest is plesiomorphic for Hadrosauroidae and that crests appeared in the earliest known and most primitive lambeosaurines during the Santonian [26, 27] as well as in at least one closely related nonhadrosaurid hadrosauroid (*Lophorhynchon*). Within Hadrosaurinae, the oldest member of that group (*Acristavus*) lacked cranial ornamentation, although bony crests later evolved in closely related brachylophosaurines (*Maiaasaura* and *Brachylophosaurus*; sensu Gates et al. [24]). The discovery of a fleshy crest in *Edmontosaurus regalis* reveals that some later hadrosaurines did not in fact lose their ornamentation but evolved an alternative solution to the bony crests that were widespread within the clade. Alternatively, fleshy crests may have appeared earlier in hadrosauroid evolution and were simply retained in *E. regalis* following the loss of a bony display structure. Based on the recent detailed analysis by Godefroit et al. [25], a clade of “flat-headed” hadrosaurines (*Edmontosaurus* plus the Russian genera *Kerberosaurus* and *Kundurosaurus*) appeared in the latest Campanian-Maastrichtian (Figure 3). As some of the last surviving hadrosaurines, this clade indicates an apparent trend

toward the loss of bony ornamentation among Hadrosaurinae at this time. However, the skull of *Edmontosaurus* bears no osteological “stamp” belying the presence of a fleshy crest that could be used to identify the presence of similar crests on other taxa. Conversely, the closely related “saurolophins” (*Prosaurolophus* and *Saurolophus*) do bear conspicuous bony crests and structures consistent with the presence of soft-tissue elaborations of the crest. *Prosaurolophus* and *Saurolophus* both present a circumnarial depression that extends posteriorly onto the nasal crest and terminates in an excavation or “pocket” at the distal end of the crest [28, 29]. The circumnarial depression has been postulated by numerous authors to be occupied by various soft-tissue structures ranging from inflatable nasal sacs and cartilaginous nasal capsules to glands [16, 30, 31]. However, the fleshy crest of *E. regalis* is in no way associated with the circumnarial depression; therefore, any soft-tissue structure—real or inferred—associated with the saurolophin crest is not homologous with that seen in *E. regalis*. Finally, the fact that unusual soft-tissue structures may be present without any clear osteological correlate (as in the case of *E. regalis*) raises the possibility that fleshy crests, wattles, and other structures existed in disparate clades not necessarily restricted to Hadrosauridae. Perhaps most obviously, the cranial crests and ornamentation found on many theropods (see Smith et al. [32] for a summary of crested theropods) may have supported more

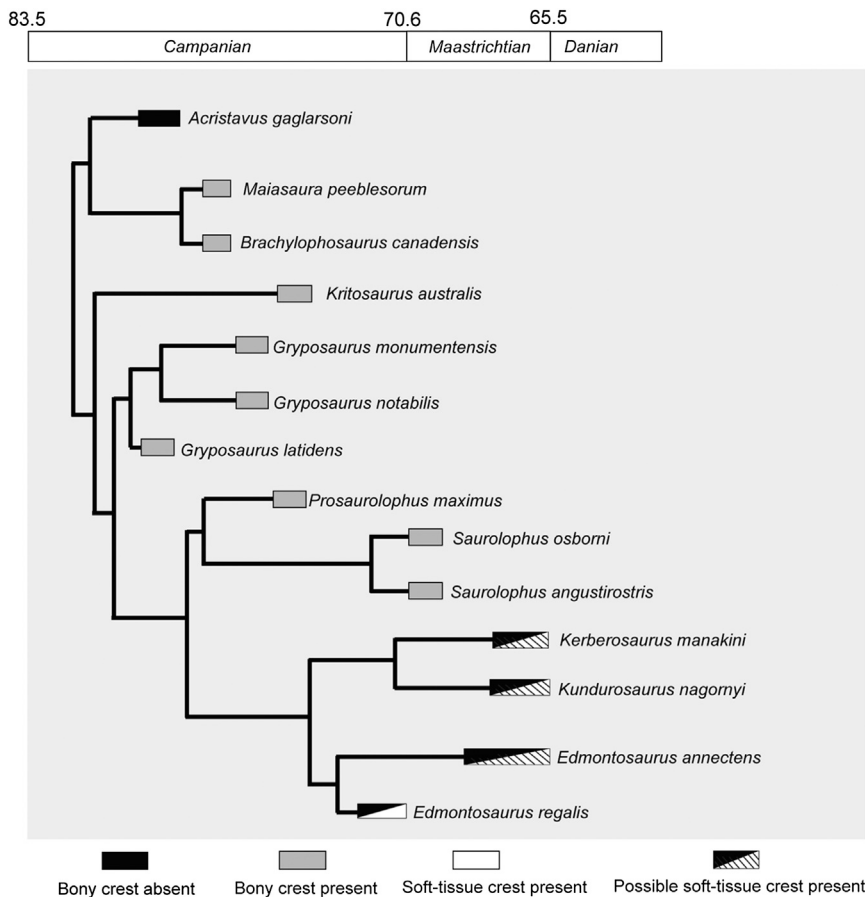


Figure 3. Time-Calibrated Phylogeny of Hadrosaurinae Showing Distribution of Crests
Cladogram based on Gates et al. [24] and Godefroit et al. [25].

the total height of the quadrate), the resulting logarithmic equation ($y = 0.9391x + 0.5541$ [$r^2 = 0.7142$]) indicates a skull length of approximately 100 cm for UALVP 53722. This value is close to the upper observed limit for skull length in that taxon (the largest specimen measures 106 cm long [12]). Therefore, the presence of a crest in a large, ostensibly somatically mature individual [35] suggests that the comb was close or had fully developed.

With the exception of sexual display, there are no other documented examples of head crests used for intra-specific communication or species recognition among extant or extinct taxa [5–7]. Although soft-tissue cranial ornaments are found in a variety of modern diapsids (e.g., dewlaps in *Anolis*; throat wattles in *Casuaris*), the fleshy, middorsal combs of extant avians provide the best analogy for the crest in *E. regalis*. In avian terminology, a comb refers to an upright, flexible integumentary outgrowth on the top of the head [1]. Single, middorsal combs are

flamboyant soft-tissue crests, which would have greatly enhanced their visual appeal.

Explanations concerning hadrosaurid crest function have included visual display, olfaction, thermoregulation, and vocalization [2–4, 15, 16]. However, most of these hypotheses are based on the hypertrophied nasal passages that invade the bony crests of lambeosaurine hadrosaurids. The crest observed in *E. regalis* differs considerably from those of all other crested hadrosaurids in its absence of osseous support. In addition, given the probable location of the nasal capsule within the bony nasal vestibule [33, 34], it is unlikely that the nasal passages occupied any part of the crest in *E. regalis*, thereby negating any connection to olfaction or vocalization. A soft crest would have been impractical for defense or intra-specific combat and would have conferred no mechanical advantage to the skull. Similarly, the relatively small size of the crest could not have stored enough fat to serve as an energy reserve for a full-grown, eight-ton (N.E. Campione, personal communication) *Edmontosaurus*. The function of a hadrosaurine soft crest therefore requires an alternative explanation, most likely related to either social signaling or sexual selection. Unfortunately, no long bones were found with the skeleton, so it was not possible to directly assess the age of the individual. To approximate the skull length and hence the relative age of UALVP 53722, a bivariate analysis of six *E. regalis* skulls was produced from the data set of Campione and Evans [12] comparing quadrate height to skull length. Assuming a quadrate height of 40 cm for UALVP 53722 (the upper part of the quadrate from the dorsal margin of the quadrate to the jugal notch to the quadrate head is roughly equivalent to half

present in a variety of modern birds [1], including domestic and jungle fowl (*Gallus* spp.), some brush turkeys (*Aepyodius arfakianus*, *A. bruijnii*), comb-crested Jacanas (*Irediparra gallinace*), and male Andean condors (*Vultur gryphus*). Avian combs are secondary sexual structures—acquired traits not associated with the reproductive system that confer an advantage over potential rivals during courtship and mating—used in female mate selection or male-male competition, where size and color (due to the highly vascularized superficial dermis and presence of carotenoid pigments [1, 36]) of a comb serve as visual cues that signal the relative health or fertility of an individual [36, 37]. Furthermore, combs may be present in both sexes of the species, so presence/absence of the comb in *Edmontosaurus* cannot be used in isolation as a proxy for sex.

The morphological similarity between the combs of *E. regalis* and modern avians, as well as their relatively close phylogenetic affinity—in combination with the aforementioned reasonings—suggest that the hadrosaurine comb played a major functional role in visual (presumably sexual) signaling (Figure 4). Such clear visual signaling structures reveal that hadrosaurids were highly visual animals, which is corroborated by various lines of evidence suggesting a high degree of visual acuity in these animals [16, 33, 38]. Furthermore, the soft-tissue crest in *Edmontosaurus* represents an unprecedented visual signaling device among dinosaurs that further illustrates the necessity of visual signals among ancestral “noncrested” forms: although auditory signaling has been posited as the main evolutionary driver in the development of lambeosaurine crests [16], evolution of the solid hadrosaurine crest (both



Figure 4. Life Reconstruction of *Edmontosaurus regalis* Showing the Soft-Tissue Comb Structure

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osseous and soft-tissue crests) clearly took a different trajectory that was most likely driven by the visual appeal of the crest.

Experimental Procedures

X-ray computed tomography (CT) scans of the specimen were acquired at the Alberta Innovates-Technology Futures facility (Edmonton, Alberta, Canada) using a Toshiba 64-slice helical CT scanner and visualized in the software program Mimics v14.01 (Materialise). Three-dimensional rendering and textured .obj files of UALVP 53722 were obtained using a Nikon D3100 camera and visualized using Agisoft PhotoScan and Meshlab softwares at the Museo Geologico Giovanni Capellini (Bologna). Use of the term Hadrosauridae and its constituent subfamilies Hadrosaurinae and Lambeosaurinae herein follow the traditional definitions of Horner et al. [15].

Accession Numbers

UALVP 53722 is permanently deposited at the University of Alberta, Edmonton, Alberta, Canada.

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