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Description of natal down of the ostrich (Struthio camelus) and comparison with common guail (Coturnix coturnix): Developmental and evolutionary implications

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Abstract

Natal down is a feather stage that differs in both form and function from the definitive feathers of adult birds. It has a simpler structure that has been speculated to be similar to the body coverings of non-avian dinosaurs. However, inference of the evolution of natal down has been limited by our understanding of its structural variation in extant birds. Most descriptive work has focused on neognathous birds, limiting our knowledge of the full diversity of feathers in extant taxa. Here, we describe the natal down of a post-hatch ostrich (Struthio camelus) and compare it to that of a post-hatch quail (Coturnix coturnix). We confirm the presence of featherless spaces (apteria) in S. camelus and the lack of barbules on the tips of natal down in both species. We also find differences between dorsal and ventral natal down structures, such as barbule density in S. camelus and the extent of the bare portion of the barb in both species. Surprisingly, we do not find that the neoptiles of either species follow the ideal morphologies for increasing insulation. Finally, we hypothesize that the different barb types present in S. camelus natal down result from a large addition of new barb ridges during development, which is not known except in feathers with a rachis. These results have implications for our understanding of how structure informs function and development in understudied feather types, such as those shared by non-avian dinosaurs.

KEYWORDS

birds, dinosaurs, down feathers, feathers, juvenile, Palaeognathae

INTRODUCTION 1

Feathers vary across ontogeny and among avian species. This variation can be influenced by several life-history constraints, such as insulation, flight, camouflage, or sexual displays (Lucas & Stettenheim, 1972; Prum, 1999; Stettenheim, 2000). Despite investigation of extant feather structure for well over 100 years (e.g., D'Alba et al., 2017; Duerden, 1922; Lefèvre et al., 2020; Michener & Michener, 1938; Nitzsch, 1867; Pycraft, 1900; Wilde, 2004), many aspects of feather diversity and function remain elusive to this day. This is partially due to a preferential focus on songbirds (Passeriformes), fowl (Galloanserae), and penguins (Sphenisciformes), many of which have been studied

extensively (e.g., Broggi et al., 2011; Butler et al., 2008; Chen et al., 2016; Clench, 1970; Dawson et al., 1999; Dove & Agreda, 2007; Fuller, 2015; Soliman, 2020; Taylor, 1986; Walsberg, 1988; Wilde, 2004; Williams et al., 2015). Another bias is the focus on adult specimens, which limits our understanding of feather variation throughout ontogeny. Both biases prevent us from understanding the full variety and potential use of feathers in extant as well as extinct taxa, many of which are described as exhibiting unusual feather morphologies outside the range of living birds (e.g., Carroll et al., 2019; Mayr et al., 2002; Saitta et al., 2017; Xu, 2020; Xu et al., 2009). Without a better understanding of feather diversity in extant birds, hypotheses concerning form, function, and evolution of such structures among Dinosauria remains limited.

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Palaeognathae, including flightless ratites and volant tinamous, with Neognathae comprise the most basal split of extant birds (e.g., Clarke et al., 2005; Cracraft, 1986; Jarvis et al., 2014; Livezey & Zusi, 2007; Yonezawa et al., 2017). Extant palaeognathous birds have feathers that are known to differ substantially from typical neognathous feathers (Bertelli et al., 2002; Chandler, 1916; Huxley, 1867; Lucas & Stettenheim, 1972; Nitzsch, 1867; Pycraft, 1900). For example, a typical adult neognath body contour feather has a pennaceous region distally and a plumulaceous region proximally and usually has a smaller afterfeather which is entirely plumulaceous (Lucas & Stettenheim, 1972). Palaeognath contour feathers, however, can vary from the bristly, twin contour feathers of emus and cassowaries to the distally fused barbules of tinamou feathers (Beddard, 1898; Chandler, 1916; Huxley, 1867; Kummrow, 2015; Lucas & Stettenheim, 1972; Pycraft, 1900). In fact, palaeognath feathers are so different from neognath feathers that many of them do not fit into the five major types of feathers outlined by Lucas and Stettenheim (1972): ratites are described as lacking down but clearly do not have pennaceous contour feathers (Bertelli et al., 2002; Chandler, 1916; Chernova & Fadeeva, 2009; DeMay, 1940; Huxley, 1867; Kummrow, 2015; Lucas & Stettenheim, 1972; McGowan, 1989; Pycraft, 1900). Thus, according to these definitions, ratite feathers are entirely plumulaceous but are not down feathers or semiplumes (though see Brush, 2000; Nitzsch, 1867). Palaeognaths may have such distinct feather types from neognaths due in part to their long separate and complex evolutionary history. Extant palaeognathous species are thought to represent three to six independent losses of flight within the clade (Harshman et al., 2008; Mitchell et al., 2014; Phillips et al., 2010; Sackton et al., 2019); this relaxation on selection for flight likely allowed for greater feather variation (Longrich et al., 2020; McGowan, 1989).

Feather morphologies that do not fit easily into categories described from neognaths have also been reported in outgroups of Aves such as pterosaurs, ornithischians, and non-avian theropods (Perrichot et al., 2008; Wang et al., 2020; Xu, 2020; Yang et al., 2019) but critically assessing the relationships among these feather types and their evolutionary implications requires a fuller understanding of extant variation in morphology and function. These unusual morphotypes include monofilamentous structures which resemble bristles or fur, branched structures that are both open- and closedvane, ribbon-like structures, scale-like structures with protruding filaments, brush-like structures, branched structures without a standard rachis, and vaned feathers with an unusually wide rachis (Chen et al., 1998; Mayr et al., 2002; Perrichot et al., 2008; Qiang et al., 1998; Rauhut et al., 2012; Wang et al., 2020; Xing et al., 2020; Xu, 2020; Xu et al., 1999, 2000; Yang et al., 2019; Zhang et al., 2006; Zheng et al., 2009). Such morphotypes are sometimes described as dissimilar to those in extant birds, which raises questions about their diversity and the evolution of feathers. It is possible that some of these do represent extant feather types that were distorted in the fossilization process (Foth, 2012; Prum, 2010; Zhao et al., 2020) and, therefore, that more extant feather morphologies could be present in extinct dinosaurs. However, if this is not the case and the

fossils represent distinct feather types, finding an extant structure to compare in the inference of non-avian dinosaur biology would be difficult given what we know from adult neognaths alone. Feather morphology data from palaeognath species and ontogenetic stages may fill some of the gaps in our knowledge and provide better comparative data for making sense of these unusual fossil morphotypes.

Despite their seamless appearance, avian plumages are not continuous and in fact form patches, or "tracts", called pterylae throughout the body (Nitzsch, 1867). The sizes of pterylae, the empty spaces (apteria), and the densities of the feathers within them are known to differ between species (Lucas & Stettenheim, 1972; Nitzsch, 1867). Clench (1970), for example, noted that pterylae patterns differed based on the climate of the species ranges, with each species having a different way of reacting to its environment. Others have noticed a trend in precocial and altricial species where increasingly altricial birds have increasingly larger apteria, which they say could be related to thermoregulation, weight reduction, or movement (Chen et al., 2019). Ostriches (Struthio camelus) have often been discussed as lacking pterylae (Allen, 1925; DeMay, 1940; Graveley et al., 2020; Leeson & Walsh, 2004; Lucas & Stettenheim, 1972), though other studies have noted that this is incorrect, as ostriches are known to have apteria when young and as adults (Clench, 1970; Cooper, 2001; Duerden, 1912; Pycraft, 1900; Stettenheim, 1972; C.A.U. pers. observation). Many extinct dinosaurs were closer in size to adult flightless palaeognaths and, therefore, may have been similarly affected by the greater heat retention of their larger body masses (Meiri & Dayan, 2003; van der Reest et al., 2016). Thus, a better understanding of feather distribution and apteria shape and size in these palaeognaths could be important for informing a possible functional model for reconstructing non-avian dinosaur biology, behavior, and energy needs.

Natal down (also called neoptiles; Figure 1b) can differ substantially from adult down (Chandler, 1916; Lucas & Stettenheim, 1972; Figure 1a). These feathers often lack a substantial rachis, as well as the characteristic nodes of the species that are present in adult down, and distinctions between proximal and distal barbules (Brush, 2000; Chandler, 1916; Foth, 2011; Lucas & Stettenheim, 1972). Like adult down, natal down is known to differ in morphology across species (Chandler, 1916; Foth, 2011; Lucas & Stettenheim, 1972) and is assumed to ensure thermoregulation in the young chick via insulation and air trapping (Ingram, 1920; Schaub, 1912; Starck & Ricklefs, 1998; Taylor, 1986). However, some studies found natal down to have additional functions related to crypsis, mimicry, and parental signaling (Ingram, 1920; Krebs & Putland, 2004; Linsdale, 1936; Londoño et al., 2015; Lyon et al., 1994; Oatley, 1982). In some cases, these other functions and selective regimes can lead to a reduction in traits considered typical to down feathers (e.g., Lyon et al., 1994). Most studies of natal down have detailed morphology in a single taxon. However, Foth (2011) compared natal down structure across a broad sample of birds with a focus on estimating ancestral traits of these feathers.

Foth (2011) identified three possible structural forms of natal down feathers: natal down with a substantial rachis in many galloanserines and palaeognaths; natal down with a reduced rachis, but an obvious central structure made of one or more barbs found



FIGURE 1 Simplified illustrations of down feathers showing the organization of anatomical structures mentioned in the text. (a), typical adult down feather with a rachis present; (b), natal down feather lacking a central rachis and with barbules restricted to only part of the barb ramus. Modified drawings of *Gallus gallus* from Lucas and Stettenheim (1972).

in S. camelus and Rhea americana; and natal down that lacked a rachis entirely, found in the remaining 30 neognath species with natal down studied, including the common quail Coturnix coturnix. An ancestral state reconstruction yielded avian natal down with a substantial rachis as present in the crown avian ancestor that was subsequently lost or reduced in Neognathae (Foth, 2011). The main difference Foth (2011) found between S. camelus and the C. coturnix natal down feathers described by Clark Jr. (1964) was that S. camelus has bilateral symmetry, and an occasional rachis, whereas C. coturnix feathers, are radially symmetric and always lack a rachis. They assessed calamus wall thickness and the presence of medullary cells in S. camelus and hypothesized these to be similar in C. coturnix based on an ancestral state reconstruction (Foth, 2011). Although this study valuably describes natal down rachis and calamus structure in detail as well as mentioning variation in size and density in feathering, Foth (2011) did not focus on barb or barbule proportions and morphology or assess whether there were significant differences in natal down characteristics in distinct body regions.

Here, to further our understanding of natal down plumage, we qualitatively and quantitatively analyze natal down feather structure and distribution in ostrich (*S. camelus*) and quail (*C. coturnix*). Because both species have different juvenile and adult body sizes, rates of growth, and evolutionary histories, we expect there to be more differences than similarities in their natal feather structures. The results of this investigation add to our knowledge of feather variation and give hints about feather development in birds, which may provide new insights into the understanding of dinosaurian integument in general.

2 | METHODS

2.1 | Specimens and feather sampling

The quail and ostrich specimens used in this study were naturally deceased animals from a farm in Valley Mills, Texas and from a private donor in the Austin, TX area. They were donated to the Vertebrate Paleontology Laboratory as part of the Texas Memorial Museum (TMM) at the University of Texas at Austin. No animals were killed for the purpose of this study. *Struthio camelus* feathers were collected from a 2-day old chick (TMM M-14775), and *C. coturnix* feathers were taken from a chick one to 2 days old (TMM M-15122). Feathers from *S. camelus* were plucked in a 2 cm² region from the left ventral side horizontal to the stifle—the "ventral patch"—and dorsal to the right scapula—the "dorsal patch" (Figure 2). Additional square patches were plucked from the dorsal and ventral sides of the proximal neck region, the dorsum of the head, the jugulum, and the proximal hindlimb dorsal to the femoral head in *S. camelus* and were included in qualitative descriptive work but were not analyzed statistically. Feathers from *C. coturnix* were plucked from sections of pterylae approximately 2 cm² from both the ventral and dorsal regions, close to the midline (Figure 2).

Apteria were documented and avoided for sampling, though they bounded both sampled patches in *S. camelus*.

2.2 | Images and data collection

All feathers taken from *S. camelus* dorsal and ventral patches were first examined without magnification for general morphology and color patterns. We noted the variation in barb forms and their frequency within the feather, color pattern within a feather and a given barb, and general feather shape. Additional qualitative notes such as nodal presence/absence and barbule orientation were made with the use of a Leica EZ4 D stereo microscope.

Four ventral and four dorsal feathers from each the ostrich and quail were selected for detailed measurements using the same microscope. An additional 5 ventral and 5 dorsal ostrich feathers as well as 9 ventral and 8 dorsal quail feathers were measured for barb density and barb lengths.

Images of feathers were taken with the Leica EZ4 D microscope connected to a computer using LAS EZ version 1.6.0 software. Photos of both the feathers and the plucked regions were analyzed using Fiji version 1.51s (Schindelin et al., 2012). Preliminary testing of image capture methods revealed a significant difference in measurement data between images taken with, and without a compressive surface to flatten



FIGURE 2 Plucked Coturnix coturnix (a, b) and Struthio camelus (c, d) dorsal (a, c,) and ventral (b, d) pterylae showing follicle density and organization. Silhouettes show the locations of the patches on the specimen. All scale bars are 1 cm.

the barbs, so all microscope images that were analyzed were taken with a clear, plastic Petri dish resting on top of the feather to reduce this variation. Photos of both the plucked areas of the specimens and individual ostrich feathers were taken with an iPhone 7 digital camera.

1010

Measurements taken from patches included the area of the plucked region in cm², the number of follicles, and the distance between follicles in mm (Figure 3a,b). Measurements of individual feathers included the number of barbs; lengths of barbs; lengths of barbule-less portions of barbs; lengths of barbules from the basal region, the middle region, and the tip region of barbs; and density of barbules from these same barb regions (Table S1; Figure 3c,d). All length measurements were taken in mm and the barbule density measurements in barbules/mm.

Due to the characteristic barbule-less tips of barbs in natal downs (Lucas & Stettenheim, 1972), the length of the portion of the barb which contained barbules (termed "vanuled length") was calculated, and all statistical analyses involving barb length were rerun with vanuled length as well. Barb and vanuled lengths used in the barb length/follicle distance ratio calculation were limited to barbs on the outermost edges of the feathers in the photo, and the ratio was measured from either side. Finally, barb aspect ratio was calculated by adding the two longest barbules of a barb (together constituting the "barb diameter") and dividing this by barb or vanuled length.

Apteria were observed in both specimens; their distribution and size were checked against published descriptions in the literature. An estimate of relative apteria percentage over the whole body was measured in Fiji using published diagrams of juvenile *S. camelus* (Duerden, 1912) and adult *C. coturnix* (Lucas & Stettenheim, 1972) feather tracts. A *C. coturnix* chick could not be used as no diagram of

juvenile *C. coturnix* pterylae could be found in the literature. As neither of these diagrams had scale bars, apteria size was calculated as a percentage out of total skin area visible in the diagram, excluding the head and any body part more distal than the distal end of the tibiotarsus (Figure 4).

2.3 | Statistical analyses

All statistical analyses were performed in R version 4.0.4 (R Core Team, 2021). Analysis of variance (ANOVAs) and Student's *t*-tests were the primary tests used when looking for significant differences between barb regions, sampling region on the body, and species. Normality assumptions were checked using the Shapiro–Wilk normality test and the non-parametric Mann–Whitney *U* test was run instead of the *t*-test when normality was not met (e.g., Heiberger & Holland, 2015). Although body size likely had a significant effect on several measurements (e.g., barb length), sample size did not allow for this to be investigated statistically.

3 | RESULTS

3.1 | Description of ostrich natal down

3.1.1 | Pterylosis

We confirm the presence of pterylae in our specimen and corroborate previous reports by Beddard (1898), Pycraft (1900), Duerden (1912),



FIGURE 3 Methods used to measure feather spacing and structure of natal down. Measured (a) dorsal skin patch in *Coturnix coturnix*; the blue outline shows the measured area, while the green dots show the counted follicles. Measured (b) follicle distance in *Struthio camelus* dorsal skin patch, (c) barbs in *C. coturnix* dorsal feather, and (d) barbule measurements in ventral *S. camelus* feather. Barbs were only measured if their entire length was visible (yellow in c); random barbules from each vanule were measured for length (d, blue), and the red line on the barb ramus (d) marks the length measured for barbule density calculations. All scale bars are 5 mm.

Clench (1970), Stettenheim (1972) and Cooper (2001) (*contra* Allen, 1925; DeMay, 1940; Lucas & Stettenheim, 1972; Leeson & Walsh, 2004; Graveley et al., 2020). Simple observations of *S. camelus* chicks and adults revealed the presence of apteria common to most other birds (Figure 4; Nitzsch, 1867). Duerden (1912) provides a detailed description of juvenile *S. camelus* pterylosis with names for each pteryla and apterium, though he did not provide any measurements. His description of ostrich apteria were corroborated by observations of TMM M-14775 with minor emendation. We summarize these below, add estimations of the area of apteria based on his figures, and calculate the feather density within pterylae from TMM M-14775.

Smaller apteria in *S. camelus* are disconnected from larger ones (Duerden, 1912; Figure 4). The spinal apterium, cloacal apterium, caudal apterium, and an occasional cranial apterium are isolated from other apteria by pterylae (Duerden, 1912), though in the case of the cloacal apterium, Duerden (1912) shows a single row of feathers which was not observed in TMM M-14775; it was continuous with the ventral and lateral apteria in our specimen. The larger apteria were all connected in our specimen, agreeing with previous reports (Duerden, 1912). Of these, the largest is the lateral apterium, which connects rostrally with the alar apterium under the wing and continues until it reaches the cloacal region, where it merges with the lateral apterium from the other side and the ventral apterium which runs along the middle of the bird. This was observed in both our specimen and previous studies (Duerden, 1912). The femoral apterium spurs off from the lateral apterium and isolates the crural pteryla from the rest of the feather tracts, which are otherwise entirely continuous (Duerden, 1912); this was corroborated in TMM M-14775.

TMM M-14775 displayed a ventral apterium that persisted on the ventral surface of the neck more distally than the condition shown in Duerden (1912), where the ventral apterium ends just past the base of the neck. Additionally, we found an upper cubital apterium on the dorsal side of the wing (Figure S1) which was not reported by Duerden (1912). As this apterium was absent from Duerden's figure, it was not included in apteria measurements; its small size would likely not have significantly changed relative estimates of bare patches. We estimated that the apteria constituted about 22.1% of the area on the dorsum and 36.2% on the ventrum (Figure 4).

Within the pterylae, the feathers in TMM M-14775 were sparsely distributed in both the ventral and dorsal regions. The dorsal patch had a density of 13.4 feathers/cm², while the ventral patch had a density of 11.8 feathers/cm² (Figure 2, Table S2). The ratio between barb length and follicle distance was different between dorsal and ventral regions—5.4 and 7.0, respectively. Thus, feathers were less dense within the sampled pterylae, and barbs were proportionally shorter on the ventrum.

3.1.2 | Morphological variation in natal down by body region

TMM M-14775 natal down displayed morphological differences between the dorsal and ventral regions of the body (Figure 5a,b;



FIGURE 4 Pterylosis and approximate apteria percentages in the ostrich chick (left) and adult quail (right). Illustrations modified from: ostrich: Duerden (1912); quail: Lucas and Stettenheim (1972). Dorsum represented on the top row and ventrum on the bottom. Blue represents feathered regions, the pterylae, and red represents apteria. Silhouettes represent the estimated size difference between the two species. Note that quail have down feathers in their apteria which are not shown here. Apteria % is estimated for the entire dorsum or ventrum area except for the region anterior of the dotted line. It does not include the small cubital apterium in the ostrich (yellow), not reported by Duerden (1912) but found in this study (Figure S1).

Table S3). Two main morphotypes, which are described here, were repeated in other body regions, generally varying from most dorsal and ventral feathers seen in the sampled patch locations and grading into each other in transition zones. A third morphotype was observed in cervical and cranial regions but was not measured. Quantitative differences in feather morphology by body region are summarized in Table S4.

Feathers typical of the dorsal region are among the most referenced types of ostrich feathers (Chandler, 1916; Foth, 2011; Jehl, 1971; Pycraft, 1900; Schaub, 1912). This feather type was comprised of 14–20 barbs (Figure 5a), most of which we term "plenary barbs," which have barbules present throughout their length. Three to four of the barbs lacked distal barbules and are referred to here as "semi-naked barbs" or more specifically as either "spade barbs" or "spine barbs" (Figure 6; see text below). Feathers sampled in the dorsal patch always had three spade barbs (Table S4), while those in transition zones (such as the lateral and neck patches) more often had four transitional spine barbs instead. The difference between the plenary and semi-naked barbs was obvious in dorsal feathers, as these feathers show no gradation between the two barb types (Figure 5a; Foth, 2009).

The two types of semi-naked barbs differed in morphology and location on the body. The standard semi-naked barb, we term a "spine barb" (Figure 6). This is a general term that applies to all semi-naked barbs except for those that have spade morphology. Spine barbs are like plenary barbs except that they have naked tips



FIGURE 5 Silhouettes and average barb composition of neoptiles from *Struthio camelus* and *Coturnix coturnix*. (a) *S. camelus* dorsal feather; (b) *S. camelus* ventral feather; (c) *C. coturnix* dorsal feather; (d) *C. coturnix* ventral feather. All scale bars are 1 cm.

of varying lengths and thicknesses, making it easy for them to grade into both plenary and spade barb types (Figure 6). It should be noted that the spine barbs in TMM M-14775 always had a vanuled region that was the same length, as the average length of the plenary barbs in the feather (Table S4); thus the naked tip made spine barbs longer than plenary barbs (Figure 6, Table S4).

Spade barbs are specialized semi-naked barbs (Figure 6) which are present only in the dorsal region. They were longer than most spine barbs in TMM M-14775 (the exception being spine barbs in the lateral regions, which were of an intermediate morphotype) and have notably thickened and concave distal ends, resulting in a spoon-like shape (Foth, 2011; Pycraft, 1900). The naked tips of spade barbs were always 1/3 or more of the total barb length (Table S4). Dorsal spade barbs had barbule-less tips that average to 45% of the total barb length; spine barbs from the ventral region had barbule-less tips which average to 31% of the total length (Table S4). The vanules on spade barbs were always diminished, bearing significantly smaller barbules than other barb types (p < 0.001, F = 76.46; Table S4; corroborated by Foth, 2011) and were often asymmetrical, with one side having longer barbules and reaching further distally on the ramus than the other. This was especially true of the central spade barbs in a feather, which often had barbules so small that they were nearly invisible to the naked eye. The short barbules and the asymmetry of the vanules likely conferred a twist to the rami of spade barbs which was not present in other barb types (Chandler, 1916; Duerden, 1911; Jehl, 1971).

As noted previously (Foth, 2011; Pycraft, 1900; Schaub, 1912), semi-naked barbs emerge from the calamus next to one another, creating an obvious midline distinction. Occasional fusion was seen at the bases of semi-naked barbs in dorsal feathers, creating what Foth (2011) identifies as a diminished rachis. However, fusion at the bases of plenary barbs was also common in dorsal feathers in our specimen. An odd spade barb was observed on three separate dorsal feathers in TMM M-14775. This barb had two rami, both of which bore barbules (Figure S2). The two rami were fused distally, appearing separate only in the vanuled region. This morphology matches that reported previously in some chicken feathers (Harris et al., 2002; Watterson, 1942), the developmental underpinnings of which were determined by Harris et al. (2002). This double-ramus morphology was not seen in feathers of any region other than the dorsal-most thoracic region, nor in any barb type other than spade barbs.

Feathers with morphologies of those present in the dorsal thoracic region also appeared on the flanks and the upper surface of the wing and leg. However, in these regions, the semi-naked barbs were spine barbs and often had an extra barb so that they bore four semi-naked barbs instead of three. Although other reports described feathers with four semi-naked barbs as coming from the dorsal region (e.g., Duerden, 1911; Foth, 2011), we only ever found three semi-naked barbs in dorsal patch feathers and feathers with four semi-naked barbs were only found in other plucked regions. The smallest feathers with this morphology were found on the knee, while the largest were found just posterior to the proximal hindlimb. Feathers in the head and neck region had spine barbs around 7mm and had few barbs, closer to 5-8 in total, with 1-3 total spine barbs. The remaining barbs were plenary barbs and, as in dorsal feathers, were significantly shorter than the spine barbs. These feathers had a brown color but were occasionally black; no color variation was observed within a single feather.



FIGURE 6 Barb types and distribution of *Struthio camelus* natal barbs drawn to scale. Plenary barbs are the shortest and the most common, appearing in both dorsal and ventral feathers. They show variable gradation into spine barbs which have shorter distal barbules and a naked tip. Spade barbs are modified spine barbs in which the naked part of the ramus is broader; they also bear short barbules in often asymmetrical vanules. Spade barbs are only found in dorsal feathers. A single ostrich feather is composed of around 15–20 plenary barbs and an average of 6 spine barbs in ventral feathers or 3 spade barbs in dorsal feathers.

We found dorsal feathers to be either heavily pigmented and appear completely black, or lightly pigmented and appear light tan. The distribution of tan and black feathers gave a peppery look to the plumage. In some cases, a feather had a mixed color, with some tan barbs and the others black. In even rarer cases, the pigmentation even differed within a single barb, with parts of the barb being tan and other parts being black; whenever this occurred, it was generally one or two changes in color.

Ventral patch feathers (Figure 5b) had 14–19 barbs, of which there was a greater number of the shorter plenary barbs (11 on average) than the longer spine barbs (six on average). The semi-naked barbs present in ventral feathers were spine barbs only and spade barbs were absent. Unlike the pattern observed in the dorsal regions, ventral feathers showed continuous variation in the distal extent of barbules; the longest plenary barbs had distal ends with barbules so small that the tips appeared bare to the naked eye, and spine barbs had shorter bare tips than in dorsal feathers (Table S4). Fusion at the base of the barbs was absent in most ventral feathers, even among the semi-naked barbs. Foth (2011) found proposed rudimentary rachises (i.e., fused barb rami) randomly distributed in all three body regions he investigated; we found such fused rami extremely rare in ventral feathers (observed in 2 out of 30 feathers) and no fusion was seen between barb tips. Despite the lack of these proposed vestigial rachises, the spine barbs all emerged from the same area of the calamus. Feathers like those on the ventral thoracic region but shorter were observed on the medial leg. Most ventral feathers were lightly pigmented and appeared whitish, though they could show black and tan coloration in lateral transition zones, especially at the base of the neck.

3.1.3 | Barbule morphology and organization

Ostrich barbules are different from the barbules of all studied birds (Chandler, 1916; Dove & Koch, 2011), although they bear a slight similarity to some barbules in tinamous (Foth, 2009). They are flat and ribbon-like, with an appearance similar to shaved or grated plastic (Figure S3; Chandler, 1916; Dove & Koch, 2011). As previously remarked (Chandler, 1916; Foth, 2009; McGowan, 1989; Pycraft, 1900), no nodes are present, though prongs are present, arising from the tips of the barbules in TMM-M14775 (Figure S3). There was no noticeable differentiation between base and pennulum at 35× magnification. These ribbon-like barbules splayed out in different directions most commonly alternating between the sides of the

Journal of Anatomy

ANATOMICAL SOCIETY-WILEY

ramus in most barbs (Figure 7). In some cases, especially in plenary barbs, these deviations were so great that both vanules reoriented to be perpendicular to typical vanule orientation. The alternation of the barbules, their organization, and their short length created barbs with a more cylindrical shape than flat. The only exception to this pattern was in spade barbs, where the barbules were very short and maintained highly organized—though very small—vanules.

In all *S. camelus* barbs, the barbules were short compared to barb length, resulting in a low barb aspect ratio (Table S4). Barbules averaged 0.8 mm but were longest near the base and shortest at the tip of the barb. Barbules were shorter in ventral plenary barbs than they were in dorsal plenary barbs (Table S4). Barbule density did not differ significantly among different barb types but was significantly different between dorsal and ventral feathers (Table S3). We ran a Mann-Whitney *U* test on plenary barbs and still found a significant difference between dorsal and ventral barbule length and density (p < 0.001, U = 346,903, N = 1389). As with barbule length, barbule density decreased towards the barb tip.

3.2 | Comparisons with Coturnix coturnix

3.2.1 | Pterylosis

Coturnix coturnix showed more individual apteria than *S. camelus* did; they tended to be thinner and were less likely to be continuous (Figure 4). For example, *C. coturnix* showed four apteria on each side of the wing, all of which are long and thin (Figure 4; Lucas & Stettenheim, 1972). *Struthio camelus*, by contrast, has two small apteria on the dorsal wing and a single large apterium on the ventral wing (Figure 4; Duerden, 1912). In *S. camelus*, the alar apterium

wraps around the digits until it is barely visible on the dorsal side caudal to the alula (Figure 4; Duerden, 1912). A small, dorsal apterium caudal to the alula also appears in *C. coturnix*, although it is isolated from instead of continuous with a ventral apterium (Figure 4; Lucas & Stettenheim, 1972). Both species have an upper cubital apterium (Figure 4, Figure 51; Lucas & Stettenheim, 1972), though this connects with the humeral apterium in *C. coturnix* which is lacking in *S. camelus* (Figure 51; Duerden, 1912). The alar apterium in *S. camelus* also follows the general pathway of the subhumeral, under forearm, and under hand apteria (Lucas & Stettenheim, 1972), though it is larger than these three combined apteria (Figure 4; Duerden, 1912). The only apteria in *C. coturnix* wings which do not have a corresponding apterium in *S. camelus* are the upper hand, ventral propatagial, and humeral apteria.

Both species have a similar spinal apterium as well as lateral apteria which connect with a medial apterium on the ventral side (Figure 4; Duerden, 1912; Lucas & Stettenheim, 1972). In C. coturnix, these apteria connect on the cranial end, whereas in S. camelus they connect on the caudal end (Figure 4). Coturnix coturnix have smaller apteria on their legs than S. camelus does; this is especially true of adults, as the crural pteryla is absent in adult ostriches though present in juveniles (Duerden, 1911). Finally, C. coturnix have apteria downs, whereas the apteria are completely bare in S. camelus. Coturnix coturnix was found to have less bare skin dorsally (~15.8%) than ventrally (~22.8%); the dorsal apteria in C. coturnix are calculated as 69% the size of the ventral apteria. Similarly, in S. camelus the dorsal apteria are calculated as 61% the size of the ventral apteria. Despite this, the ratios between apteria and pterylae area are found to differ substantially between species, with S. camelus showing more bare skin in both ventral and dorsal regions than C. coturnix (Figure 4).



FIGURE 7 Barbule orientation in *Struthio camelus* and *Coturnix coturnix* natal down showing differences in vanule organization. Left: mid region of a single barb from a ventral *S. camelus* feather showing the "chaotic" orientations of the ribbon-like barbules. Right: mid region of a single barb from a ventral *C. coturnix* feather showing how the barbules are organized into a simple vanule resembling a pennaceous arrangement. The dorsal feathers of each species mirror the vanule texture of their respective ventral feathers. Both images are to scale; scale bar = 0.5 cm.

WILEY-ANATOMICAI

Journal of Anatomy

Feather density was greater in the sampled *C. coturnix* pterylae than in the sampled *S. camelus* pterylae (Figure 2). Feather density was greater in the sampled ventral region (116 feathers/cm²) than the dorsal region (66 feathers/cm²; Figure 2). The ratio between barb length and follicle distance was much more similar between dorsal and ventral regions in *C. coturnix* (dorsal: 6.4, ventral: 6.7) than it was in *S. camelus* (Table S2).

3.2.2 | Barb morphology and variation in dorsal and ventral patches

Like *S. camelus*, the sampled *C. coturnix* showed dorsal and ventral differences in natal down morphology. These differences in *C. coturnix* are described first and then compared to *S. camelus*.

Coturnix coturnix dorsal natal down feathers (Figure 5c) had a low barb density with 8 barbs on average. In most cases, these feathers only constituted spine barbs (Figure S4a), but on rare occasions a small plenary barb was present. No fusion was seen between the barb rami which might be homologous with a vestigial rachis (Clark Jr., 1964; Foth, 2011) or afterfeather. The dorsal feathers were mostly black but often had a few barbs of a lighter, tan color. In many cases, these lighter barbs alternated between black and tan, with black more common at the base.

Coturnix coturnix ventral feathers (Figure 5d) were looser with extremely flexible barbs reminiscent of adult down feathers. The rami were much thinner and more flexible than those in dorsal feathers. They had an average of 11 barbs per feather, most of which were spine barbs, but most feathers had two or three plenary barbs which were either long or short (Figure S4b,d). Just as in dorsal feathers, quail ventral feathers lacked all signs of fusion among the barb rami. Ventral spine barbs also tended to have shorter distal barbule-free portions (Figure 8). In *C. coturnix*, the dorsal barbs had barbule-less tips that averaged to 28% of the total barb length; comparable ventral barbs averaged only 12% of the total barb length lacking barbules, and they were often much shorter than that (Figure 8). A few *C. coturnix* ventral plenary barbs were extremely short, and the barbules did not diminish in length or density towards the tip (Figure S4d). We cannot rule out that this morphology is simply a broken barb form, leaving only the basal portion remaining. If these are broken barbs, the consistency of the break point and presence in ventral feathers may point to there being structural differences in the ventral natal down and its exposure to wear. *Coturnix* coturnix ventral down is white.

Coturnix coturnix natal down showed stark differences from *S*. camelus natal down (Figure 5). Coturnix coturnix feathers showed no signs of barb fusion while *S*. camelus feathers showed fusion in some barbs interpreted as a diminished or vestigial rachis (Foth, 2011). Additionally, *S*. camelus natal down feathers had larger numbers of barbs (Figure 5). Another difference was the relative rarity of plenary barbs (i.e., barbs with barbules extending to the tip of the ramus) in *C*. coturnix natal down compared to *S*. camelus. In *S*. camelus, plenary barbs were the most common barb type in both dorsal and ventral feathers (Figure 5, Table S4). However, in *C*. coturnix, spine barbs were by far the most common, with plenary barbs being limited to one or two per feather, if any (Figure 5). Finally, as noted by Foth (2011), quail natal down feathers lacked signs of medullary cells and had no barbs which were extremely more elongate than the majority unlike *S*. camelus (Figure 5).



FIGURE 8 Comparison of absolute and relative lengths of the barbule-less regions of semi-naked barbs in *Struthio camelus* and *Coturnix coturnix*. Both *S. camelus* (% barbule-less: p < 0.001, U = 212; barbule-less length: p < 0.001, U = 216) and *C. coturnix* (% barbule-less: p < 0.001, U = 1039; barbule-less length: p < 0.001, U = 1008) differ significantly by body region; dorsal feathers show longer barbule-less tips. Significance level (***) defined as p < 0.001.

3.2.3

Journal of Anatomy

or even a single barb, with the dominant color being black. Struthio camelus feathers were more often uniform in color, either black or tan, though they occasionally had both colors in the same feather. Barbule morphology and orientation 4 All sampled C. coturnix barbules differed from the sampled S. camelus in their densities, their shapes, their orientation, and in their relative lengths. Additionally, C. coturnix barbules showed differences between dorsal and ventral regions that were not seen in the S. camelus specimen.

Both S. camelus and C. coturnix had white ventral feathers and

mixed black/tan dorsal feathers. However, dorsal C. coturnix feathers

appeared to more commonly to have both colors in a single feather,

Coturnix coturnix barbules were long, round, and thin. They were less dense than S. camelus barbules throughout the barb length (Figure 7), with an average of 10 barbules per mm. Barbules became steadily shorter distally. In S. camelus, the barbules become steadily shorter until they appear as tiny tabs off the barb ramus (Foth, 2009). In the sampled C. coturnix, however, the barbules did not reach such a small size and simply stopped forming along the ramus. Although adult C. coturnix down is known to have nodes (Lucas & Stettenheim, 1972; Soliman, 2020), we could only detect nodes on the barbules from the ventrum, and no nodes were seen on barbules in sampled C. coturnix natal down from the dorsum. It is possible that nodes would be visible in the dorsal barbules at higher magnifications; in this case, the ventral nodes would be larger than the ones in the dorsum in this specimen. The barbules were around the same absolute lengths as those of S. camelus, though still significantly shorter (Table S3), and their relative length compared to the ramus was longer, giving C. coturnix barbs higher aspect ratios than S. camelus barbs (C. coturnix ventral barb aspect ratio was 0.386 on average, while dorsal was 0.264 on average with both total and vanuled lengths). A Mann-Whitney U test revealed a significant difference between C. coturnix dorsal and ventral barbule length (Table S3). However, the means of the sampled C. coturnix dorsal and ventral barbule lengths were similar (p=0.247, diff.=-0.026 using Tukey's range test; Figure S5).

Unlike S. camelus, the orientation of the barbules in C. coturnix barbs differed depending on location on the barb in both dorsal and ventral feathers (Figure 7). Basally, the barbules splayed in all directions, creating a poorly organized proximal region that was extremely dense when combined with the basal barbules from other barbs. In the mid region, however, the barbules abruptly became organized and formed very discrete vanules (Figure 7); this pattern continued for the rest of the barb. In this region, each barbule projected in the same direction as the ones next to it, as is the case in a pennaceous vanule. The resulting texture was similar to the open-pennaceous texture created by reduced pennaceous or plumulaceous barbules found on adult neognath contour and downy feathers (Lucas & Stettenheim, 1972). The sampled C. coturnix thus had organized barbules, with a similar vanule plane orientation distal to the first 1/3 of the barb length; this transition was abrupt (Figure S4). Barbules from

the sampled S. camelus were projected in a similar plane only when at their shortest, closer to the tip of the barb or in spade barbs; this transition was gradual (Figure 6). While S. camelus barbs were almost conical due to the different projection planes of their vanules, C. coturnix barbs were only conical at their bases and transitioned to a very flat, planar surface about a third of the way from their bases.

DISCUSSION

We confirm the presence of apteria in S. camelus including the lateral, femoral, spinal, ventral, alar, and cubital apteria. These apteria followed the same organization as those found in C. coturnix, showing their importance to integument patterning in species with disparate evolutionary histories and ecologies. We estimate that the sampled S. camelus has ~10% more bare skin than the sampled C. coturnix, with most of this additional bare space on the proximal hindlimb (Figure 4). Highly precocial chicks such as quail and ostrich have less bare skin (Chen et al., 2019). If this larger bare space in ostrich than in quail is confirmed with greater sampling, the slightly larger percentage in ostrich may be related to environmental and thermoregulatory differences; ostriches are significantly larger as both chicks and adults than quail, and therefore, heat loss may be a competing selective constraint (Barve et al., 2021; Meiri & Dayan, 2003).

The sampled juvenile C. coturnix showed denser feathering within pterylae and a large difference in density between dorsal and ventral tracts (Figure 2). Differences in the feather density of dorsal and ventral body regions have rarely been reported, although they have been noted in adult penguins (Williams et al., 2015). The limited difference in feather density between regions in the S. camelus specimen may reflect environment and ecology, which affect overall feather density in birds (Osváth et al., 2017; Pap et al., 2020). Further work on a larger sample is needed to investigate patterns of dorsoventral differences in feather density in birds and potential causal factors in such variation.

Barb length scaled tightly with follicle distance (Table S2) in the compared specimens, despite differing ecologies and evolutionary histories. This could imply conserved developmental linkages between follicle spacing and feather scaling. However, these findings need to be confirmed with greater sampling; there are many possible factors that can affect barb length (Barve et al., 2021; Butler et al., 2008; Osváth et al., 2017; Pap et al., 2017, 2020).

Both specimens showed significant differences in the morphology of dorsal and ventral natal feathers (Table S3, Figures 8 and 9); ventral feathers show shorter barbule-less tips and more continuous variation in morphology. Barb density differed across these regions in the sampled C. coturnix but not in the sampled S. camelus (Table S3). Barbule density, length, and the frequency of barb ramal fusion also differed between dorsal and ventral feathers in S. camelus (Figure 9). These patterns were not clear in C. coturnix due to different tests giving different significance results (Figure S5). Morphological differences between dorsal and ventral natal down feathers in ostrich and other species have been infrequently noted (Duerden, 1911; Foth, 2011; Pap et al., 2020: Supplementary Information) but never

WILEY-ANATOMICAI

described in detail nor statistically assessed within a single species. Only in *Strix aluco* has adult down barbule density been reported to significantly differ between these regions (Koskenpato et al., 2016). More exemplars within a single species and a larger taxonomic sample are needed to understand how consistent these patterns may be intraspecifically and how they may vary across Aves.

Barb rami fusion in the *S. camelus* specimen was common in dorsal but not ventral feathers; it was not present in the sampled *C. coturnix. Struthio camelus*, *R. americana*, and *Crax*. sp. have been previously reported to have randomly distributed barb fusion (Foth, 2011), but other reports have found such fusion to be more common in specific body regions in the domestic chicken (*Gallus gallus*; Watterson, 1942). If the pattern observed in TMM M-14775 is confirmed with increased sampling, an ecological or developmental explanation for such a regional difference is wanting. We cannot not rule out, however, that it may be an artifact of a small, if random, sample of the entire ventral tract in a single specimen.

Previous work has proposed a set of down traits as associated with insulatory function. However, natal down of the sampled ostrich and quail show different combinations of these traits. The low barbule density and relatively longer barbules seen in the sampled *C. coturnix* match described modifications for trapping air (Broggi

et al., 2011; Butler et al., 2008; D'Alba et al., 2017; Fuller, 2015; Lucas & Stettenheim, 1972; Pap et al., 2017), but their naked tips, absolutely shorter barbules, well-organized vanules, and inconsistency of node presence contrast with described modifications for insulation (Butler et al., 2008; D'Alba et al., 2017; Dove, 2000; Dove & Agreda, 2007; Fuller, 2015; Lucas & Stettenheim, 1972; Pap et al., 2017, 2020). Struthio camelus, by contrast, has short, ribbonlike barbules which lack nodes and extend to the tip of the ramus of most barbs (Figure 6; Chandler, 1916; Dove & Koch, 2011). Barbule orientation in our specimen was also disordered for more of the length of the barb ramus than in the sampled C. coturnix. Both species showed differing combinations of proposed insulatory down traits. Increased sampling within the two species and across Aves is needed to fully understand how much neoptiles diverge from morphologies described as optimal for insulation. Without modeling air-trapping effects of the two morphologies found here, it is impossible to say which downy feather provides more insulation. Other features not examined in this study, such as node and prong shape, affect insulation; these features need to be examined with scanning electron microscopy (SEM; see examples in D'Alba et al., 2017; Dove, 2000; Foth, 2009; Fuller, 2015; Soliman, 2020), which were beyond the scope of this study.



FIGURE 9 Barbule density for all barb types from the dorsal and ventral regions in both species. *Struthio camelus* barbule density is significantly different from that of *Coturnix coturnix* (p<0.001, U=2827.5), while dorsal *S. camelus* densities are significantly different from ventral *S. camelus* densities (p<0.001, t=8.486). Dorsal and ventral barbule densities in *C. coturnix* are not significantly different (p=0.776, U=3916.5). Significance level (***) defined as p<0.001.

The distribution of long and short barbs in *S. camelus* natal down feathers may imply a distinct developmental pattern in this species. Ostrich natal feathers have been consistently noted by previous authors to display a small number of significantly longer barbs and a larger number of shorter barbs as described here (Table S4; Duerden, 1911; Foth, 2009; Pycraft, 1900). This morphology is consistent with a large addition of barb ridges later in feather development (Figure 10) due to expansion of the follicle (Harris et al., 2005; Prum & Williamson, 2001; Watterson, 1942) or a late release of transcription factors (Yu et al., 2002) in ostrich neoptile development. Both mechanisms have been described in adult feather development (Alibardi, 2009; Harris et al., 2002; Prum & Williamson, 2001; Yu et al., 2002).

Our specimens, consistent with reports on these and other species (e.g., Clark Jr., 1964; Hosker, 1936; Lucas & Stettenheim, 1972; Pycraft, 1900), lack barbules in the distal tips of the barb rami. All barbules began at approximately the same heights on the barb rami within a single feather (Figure 10). The appearance of barbules in natal down seems to follow the pattern for an isocline ('Espinasse, 1939; Lucas & Stettenheim, 1972; Prum & Williamson, 2001) which, if confirmed with greater sampling, implies that barbule development is triggered at a certain point during neoptile development. Unfortunately, there has been no investigation into how naked barb rami form (Prum & Dyck, 2003). There have been proposed hypothetical scenarios (e.g., Alibardi, 2006) and two major hypotheses put forward: i.e., (1) the barbule plates do not form in the distal end of the barb ridges (Watterson, 1942); and (2) the barbule plates form but are later resorbed in the distal end of the barb ridges (Matulionis, 1970). Either or both developmental strategies could be employed by neognaths and palaeognaths.

4.1 | Paleontological implications

Fossil discoveries relevant to the evolution of follicle spacing are limited. Some studies report scattered and unorganized follicles in stem lineage taxa proposed to glide or show active flight (Navalón et al., 2015; Wang et al., 2017). Others show lightly-defined, distinct rows in species proposed to be volant (van der Reest et al., 2016) and those proposed to be non-volant (Xing, McKellar, Wang, et al., 2016). *Struthio camelus* shows a less tight organization of follicles within pterylae also hypothesized to be related to the loss of flight (Ho et al., 2019). However, our specimen still displayed the same average barb length to follicle distance ratio as the sampled *C. coturnix*. If this relationship is confirmed with greater sampling, this scaling constraint could be expected in extinct stem taxa, even when the follicles are less organized or a taxon is non-volant.

Fossil discoveries of potential neonatal feathering are rare but have been reported in at least three instances (Xing et al., 2017, 2020; Xing, McKellar, Xu, et al., 2016). Most of these feathers were described as an unusual neoptile type with both a rachis and reduced pennaceous barbules organized into a simple vanule instead of the disorganized plumulaceous barbules common to adult down. Organized barbules occurred only in a portion of each natal down feather in the sampled *C. coturnix* natal down feathers and were not present in the *S. camelus* specimen; all barbules were consistently flexible and disorganized. We could not determine whether these organized barbules in *C. coturnix* were pennaceous or plumulaceous; a more detailed analysis utilizing SEM may be needed. All but one of the fossil feathers to possibly comprise neonatal down (Xing et al., 2017, 2020; Xing, McKellar, Xu, et al., 2016) show barbules



FIGURE 10 Implications of neoptile development based on feather morphology. Lines intersecting the feathers (a, *Struthio camelus*; b, *Coturnix coturnix*) represent isoclines that occur early (red) and late (blue) in the feathers' development. The diagrams below each feather show hypothesized follicular cross sections at each isocline based on feather morphology. Lines within barb ridges represent barbule plates. Both feathers have no barbule plates in early development (c, e). *S. camelus* has few barb ridges in early development (c) and gains more later (d), while *C. coturnix* retains approximately the same number of barb ridges throughout development (e, f).

WILEY-ANATOMICAL

Journal of Anatomy

through the entire length of the barb ramus. Only one fossil bears naked tips (Xing et al., 2017), but in this case barbules did not appear present in any part of the feather, and the authors concluded that these feathers were more likely newly erupting adult feathers. By contrast, all described extant avian natal down includes at least some barbs with barbule-less tips, generally the longest and earliest developing in the feather (Clark Jr., 1964; Hosker, 1936; Lucas & Stettenheim, 1972; Pycraft, 1900; Watterson, 1942). Our results are consistent with these previous studies. If these fossil feathers do exemplify natal down, that would imply that natal down in some or all extinct stem taxa lacks semi-naked barbs and is instead closer in morphology to the adult feathers of modern birds, as hypothesized in previous studies (O'Connor et al., 2020; Xing et al., 2017; Xing, McKellar, Wang, et al., 2016; Xing, McKellar, Xu, et al., 2016). Previous studies have also shown that some fossilized feathers lack barbules partially or entirely, though they never show the naked tips seen in extant bird natal down (Kundrát et al., 2020; Lefèvre et al., 2017; Perrichot et al., 2008; Sayão et al., 2011; Xing et al., 2017; Xing, Cockx, et al., 2018; Xing, McKellar, et al., 2018; Xing et al., 2020). Whether extinct species did this in their neoptile plumage is uncertain, but if the currently identified neoptile feathers are indeed natal down, then semi-naked barbs in natal down would represent a synapomorphy of crown birds. Such a conclusion brings new questions as to why crown birds evolved this trait and if it has some selective advantage.

5 | CONCLUSIONS

We compare in detail the natal down of two exemplars of neognaths and palaeognaths, finding significant differences in their neoptile structures and establishing a framework in which further comparative study can be done. These results, though limited by a small sample size, illuminate patterns that had been overlooked in previous investigations. Examples include differences in feather density, structure, and barb rami fusion between the ventrum and dorsum, the developmental questions raised by the two barb morphologies in S. camelus, and variation in the neoptiles with respect to traits proposed to be insulator adaptations. Further studies using larger sample sizes are needed to corroborate the patterns observed in the S. camelus and C. coturnix specimens studied here and to determine whether these are present in other neognath and palaeognath species. Future studies utilizing SEM to illuminate nodal and naked tip microstructures (e.g., Foth, 2009) would be especially valuable. Understanding the formation of bare, barbule-free barbs in crown birds will inform future interpretations of feather evolution and diversity in extinct dinosaurs. This trait could represent a plesiomorphic character state for dinosaurs. However, given that all described extinct taxa, including enantiornithine birds, lack this trait, this morphology could also represent an apomorphic feature possibly associated with unidentified selective pressures in these species or simply has not yet been sampled in the sparse array of potential natal down feathers from extinct taxa. Further

URBAN ET AL.

investigation of the relationships between development, structure, and function in extant natal down are needed with increased fossil sampling that can inform the evolution of feathering across ontogeny in dinosaurs.

AUTHOR CONTRIBUTIONS

Carmen A. Urban and Julia A. Clarke designed the research. Carmen A. Urban acquired the data. Carmen A. Urban and Lucas J. Legendre analyzed the data. Carmen A. Urban and Julia A. Clarke wrote the manuscript. All authors contributed to and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

OPEN RESEARCH BADGES

This article has earned Open Data, Open Materials and Preregistered Research Design badges. Data, materials and the preregistered design and analysis plan are available at http://doi.org/10.17605/OSF. IO/DM6CK.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Open Science Framework at http://doi.org/10.17605/OSF. IO/DM6CK.

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1023