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Nonavian Feathers in a Late Triassic Archosaur

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Longisquama insignis **was an unusual archosaur from the Late Triassic of central Asia. Along its dorsal axis *Longisquama* bore a series of paired integumentary appendages that resembled avian feathers in many details, especially in the anatomy of the basal region. The latter is sufficiently similar to the calamus of modern feathers that each probably represents the culmination of virtually identical morphogenetic processes. The exact relationship of *Longisquama* to birds is uncertain. Nevertheless, we interpret *Longisquama*'s elongate integumentary appendages as nonavian feathers and suggest that they are probably homologous with avian feathers. If so, they antedate the feathers of *Archaeopteryx*, the first known bird from the Late Jurassic.**

Longisquama insignis was a small, Late Triassic [Norian, ~220 million years ago (Ma)], gliding archosaur with unusual integumentary appendages (*1*–*3*). Fossils are known only from lacustrine deposits in central Asia [Madygan, Osh Province, Kyrgyzstan (*1*, *2*)]. The most complete specimen consists of a slab and counterslab that contains articulated elements from the skull, vertebrae, ribs, furcula, and forelimbs and impressions of much of the integument (Fig. 1 and Web fig. 1). There are five other fossils of integumentary appendages from the same site (*1*, *4*).

The anterior portion of *Longisquama*'s body was covered with imbricating, scalelike appendages; those on the chin and neck were particularly delicate and elongate (Fig. 1, upper left inset). In addition, a series of scales (*1*) formed an apparent aerofoil-like surface along the postaxial margins of the forelimbs (Fig. 1, lower right inset). Most remarkable, however, are the series of six to eight pairs of bilaterally placed, markedly elongate, pinnate, integumentary appendages that occurred at segmental intervals along the animal's dorsum (Fig. 1 and Web fig. 1).

Longisquama's pinnate integumentary appendages each consisted of a distinct shaft that included a distally expanded vane. At its base, the elongate shaft was tubular, with a solid wall that surrounded a number of transverse partitions. Four to six of these partitions are visible in one particularly well-preserved shaft (Fig. 2). Additionally, as seen in three successive units immediately adjacent to the dorsal vertebrae, the broad, tubelike bases of the appendages were approximately barrel-shaped and tapered proximally—a morphology consistent with their placement within, and origin from, follicles (Fig. 2).

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Beyond its base, each shaft consisted of an uninterrupted central axis from which radiated a continuous series of pinnae (Fig. 1, Figs. 3 through 5, and Web figs. 1 and 2). Portions of the central axis appear to have been hollow and unsubdivided (Fig. 4).

At their distal extremities, the shafts were vanelike and consisted of distinct markedly elongate pinnae that branched regularly from the central axis (Figs. 4 and 5 and Web fig. 2) (*5*). Some of the individual pinnae appear to have been branched, and the distal ends of successive pinnae formed a ribbonlike margin that was more delicate along the trailing edge of the vane (Fig. 4). In addition, pinnae at the distal extremities of the integumentary appendages were sufficiently delicate that details of their morphology can be resolved even when they are overlain by other units (Fig. 5).

Proceeding proximally from the expanded vanelike portions of the shaft, the pinnae became increasingly abbreviated, massive, and less delicate, so that the long proximal portion of the shaft consisted largely of the central axis and a long series of short, less delicate pinnae. In addition, an extensive sheath was retained in this region as an integral part of the shaft, where it formed a distinct robust jacket that fully enclosed the central axis and its associated pinnae (Figs. 1 and 3).

Longisquama's elongate integumentary appendages have previously been described as "long scales" or "extremely modified horny scales" (*1*, *3*). However, a pinnate shaft, vane, and sheath are not attributes of reptilian scales (*6*). Additionally, because the morphology of the shaft base in *Longisquama* was consistent with each unit having developed within a follicle, each must have been formed, and therefore shed, individually. This differs sharply from epidermal replacement of a reptilian scale. Because the latter lacks a follicular morphology, mature corneous materials form, and are shed, in large flakes or continuous sheets (*6*).

Like *Longisquama*'s pinnate integumentary appendages, avian feathers are elongate, individually distinct, follicular units that bear pinnae, or barbs. Additionally, as in the rachis of many feathers, the axes of *Longisquama*'s appendages spanned most of their overall length. The apparently hollow remnant of the spongy air-filled pith in the rachis of many feathers closely resembles hollow portions of the axis in *Longisquama*'s appendages (Fig. 4).

Pinnations in *Longisquama*'s integumentary appendages, and especially those in the distal vane, are generally comparable to feather barbs (Figs. 4 and 5 and Web fig. 2). However, barbulelike structures were not present in *Longisquama*, and the aforementioned branching and comparable distal connections between consecutive pinnae are uncommon in feather barbs of extant birds. Nevertheless, branching of individual barbs and fusion of successive barb tips in avian feathers resulting from modulations of cellular activities within the ramogenic zone at the base of the follicle during feather replacement are well documented (*7*–*9*). Additionally, examples of *Longisquama*-like barb structure can be found in some modern avian feathers (*9*). As in *Longisquama*'s pinnae, individual feather barbs may be branched (for example, in downy feathers of the jungle fowl, *Gallus*) (*8*) and successive barbs may be fused distally (for example, in spangled feathers of the curl-crested aracari, *Pteroglossus beauharnaesii*, and the scaled cuckoo, *Lepidogrammus cumingi*) (*9*).

The sheath that surrounded the extensive proximal region of the central axis and its more massive pinnae created the unusual appearance of *Longisquama*'s integumentary appendages (Figs. 1 and 3) (*10*). Although the sheath of an avian feather cracks and flakes and is usually eliminated by preening (*8*), its morphology and spatial relationships are closely comparable to those of the epidermal sheath in *Longisquama* (Fig. 3).

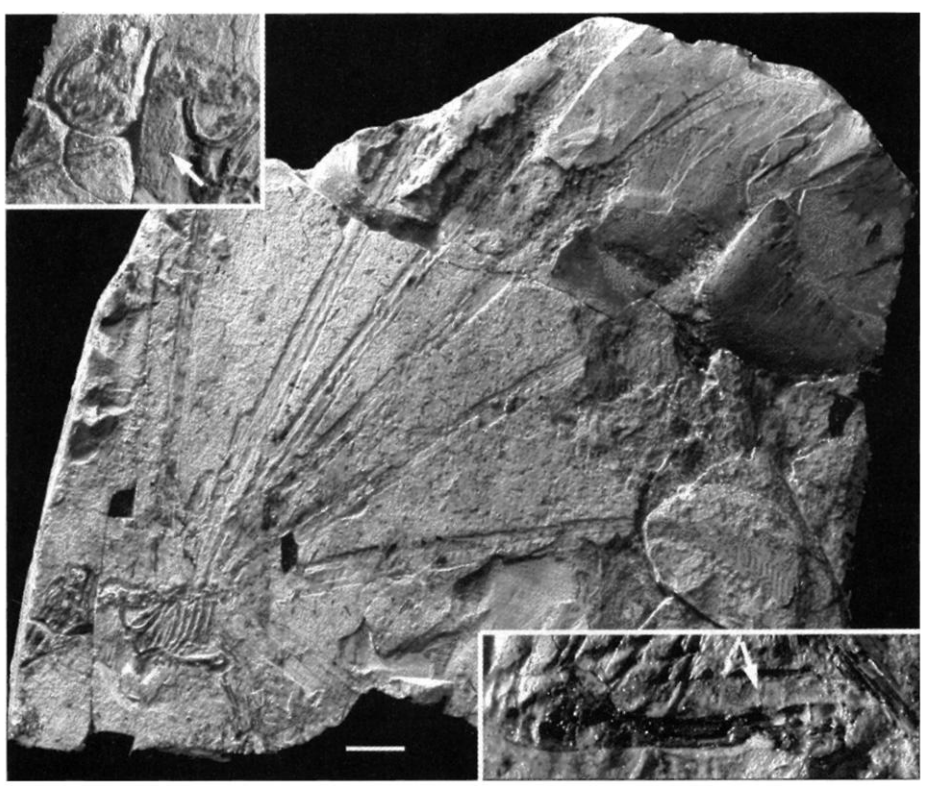

Fig. 1. Holotype of *L. insignis* from Late Triassic lacustrine deposits, Madygan (southern Fergana Valley), Osh Province, Kyrgyzstan (PIN 2584/4). (**Inset above**) Skull and neck; the arrow points to impressions of the elongate scales of the chin and neck. (**Inset below**) The left humerus [digitally reversed from the counterslab (PIN 2584/4)] the elongate postaxial scales are indicated by the arrow. Scale bar, 1 cm.

Fig. 2. Tubular bases of three successive shafts that inserted on the left dorsum above the ribs (asterisks) of *L. insignis* (PIN 2584/4). Note the proximal tapering as well as the distinct, transversely subdivided, hollow core (indicated by arrows) of each tubular base. The morphology of these bases strongly implies that development of *Longisquama*'s elongate integumentary appendages took place within a follicle. Apparent pulp cavities (p) are also preserved. Scale bar, 5 mm.

The bases of *Longisquama*'s integumentary appendages also resemble those of avian feathers. Both exhibit a tubular morphology consistent with development within a follicle (Figs. 2 and 6). Additionally, in feathers, the hollow base, or calamus, has a tubular outer wall surrounding an inner thin-walled tube that is transversely partitioned by a series of cornified pulp caps (Fig. 6) (*8*). The calamus bears a striking resemblance to the transversely subdivided tubular base of *Longisquama*'s appendages (Fig. 6).

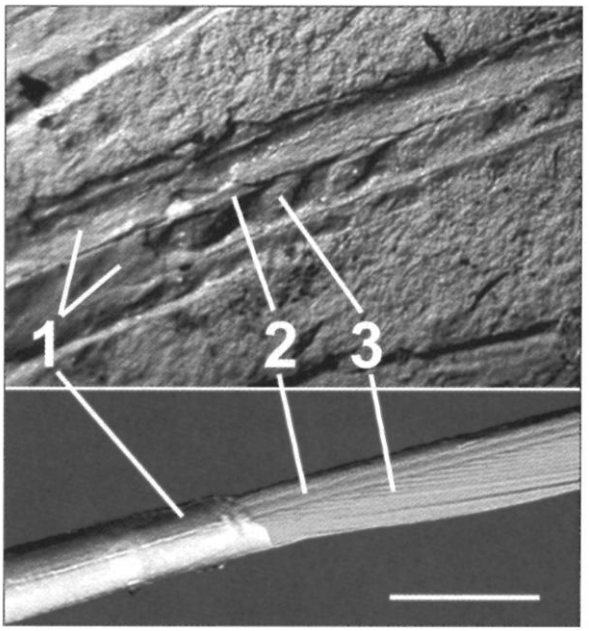

Fig. 3. The sheath/axis/pinna complex of the proximal vane of *L. insignis* (PIN 2584/4) (**above**) and the sheath/rachis/barb complex in a primary feather of a juvenile Goffin's cockatoo (*Cacatua goffini*) (**below**). 1, the epidermal sheath; 2, the central axis and rachis in *Longisquama* and *Cacatua*, respectively; 3, pinna and barbs in *Longisquama* and *Cacatua*, respectively. In both cases, the sheath has broken away to reveal the underlying structures. Scale bar, 5 mm.

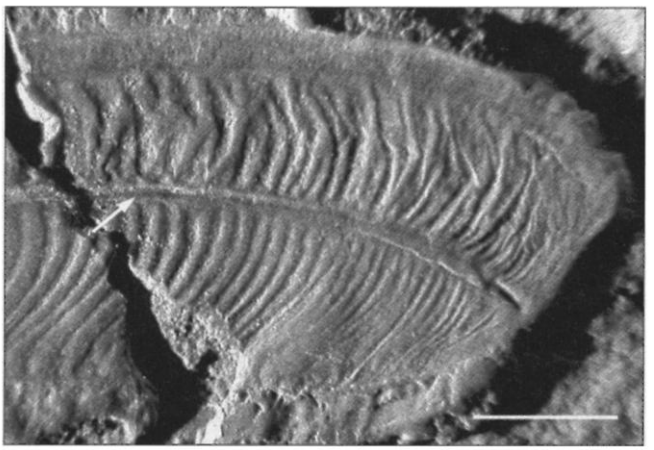

Fig. 4. The distal portion of the vane of *L. insignis* (PIN 2584/5). The arrow denotes where breakage reveals the hollow remnant of spongy air-filled pith of the central axis. Note the distal fusion of the pinnae at both the leading edge (**above**) and trailing edge (**below**) of the vane. Pinnae are clearly distinct from one another except where they are fused distally and where they join the central axis (*5*). Postmortem disturbance probably resulted in the apparent overlapping of some pinnae. Scale bar, 2.5 mm.

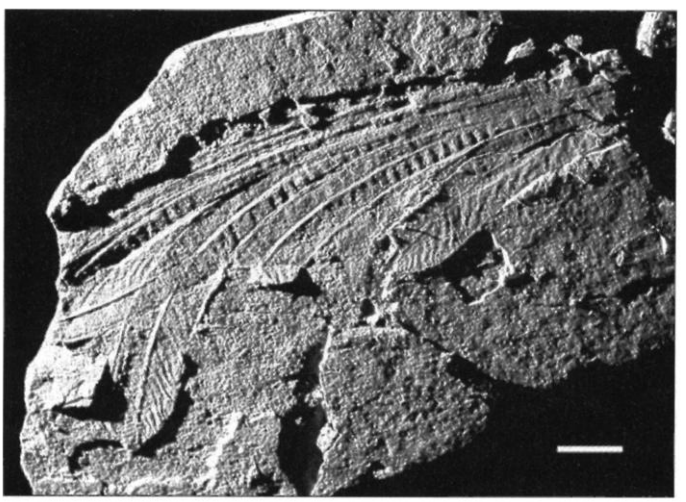

Fig. 5. Overlapped distal ends of elongate integumentary appendages in *L. insignis* (PIN 2584/9). Vanes were sufficiently delicate that the structure of underlying vanes remains visible. Scale bar, 5 mm.

The calamuslike anatomy of the base of *Longisquama*'s integumentary appendages may provide insight into their mode of development. Feathers form from the circular epidermal collar of a follicle. The invaginated base of the follicle houses a dermal papilla. This organization of the follicle is the defining developmental and morphological characteristic of feathers (*8*). In the mature feather, only the feather base or calamus remains tubular, so that it encloses the pulp caps, unique structures that result from regression of the dermal papilla during late feather growth (*8*). Consequently, the structure of the calamus is a signature of the complex developmental patterns distinct to feathers. Thus, it is particularly noteworthy that preservation of a follicular, calamuslike base in *Longisquama*'s appendages is consistent with a developmental pattern heretofore known only in avian feathers.

Both birds and *Longisquama* are archosaurians. Beyond this, the taxonomic status of *Longisquama* is poorly understood; thus, the relation between integumentary derivatives in birds and *Longisquama* remains unclear. Nevertheless, because feathers are perhaps the most complex derivatives of the integument in any vertebrate (*8*, *9*), we suggest that the combination of shared, specialized morphological characters (apomorphies) of avian feathers and the pinnate integumentary appendages in *Longis-*

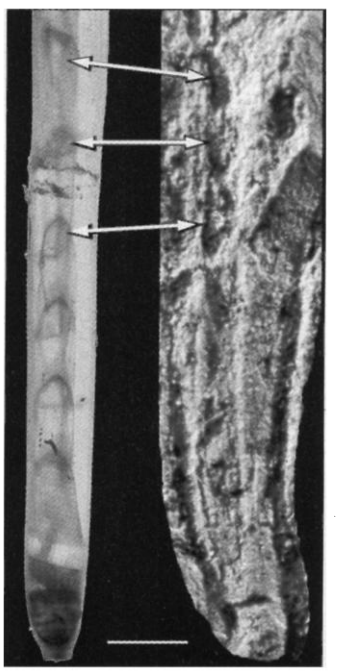

Fig. 6. Calamus of a green wing macaw (*Ara chloroptera*) tail feather (**left**) and one of the tubular bases of the elongate integumentary appendages of *L. insignis* (PIN 2584/4) (**right**). Arrows indicate pulp cavities. Scale bar, 2.5 mm.

quama were unlikely to have evolved more than once. Significantly, the development of *Longisquama*'s integumentary appendages probably followed complex specialized patterns previously thought to be distinct to avian feathers. Thus, we interpret the pinnate appendages of *Longisquama* as nonavian feathers, probably homologous to those in birds.

Archaeopteryx, the earliest known bird (145 Ma), possessed a complete plumage of flight feathers that differed little from those of many extant birds (*8*, *11*). Consequently, factors associated with earlier stages of feather evolution, the morphology of the earliest feathers, and the taxonomic groups in which they first occurred remain uncertain. Nevertheless, if *Longisquama*'s integumentary appendages are homologous with those of birds, they may provide insight into an evolutionary grade through which feathers passed almost 75 million years before *Archaeopteryx* and perhaps before the origin of Aves itself.

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4. All known specimens of *L. insignis* are part of the collection of the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). These include specimen number PIN 2584/4: the holotype specimen, slab (and counterslab) of the anterior portion of the body [see Figs. 1, 2, and 6 (right)]; PIN 2584/5: a partial single elongate integumentary appendage (no shaft base preserved) (Fig. 4); PIN 2584/6: the mid-regions of two incomplete elongate integumentary appendages; PIN 2584/7: a partial individual elongate integumentary appendage (no shaft base preserved); and PIN 2584/9: associated distal portions of approximately six incomplete elongate integumentary appendages (Fig. 5). We directly examined these specimens at the University of Kansas, Lawrence, in April 1999.
5. We interpret pinnae to have been distinct from one another, rather than merely plications on a continuous surface, for two reasons. First, the texture and color of the matrix composing the surfaces of the pinnae are qualitatively different from that of the matrix between the pinnae. In a continuous surface, matrix quality would have been more homogenous. Second, some pinnae appear to have been disturbed post-depositionally and are preserved in overlapped positions (Web fig. 2).
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10. The animal apparently was preserved in a quiet lacustrine environment. Some skeletal elements were preserved, but most of the right-side elongate integumentary appendages either floated away or rotated caudally. Their preservation probably resulted from infill by fine-grained sediment. Proximally, a few of the left-side shaft bases maintained themselves as hollow tubes that eventually fractured down their centers during compaction. The outer surface of the sheath was essentially featureless, although underlying compacted structures pressed outwardly against it. In the mid-shaft region, the axis and pinnae are sharply defined in places where parts of the epidermal sheath broke away during collection of the specimen. Preservation of the axis and individual pinnae in this region is consistent with there having been enough empty space within the sheath that, when filled with fine-grained mud, the morphology of the structures within was faithfully recorded.
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12. We thank S. Poitras, C. Campbell, S. Olson, and the Palaeontological Institute of the Russian Academy of Sciences for assistance in procurement of specimens. T. Dujsebayeva's English translation of Sharov's original paper, photographs of modern bird feathers by A. Brower, and J. Atkinson's assistance with juvenile birds were invaluable. Supported by an NSF grant to J.A.R. and W.J.H. and by a Russian Fund for Basic Research Grant to E.N.K. and V.A.

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A Metalloprotease Disintegrin That Controls Cell Migration in *Caenorhabditis elegans*

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In *Caenorhabditis elegans*, the gonad acquires two U-shaped arms by the directed migration of its distal tip cells (DTCs) along the body wall basement membranes. Correct migration of DTCs requires the *mig-17* gene, which encodes a member of the metalloprotease-disintegrin protein family. The MIG-17 protein is secreted from muscle cells of the body wall and localizes in the basement membranes of gonad. This localization is dependent on the disintegrin-like domain of MIG-17 and its catalytic activity. These results suggest that the MIG-17 metalloprotease directs migration of DTCs by remodeling the basement membrane.

Many new insights into the molecular mechanisms controlling cell migration have been gained by the genetic analysis of model organisms such as the nematode *C. elegans*. The shape of the *C. elegans* hermaphrodite gonad is determined by the migration path of the DTCs during larval development (*1*). DTCs migrate in a complex trajectory consisting of three linear phases punctuated by two orthogonal turns (Fig. 1, A and B). DTCs are generated at the ventral midbody and migrate in opposite directions along the basement membranes of ventral body wall muscles. Mutation of the *mig-17* gene alters DTC migration (*2*): initially, migration along the ventral body wall muscles is normal, but the migration path deviates from normal after the dorsal turn (Fig. 1C). In addition, these DTCs often detach from the dorsal muscles and migrate along the intestine or gonad. As a result of this misdirected migration, *mig-17* mutants exhibit morphologically abnormal gonadal arms (*3*). These results indicate that *mig-17* is not required for DTC migration per se, but rather influences the route of migration.

A similar defect is observed in the male gonad of *mig-17* mutant worms. In wild-type worms, the male linker cell (MLC) migrates anteriorly, then reflexes and migrates to the posterior end of the worm (Fig. 1, D and E) (*1*). In *mig-17* mutants, the MLC fails to migrate correctly (Fig. 1F). However, mutation of *mig-17* does not affect the migration of other cell types such as HSN neurons and Q neuroblasts (*2*). Therefore, *mig-17* does not affect cell migration generally, but rather is required specifically for the correct migration of gonadal leader cells.

We cloned the *mig-17* gene by positional mapping followed by transformation rescue (*4*). Fragments containing only the F57B7.4 gene rescued *mig-17(k174)*. The *mig-17* gene encodes a single protein of 509 amino acids length (Fig. 2A). The MIG-17 protein is a member of the metalloprotease-disintegrin protein (ADAM) family (*5*). It contains a signal sequence followed by a pro-domain, a catalytic domain, a disintegrin-like (DI) domain, and a cysteine-rich domain (Fig. 2B). MIG-17 also lacks a transmembrane domain, suggesting that it is secreted. Comparison with the ADAM family members indicates that MIG-17 is most similar to the mouse ADAMTS-1 (*6*). The metalloprotease and DI domains are relatively well conserved (Fig. 2A). However, the domain organization in the COOH-terminal region following the DI domain of ADAMTS-1 diverges from that of MIG-17 in that ADAMTS-1 possesses the thrombospondin type I motif (*6*), whereas MIG-17 does not.

We sequenced four *mig-17* mutant alleles

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