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ON THE STRUCTURE AND HOMOLOGY OF THE TAIL BRISTLES OF *PSITTACOSAURUS*

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Abstract: We examined bristle-like appendages on the tail of the Early Cretaceous basal ceratopsian dinosaur *Psittacosaurus* with laser-stimulated fluorescence imaging. Our study reveals previously unknown details of these structures and confirms their identification as integumentary appendages. For the first time, we show that most bristles appear to be arranged in bundles and that they exhibit a pulp that widens towards the bristle base. We consider it likely that the psittacosaur bristles are structurally and developmentally homologous to similar filamentous appendages of other dinosaurs, namely the basal heterodontosaurid *Tianyulong* and the basal therizinosauroid theropod *Beipiaosaurus*, and attribute the greater robustness of the bristles of *Psittacosaurus* to a higher degree of cornification and calcification of its integument (both skin and bristles). Although the psittacosaur bristles are probably homologous to avian feathers in their origin from discrete cell populations, it is uncertain whether they developed from a follicle, one of the developmental hallmarks of true feathers. In particular, we note a striking resemblance between the psittacosaur bristles and the cornified spine on the head of the Horned Screamer, *Anhima cornuta*, an extant anseriform bird. Similar, albeit thinner keratinous filaments of extant birds are the "beard" of the Turkey, *Meleagris gallopavo*, and the crown of the Congo

Peafowl, *Afropavo congensis*. All of these structures of extant birds are distinct from true feathers, and because at least the turkey beard does not develop from follicles, detailed future studies of their development would be invaluable towards deepening our understanding of dinosaur filamentous integumentary structures.

Running Head: Psittacosaur tail bristles

Key words: ceratopsian dinosaur, feather evolution, laser-stimulated fluorescence imaging, *Psittacosaurus*, tail bristles

DINOSAURIA comprises two major clades, Saurischia and Ornithischia, with birds being nested in the saurischian subclade Theropoda. In the past two decades, filament-like integumentary appendages were reported from a variety of non-avian dinosaurs. Many of these structures stem from theropods, so that homology with avian feather precursors ("protofeathers") is likely (e.g., Chen *et al.* 1998; Xu *et al.* 1999a, b, 2012, 2014). A number of specimens with unusual integumentary structures are, however, also known from dinosaurian groups that are only distantly related to birds.

One of the most remarkable instances concerns a fossil of the basal ceratopsian ornithischian *Psittacosaurus* from the Early Cretaceous Jehol Biota of China in the collection of the Senckenberg Research Institute. This specimen preserves most of the skin in exceptional detail and is most unique because of long bristle-like appendages on the proximal portion of the tail (Fig. 1). This psittacosaur fossil represents one of the first non-avian dinosaurs, for which integumentary appendages have been reported (Mayr *et al.* 2002), and it was the first ornithischian, for which integumentary structures other than scales were described.

Mayr *et al.* (2002) noted differences between the psittacosaur bristles and the filamentous theropod "protofeathers" known at that time and cautioned against considering them to be homologous. Filamentous integumentary appendages were subsequently reported from two other ornithischian taxa, the Early Cretaceous basal heterodontosaurid *Tianyulong* (Zheng *et al.* 2009) and the Middle-Late Jurassic basal neornithischian *Kulindadromeus* (Godefroit *et al.* 2014; Alifanov and Saveliev 2014). The hypothesis that these structures are homologous to avian feathers has been put forward by multiple authors (Xu *et al.* 2009; Godefroit *et al.*

2014), but most recently it was suggested that that filamentous integumentary appendages might have evolved independently in theropods and ornithischians (Barrett *et al.* 2015).

The psittacosaur bristles shown here are arguably amongst the best preserved integumentary appendages of any non-avian dinosaur, but they have only been briefly described and their significance has yet to be fully appreciated. This fossil has therefore been restudied with laser-stimulated fluorescence (LSF) imaging, a powerful tool for the analysis of fossil soft tissue (Kaye *et al.* 2015). The results for the skin will be described elsewhere (Vinther *et al.* in press) and here we focus on a detailed description of the tail bristles.

Given that the named species of *Psittacosaurus* mainly differ in skull proportions, which are difficult to evaluate in the crushed Senckenberg specimen, and that the taxonomy is currently in flux with various species being synonymized (Hedrick and Dodson 2013), we refrain from identifying the fossil at the species level. Three species of *Psittacosaurus* have been described from the Lujiatun Beds of the Yixian Formation (You *et al.* 2003; Zhou *et al.* 2006; Lü *et al.* 2007). These are now considered to be growth stages of the same species, for which *Psittacosaurus houi* has nomenclatural priority (Hedrick and Dodson 2013). Although the exact provenance of the Senckenberg psittacosaur is unknown, the sedimentology of the matrix, which consists of a finely laminated mudstone, indicates that it is not from the tuffaceous Lujiatun Beds (*contra* Sereno 2010: 22), but from the Dawangzhangzi or Jiangshou beds of the Yixian Formation, or even from the overlying Jiufotang Formation, so that an identity with *P. houi* ("*P. lujiatunensis*" *sensu* Sereno 2010: 28) is anything but certain.

MATERIAL AND METHODS

The psittacosaur fossil is on public display at the Senckenberg Natural History Museum, Frankfurt am Main, Germany (SMF), where it is catalogued under the number SMF R 4970. LSF imaging was performed with a custom device (KayeT Scanner 3.0). A 405 nanometer, 500 milliwatt violet laser was interfaced with a Powel line lens, which projected an even vertical line across the specimen that was scanned horizontally by a motor assembly. Photos were taken with a Nikon D810 camera, with a 425 nanometer long pass filter in front of lens that blocked the laser light. Images were post processed and the bright fluorescence of dust particles embedded in the specimen's lacquer coating was removed by specific colour subtraction during conversion from the NEF image.

RESULTS

Most bristles extend beyond the margin of the fossil slab and lack their tips, with the bristle tuft having therefore been larger than what is preserved (Fig. 2B). The LSF images allow most of the individual bristles to be traced such that the bases of 91 bristles can be distinguished, which is probably a slightly underestimated number given that not all bristle bases are clearly discernible. The fluorescent colour of the bristles matches that of the skin remains (see also Vinther *et al*. in press: Fig. S3).

For the first time, we note that the bristles are not evenly distributed along the dorsum of the tail, and many are arranged in clusters of 3-6 individual bristles, which appear to have been tightly grouped at their bases (Fig. 2). Most bristles have a width of about 1 mm at their bases, but the bristles in the distal tail section are thinner than the more proximal ones. Some thinner bristles also occur in the proximal section of the tail, and these are more strongly bent or erupted from the skin at a lower angle (Figs 2, 3D, E). These narrow bristles are fairly evenly distributed over the proximal bristle section, with most bristle bundles containing 2-3 narrow bristles. Many of the narrow bristles are short and may represent growing bristles. However, there are also several very long and narrow bristles, some of which have an equal width throughout their length, whereas others become gradually wider towards the base. The preserved bristle tips seem to have been blunt rather than sharply pointed.

In their initial description, Mayr *et al.* (2002) reported midline stripes in some bristles, which were considered to differ in width, but the authors did not adequately distinguish between what appear to be three different origins and preservation modes of these stripes. The LSF images of SMF R 4970 reveal that a lighter-fluorescing midline stripe is an attribute of most bristles. This midline stripe becomes wider towards the bristle base and suggests a pulp, that is, a bristle lumen (Figs 3B-D, 4E, F), which may have been filled with connective tissue as in the spine of the extant Horned Screamer (see discussion and Fig. 4D). In some bristles, the midline stripe is furthermore defined by dark, organic material visible under natural light (Figs 3E, 4F; Mayr *et al.* 2002: fig. 3), which appears to be due to infilling with recalcitrant organic material. These midline stripes, which seem to be a property of all bristles, are to be distinguished from broad dark stripes, which extend over most of the bristle width in a few bristles (Fig. 3F). These broad dark stripes do not fluoresce under LSF, and here we hypothesize that they represent melanin deposits within the keratin matrix, similar to those found on the integumentary scales in the same specimen.

Three bristles in the most proximal area of the tail extend well into the preserved integument and reach the vertebral bodies (Fig. 3G), and Mayr *et al.* (2002) posited that they may have been anchored deeply in the skin. However, the skin on the dorsal side of the tail does not follow the course of the neural spines and the fossilized integument probably does not reflect the exact tail outline of the animal (Fig. 2). Because the skin covered the skeleton after the decay of the muscular soft tissue, it is likely to have been displaced relative to the original body contour. In addition, the fossil appears to have been compacted in an oblique embedded position. A skin flap may therefore conceal the bristle bases in the proximal tail section, which, even in comparison with modern feathers, would be anchored unusually deep in the skin. Here, we consider it uncertain how deeply the psittacosaur tail bristles extended into the skin if at all.

We furthermore note that preparation after the initial description of the specimen revealed soft tissue remains next to the jugal horn, which are suggestive of a keratinous sheath (Fig. 3H). The presence of such a sheath in the living animal can be deduced from numerous vascular grooves on the surface of the jugal horn (Sereno 2010). However, although the dark soft tissue structure that is now situated underneath the jugal horn of SMF R 4970 matches the presumed shape of a keratinous sheath, it is significantly larger than the jugal horn itself. Moreover, these soft tissue remains do not cover the bony jugal horn but are situated beneath (i.e., anatomically dorsal) and rostrally of it, so that the keratinous sheath must have slipped off the bony core, if it fully enclosed the jugal horn. Given the otherwise reasonably undistorted nature of the skeleton, a removal of the sheath from the jugal horn is difficult to explain, as keratinous sheaths – like teeth - are rigidly attached to bone via Sharpey's Fibers, which are mostly collagen-based (e.g., Horner and Goodwin 2009). However, protein decay of such fibers combined with cracking of the sheath as a result of keratin degradation could have led to a split jugal horn sheath that no longer attached to the bone.

DISCUSSION

LSF imaging confirms that the fluorescent colour of the bristles matches that of the skin remains. Given that laser-stimulated fluorescence closely reflects the geochemistry of the involved structures (Kaye *et al.* 2015), we conclude that the fossilized bristles and the skin have a similar geochemical composition. The skin of the specimen shows an equal fluorescence across the body (Vinther *et al.* in press: Fig. S3), and we consider it more likely that the preserved soft tissue remains represent remains of the keratinous epidermis rather

than collagen fibers of the dermis (*contra* Feduccia *et al.* 2005). This assumption is also supported by the fact that in many cases clearly defined scales are visible (Vinther *et al*. in press: Fig. S3). Unlike chemically more stable polysaccharids (e.g., chitin and cellulose) and lipids (e.g., waxes), keratins of the vertebrate integument are proteins, meaning they have a low fossilization potential (Briggs and Summons 2014). We therefore hypothesize that preservation of the psittacosaur integument, in both the scales and bristles, is potentially due to calcium phosphate residues from embedded mineral salts, which are commonly found in vertebrate epidermis (Pautard 1964). Collagen fibers, by contrast, are unlikely to calcify across the entire integument, and no preservational mechanisms are known to us that would result in an extensive preservation of collagen in the absence of other protein-based soft tissue structures, such as internal organs.

A strongly calcified epidermal integument would not only account for the exceptional preservation of the skin in this psittacosaur specimen and others from the Jehol Biota (Ji and Bo 1998), but also for its distinct fluorescence under LSF. Claw sheaths are similarly preserved in many specimens of *Archaeopteryx* (Wellnhofer 2009) and *Confuciusornis* (Chiappe *et al.* 1999), which is also true for the rachises of feathers of some fossil birds (Bergmann *et al.* 2010). By contrast, most dark soft tissue traces seen under naturally occurring light in the psittacosaur fossil that do not fluoresce under LSF are carbonaceous residues derived from melanin pigmentation (Vinther *et al.* in press).

The soft tissue remains of the jugal horn show no fluorescence under LSF, which indicates that they exhibit a different geochemistry than the skin and bristles. Possibly, the calcium phosphate residues of the keratinous sheath are masked by layers of non-fluorescing melanin, although we currently cannot exclude the possibility that the soft tissue remains preserved underneath and next to the jugal horn are remains of a skin flap, which was situated dorsal of the jugal horn.

Our study therefore confirms previous hypotheses that the tail bristles of *Psittacosaurus* were epidermal appendages. The fact that some bristles are very thin and most appear to be arranged in bundles would make them poor support structures of a membranous frill for which we find no preserved evidence (contra Lingham-Soliar 2010).

Compared with the known integumentary appendages of other non-avian dinosaurs, the bristles of SMF R 4970 most closely resemble the "elongated broad filamentous feathers" of the basal therizinosauroid *Beipiaosaurus* (Xu *et al.* 2009) in their shape and presumed rigidity. In *Beipiaosaurus*, these structures are, however, more widely distributed over the body surface, occurring along the dorsal and ventral sides of the neck, as well as on the back

of the animal and in the distal tail section. Greatly elongated filament-like appendages were also found in the basal heterodontosaurid *Tianyulong* (Zheng *et al.* 2009). The filaments of *Tianyulong* are somewhat narrower than most psittacosaur bristles and appear to have been less rigid, but like many of the *Psittacosaurus* bristles, they exhibit a dark melanized midline stripe (Zheng *et al.* 2009: fig. 2d) and are particularly long in the proximal section of the tail, with filaments being absent on the distal portion of the *Tianyulong* tail. Unlike in *Psittacosaurus*, shorter filamentous appendages are also found along the ventral and dorsal sides of the neck of *Tianyulong*. As noted by Godefroit *et al.* (2014), the monofilamentous integumentary structures associated with the ornithischian *Kulindadromeus* are shorter and thinner than those of *Psittacosaurus*.

A distinctive feature of the *Psittacosaurus* tail bristles is their thickness and apparent rigidity. This unusual robustness is likely to be correlated with a high overall degree of cornification of the skin of psittacosaurs, which seems to have been very thick (Feduccia *et al.* 2005). The presumed high degree of calcification of the keratin probably also accounts for the preservation of the light brown bristles of SMF R 4970 as structures with some degree of preserved topography, whereas the darker integumentary appendages of *Beipiaosaurus*, *Tianyulong*, and other dinosaurs from the Jehol Biota usually represent very thin layers of melanin residues (Li *et al.* 2010; Zhang *et al.* 2010), which show very little to no fluorescence under LSF.

Psittacosaur fossils are not uncommon in the Jehol Biota, but tail appendages have so far only been reported from SMF R 4970. With a skull length of about 18 cm, this specimen is one of the largest psittacosaurs known from the Jehol Biota, and long bristles may therefore have been a feature of mature animals. Because of their restriction to only a small part of the body, we consider it unlikely that the psittacosaur bristles fulfilled the same function as maniraptoran "protofeathers", which seem to have covered the entire body and may have served to insulate the body of these animals. Mayr *et al.* (2002) assumed a possible display or signaling function of the psittacosaur tail bristles, but did not elaborate this hypothesis further. An origin for display has subsequently also been assumed for filamentous integumentary structures in other non-avian dinosaurs (e.g., Xu *et al.* 2009). Our interpretation of the wide dark stripes along some of the bristles (Fig. 3F) as probable melanin residues indicates a former colour pattern and corroborates the hypothesis of a display function, which was also assumed for the similar appendages of *Beipiaosaurus* (Xu *et al.* 2009). If the psittacosaur bristles evolved for display, these structures could have served for silhouette enlargement of the animal, similar to the mane on the back of many mammals or the scale-derived dorsal

spines of various squamates, such as the Green Iguana (*Iguana iguana*) and the Marine Iguana (*Amblyrhynchus cristatus*; Eibl-Eibesfeldt 2008). Mammalian manes usually have an intraspecific signaling function (e.g., Nagel *et al.* 2003; Yamaguchi *et al.* 2004) and either increase male attractiveness to females, or are found in social species that engage in territorial or courtship combats (e.g., hyenas and many artiodactyls). Psittacosaurs were gregarious animals (Zhao *et al.* 2007) and intraspecific combats appear to have been common in ceratopsians (Farlow and Dodson 1975), so that a display or signaling function of the psittacosaur bristles remains a viable hypothesis. The occurrence of elongated filaments in the same tail regions of the ornithischian taxa *Psittacosaurus* and *Tianyulong* is remarkable and may indicate that a pronouncement of the dorsal ridge of the tail base played a role in the social or sexual behavior of these animals.

Some earlier authors already hypothesized that avian feathers developed from monofilamentous integumentary appendages (e.g., Schorger 1957), and after discovery of such filaments in maniraptoran theropods, detailed evolutionary models for the origin of feathers from monofilamentous structures were proposed (Prum and Brush 2002). Genetic studies furthermore showed that most regulatory elements associated with feather development appear to have been present in non-avian dinosaurs (Lowe *et al.* 2014), although some of the feather β-keratins occurred late in avian evolution (Greenwold and Sawyer 2011). Therefore, the integument of the last common ancestor of psittacosaurs, heterodontosaurids, and therizinosauroids – at the node Dinosauria – most likely had the potential to produce filamentous or bristle-like appendages, which are homologous to avian feathers in their developmental origin from discrete cell populations. This is so much the more true, if "reptilian" scales, mammalian hair, and avian feathers indeed have a common developmental origin, as has recently been proposed (Di-Poï and Milinkovitch 2016). Still, the psittacosaur bristles are much longer and more rigid than the integumentary appendages of maniraptoran theropods. Because the integument of some extant birds produces filament-like appendages which are structurally and developmentally different from feathers (see below), we recommend reservation in calling the appendages of *Psittacosaurus* and other ornithischians "feathers" (*pro* Barrett *et al.* 2015; *contra*, e.g., Xu and Guo 2009; Godefroit *et al.* 2014).

Sawyer *et al.* (2003a) noted that the filamentous integumentary appendages found in non-avian dinosaurs show a resemblance to the "beard" in the breast region of turkeys (*Meleagris gallopavo*) (Fig. 4A). Unlike feathers, these bundles of keratinous filaments do not develop from follicles, but from epidermal papillae (Schorger 1957; Lucas and Stettenheim 1972). The bristles of the turkey beard exhibit a lumen (which can be filled with connective tissue), are

devoid of barbs, and are tightly connected at their bases, which are features shared with the integumentary appendages of psittacosaurs. We consider it probable that, like the turkey beard, the psittacosaur bristles were continuously growing, whereas feathers have a terminated growth phase. Filamentous integumentary appendages resembling the turkey beard also occur on the head of the male Congo Peafowl, *Afropavo congensis* (Fig. 4C), with these rigid and unbranched bristles being different from the feather crown of the Indian Peafowl (*Pavo cristatus*) and other pheasants. The psittacosaur bristles are proportionally much wider than the filaments of the turkey beard and the crown of the Congo Peafowl, but, as noted above, their unusual thickness may be the result of a strong cornification and calcification of the psittacosaur skin.

With regard to their thickness, the psittacosaur bristles are a closer match to the cornified spine on the head of another bird, the Horned Screamer, *Anhima cornuta* (Fig. 4B). This epidermal outgrowth is sometimes erroneously considered to be a modified feather shaft (Carboneras 1992), but unlike feathers the *Anhima* spine shows continuous growth and is a brittle structure (Stettenheim 2000). The *Anhima* spine furthermore has a pulp, which, unlike the pulp of true feathers, is infilled with dense connective tissue (Fig. 4D). Ontogenetic data on its development seem to be lacking, but even in chicks, it forms a cylindrical structure that is clearly distinguished from the surrounding feathers (GM, pers. obs.).

The exact evolutionary transition of dinosaurian filaments into true feathers is poorly known, not least because data on the ontogenetic development of these structures in fossil taxa is lacking. In particular, it is unknown, when a follicle evolved, which is one of the major developmental characteristics of feathers. In Prum and Brush's (2002) model of feather evolution it is assumed that follicles, that is, invaginated epidermis surrounding early ontogenetic feather filaments, were already present in the initial, filament-like stages of feather evolution. However, as exemplified by the turkey beard, follicles are not requisite for the development of filamentous integumentary appendages, and it is possible that their origin coincides with that of barb ridges, which are a key characteristic of modern-type, branched feathers. This hypothesis corresponds with ontogenetic evidence that "[d]eveloping feathers of modern birds first produce an embryonic feather filament […] prior to making a follicle" (Sawyer *et al.* 2003b: 20).

It is notable that, amongst extant birds, filamentous structures that are not highly modified feathers (such as eyelashes and filoplumes) only occur in the basally diverging clade Galloanseres. Although their ontogenetic development deserves future scrutiny, we consider it possible that they develop through a heterochronic process from feather primordia before

invagination of a follicle occurs (Yu *et al.* 2004), which is certainly the case for the turkey beard (as noted above, developmental data on the *Anhima* spine and the *Afropavo* crown are lacking). Similarly, monofilamentous structures in non-avian dinosaurs may go back to filament primordia before the evolutionary origin of follicles, in which case they would not be "feathers" *sensu* Prum and Brush (2002).

While recent fossil finds and developmental studies suggest an evolutionary origin of integumentary appendages homologous to feathers deep within Dinosauria, the potential resemblance of the psittacosaur bristles to non-feather integumentary structures in extant birds may indicate that these structures were still fundamentally different from true feathers. That the genetic pathways for integument formation in ornithischians substantially differed from those of theropods is suggested by the fact that the trunk skin of ornithischians can form both filaments and scales. In birds and non-avian maniraptoran theropods, by contrast, scales only occur on the feet (e.g., Foth *et al.* 2014), whereas the trunk is entirely clad in filaments or feathers.

Here we posit that the turkey "beard", the crown of *Afropavo*, and the cornified spine of *Anhima* are the closest integumentary equivalents of the psittacosaur bristles among extant vertebrates. The turkey beard has previously been compared with the integumentary appendages of non-avian dinosaurs, albeit not with those of *Psittacosaurus* (Sawyer *et al.* 2003a), and its histology and ontogenetic development has been studied in detail (Schorger 1957; Lucas and Stettenheim 1972). Our identification of the *Afropavo* crown and the *Anhima* spine as possible developmental homologues to the psittacosaur bristles is novel, but unfortunately no data on the ontogenetic development of these structures are currently available. As such, future studies of both these structures would be invaluable towards deepening our understanding of dinosaur filamentous integumentary structures.

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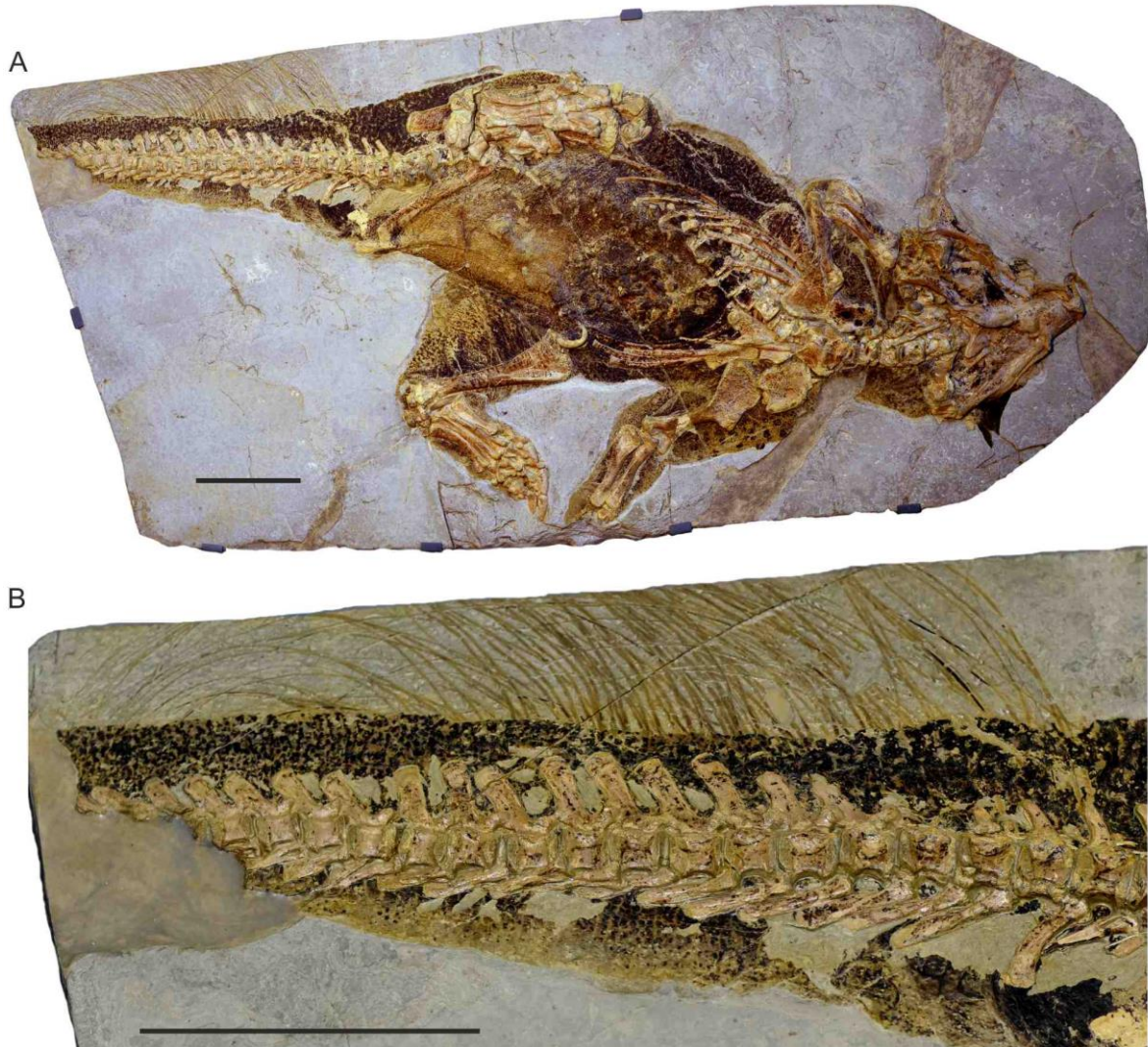
Fig. 1. *Psittacosaurus* sp. from the Early Cretaceous Jehol Biota of China (SMF R 4970). A, Overview of specimen. B, Detail of tail section with bristles. The scale bars represent 10 cm.
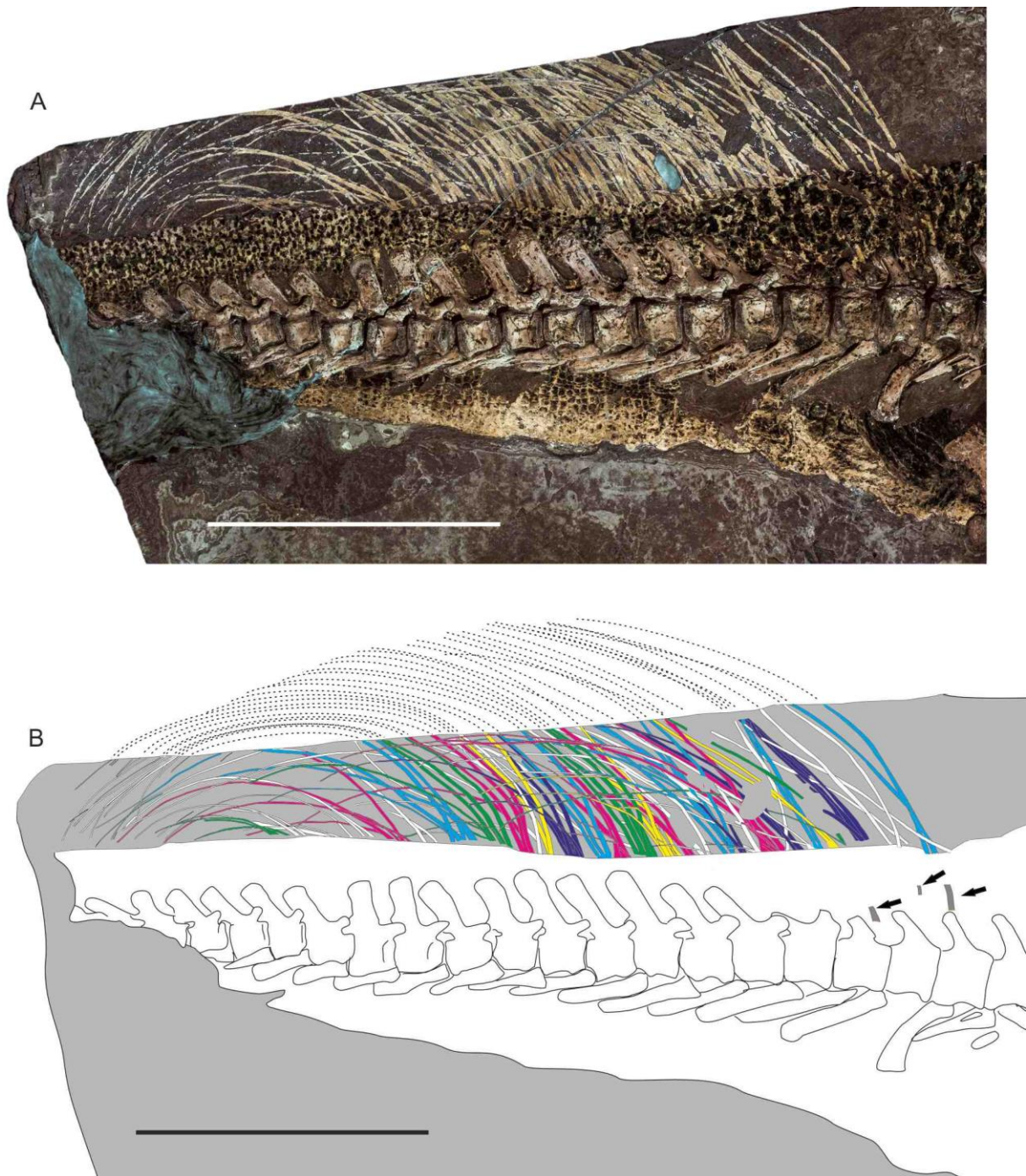
Fig. 2. A, LSF image of the *Psittacosaurus* tail section (SMF R 4970). Areas that were restored with artificial resin show a turquoise blue fluorescence. B, Interpretive and schematic drawing of the bristles. Presumed bristles bundles are coloured, whereas individual bristles and those that could not be unambiguously traced are shown in white. The dashed lines reconstruct the missing bristle portions, with their hypothetical lengths having been deduced from those of the complete bristles in the distal tail section. The arrows point to three bristle bases that appear to extend deeply into the integument (also shown in Fig. 3G). The scale bars represent 10 cm.
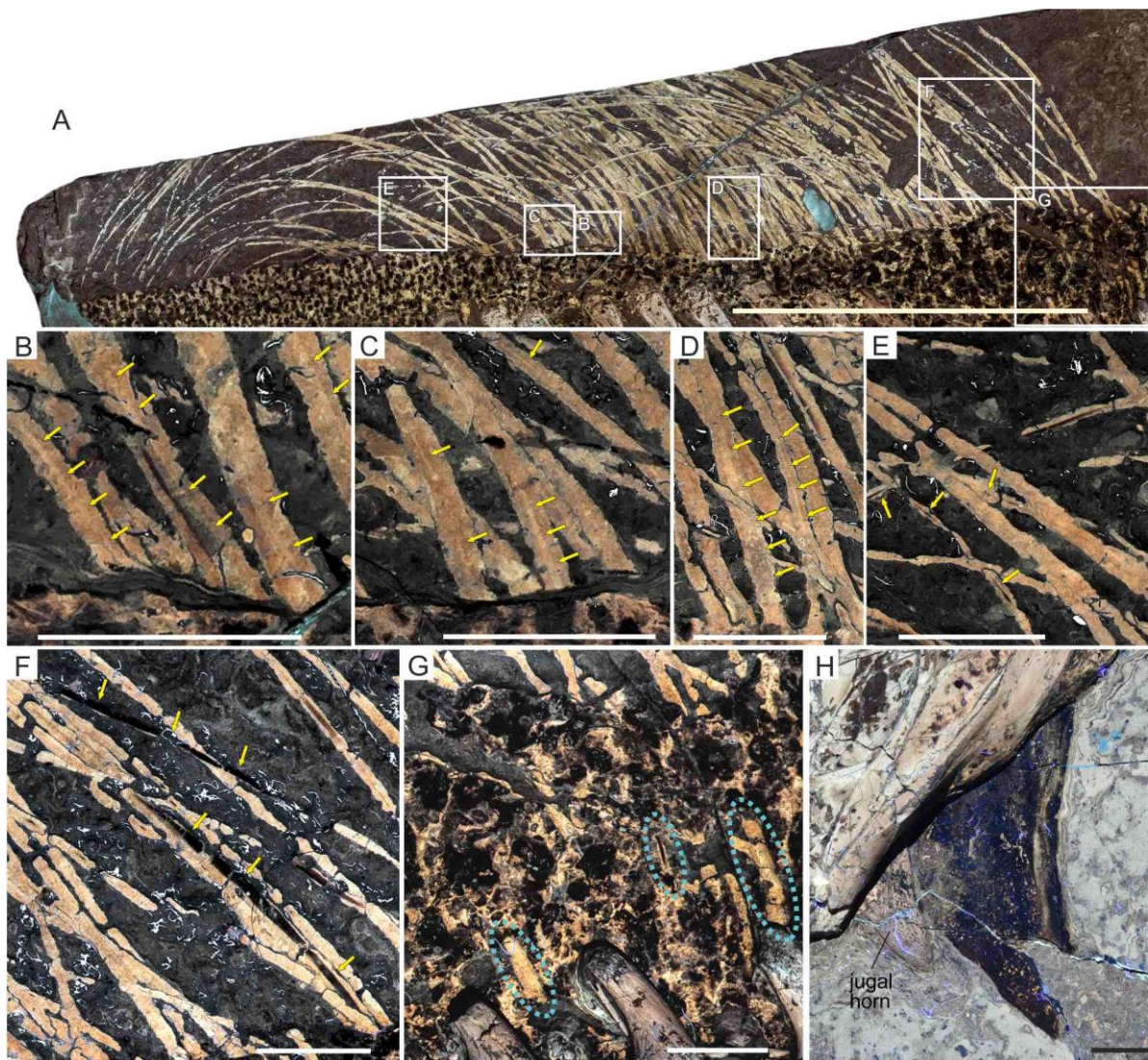
Fig. 3. LSF images of details of the *Psittacosaurus* integument (SMF R 4970). A, Bristle section of tail, with white frames indicating the position of the details shown in B-G. B-D, Bases of bristle clusters, with bristles featuring bright, fluorescing midline stripes (arrows), which are here considered to be indicative of a pulp. E, Bristle section with bristles showing dark (i.e., non-fluorescing) midline stripes interpreted to be organic infillings of the pulp (arrows). F, Bristle section with bristles showing wide dark stripes interpreted to be melanin (arrows). G, Three bristle bases that extend into the preserved integument (dashed circles). H, Dark soft tissue remains preserved beneath and next to the jugal horn. The scale bar represents 10 cm for A and 10 mm for B-H.
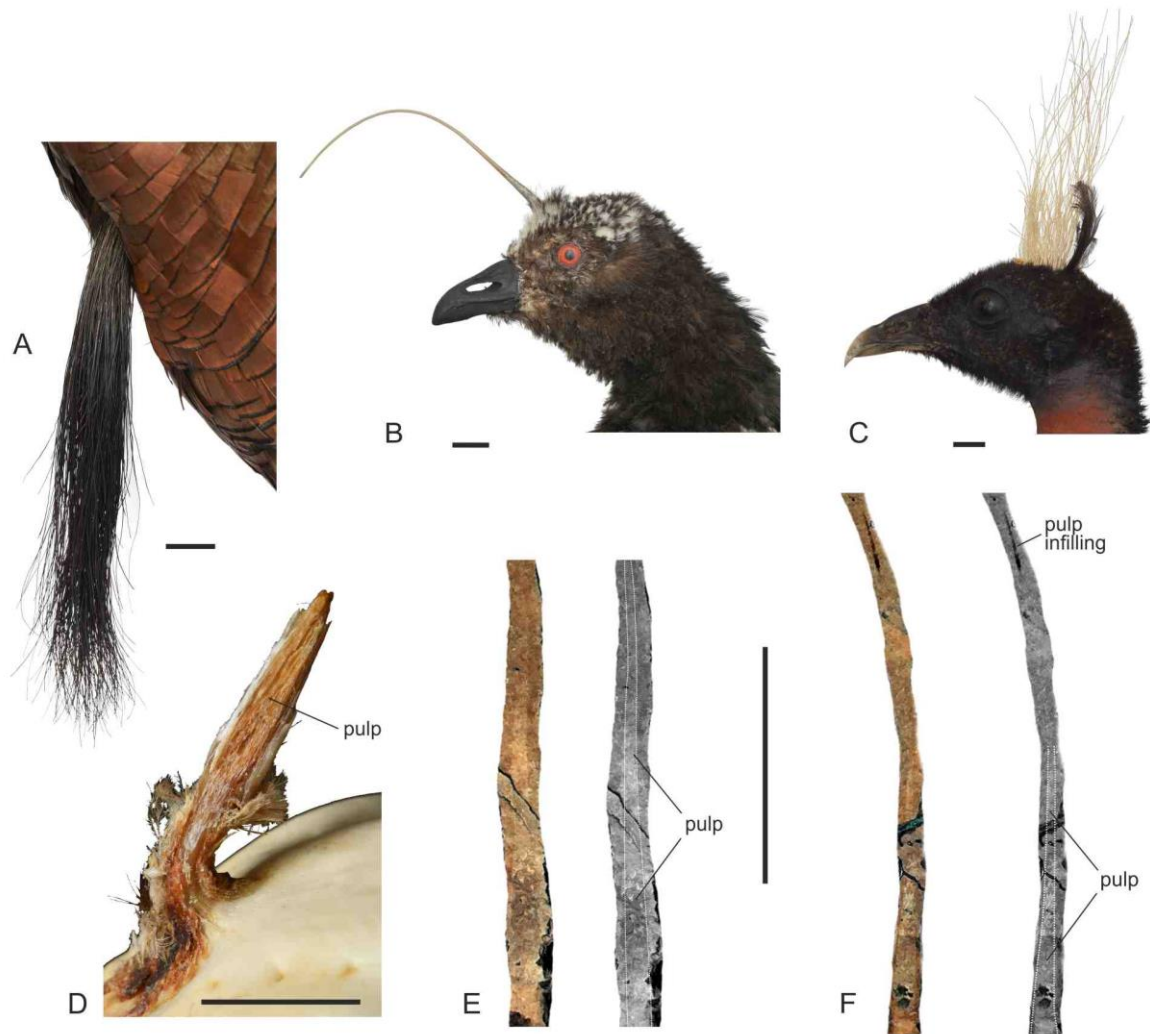
Fig. 4. A, The "beard" of the Turkey, *Meleagris gallopavo* (Galliformes; uncatalogued mounted specimen on display in Senckenberg Natural History Museum). B, The spine on the head of the Horned Screamer, *Anhima cornuta* (Anseriformes; uncatalogued mounted specimen on display in the Senckenberg Natural History Museum). C, Bristles on the head of the Congo Peafowl, *Afropavo congensis* (Galliformes; uncatalogued mounted specimen on display in Senckenberg Natural History Museum). D, Detail of longitudinal section through the base of an *Anhima* spine attached to a macerated skull (SMF 2479) to show the pulp, which is infilled with dense connective tissue; the tip of this spine is broken. E, F, Detail of two psittacosaur bristles with pulp indicated by dashed lines in the greyscale images to the right. The scale bars represent 10 mm.