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SHORT COMMUNICATION

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Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*

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Abstract A specimen of the horned dinosaur *Psittacosaurus* from the early Cretaceous of China is described in which the integument is extraordinarily well-preserved. Most unusual is the presence of long bristle-like structures on the proximal part of tail. We interpret these structures as cylindrical and possibly tubular epidermal structures that were anchored deeply in the skin. They might have been used in display behavior and especially if one assumes that they were colored, they may have had a signal function. At present, there is no convincing evidence which shows these structures to be homologous to the structurally different integumentary filaments of theropod dinosaurs. Independent of their homology, however, the discovery of bristle-like structures in *Psittacosaurus* is of great evolutionary significance since it shows that the integumentary covering of at least some dinosaurs was much more complex than has ever been previously imagined.

Introduction

Filamentous integumentary structures have been described in a number of theropod dinosaurs from the early Cretaceous of China and have been considered to be possibly homologous to avian feathers (Chen et al. 1998; Xu et al. 1999a, b, 2000, 2001; Ji et al. 2001). Similar structures are, however, unknown in non-theropod dinosaurs concerning whose integument little is known. The discovery of bristle-like protrusions at the tail of an extraordinarily well-preserved specimen of a psittacosaur (parrot-beaked dinosaur) from the early Cretaceous of Liaoning Province in China has attracted much recent attention (Buffetaut 2001; Dalton 2001a, b; Stokstad 2001), because psittacosaurs rank among the Ceratopsia (horned dinosaurs), which occupy a phylogenetic position far removed from theropod dinosaurs (Sereno 1990, 1999). Here we give a first formal description of these structures.

We are aware of the controversial debate concerning the legal ownership of this and other Chinese fossils (Dalton 2001a). However, arrangements concerning its repatriation to China have not yet proved successful (Dalton 2001a), and this important specimen was acquired in order to prevent its sale into private hands and to ensure its availability for future scientific examination. Since much unauthorized information on the specimen has already been widely published (Buffetaut 2001; Dalton 2001a, b; Stokstad 2001), we feel obliged to correct some statements and to describe the most important features, in order to prevent speculation. The fossil was originally offered for sale at a fossil fair in Tucson, USA. After an odyssey through Europe (Dalton 2001a), it finally came to Forschungsinstitut Senckenberg where it is currently inventoried; comments on its price are inappropriate.

Although some specimens from Liaoning have been shown to be forgeries (Simmons 2000), this possibility can be safely excluded for the integumentary structures in the *Psittacosaurus* specimen described in this study. Much of the preparation was done before we obtained the specimen, but some of the best preserved parts of the integument were prepared at Forschungsinstitut Senckenberg prior to which they were completely covered with sediment. This is also true for the ends of some of the tail "bristles".

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Systematic paleontology

Ornithischia Seeley 1888

– Ceratopsia Marsh 1890
– Psittacosauridae Osborn 1924
– *Psittacosaurus* sp.

Fig. 1 Skeleton of *Psittacosaurus* sp. with bristle-like integumentary structures at the tail (specimen SMF R 4970, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany). The skeleton is seen from its ventral side, the *frames* indicate the position of the details seen in Figs. 2a and b

Referred specimen

SMF R 4970, a largely complete and well-preserved skeleton exposed from its ventral side (Fig. 1), which is deposited in Forschungsinstitut Senckenberg, Frankfurt am Main, Germany. There are ongoing negotiations concerning repatriation of the specimen to China which have, however, not been finalized at the time this manuscript was accepted for publication.

Locality and geological setting

The exact locality within Liaoning Province in which the specimen was found is unknown; most likely, however, it comes from the Yixian Formation of Sihetun near Beipiao City where other psittacosaurs and many of the "feathered" theropods were found (Chen et al. 1998; Xu and Wang 1998; Xu et al. 1999a, b). Also known from this locality are psittacosaur specimens with remains of skin impression (Ji and Bo 1998). There is general agreement that the *Psittacosaurus*-bearing localities in Liaoning Province are early Cretaceous in age (Xu and Wang 1998).

Description

The skeleton of *Psittacosaurus* is sufficiently well known, and the osteology of the new specimen in Forschungsinstitut Senckenberg will be described in detail elsewhere. Derived features supporting an assignment to the genus *Psittacosaurus* are the presence of a bulbous primary ridge on the dentary crown and the reduction of the fourth and fifth manual digit (Sereno 1990). As in *Psittacosaurus sinensis* there is a strongly laterally protruding horn on the jugal. From Liaoning Province, three species of the genus *Psittacosaurus* have been reported; *Psittacosaurus mongoliensis*, *P. meileyingensis*, and an as yet unnamed taxon (Sereno et al. 1988; Sereno 1990; Xu and Wang 1998). Unfortunately, the skull is exposed from its ventral side and since important diagnostic species-level characters are thus not clearly visible, a reliable assignment to any of the fairly similar psittacosaurid species is difficult and depends on further preparation of the specimen.

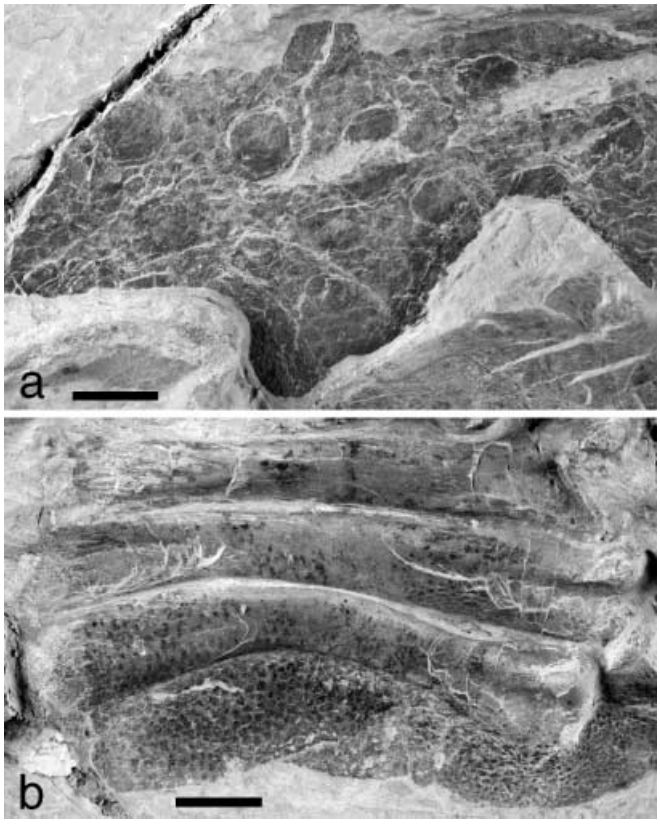

Fig. 2 a Detail of the skin preservation of the left shoulder. **b** Detail of the skin preservation at the left foot. The *scale bars* equal 10 mm

In the area of the former stomach numerous gastroliths can be discerned which are also known from other specimens of the herbivorous psittacosaurs (Sereno

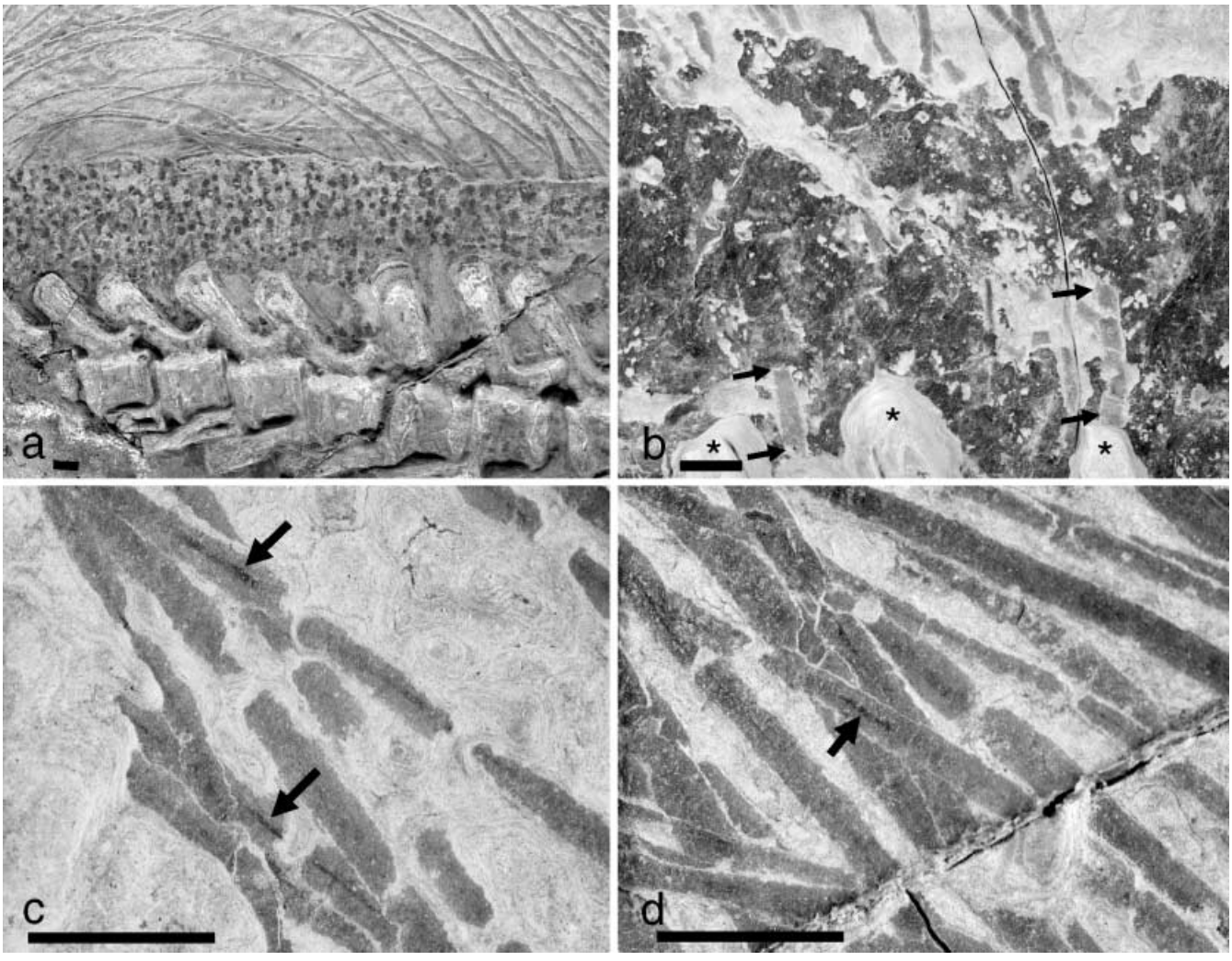

Fig. 3 **a** Ultraviolet-induced fluorescence photograph of the tail, showing numerous small scales. **b** Detail of the proximal area of the tail, showing that the "bristles" extend deeply into the skin (*arrows*) and terminate directly at the vertebrae; the neural spines of the vertebrae are indicated by *asterisks*. **c**, **d** Details of the "bristles", showing the narrow dark stripe along the midline which possibly indicates a tubular structure of these appendices (*arrows*). The *scale bars* equal 5 mm

1990). Large parts of the integument are preserved as a thin layer of dark carbonized matter. At the shoulder, the skin structure corresponds well to that seen in skin impressions of the more advanced ceratopsian genus *Chasmosaurus* (Sternberg 1925; Czerkas 1997), in that irregular rows of large, round, and plate-like scales are separated by numerous small, polygonal, and tubercle-like ones (Fig. 2a). At the limbs and the tail only the small tubercle-like scales are visible (Figs. 2b, 3a; see also Czerkas 1997; Ji and Bo 1998).

The most unusual feature, and the reason for the recent excitement among vertebrate paleontologists, is the presence of about 100 long bristle-like structures on the tail (Figs. 1, 3). These structures are restricted to a 235-mm long stripe along the dorsal surface of the proximal third of the tail (measured from the base of the most proximal to the base of the most distal "bristle"), extending over 14–15 caudal vertebrae. They are not discernible anywhere else on the tail nor anywhere else on the specimen. The middle parts of the longest ones reach beyond the margin of the slab, but their overall length, from the base to the tip, can be estimated to be about 160 mm. At their base, they are about 1 mm wide; all of the preserved tips taper into a point. These "bristles" are preserved as a very thin brown layer which is somewhat brighter than most of the dark substance of the skin; however, they exhibit a completely different texture than the ossified tendons which are preserved along some of the tail vertebra of the specimen (and which are also found in other psittacosaurs, see Sereno 1990). Under ultraviolet light they show the same fluorescence as the epidermal scales, which indicates that they might have been keratinized. The possibility that these structures are plant remains attached to or lying under the tail can be safely excluded by their morphology (V. Wilde, personal communication).

Because of diagenetic compression, the "bristles" are completely flat, but we assume that they were originally cylindrical and possibly tubular. Most of the "bristles" are more or less bent towards the caudal end of the tail

and if they originally were flat and ribbon-like, one would expect to see some twisting of the shaft which cannot be observed.

Most "bristles" exhibit a dark stripe of varying width along at least a part of their midline (Fig. 3), which possibly indicates the presence of a hollow lumen inside these structures, as in the filamentous structures of some theropods (Schweitzer et al. 1999). However, the "bristles" of *Psittacosaurus* are oriented in parallel, whereas at least some of the filaments of theropods originate from a single point and form a radiating spray (Ji et al. 2001; Xu et al. 2001). Furthermore, they do not show any branching, which was recently reported for the filaments of the theropod genera *Beipiaosaurus* and *Sinornithosaurus* (Xu et al 1999a, 2001).

Virtually all of the exposed integument of the tail is from the right lateral side of the animal, which can be deduced from the fact that it is continuous with the integument that covers the bones in the abdominal region of the specimen. The "bristles" extend under this skin layer and nowhere lie above it, which indicates that they were attached to the dorsal midline of the tail only.

Careful preparation of some "bristles" revealed that these terminate directly at the vertebrae, at the tip of the neural spine in one case and at the prezygapophysis in the other (Fig. 3b). Since the more proximal caudal vertebrae have shorter and smaller neural spines than the more caudal ones, the "bristles" extend further into the skin in the proximal part of the tail.

Discussion

Little is known about the integument of ornithischian dinosaurs, and the few known fossil specimens with skin preservation show typical reptilian scales and dermal spines; "bristle"-like structures have not been reported so far (Czerkas 1997).

Apart from their existence per se, it is very unusual that the "bristles" of *Psittacosaurus* are restricted to the dorsal midline of the proximal part of the tail. Considerations on their functional significance have to remain speculative since there is no analog in any other fossil or extant animal. Almost certainly, and possibly in contrast to the filamentous covering of certain theropods (Sues 2001), they had no thermoregulatory function, as they only cover a very small part of the integument. A possible explanation is that these "bristles" were used in some sort of display behavior. Especially if one assumes that they were colored – an admittedly entirely speculative supposition (see Ryan and Russell 1997) – they may have had a signal function as, for example, the ornamental feathers of many birds. Many of the more derived ceratopsian dinosaurs exhibit frills and horns which were assumed to have had a function in intraspecific agonistic or sexual behavior (Farlow and Dodson 1975). A complex social behavior in horned dinosaurs would be in concordance with the assumption of a display function of the tail "bristles" in *Psittacosaurus*. The facultatively bipedal psittacosaurs lack the horns and frills of the more advanced ceratopsians in which display behavior might have become more cephalized.

It was recently assumed that filamentous epidermal appendages evolved in terrestrial theropod dinosaurs before the origin of flight (Xu et al. 1999a, 2001; Brush 2001; Ji et al. 2001; Sues 2001). Although the "bristles" of *Psittacosaurus* distinctly differ from the known integumentary structures of theropod dinosaurs in being much longer, apparently more rigid, and much thicker, there is comparable variation between the hairs of extant mammals (as, for example, shown by the spines of porcupines and hedgehogs and the fur of most other species). If the "bristles" of *Psittacosaurus* can be shown to be homologous to the filamentous structures of theropod dinosaurs, similar structures may have already been present in a more comprehensive clade including ornithischian dinosaurs. At present, however, this conclusion would be premature and more detailed investigations on the microstructure and biogeochemistry (Schweitzer et al. 1999; Schweitzer 2001) of the integumentary structures of *Psittacosaurus* and theropod dinosaurs need to be carried out. Without further evidence, there remains the possibility that the "bristles" of *Psittacosaurus* are greatly modified scales, as has been suggested by Reisz and Sues (2000) for the – structurally different – appendages of the Triassic reptile *Longisquama*.

Independent of their homology, however, the discovery of bristle-like structures in *Psittacosaurus* is of great evolutionary significance since it shows that the integumentary covering of at least some dinosaurs was much more complex than has ever been imagined before.

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