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ORIGINAL PAPER

The integument of *Psittacosaurus* from Liaoning Province, China: taphonomy, epidermal patterns and color of a ceratopsian dinosaur

Theagarten Lingham-Soliar · Gerhard Plodowski

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Abstract Preserved skin of small dinosaurs is rare. Here, a specimen of the ceratopsian dinosaur, *Psittacosaurus*, presents some of the best preserved epidermal scales observed to date in a relatively small dinosaur, over wide areas extending from the head to the tail. We study the preserved epidermis of SMF R 4970, the different types of scales, color, and patterns, and their respective locations in the body. We use modern application of high-power digital imaging for close-up analysis of the tubercles and fragments of preserved color. Three types of scales are preserved, large plate-like scales, smaller polygonal scales or tubercles, and round pebble-like scales. The sizes of the plate-like scales vary in different parts of the body and vanish altogether posteriorly. Light and dark cryptic patterns are created by the associations of the tubercle and plate-like scales, and there is also evidence of countershading in the proximal caudal region, the body darker dorsally and lighter ventrally. Perhaps most impressive are the distinctive pigmented impressions of scales over most of the skeletal elements. The pigmentation follows the curvature of the bones implying that when it was deposited, the skin was still pliable and able to wrap around the visible parts of the elements. The present record of color is the first in a non-theropod dinosaur and only the second record in a non-avian dinosaur. Because of its resistance to degradation and ability to produce various color tones from yellows to blacks, we suggest that melanin was the dominant chemical involved in the coloration of *Psittacosaurus*. The data here enable us to reconstruct the colors of *Psittacosaurus* as predominantly black and amber/brown, in cryptic patterns, somewhat dull, but useful to a prey animal. Indeed, skin pigment within a partially degraded bone indicates that *Psittacosaurus* was scavenged shortly after death. The theropod dinosaur *Sinosauropteryx* has recently been reported to have naturally pigmented integumental structures, which the authors interpret as proof that they are protofeathers and not support fibers of collagen. Our findings in *Psittacosaurus*, on the other hand, indicate a more parsimonious and less profound alternative explanation, i.e., decomposition of the skin releases pigments that readily permeate underlying structures.

Keywords *Psittacosaurus* · Epidermal scales · Skin color · Skeletal pigmentation · Pigment diffusion · Crypsis

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T. Lingham-Soliar (✉)
Biological and Conservation Sciences,
Biological Sciences Building, University of KwaZulu-Natal,
Westville Campus, P. Bag X54001, Durban, South Africa
e-mail: linghamst@ukzn.ac.za

G. Plodowski
Forschungsinstitut Senckenberg,
Senckenberganlage 25,
60325 Frankfurt am Main, Germany

Introduction

Fossilized skin impressions of dinosaurs can provide tangible evidence of what the animal looked like in real life (Czerkas 1997). The best known skin impressions are from the larger dinosaurs such as hadrosaurs (Matthew 1915; Czerkas 1997) and sauropods, and a few instances from large theropods, e.g., *Ceratosaurus*, *Carnotaurus*, and a tyrannosaurid (Czerkas 1997). Lull (1933) described large, round, plate-like scales separated by polygonal tubercles in the integument of several of the larger ceratopsids. Among small non-volant theropods scale impressions are rare. Uniformly sized tubercles were described in the theropod dinosaurs *Juravenator* (Göhlich and Chiappe 2006) and *Compsognathus* (Peyer 2006). Skin impressions from small non-theropod dinosaurs were almost as rare as those of theropods. Czerkas (1997) refers to a small section of preserved skin impressions from the ankle of a *Psittacosaurus*. However, the prolific Jehol biota of the Lower Cretaceous Yixian Formation of China has the potential of changing this apparent paucity. Ji and Bo (1998) noted large areas of tubercles in a psittacosaur from the Yixian Formation of China, and Mayr et al. (2002) mentioned a small area of preserved tubercles and plate-like scales in *Psittacosaurus* SMF 4970, also thought to be from the Yixian Formation.

Psittacosaurus was a small ceratopsian, herbivorous dinosaur (Averianov et al. 2006; Zhou et al. 2006) about 1.5–2 m long, which may occasionally have adopted a bipedal stance. *Psittacosaurus* SMF R 4970, the focus of the present study, has substantial areas of integument preserved. This specimen is known for preservation of filamentous structures in the tail region of the animal (Mayr et al. 2002). Here, we study the preserved epidermis of SMF R 4970, the different types of scales, color, and patterns, and their respective locations in the body.

Material

Psittacosaurus specimen SMF R 4970 is housed in the Forschungsinstitut Senckenberg, Germany (Mayr et al. 2002). Two new species *Psittacosaurus lujiatunensis* (Zhou et al. 2006; Averianov et al. 2006) and *Psittacosaurus major* (You et al. 2008) have been described from the Yixian Formation of China, increasing the taxonomic diversity of psittacosaurs to at least nine valid species.

One of us (GP) has been closely involved in the lithology of the specimen and in its preparation since its acquisition. This has been of invaluable help in understanding the preservation of the scales and quality and reliability of the preparation for the purposes of this study. For example, the bristles, which do not concern this study, were crudely preserved prior to acquisition by coarse air abrasive, but fortunately, the scales were prepared by the Institute's preparator (Olaf Vogel) using fine needle preparation (GP). Apart from the plate-like scales, the tubercular scales (~1 mm diameter) are barely discernable with the naked eye and uninformative. Hence, the observations and analyses of these structures and areas within (1/4–1/3 mm diameter) are based on detailed high-power digital close-up images (~×10–20 magnification) and artificial lighting (we provide relevant high resolution digital images online allowing quality magnification up to ~×40; see Lingham-Soliar [2010] on the use of digital imaging in the analysis of fossil micro-structures, e.g., integumental structural proteins). Digital images were taken by Sven Tränkner (photographer, Forschungsinstitut Senckenberg) with a Nikon Professional digital camera with 12.5 Megapixels chip (35 MB tiff images) under artificial lighting at 3100°K. The tubercles seen with the naked eye, and up to ~×2–3 magnification, are black in color, allowing very little information. However, when viewed under higher magnification and adequately lit, traces of brown color are obvious (Figs. 2d, 3d; ESM S1; this is analogous to being able to discern the primary colors in photos only under magnification). This can easily be tested in the tubercle impressions over bone (e.g., top left Fig. 3 by simply enlarging from normal size (~1 mm) to ×10–20—the large MB tiff images online are ideal). There will inevitably be some minor color differences (i.e., variations between warm and cold) in photographic images depending on the type of lighting but these are unavoidable, and as microstructures, there is no other frame of reference such as the naked eye (the human eye itself has significant variations in individuals anyway). The complete view of *Psittacosaurus* in Fig. 1 is based on a high-resolution 28.5 MB tiff image.

Fig. 1 *Psittacosaurus* SMF R 4970. *Scale bar*=10 cm

Description

The surrounding matrix of *Psittacosaurus* SMF R 4970 is preserved as a carbonaceous clay material with an admixture of a fine silty material. The head and thoracic regions (up to the posterior limbs) are compressed dorsoventrally (Fig. 1) with only a trace of the latero-thorax visible. Only in the posterior part of the body (lumbar region) and in the tail are notable lateral and ventrolateral regions of the body visible. The epidermal preservation in SMF R 4970 represents actual scales in contrast to most cases of skin preservation in dinosaurs that are of a mold of the scales. Scales occur over most parts of the body including in a thin strip along the throat, left and right shoulders, right dorsal surface, dorso-ventral caudal regions, and areas of the left anterior and posterior limbs. Scale impressions (pigmentations) are preserved over most of the skeletal elements.

Three types of scales are preserved: (1) large, round plate-like scales, (2) polygonal scales or tubercles, and (3) small rounded pebble-like scales. The best preservation of the plate-like scales is in the shoulder region (Figs. 2d, 3a). They vary in size, the largest approximately 10 mm in diameter, decreasing in size ventrad along the arm to approximately 4 mm diameter. Well-preserved dark pigment impressions of three plate-like scales (black), surrounded by amber/brown impressions of tubercles, overlie the base of the left scapula (Fig. 2d; ESM S1).

The tubercles are numerous, small, and polygonal-shaped. They vary in size from approximately 0.75–1.5 mm in diameter and also vary in tone from light to dark brown. Remarkably preserved tubercles and plate-like scales occur in both shoulder regions (Figs. 2c, 3a). Pigmented impressions of the scales found imprinted over virtually all the skeletal elements of the specimen give a very vivid impression of color and patterns, no more so than those at the base of the left scapula, probably articular cartilage, which shows a well defined ring-like pattern of amber tubercles surrounding the dark plate-like scales (Fig. 2d, white arrows; ESM S1). The ring has possibly survived better over bone (ESM S3) given that the skin as it contracts (as over a drum) is probably less likely to crease and distort as it might over muscle. The color too is generally brighter over bone—a brighter amber/brown and deeper black (Figs. 2d, 3d, e; ESM S1), presumably because the pigment has less chance to permeate bone or cartilage and dissipate as over soft tissue (see "Discussion"), analogous to the way color is brighter when printed on glossy rather than matt absorbent paper. Dark tubercles are preserved at the boundary of the upper proximal part of the tail along the vertical midline and in the upper lumbar region (Fig. 2g, h).

Small, light, pebble-like scales occur in a small section of skin in the region of the throat and in the ventro-lateral regions of the posterior body and tail (Fig. 2a, h). These are assumed to have sparse pigmentation in life.

Of interest are the color patterns in SMF R 4970, most notably in the right and left shoulder regions. The dark plate-like scales regularly dispersed among the amber brown tubercles would almost certainly have created an effective cryptic pattern on the body of *Psittacosaurus* (Figs. 2c, 3a). Conceivably, differences in color tones of the tubercles themselves may even have contributed to the cryptic patterns (Figs. 2c, 3b, c, d) as in *Agama* (Fig. 2j). Another form of crypsis, common in many extant animals, is also evident—countershading, i.e., a dark dorsum and light ventrum (Fig. 2h)

Discussion

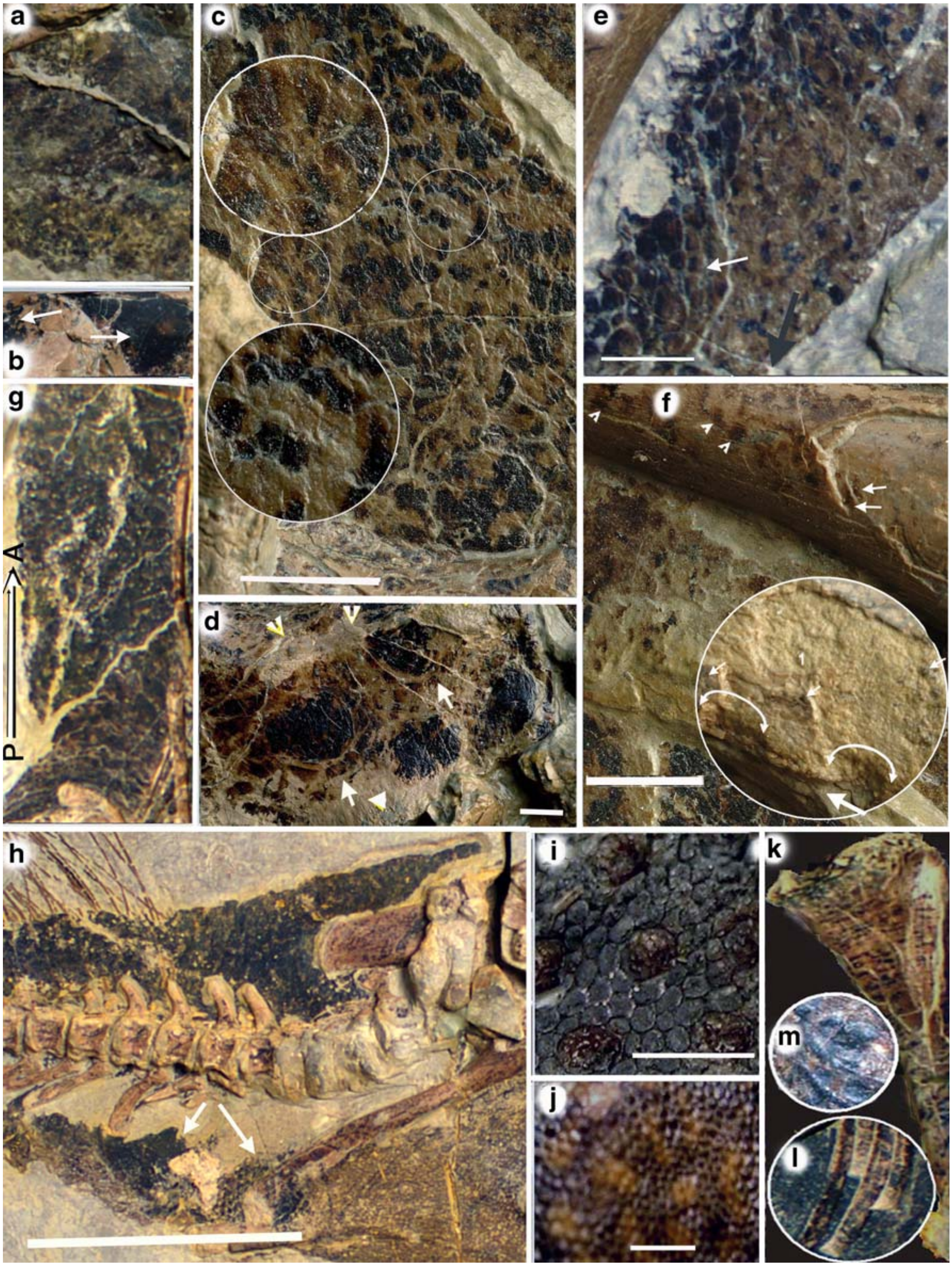
The scales of reptiles are in the main epidermal derivatives in contrast to those of fishes, which are derived from the dermis (stratum spongiosum; Lingham-Soliar 2005). In contrast to the rare insight into the dermal structure of the skin in *Psittacosaurus* MV53 (Lingham-Soliar 2008), SMF R 4970 presents equally rare information through exceptional preservation of the epidermis and scales that allow the most complete assessment of the external appearance of a small non-avian dinosaur to date.

Comparisons of the epidermis of *Psittacosaurus* with that of other taxa

A distinctive ring of evenly sized tubercles surrounding the plate-like scales (Fig. 2d, white arrows; ESM S1) is also evident in another ceratopsian dinosaur, *Chasmosaurus* (Lull 1933, p. 69–70). Also, comparable with *Chasmosaurus* (Lull 1933) is a decrease in size of the large plate-like scales from the dorsal surface of the body ventrad. In the ceratopsian, *Centrosaurus* the skin tubercles are beautifully preserved (Lull 1933, p. 66, plate 3b), but unlike in *Chasmosaurus* and *Psittacosaurus*, they are generally consistent in size, and the plate-like scales are disposed in rows.

Details of the plate-like scales (Figs. 3a, 4a) show they are considerably eroded, also indicated by the presence of underlying collagen fibers (Lingham-Soliar 2008, Fig. 1c). They are demarcated largely by color. Strong wear of the surface of the scales is also seen in a hadrosaur (Figs. 32, 33 of Matthew 1915; ESM S4). Although there are in *Psittacosaurus* possible traces along the edges of the plate-like scales of a papillose surface (Fig. 4a, circled; edges of scales in Matthew's hadrosaur, ESM S4), they could equally be artifacts of wear.

Preservation of color in fossils is rare and largely restricted to invertebrates. To our knowledge, this is only the second record of color patterns in a non-avian dinosaur



and the first in a non-theropod. Because of the potential importance of color as a key to understanding physiological and behavioral processes in extinct animals (Mapes and Davis 1996), we attempt to assess the color patterns in *Psittacosaurus*, aware of the constraints with respect to diagenetic processes (Kobluk and Mapes 1989).

As in many of the invertebrate fossils manifesting color, the key question is whether or not they are a reasonably true representation of the animal's color, i.e., preserved as original pigment or whether the color emanates from diagenesis whereby the original pigment may be substituted by another organic or inorganic compound (Nitecki and

◀**Fig. 2** Preserved scales in *Psittacosaurus* SMF R 4970. **a** few dark scales in the ventral throat region; **b** dark pigment on the skull bones; **c** left shoulder, details shows cryptic patterns created by light and darker brown tubercles, many in relief ; **d** dark plate-like scales surrounded by rings of amber/brown tubercles (*white arrows*) preserved over the base of left scapula, grayish in color (*arrowheads*); **e** lower part of left anterior limb (tubercles, *arrow*); **f** right radius with tubercle impressions both on the external surface (*arrowheads*) and within the fracture (*arrows*), with scale patterns on skin directly below; *inset* shows anterior of bone with possible tooth impressions (*curved double-headed arrows*); **g** right dorsal surface (*vertical*, *arrow* shows anterior–posterior [A–P] direction of dinosaur) of the thoracic-lumbar region; **h** dark scales of proximal caudal dorsal area and light scales in the proximal caudal ventral region (*arrows* show displacement of skin); **i**, **j** scales in *A. atricollis*. **k**, **l** Pigment imprints in *Psittacosaurus* preserved over the femur and ribs respectively. **m** Pigment imprint preserved over ribs in decomposing dolphin. *Scale bar*: **c**, **g**=10 mm; **e**=2.5 mm; **f**=1 cm; **d**, **i**, **j**, **k**=5 mm; **h**=10 cm

Sadlick 1968; Kriz and Lukes 1974; Hagdorn and Sandy 1998), an ongoing problem. Without comparative chemical analysis (invariably impractical because of, e.g., destruction to rare material) of recent and fossil pigments to test for diagenetic alteration, the question cannot be directly resolved. As in the fossil invertebrates, we also invoke a number of lines of strong circumstantial evidence that, in our view in totality, strengthen the arguments for the preservation of genuine color in *Psittacosaurus*.

Although many different kinds of pigments (biochromes) are present in modern-day organisms, two sorts, melanin and members of the porphyrin group of tetrapyrroles, are known to be preserved in fossils (Hollingworth and Barker 1991). The dominant colors preserved in *Psittacosaurus* are black and amber/brown. Melanin is a black pigment that can appear as black, gray brown, reddish brown, or even yellow depending on the size and distribution of the melanin granules and consequently could account for all the colors observed in *Psittacosaurus* (e.g., Figs. 2d, f, 3a, d, e). The porphyrins, however, do not appear commonly, if at all in reptile scales (Dr. Kevin McGraw pers. communication 2008). Melanins are insoluble in most liquid media (Kriz and Lukes 1974) and thus have a better chance of being preserved during the complicated process of postmortem diagenesis and fossilization.

Of considerable interest to our hypothesis on color are the pigmented impressions of the scales that overlie virtually all the skeletal elements of SMF R 4970 (e.g., Figs. 2d, f, k, l, 3d, e, 4b; ESM S1, S2, S5, S6, S7). Such widespread preservation of pigment over the skeletal elements has not previously been recorded in fossil vertebrates, including those from Liaoning—only traces of structural proteins have been noted over skeletal elements, e.g., over the vertebrae of the ichthyosaur *Stenopterygius* (Lingham-Soliar 2001) and the surangular and dentary of *Ichthyosaurus* (Lingham-Soliar 1999) and caudal vertebrae of the dinosaur *Sinosauropteryx* (Lingham-Soliar et al. 2007). What is the reason for this unusual preservation in SMF R 4970? Chromatographic analysis of the hypodermal tissue taken from a decomposing dolphin showed that one of the earliest decay processes is pronounced oxidation of the unsaturated lipids and leaching into the surrounding substrate (Lingham-Soliar 2003). Rapid removal of fat beneath the skin of *Psittacosaurus* would have resulted in the skin collapsing onto the skeletal elements, exactly as seen in the decomposing dolphin in which some of the best and widespread preservation of skin occurred over the skeletal elements (Lingham-Soliar 2003; Fig. 2m; ESM S3). This raises another important point. The skin impressions in *Psittacosaurus* SMF R 4970 in most cases appear closely "wrapped" around the visible bone (Figs. 2d, f, k; ESM S5, arrows) strongly suggesting the plasticity of the epidermis at the time the pigmented impressions on the skeletal elements formed and that they occurred before mineralization and rigidity of the integument (Lingham-Soliar & Wesley-Smith 2008, p. 2210–2211). Further evidence that mineralization had probably not yet occurred is revealed by a torn segment of skin displaced onto the distal extensions of the ischium and pubis and presence of a crease in the skin as it pressed against the ischium (denoted by the tubercles becoming sharply attenuated) and molded itself over it (Fig. 4b; ESM S6, arrowheads). Similar pigmented imprints from the skin over underlying structures (not just bone but cartilage and structural fibers) in other dinosaurs from Liaoning, including theropods, is not just likely but predictable.

Although the colors observed in *Psittacosaurus* are all capable of being produced by melanin, the possibility of a secondary, carotenoid pigment, commonly found in vertebrates including reptiles (Macedonia et al. 2000), is also considered. Carotenoids produce red, orange, and yellow pigments and virtually every color known. Animals, however, cannot synthesize carotenoids but obtain them in the diet from plants, fungi, algae, and certain microorganisms. *Psittacosaurus*, a herbivore, would easily have acquired the pigment from its diet. Carotenoids are not normally water soluble, but they are soluble in lipids (Borel et al. 1996). Leaching of the lipids would indirectly have aided the dissolution of the carotenoids and facilitated more or less permanent widespread staining from the epidermis over skeletal elements (e.g., Figs. 1, 2d, q, r, 3d, e), a condition demonstrated for the first time in a dinosaur—with further implication for genuine preservation of pigments in *Psittacosaurus*. The organic nature of the scales and bristles of SMF R 4970, which was suggested from ultraviolet examination (Mayr et al. 2002), provides another line of evidence that the colors were probably original rather than diagenetically transformed (*Scelidosaurus*, Martill et al. 2000).

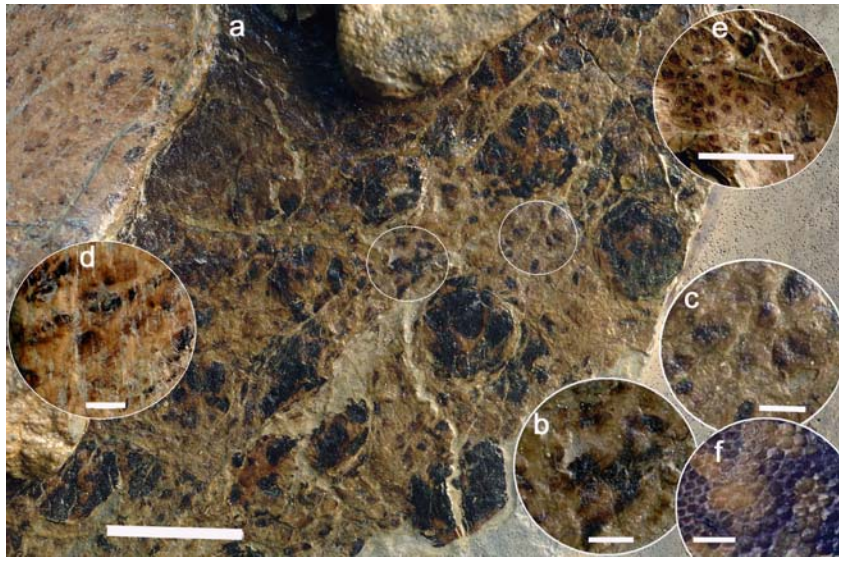


Fig. 3 Left shoulder of *Psittacosaurus* SMF R 4970. **a** tuberculate and large plate-like scales. **b** light and dark brown tubercles; **c** polygonal tubercles in relief showing traces of dark pigment; **d** amber/brown and dark tubercle pigment imprints on the upper part of left humerus (lower humerus in view); **e** tubercle pigment imprints on left coracoid; **f** skin of *A. atricollis*. *Scale bar*. **a**, **e**=10 mm; **b**, **c**, **d**=2 mm; **f**=5 mm

Distinctive and consistent cryptic patterns (antlion, Heads et al. 2005), formed widely over the body by the two dominant colors found in *Psittacosaurus*, black and amber/brown, are unlikely to be achieved by random diagenetic transformations or weathering. The most striking crypsis is a consequence of the large dark plate-like scales set amidst smaller, lighter, tubercles, most noticeable in the shoulder region of *Psittacosaurus* (Figs. 2c, 3a; ESM S1). While the brown coloration of the tubercles has apparently leached more readily in areas overlying soft tissue, they are often more strongly preserved over bone (Figs. 2d, 3d, e) for reasons mentioned earlier. The pattern created by the tubercles and plate-like scales are reminiscent of that in the lizard *Agama atricollis* (Figs. 2i), i.e., a precise pattern of large dark spiny scales surrounded by smaller and lighter tubercles. Bleaching and weathering may have affected the intensity of the color (Hagdorn and Sandy 1998) (Fig. 3b, c), but a combination of data from color overlying bone and soft tissue allows a more reliable assessment.

We also briefly mention the phenomenon known as counter-shading or Thayers' Law (Fig. 1; ESM S6, S8), a form of camouflage wherein an animal is darker dorsally and lighter toward the ventral parts of the body, which is quite striking in the anterior part of the tail of *Psittacosaurus* (unfortunately along the body it is mostly the ventral part that is exposed). Matthew's (1915) hypothesis on shading in hadrosaurs is pertinent: "Larger tubercles concentrate and become more numerous on all those portions of the body exposed to the sun,…and appear to increase also along the sides of the body and to be more concentrated on the back."

The basic color of *Psittacosaurus* in life would overall have been a dark brownish hue, created by cryptic

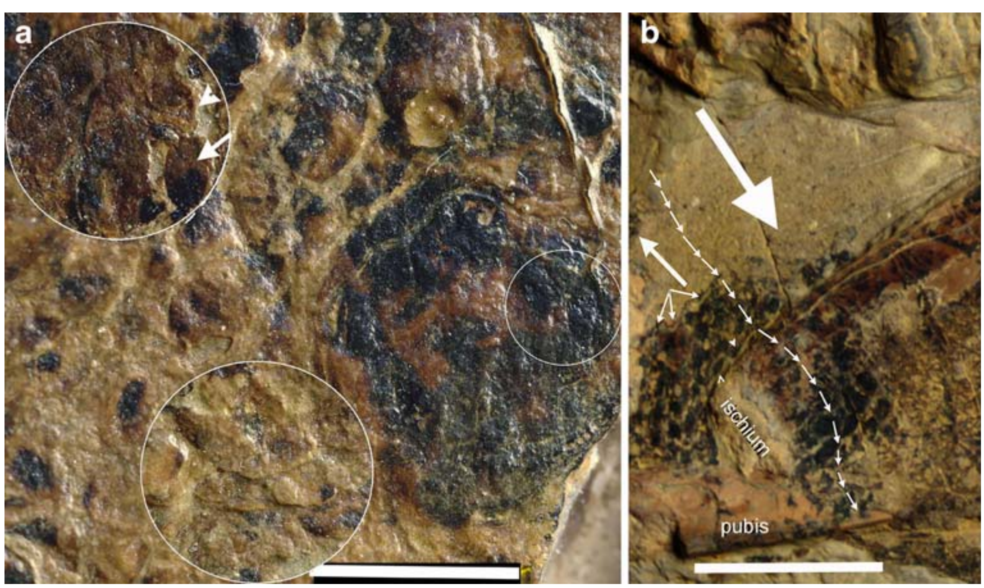


Fig. 4 *Psittacosaurus* SMF R 4970. **a** left Shoulder. Plate-like scales eroded and exposing pigment below. *Circled* pappilose surface (see text). Lower and upper details, light (strongly leached) and brown pigmented tubercles, respectively (*arrow*, dislodged tubercles; *arrowhead*, crack in skin). **b** Skin from ventral to caudal vertebrae has displaced downward and wrapped itself over part of the ischium (see text). *Scale bar* **a**=5 mm; **b**=2.5 cm

associations of black and amber-brown scales, but somewhat lighter in the forequarters. The dorsal areas were darkest, almost black and the ventral areas lightest—light gray-brown. Certainly, as one might expect, the colors in *Psittacosaurus*, a prey animal, are not flamboyant. The dark plate-like scales dorsally would have affected the basic color considerably depending on their concentration (Fig. 2c, g, h). Cryptic skin patterns (Fig. 3) allow an otherwise visible organism to remain relatively indiscernible from its environment, e.g., muddy banks to woodlands and savannas—how it works is a topic of ongoing debate (Ruxton et al. 2004).

How did *Psittacosaurus* SMF R 4970 die?

Preservation of tubercle impressions over skeletal elements also gives a clue to circumstances surrounding the death of *Psittacosaurus* SMF R 4970. A fracture of the right radius shows traces of pigmented impressions (arrows) from the torn decomposing skin on inner layers of the bone (Fig. 2f; ESM S7—arrowheads and arrows show stains in the radius on external and internal surfaces, respectively). Color from the epidermis impregnating inner layers of bone could only have occurred shortly after damage to the bone—i.e., proof that this damage was not a consequence of later degradation and erosion (post-fossilization) but from bites from an animal. Crushing and stripping of the bone as noted (ESM S7) suggests one probable dinosaur candidate, the heterodontorosaurid dinosaur *Tianyulong* (Zheng et al. 2009), known from the Jehol biota. This contrasts with the bite impressions in *Psittacosaurus* MV53 (Lingham-Soliar 2008) in the soft belly region and in which the tooth impressions appear more typically reptilian. We are getting a better idea of the life and death struggles of these dinosaurs showing that they were an important prey item in the Jehol biota for probably a variety of animals.

An accumulation of evidence, some uniquely observed such as widespread deposition of pigment over bone, indicates a high probability that the color patterns observed in *Psittacosaurus* SMF R 4970 are genuine and we reasonably rule out diagenetic transformation (above). Nevertheless, as in most formative investigations, the present study raises as many questions as are answered, but we believe it opens a window of possibilities for future studies. The view that color holds vital information on the evolution of animals (Kobluk and Mapes 1989; Taylor and McGraw 2007) may prove particularly fascinating with respect to the dinosaurs. There are many vertebrates of the Jehol biota (see, e.g., Figs. 96, 112, 127, 132, and 206 of Mee-mann et al. 2003) that potentially preserve color and merit investigation. Furthermore, SEM investigations of pigmentation in a 100-Ma fossil feather (Vinther and Briggs 2008) and of ultrastructural details in ichthyosaur skin (Lingham-Soliar & Wesley-Smith 2008) point to new methods of investigating fossilized integumental structures when rare material can be spared. Most recently, an SEM image on the theropod dinosaur, *Sinosauropteryx* (Zhang et al. 2010) from the Jehol biota purportedly shows the presence of melanosomes (see Lingham-Soliar and Glab (2010) for an alternative explanation) in the integumental structures of the tail, which the authors state is evidence that these structures were pigmented protofeathers and not support fibers of collagen (e.g., Lingham-Soliar et al. 2007). Our findings in *Psittacosaurus* on the other hand indicate a more parsimonious and less profound alternative explanation (accepting for the present that the structures identified were indeed melanosomes)–pigment in the integumental structures of *Sinosauropteryx* could easily have been absorbed from the overlying decomposing skin, a phenomenon amply demonstrated in the present study in *Psittacosaurus* SMF R 4970, also from the Jehol biota.

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Author contributions

GP—detailed examination of SMF R 4970 with respect to the material's geology, lithology, preparation, and photography. TL-S—detailed analysis of the integument of *Psittacosaurus* SMF R 4970 based on digitized images of microstructures, zoological, paleontological and taphonomic interpretations, and writing the paper. This is an equal joint publication.