

A new Chinese specimen indicates that ‘protofeathers’ in the Early Cretaceous theropod dinosaur *Sinosauropteryx* are degraded collagen fibres

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Alleged primitive feathers or protofeathers in the theropod dinosaur *Sinosauropteryx* have potentially profound implications concerning feather morphogenesis, evolution of flight, dinosaur physiology and perhaps even the origin of birds, yet their existence has never been adequately documented. We report on a new specimen of *Sinosauropteryx* which shows that the integumental structures proposed as protofeathers are the remains of structural fibres that provide toughness. The preservation in the proximal tail area reveals an architecture of closely associated bands of fibres parallel to the tail’s long axis, which originate from the skin. In adjacent more exposed areas, the fibres are short, fragmented and disorganized. Fibres preserved dorsal to the neck and back and in the distal part of the tail are the remains of a stiffening system of a frill, peripheral to the body and extending from the head to the tip of the tail. These findings are confirmed in the holotype *Sinosauropteryx* and NIGP 127587. The fibres show a striking similarity to the structure and levels of organization of dermal collagen. The proposal that these fibres are protofeathers is dismissed.

Keywords: theropod; *Sinosauropteryx*; collagen; protofeather

1. INTRODUCTION

Despite wide acceptance that integumental structures found in theropod dinosaurs such as *Sinosauropteryx* represent feather progenitors or ‘protofeathers’ (Chen *et al.* 1998; Currie & Chen 2001; Norell & Xu 2005; Prum & Brush 2002), the view is poorly supported (Feduccia 1999; Ruben & Jones 2000; Lingham-Soliar 2003a,b; Feduccia *et al.* 2005). The idea of protofeathers has strengthened the resolve of many palaeontologists that birds are direct descendents of theropod dinosaurs (e.g. Chen *et al.* 1998; Currie & Chen 2001; Prum & Brush 2002; Norell & Xu 2005). The spectacular Early Cretaceous Jehol biota in Liaoning Province, China has thus added a potentially powerful new dimension to the hypothesis of the dinosaurian origin of birds with the discovery of *Sinosauropteryx*, proclaimed to be a ‘feathered’ dinosaur (Chen *et al.* 1998; Currie & Chen 2001). The objective of the present study is to try to understand the nature of the integumental structures in *Sinosauropteryx*. Clearly, the results on whether or not they are protofeathers will impact on the vital question of feather origins, dinosaur physiology and bird flight (Feduccia *et al.* 2005 and references therein); on the other hand, we emphasize, the wider question of whether or not birds originate from dinosaurs does not concern the present study.

Both studies purporting protofeathers in *Sinosauropteryx* (Chen *et al.* 1998; Currie & Chen 2001) lack adequate

morphological analyses and detailed representations of the integumental structures via e.g. microscopy or macro-photography. For instance, there is not a single close-up representation of the integumental structure alleged to be a protofeather. Given its pivotal importance if true, i.e. that this structure is the progenitor of a unique structure in evolutionary biology, the feather, and given that such intermediate functional structures connecting one species to another, are among the most elusive in the history of life on Earth (Darwin, *On the Origin of Species*, p. 124), scientific rigour is called for. For instance, the authors (Currie & Chen 2001, p. 1721) state that ‘the integumentary structures are piled so thick that it has not been possible to isolate a single one for examination’. Despite this alleged obstacle, they speculate that ‘structurally, the integumentary structures seem to most closely resemble plumules of modern birds’ and that they may have been hollow. Furthermore, our examination of the holotype (Chen *et al.* 1998, fig. 5) shows large tracts of integumental structures in a single layer with a number of reasonably isolated fibres.

The major evolutionary ramifications, if these structures were indeed feather progenitors require (i) sound analytical methods and minimal speculation, (ii) support for findings from extant and extinct vertebrates, (iii) an appreciation of decomposition and taphonomic processes, and (iv) open presentation of data and photos in support of any proposals. We employ these principles to crucially determine whether or not there is evidence for a herringbone-like pattern that would justify claims of a ‘rachis and barbs’, which in addition

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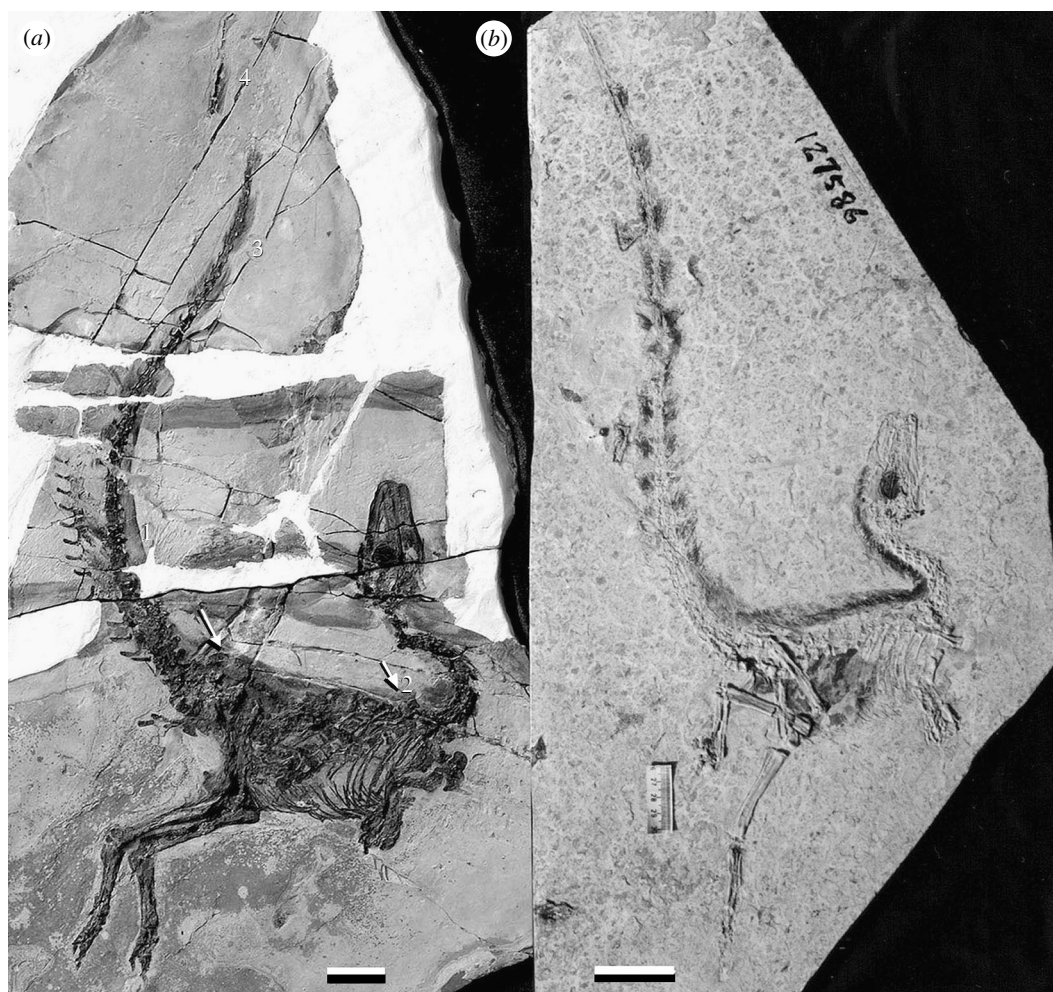


Figure 1. The theropod dinosaur *Sinosauropteryx*. (a) A new specimen of *Sinosauropteryx* IVPP V12415 (chevrons and tip of tail are displaced). Numerals 1–4 represent main areas of study (material courtesy of Dr Zhonghe Zhou, Beijing Museum, Chinese Academy of Sciences). (b) The holotype *Sinosauropteryx*, a small specimen, possibly a juvenile (photo courtesy of Dr Pei-Ji Chen, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences). Scale bars, (a,b) 5 cm.

were alleged to be ‘soft and pliable’ (Currie & Chen 2001), or for some other pattern altogether unrelated to either primitive or advanced feathers.

2. MATERIAL AND METHODS

A window on understanding these interesting integumental structures is presented by a recently discovered new specimen of *Sinosauropteryx*, IVPP V12415 (figure 1a) collected from the Dawangzhangzi locality in Lingyuan, Liaoning Province (Yixian Formation, Early Cretaceous). The skeleton is excellently preserved, with some displacement of individual bones (dorsal vertebrae, chevrons and terminal caudal vertebrae) and includes preservation of soft tissue. Assignment to *Sinosauropteryx* is by Z. Zhou (personal communication, Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, 2006) and one of us (X.W.). Our investigation uses conventional microscopy, which we believe has proved more than adequate in studies on dermal collagen fibre and fibre bundle organization in, e.g. modern day animals such as sharks (Motta 1977; Lingham-Soliar 2005a,b), dolphins (Pabst 1996; Lingham-Soliar 2003b), reptiles (Lingham-Soliar in Feduccia *et al.* 2005), the extinct ichthyosaurs (Lingham-Soliar 1999, 2001; Lingham-Soliar & Plodowski 2007) and pterosaurs (Unwin & Bakhurina 1994). Finer details down to the collagen fibril level (approx. 50–100 nm

thickness), which ordinarily might benefit from scanning electron microscopy (SEM) analysis, are highly unlikely in pyritic fossil preservations and the cost of searching in terms of damaging valuable material would be too great to justify.

3. RESULTS

(a) Microscopy of the integumental structures

The integumental structures in the new *Sinosauropteryx* specimen occur as high-fidelity mineralized impressions (SEM on less rare Jehol biota soft-tissue specimens show pyrite as a consistently important mineral component; Leng & Yang 2003). The structures occur in several areas (figure 1a) comparable to that of the holotype NIGP 127586 (figure 1b) and NIGP 127587, including in a recess left by the proximal part of the tail (site 1; figures 1a, 2a,b and 3a,b), along the neck (site 2; figure 2c), back and the distal part of the tail (sites 3 and 4; figures 2d–f and 3c,d); also overlying well-preserved vertebrae (figure 2b). We also show identical structures in *Sinosauropteryx* NIGP 127587 (figure 4). Unravelling the nature of the preserved integumental structures in IVPP V12415, as in the other specimens, is complex but we suggest the same structures occur in the skin and frill (figures 2 and 3).

In site 1 (tail recess, see above), the regular, compact pattern of the preserved structures indicate they were part of the skin. Along the dorsal ascending part of the tail recess,

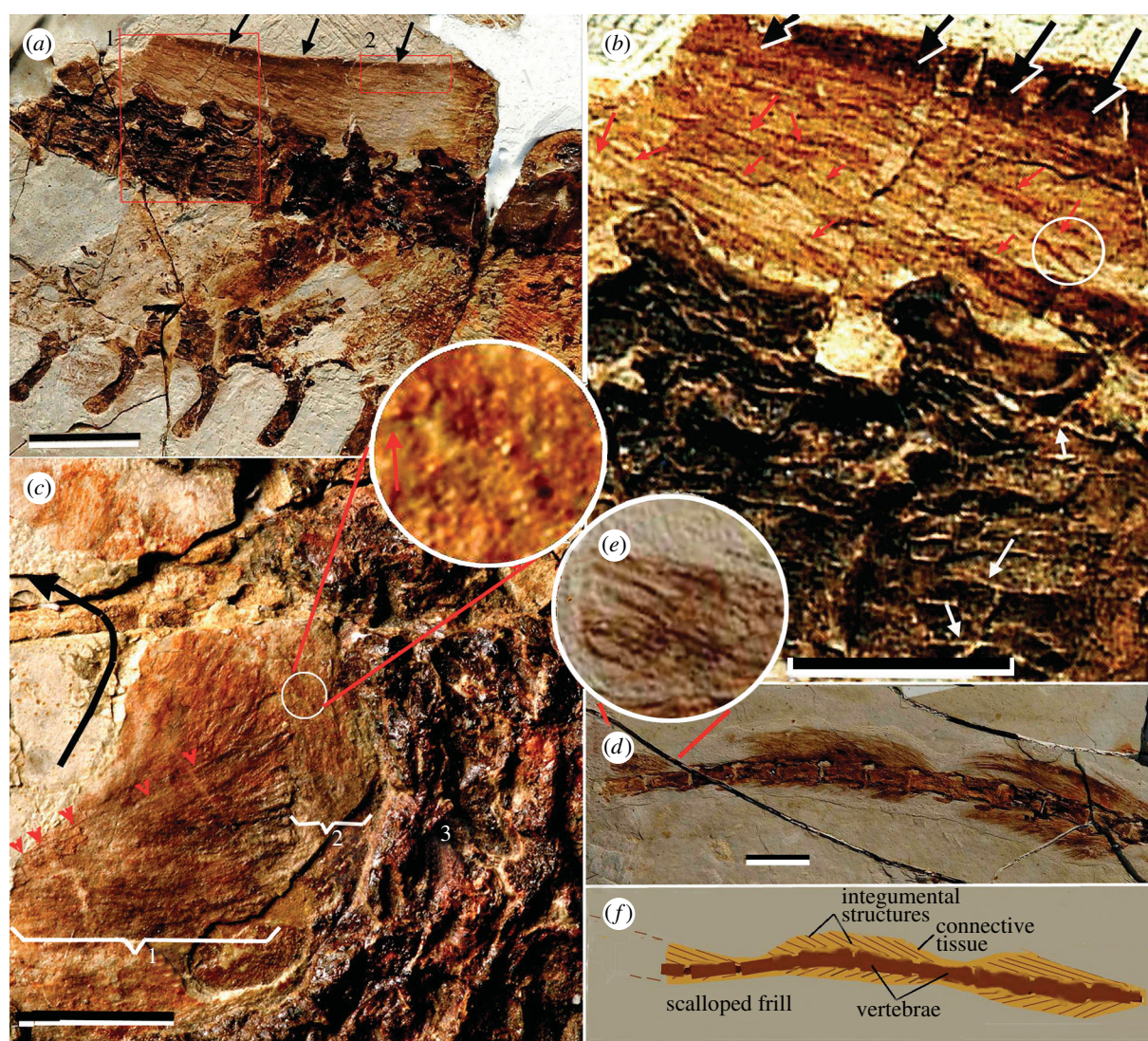


Figure 2. *Sinosauropteryx* IVPP V12415. Integumental structures. (a) Overview of the area with significant soft-tissue preservation within the body rather than coronal. Integumental structures occur in the tail recess and overlying the vertebrae; the chevrons have been displaced. (b) Detail in (a). Red arrows show some isolated integumental structures; white arrows show integumental structures closely associated to give the impression of branching; white circle shows two closely associated integumental structures (detail in figure 3b₅); large black arrows shows the vertical part of the excavation in which the best preservations occur. (c) Integumental structures at the juncture between the neck and body, detail in circle shows the angles of the beaded fibres (site 2 in figure 1a); numerals 1, 2, indicate integumental structures of the frill and skin/muscle, respectively, and 3, the cervical vertebrae, curved arrow shows the sharp backward recurvature of the neck; arrowheads show straight fibres. (d) Integumental structures in the distal part of the tail showing gaps between preserved tissues (cf. holotype, figure 1b). (e) Detail, showing beaded integumental structures. (f) Schematic of (d). Scale bars, (a, d) 2 cm and (b, c) 1 cm.

within a slight concavity (figure 2a, b, black arrows in b), the integumental structures extend in rows parallel to the long axis of the tail (figure 3a). In extant animals (Lingham-Soliar 2005a, b) and in an ichthyosaur (Lingham-Soliar & Plodowski 2007), dermal collagen fibres orient in the same direction in numerous consecutive layers. Both patterns are consistent with the structural organization of dermal collagen. Towards the central, more exposed part of the tail recess, the integumental structures become fragmented, disorganized and scanty (figure 3a). As in our *Sinosauropteryx*, NIGP 127587 also shows clear signs of a recess formed by the proximal part of the tail (Chen *et al.* 1998) and it is probable that the fibres therein also emanate from the skin.

Figure 3a provides a crucial insight into the nature of the integumental structures as well as into the process of degradation (note that the terms degrade or degradation define both biological and geological erosion and are

especially useful where such distinctions are difficult). Breakdown into disorganized structures is initiated in the tissue. The degradation may be exacerbated during fossilization by the agents of erosion, e.g. wind and water especially in the more exposed central area of the preservation (site 1). In addition, fragments of decomposing tissue may have been better protected in niches rather than exposed areas. We observe the inception of degradation in *Sinosauropteryx* NIGP 127587 (figure 4b, arrows) from geometrically precise bands of parallel integumental structures, oriented at acute angles to the tail's long axis (figure 4a, arrows 1–4). These bands are evidently the remnants of a finely assembled fibre architecture occurring in several bands of overlying layers (figure 4a, arrowhead shows overlap) consistent with structural reinforcement of the skin (Lingham-Soliar 2005a, b). Fibres between the chevrons extend parallel to the long axis of the tail and probably represent the skin or

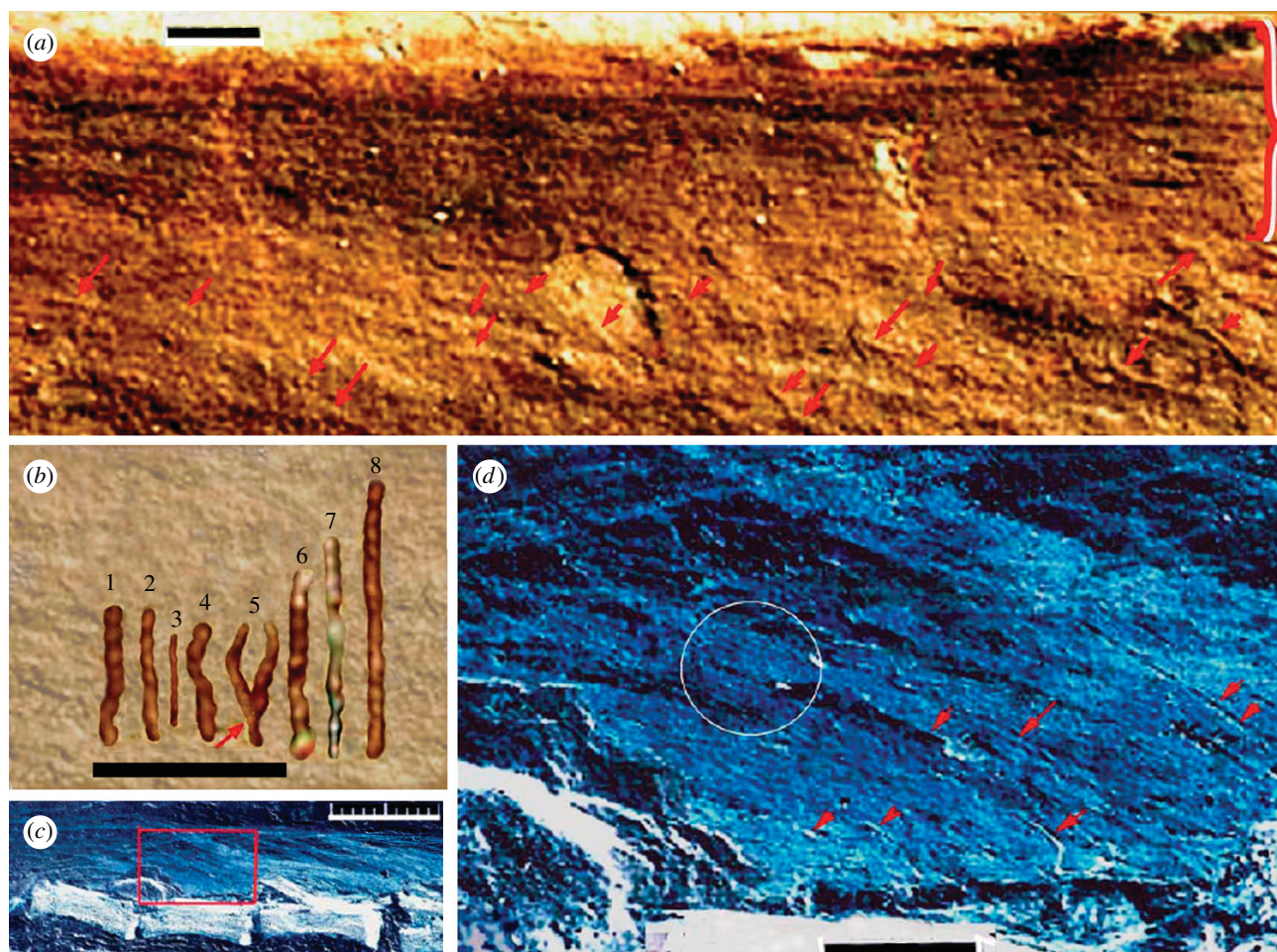


Figure 3. Integumental structures in *Sinosauropteryx* IVPP V12415. (a) Integumental structures in the proximal tail area (area 1 in figure 1a); at the top, they are in regular parallel association (red bracket); below the integumental structures are more random. (b) Isolated integumental structures from various parts of the preservation, reoriented for ease of viewing; $b_{1-6,8}$, from the integument within body outline; b_5 circled in (figure 2b), b_7 represents integumental structure overlying well-preserved vertebrae (see text). (c) Integumental structures in the last but three terminal caudal vertebrae preserved. (d) Detail of (c) showing integumental structures as part of a matrix of connective tissue at their lower half, while in the distal half, the individual structures are more evident (circled), becoming progressively more degraded towards the tips; circle shows mid-stage of regular, tight, parallel fibre associations. Scale bars, (a,b) 1 mm, (c) 1 cm and (d) 2 mm.

longitudinal musculature. The inception of the break-up of the fibre architecture, i.e. just a few loose fibres (figure 4b, arrows) is analogous to short stitches pulled from clothing during wear. It is a clear indication of how the aberrant integumental structures (whether from skin, muscle or frill), popularly referred to as protofeathers, originated.

Fibres preserved over caudal vertebrae in the proximal part of the tail (adjacent to site 1; figure 2b, detail in figure 3b₇) occasionally formed aberrant associations with others. In site 2, where the neck arches strongly over the body, there are two discrete groups of fibres; the first located distally is oriented at right angles to the second (figure 2c, numbered 1 and 2, respectively), which lies adjacent to the cervical vertebrae. This vital preservation provides compelling evidence concerning the origin of coronal fibres (fibres peripheral to the body outline). Directly adjacent to the cervical vertebrae, the non-coronal soft tissue apparently represents part of the skin or epaxial musculature (*Longissimus cervico-capitis*), its fibres (beaded) extend parallel to the neck's long axis (figure 2c, detail) in striking contrast to those of the distal soft tissue, which lie at right angles to them. In the holotype, restriction of the integumental structures to a

corona was thought to be a preservational bias (Currie & Chen 2001), i.e. the marginal substrate provided better conditions for soft-tissue preservation, which is clearly not the case here where fibres are also preserved within the body outline (also at site 1 and in NIGP 127587). The sharp demarcation of the distal fibres along the animal's margin may be considered therefore a primary condition, not connected with any preservational bias. Protofeathers in such circumstances would have a high probability of more random points of origin and orientations and not the clean-cut corona noted. The most parsimonious explanation with respect to the above observations is that the marginal fibres belonged to a frill. Furthermore, the fibres nearest to the juncture between the neck and body converge distally more or less to a point probably a consequence of the frill being somewhat squashed as the neck arched strongly backward during rigour mortis. Despite this, these long fibres retain a remarkable straightness (figure 2c, arrowheads), consistent with high tensile stiffness and protection within the collagenous matrix of a frill. Such features are almost identical in the holotype (Nature, doi:10.1038/34356). The improbability that these fibres represent 'protofeathers', described as 'soft and pliable' (Currie & Chen 2001), and

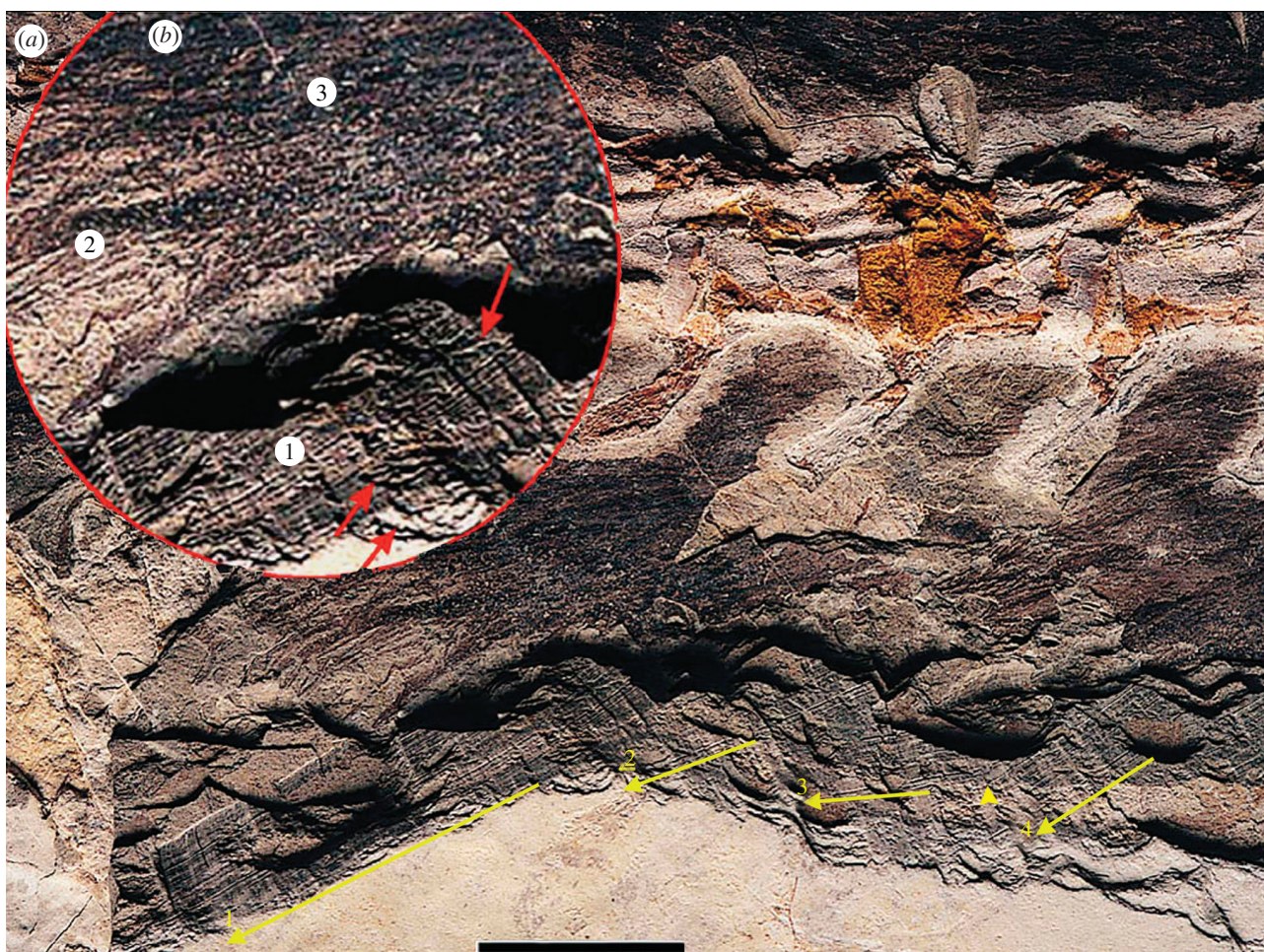


Figure 4. Integumentary structures in *Sinosauropteryx* NIGP 127587. (a) Integumental structures (fibres) in at least three stages of preservation as (1) architecture of numerous parallel strands in tight formation (our inserted arrows show four broad bands of parallel fibres along the ventral area of the preservation), (2) parallel slightly thicker strands (onset of diagenesis) and (3) short, disorganized, occasionally sinuous structures (degraded). Between the chevrons the fibres parallel the long axis of the tail (Reprinted with permission from [Chen *et al.* \(1998\)](#)). Copyright © Macmillan Publishers Ltd). (b) Our detail shows the above three stages (numbered 1–3) including initialization of the breakdown of the geometric architecture (1) both within and along the edges, analogous to threads pulled from clothing (red arrows). Fibre structures in (a,b) are at higher magnifications than in [Chen *et al.* \(1998\)](#), where these structures are not mentioned. Scale bar, 1 cm.

that they escaped becoming tangled and matted in the mud prior to fossilization, is evident (see also [figure 3d](#)).

Although the frill is poorly preserved over the animal's back, traces of fibres sharply angled away from the body are evident in the shoulder and sacral area (see below; arrows, [figure 1a](#)). Integumental structures at the tip of the tail are also considered to belong to the frill (sites 3 and 4). In our specimen, as well as in the holotype (our observations, [figure 1b](#)), the fibres in the distal tail occur in regularly spaced patches, which we believe is a primary condition consistent with the gaps in a scalloped frill ([figure 2d](#)). Along the terminal vertebrae ([figure 3c](#)), the lower parts of the integumental structures (approx. half their lengths) across a broadband are barely distinguishable, compacted together as in a matrix of connective tissue, becoming discernible towards the mid-point ([figure 3d](#), circle), and separating as they degrade or become 'unglued' ([Lingham-Soliar 2003b](#)) at the tips. Such features are comparable with stages in the degradation of collagenous architectures in decomposing dolphin hypodermis ([Lingham-Soliar 2003b](#)). We would expect protofeathers to be rather sparse at this terminal part of the tail where the skin would be thinnest.

Our results show no herringbone patterns connected with the integumental structures or patterns that might resemble the plumules of birds ([Currie & Chen 2001](#)), but rather that the patterns are of geometrically precise bands of parallel fibres ([figure 4](#)). Short, randomly oriented, sinuous strands, interpreted as protofeathers ([Currie & Chen 2001](#)), are demonstrably a consequence of the degradation of the regular structures of bands of parallel fibres ([figures 3a and 4](#)). The geometric pattern noted is maintained so long as there is tension in the tissue whether this is in the skin, muscle or frill. Once tension is lost, the fibres may take on a sinuous appearance ([Gordon 1978](#); [Lingham-Soliar 2003a,b](#)).

(b) Thickness measurements of the integumental structures

Isolated integumental strands ([figures 2b and 3b](#)) from site 1 of our *Sinosauropteryx* show a distinct beaded structure. The strands range in thickness from 80 to 120 μm , but rarely as thin as 65 μm as in [figure 3b₃](#) (mean, 88 μm ; $n=100$; s.d., 14.98). Over the caudal vertebrae, the thickness ranged from 50 to 95 μm (mean, 71.3 μm , $n=75$; s.d., 11.24). These measurements were consistent for the other sites.

Some strands lie close to or overlies others as would be expected during the process of decay and decomposition (Lingham-Soliar 2001, 2003a,b; Feduccia *et al.* 2005; figure 2b, white arrows and circle and figure 3b₅). Figure 3b₇ shows swelling towards the centre of the integumental structure indicating the probable onset of diagenetic transformations, which include distortion in shape and thickness (Allison 1988a,b; Allison & Briggs 1991; Lingham-Soliar 2001, 2003b; Briggs 2003), cautioning that measurements be treated as approximations.

4. DISCUSSION

(a) Structure of the fibres

Under close-up examination, the integumental structures frequently show remarkable straightness (figure 3b_{1-3,6-8}), consistent with high tensile fibres, whereas sinuousness (figure 3b₄) was more infrequent. All integumental structures examined show the beaded form noted, e.g. in collagen fibre bundles in the dermis of sharks (Lingham-Soliar 2005a,b), modern-day reptiles (Lingham-Soliar in Feduccia *et al.* 2005), ichthyosaurs (Lingham-Soliar 1999, 2001) and dinosaurs (Feduccia *et al.* 2005) as well as individual mammalian collagen fibrils (Reichlin *et al.* 2005). Beading in histological preparations of collagen fibre bundles is thought to occur during dehydration with contraction in regular short waves of approximately 50 µm, more or less, dependant on the thickness of the fibre bundle (Lingham-Soliar 2003b). A tendency for collagen fibres to twist into rope-like structures (Young 2003) may also account for the beaded appearance. However, we emphasize that our objective is primarily to show that the integumental structures in *Sinosauropteryx* are structural fibres of soft tissue which form characteristic patterns in a wide variety of animals (Feduccia *et al.* 2005) and that they are collagenous is of secondary importance.

(b) Preservational biases during an animal's taphonomic history

Preservational bias of fibres, e.g. occurrence in one well-preserved specimen and not in another is one of the enigmas of fossilization frequently noted in different specimens. For example, in the ichthyosaur *Stenopterygius* dermal fibres were preserved over vertebrae and substrate in one soft-tissue specimen but solely within the body in another (Lingham-Soliar 2001) and similar differences are noted in soft-tissue preservation in the two *Psittacosaurus* specimens mentioned above (Mayr *et al.* 2002; Lingham-Soliar in Feduccia *et al.* 2005). Preservation of a hypothesized frill occurs in our specimen over the neck and tail (with scanty remains over the animal's back). In the holotype (Chen *et al.* 1998), it is virtually complete from the neck to the tip of the tail (figure 1b). Differences of preservation may depend, e.g. on how much of the animal was imbedded in the sediment (mud) immediately after death. For instance, among the many complexities of preservation (Briggs 2003), if the frill at the highest part of an animal lying on its side, i.e. the body and thicker part of the tail, was not rapidly and completely imbedded in the sediment (a possible fate in our specimen) then rapid degradation and destruction of the frill may occur by e.g. mechanical agents (albeit not exclusively) such as wind, water and scavengers. Initially, the matrix of the frill would

permit the fibres a good degree of tension, but with decomposition, this tension will inevitably be lost.

(c) Functional consequences of skin stiffness

In *Sinosauropteryx*, with the longest tail known for any theropod (Ji *et al.* 2001), the caudal vertebrae are not especially modified for stiffness as in *Deinonychus* (Weishampel *et al.* 1990). A fibre-reinforced skin, which, e.g. may account for 40–50% total tail stiffness in sharks (Wainwright *et al.* 1976; Lingham-Soliar 2005b), may have helped to maintain a stiff tail in *Sinosauropteryx*. In addition to a decorative role, perhaps the primary function of the tail frill in *Sinosauropteryx* was one of stiffness.

In both the nature of the fibrous structures and the structural architectures (geometrically parallel) they comprise in *Sinosauropteryx* (e.g. figures 3a and 4), they compare with collagenous fibre reinforcements of the dermis in living animals (Feduccia *et al.* 2005 and references therein; Lingham-Soliar 2005a,b). We suggest therefore that they were collagenous. As in many vertebrates including modern reptiles, the collagen probably occurred in numerous layers of the skin (Feduccia *et al.* 2005; Lingham-Soliar 2005a,b; Lingham-Soliar & Plodowski 2007), which would account for their density in preserved material (Chen *et al.* 1998; Currie & Chen 2001). The relatively inextensible nature of collagen makes it an ideal material for fibre architectural systems and accounts for its ubiquitous occurrence in the skin of vertebrates and invertebrates (Gordon 1978; Lingham-Soliar in Feduccia *et al.* 2005). In a unique preservation of a cross-section into the skin of a psittacosaur, more than 25 layers of fibres are observed (T. Lingham-Soliar 2007, unpublished results). We propose that multiple layers of collagen in the skin of dinosaurs function to stiffen the tissue at high strain and, importantly, provide toughness against injury, which would be particularly useful in less heavily armoured dinosaurs.

(d) Biological and evolutionary implications of a fibre-reinforced skin in dinosaurs

The pervasiveness of the beguiling, yet poorly supported, proposal of protofeathers in *Sinosauropteryx* has been counterproductive to the important question of the origin of birds. For instance, *Juravenator* (Gohlich & Chiappe 2006), a new Solnhofen compsognathid closely related to *Compsognathus* and *Sinosauropteryx*, as well as re-examined French Tithonian *Compsognathus corallestris* (Peyer 2006) were not only devoid of any trace of protofeathers/feathers, but had fairly typical tuberculated dinosaur skin (Gohlich & Chiappe 2006). Although a severe setback to the view that coelurosaurs possessed feathers, not scales, the authors (Gohlich & Chiappe 2006) challenge their own evidence by proposing that coelurosaurs 'may have differed greatly in the extension of their feathery covering', from 'for the most part feathered' in *Sinosauropteryx* to scantily feathered in *Juravenator*. Even if plausible, the unwillingness to consider the realistic alternative that coelurosaurs may simply have been scaly theropods is a cause for concern.

As in *Sinosauropteryx*, proposals that integumental structures preserved in *Sinornithosaurus* (Xu *et al.* 2001) and tyrannosauroids (Xu *et al.* 2004) are the remains of protofeathers/feathers do not withstand scientific scrutiny (Lingham-Soliar in Feduccia *et al.* 2005). On the other hand, *Sinosauropteryx* IVPP V12415 provides a

remarkable opportunity to understand dermal and subdermal fibre reinforcements in dinosaurs and helps to further our insights into taphonomic processes (Allison & Briggs 1991) without recourse to arbitrary conjectures on feather origins.

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REFERENCES

- Allison, P. A. 1988a Phosphatized soft bodied squids from the Jurassic Oxford Clay. *Lethaia* **21**, 403–410.
- Allison, P. A. 1988b Konservat-Lagerstätten: cause and classification. *Paleobiology* **14**, 331–334.
- Allison, P. A. & Briggs, D. E. G. 1991 The taphonomy of soft-bodied animals. In *The process of fossilization* (ed. S. K. Donovan), pp. 120–140. London, UK: Belhaven Press.
- Briggs, D. E. G. 2003 The role of decay and mineralization in the preservation of soft-bodied fossils. *Annu. Rev. Earth Planet. Sci.* **31**, 275–301. (doi:10.1146/annurev.earth.31.100901.144746)
- Chen, P.-J., Dong, Z. M. & Zheng, S. N. 1998 An exceptionally well preserved theropod dinosaur from the Yixian Formation of China. *Nature* **391**, 147–152. (doi:10.1038/34356)
- Currie, P. J. & Chen, P.-J. 2001 Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Can. J. Earth. Sci.* **38**, 1705–1727. (doi:10.1139/cjes-38-12-1705)
- Feduccia, A. 1999 *The origin and evolution of birds*, 2nd edn. New Haven, CT: Yale University Press.
- Feduccia, A., Lingham-Soliar, T. & Hinchcliffe, J. R. 2005 Do feathered dinosaurs exist? Testing the hypothesis on neontological and paleontological evidence. *J. Morphol.* **266**, 125–166. (doi:10.1002/jmor.10382)
- Gohlich, U. B. & Chiappe, L. M. 2006 A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature* **440**, 329–332. (doi:10.1038/nature04579)
- Gordon, J. E. 1978 *Structures*. Harmondsworth, UK: Penguin.
- Ji, Q., Norell, M. A., Gao, K.-Q., Ji, S.-A. & Ren, D. 2001 The distribution of integumentary structures in a feathered dinosaur. *Nature* **410**, 1084–1088. (doi:10.1038/35074079)
- Leng, Q. & Yang, H. 2003 Pyrite framboids associated with the Mesozoic Jehol biota in northeastern China: implications for microenvironment during early fossilization. *Prog. Nat. Sci.* **13**, 206–212.
- Lingham-Soliar, T. 1999 Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England. *Proc. R. Soc. B* **266**, 2367–2373. (doi:10.1098/rspb.1999.0933)
- Lingham-Soliar, T. 2001 The ichthyosaur integument: skin fibers, a means for a strong, flexible and smooth skin. *Lethaia* **34**, 287–302. (doi:10.1080/002411601753293042)
- Lingham-Soliar, T. 2003a Evolution of birds: ichthyosaur integumental fibers conform to dromaeosaur protofeathers. *Naturwissenschaften* **90**, 428–432. (doi:10.1007/s00114-003-0448-x)
- Lingham-Soliar, T. 2003b The dinosaurian origin of feathers: perspectives from dolphin (Cetacea) collagen fibers. *Naturwissenschaften* **90**, 563–567. (doi:10.1007/s00114-003-0483-7)
- Lingham-Soliar, T. 2005a Dorsal fin in the white shark *Carcharodon carcharias*: a dynamic stabilizer for fast swimming. *J. Morphol.* **263**, 1–11. (doi:10.1002/jmor.10207)
- Lingham-Soliar, T. 2005b Caudal fin in the white shark, *Carcharodon carcharias* (Lamnidae): a dynamic propeller for fast, efficient swimming. *J. Morphol.* **264**, 233–252. (doi:10.1002/jmor.10328)
- Lingham-Soliar, T. & Plodowski, G. 2007 Taphonomic evidence for high-speed adapted fins in thunniform ichthyosaurs. *Naturwissenschaften* **94**, 65–70. (doi:10.1007/s00114-006-0160-8)
- Mayr, G., Peters, D. S., Plodowski, G. & Vogel, O. 2002 Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften* **89**, 361–365. (doi:10.1007/s00114-002-0339-6)
- Motta, P. J. 1977 Anatomy and functional morphology of dermal collagen fibers in sharks. *Copeia* **1977**, 454–464. (doi:10.2307/1443263)
- Norell, M. A. & Xu, X. 2005 Feathered dinosaurs. *Annu. Rev. Earth Planet. Sci.* **33**, 277–299. (doi:10.1146/annurev.earth.33.092203.122511)
- Pabst, D. A. 1996 Morphology of the subdermal connective sheath of dolphins: a new fiber-wound, thin-walled, pressurized cylinder model for swimming vertebrates. *J. Zool. Lond.* **238**, 35–52.
- Peyer, K. 2006 A reconsideration of *Compsognathus* from the Upper Tithonian of Canjuers, southeastern France. *J. Vertebr. Paleontol.* **26**, 879–896. (doi:10.1671/0272-4634(2006)26[879:AROCFT]2.0.CO;2)
- Prum, R. O. & Brush, A. H. 2002 The evolution and diversification of feathers. *Q. Rev. Biol.* **77**, 261–295. (doi:10.1086/341993)
- Reichlin, T., Wild, A., Dürrenberger, M., Daniels, A. U., Aebi, U., Hunziker, P. R. & Stolz, M. 2005 Investigating native coronary artery endothelium *in situ* and in cell culture by scanning force microscopy. *J. Struct. Biol.* **152**, 52–63. (doi:10.1016/j.jsb.2005.07.009)
- Ruben, J. A. & Jones, T. D. 2000 Selective factors associated with the origin of fur and feathers. *Am. Zool.* **40**, 585–596. (doi:10.1668/0003-1569(2000)040[0585:SFAWTO]2.0.CO;2)
- Unwin, D. M. & Bakhurina, N. 1994 *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature* **371**, 62–64. (doi:10.1038/371062a0)
- Wainwright, S. A., Biggs, W. D., Currey, J. D. & Gosline, J. M. 1976 *Mechanical design in organisms*. London, UK: Edward Arnold.
- Weishampel, D. B., Dodson, P. & Osmolska, H. (eds) 1990 *The Dinosauria*, 2nd edn. Berkeley, CA: University of California Press.
- Xu, X., Zhou, Z. & Prum, R. O. 2001 Branched integumental structures in *Sinornithosaurus* and the origin of birds. *Nature* **410**, 200–204. (doi:10.1038/35065589)
- Xu, X., Norell, M. A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. 2004 Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680–684. (doi:10.1038/nature02855)
- Young, M. F. 2003 Bone matrix proteins: their function, regulation, and relationship to osteoporosis. *Osteoporos Int.* **14**(Suppl. 3), S35–S42.