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Short Communication

Evolution of birds: ichthyosaur integumental fibers conform to dromaeosaur protofeathers

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Abstract Filamentous integumentary structures have been reported as protofeathers in dromaeosaurs (non-avian dinosaurs). This hypothesis is considered against data on the complex architecture of dermal and subdermal collagenous fibers widely prevalent in living and extinct animals. Ichthyosaur integumental fibers, as dromaeosaur "protofeathers", are the most external structures preserved. Marked similarities are shown in branching patterns of these fibers compared with those of the dromaeosaur *Sinornithosaurus*; hence distinguishing between aberrant and primary features is difficult. Analysis of a pterosaur specimen shows that bent and straight fibers on the wings have functional implications. The fibers conform to the twofold shape of collagen and contradict the notion that bent integumental structures in the dinosaur *Sinosauropteryx* indicate softness and pliability. A suggestion also concerning *Sinosauropteryx* is that integumental structures with darker edges, compared with the middle, imply that they were hollow. Investigation of a similar condition in an ichthyosaur shows that it is more likely a consequence of mineralization. Dermal collagen fibers in, for example, sharks, dolphins, snakes, and turtles are shown to be grouped in bundles of varying sizes. Degradation of the dermis results in the breakdown of the fiber bundles and formation of myriad patterns of the disrupted fibers, as noted in decomposed dolphin skin. The overall findings of the study are that the thesis of dinosaur "protofeathers" requires more substantial support than exists at present.

Introduction

The now popular idea that feathers developed from filamentous integumentary structures in theropod dinosaurs before the development of avian flight (Prum *1999*) has broad implications for everything from the origins of endothermy to flight and bird origins. Over the last 10 years "feathered dinosaurs", "non-avian theropods", and "dromaeosaurs with integumental structures" have regularly featured in high-profile journals. Many of these discoveries have been so highly sensationalized that it is difficult to separate fact from fiction. Titles of articles (Xu et al. *2001*; Ji et al. *2001*) that proclaim "feathered dinosaurs" actually describe integumentary fibers or feather-like structures, which are not the same as avian feathers, as some of these authors recently noted (Norell et al. *2002*). Inconsistencies such as those of another author's support of a "filament to feather" model in one paper (Xu et al. *2001*), and the classical "scale to feather" model in another (Zhang and Zhou *2000*) cloud one of the important questions in evolutionary biology, the evolution of the avian feather. The subject necessitates that the suggested presence of protofeathers in dinosaurs must be proven or rejected based on incontrovertible evidence, especially given the presence of similar filamentous structures in other groups of fossilized archosaurian and non-archosaurian reptiles (Mayr et al. *2002*; Wang et al. *2002*; Lingham-Soliar *2001*) and mammoths (Kukhareva and Ileragimov *1981*).

The objective of the present study is to consider the popular idea of "protofeathers" in dromaeosaurid dinosaurs by examining our current understanding of dermal and subdermal fibers in vertebrate groups, living and extinct. The debate concerning whether or not birds originate from dinosaurs is not pertinent to the study.

Material

The soft-tissue ichthyosaur specimens discussed in this paper are probably amongst the best preserved in the world. The complete specimens, PMU R435 and SMF 457 are of the ichthyosaur *Stenopterygius quadricissus*, from Holzmaden in Southern Germany. *Ichthyosaurus*, GLAHM V1180a, is from the Lower Lias, Gloucestershire, England (Lingham-Soliar *1999*, *2001*). Cross-sections of skin of the white shark, *Carcharodon carcharias*, and bottlenose dolphin, *Tursiops truncatus*, were examined.

Observations and discussion

Studies of integumentary filamentous structures in fossils are not new (Broili *1942*; Wiman *1946*; Delair *1966*; Sharov *1971*) and have been beset with problems relating to the complexity of skin fibrous systems that we are only recently beginning to understand in extant vertebrates (Wainwright et al. *1978*; Hebrank and Hebrank *1986*; Pabst *1996*). Such problems in fossils are compounded by taphonomic processes (Allison and Briggs *1991*) that result in gross morphological and pattern changes, fibers break and rejoin in any number of patterns and are altered by complex chemical and microbial activity (Fig. 1a; Lingham-Soliar *2001*).

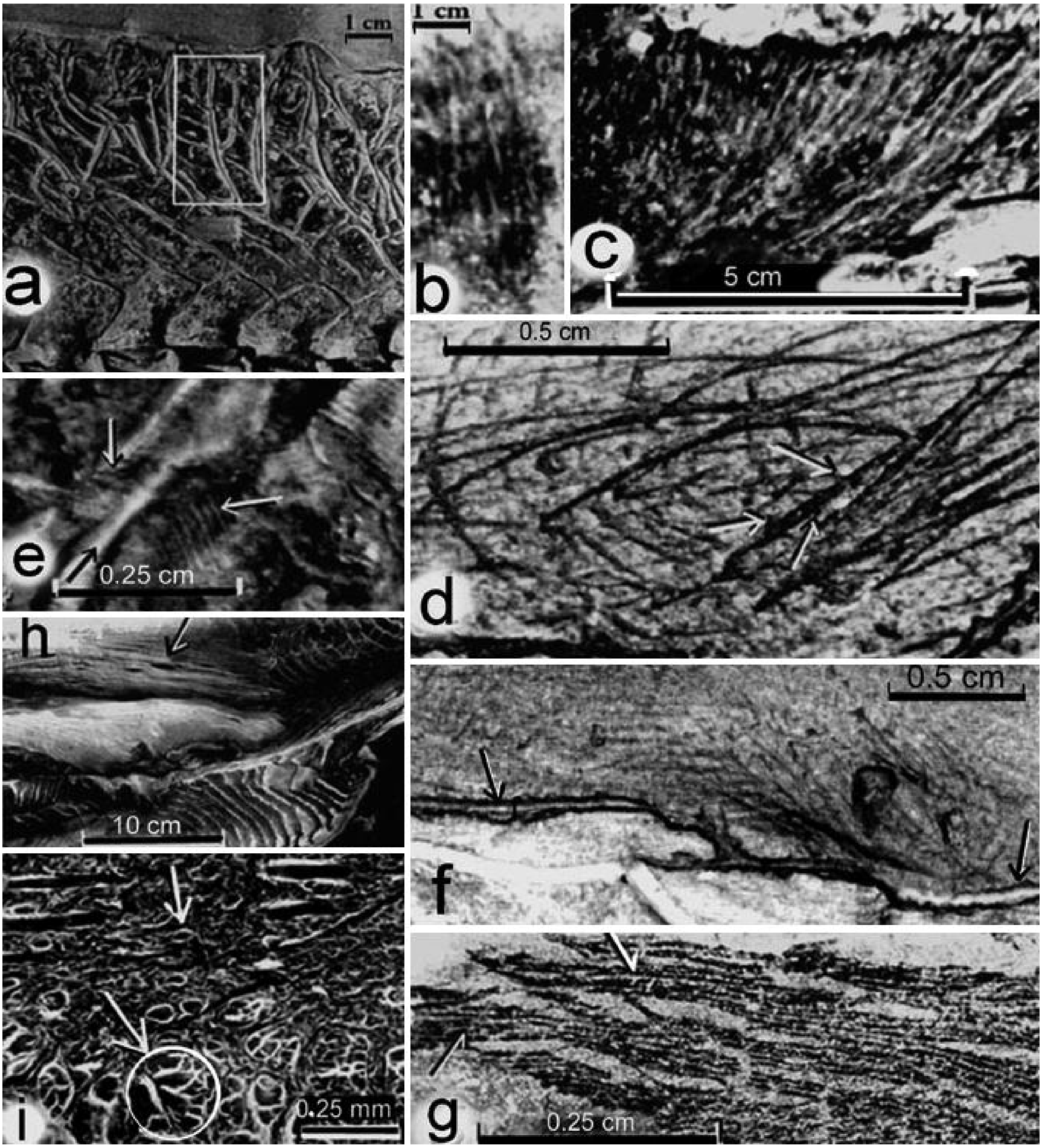

Fig. 1a–i. Integumentary fibers in three ichthyosaurs. **a** SMF 457, disorganized fibers on the posterodorsal surface; the result of. for example. fiber breaks and false joins; **b**, **c** PMU R435, tufts of fibers apparently branching from a narrow basal point; **d** SMF 457, integumentary fibers on the matrix near the anterodorsal surface showing rachis-like filaments and stubs (*arrows*); **e** SMF 457, posterolateral surface showing fine fibers preserved over thick fibers, resembling rachis and barbs (*arrows*); **f** SMF 457, matrix above posterodorsal surface showing fibers resembling rachis and barbs; *arrows* show ?mineralization of long fiber; **g** GLAHM V1180a shows two integumentary fiber layers, the patchy top one impresses on those below. Note, "bending" of fibers (in life). Shark integument: **h** fibers in the white shark, *Carcharodon carcharias*, just anterior to dorsal fin (T. Lingham-Soliar, unpublished data) showing instances of herringbone patterns and an example of fibers curving around openings in tissue (*arrow*); **i** cross-section of the skin and

fibers showing thin collagenous fibers in the superficial dermis (*arrow*) and thick fiber bundles in the deeper dermis (*arrow/circled*). Note that the large fiber bundles are divided like muscle fasciculi into smaller fiber bundles and ultimately fibrils (the latter seen under SEM). Abbreviations: *SMF* Senckenberg Museum Frankfurt, *PMU* Paleontological Museum Uppsala, *GLAHM* Glasgow Hunterian Museum

Xu et al.'s (*2001*) report on integumental structures associated with a dromaeosaur exemplifies some of the problems mentioned above. The authors identify fiber-like structures in *Sinornithosaurus*. They allege that two different forms of "integumental appendages" are present, which coincide with part of their model of feather evolution. Firstly, they describe fibers apparently joined in a basal tuft (stage II in their figure 6). Given its isolated occurrence, and given a number of similar observations in ichthyosaurs (Fig. 1b, c), it is probable that it represents a taphonomic aberration. In another example, the authors' assertion that patches of multiple filaments represent a primary condition, i.e., "integumental appendages", is speculative and unconvincing. Most fibers are near-parallel (Fig. 2) and the few instances of divergence can easily be accounted for by taphonomic processes. Their contention that the different orientations of these "appendages" argue against them being attached to a single piece of skin might hold for fresh skin, but decaying skin may wrinkle and crease and over time decompose through chemical and microbial activity in patches, not to mention the vagaries of mechanical erosion (Fig. 2g). Hence, the constituent fibers could potentially form any number of orientations. They may also belong to different fiber layers with different orientations. Secondly, Xu et al. (*2001*, p 202) describe some filaments as forming a pattern "...in the manner of rachis and barbs in a pinnate feather" (stage IIIa in their figure 6). Two problems are noteworthy: (1) there are only two places showing apparent signs of fibers diverging from the alleged rachis (Xu et al. *2001*, figure 5a, b). Disregarding whether or not this is a primary condition, it seems inconceivable that such an important question as the structure of a pinnate feather can be contemplated on such tenuous evidence (also see Prum *1999*); (2) toward the tip (their figure 5b) there are three fibers lying parallel with the alleged rachis and of equal length. They do not resemble branching barbs and while this may result from poor preservation, so equally might other phenomena in the study. Indeed, there is nothing to preclude the structures being modified, elongated scales, as in some modern reptiles. Indeed, Mayr et al. (*2002*) described a significant find of bristle-like structures in the tail of *Psittacosaurus* (non-theropod), which according to them differ from the known integumentary structures of theropod dinosaurs in being "much longer, apparently more rigid, and much thicker...". Moreover, taphonomic problems, which plague paleontological research, have been ignored by Xu et al. (*2001*), as by many recent studies of Chinese dromaeosaur integument (see below).

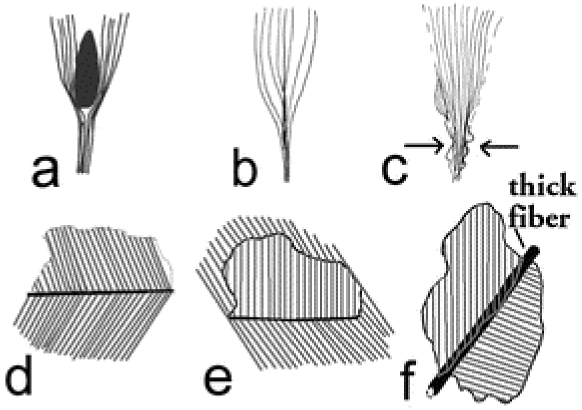

Fig. 2a–f. Models of how some taphonomic aberrations occur in preserved integuments. **a** Impressed object/s cause fibers to diverge before fossilization; **b** false joins produce a branching pattern; **c** creasing of skin at the base results in fluting of the fibers; **d**, **e** produce herring-bone patterns, **d** two opposing flaps of skin join as pages in a book, **e** loose flap of skin overlying another, **f** flaps of skin as in **d** overlain by thicker fiber(s). Such aberrations were found in ichthyosaur integuments (see Fig. 1a–g; also Lingham-Soliar *1999*, *2001*)

Ji et al. (*2001*) reported a dromaeosaur with integumentary structures, but discerning an association of very fine and thick fibers is difficult (their figure 5a–c). If rightly identified, a tiny patch shows exceedingly fine fibers forming a herringbone pattern, but not comparable to the barbs in other hypothesized feathered dinosaurs. Nevertheless, these are among the most convincing representations of feather impressions in a dromaeosaur. However, a serious problem in many such reports is the absence of fundamental data regarding dimensions (including those of alleged rachis and barbs) and concentrations of the filaments per unit area. The short, knobby thick fibers, on the other hand, are very similar to extensively preserved fibers, complete with tiny stubs along the pseudo-rachis, in an ichthyosaur (Fig. 1d). In other places on the same ichthyosaur specimen, fine fibers of one layer are compressed onto thick fibers of another, giving an uncanny resemblance to rachis and barbs (Fig. 1e). In Ji et al.'s (*2001*) report (their figure 6) fine fibers elsewhere near the ulna are obvious (clearly thicker than the ultra-fine fibers mentioned above), with some forking, but thick fibers are not apparent.

The hypothesis of dromaeosaur feathers should not be considered to be a fait accompli and any theory must consider the aberrations of preservation that may account for fibers diverging or forming herringbone and barb-like patterns (Fig. 1e, f). For instance, before fossilization, overlying structures pressed into the fibers below during compaction could cause the fiber paths to diverge (Lingham-Soliar *1999*) (Fig. 1g), in addition to the situation when curvature and sudden change in pitch reflects a primary feature (Hebrank and Hebrank *1986*). Creases, kinks and tears in the skin could also have a similar effect, a problem complicated by the numerous layers of integumentary fibers in a single animal, frequently having different dimensions and orientations (also see perimysial fibers in shark skin, Fig. 1h). In two-dimensional preservations it is almost impossible to separate one layer from another (Fig. 2). Thus, this complexity of fibers gives Prum's (*1999*) proposed model of the evolution of the feather a predictive vagueness and might fit into almost anything associated with the integument of diverse groups of animals.

Would the discovery of true feathers in non-avian dinosaurs support the filamentous "protofeather" stage in Prum's (*1999*) model? Not necessarily. "Protofeathers" would still have to be conclusively distinguished from fibers of the skin. For instance both hair and collagenous fibers have been discovered in mammoths (see Kukhareva and Ileragimov *1981*), with obviously no evolutionary connection.

The assumption that integumentary structures along the tail of the dromaeosaur *Sinosauropteryx* are feather-like (Chen et al. *1998*) is speculative, and no more convincing in a subsequent study of new material (Currie and Chen *2001*). Currie and Chen's (*2001*, p 1719) comment that the fossilized integumentary structures were "soft and pliable" is perplexing, given that we do not know their biological composition. Fibers composed of collagen have different forms (e.g., straight or bent), which are affected by various conditions including decay. The authors add that under magnification the margins of the larger structures are darker along the edges but light medially (?middle), which in their view suggests that they may have been hollow. Investigation in the ichthyosaur SMF 457, however, indicates that different stages of mineralization seem more likely (Fig. 1f, arrows).

The dromaeosaur tail is a relatively stiff organ, achieved by powerful bands of ligaments that extend along the dorsolateral and ventrolateral surfaces of the tail vertebrae. Enlarged interspinal ligaments also occur on the dorsal vertebrae (Weishampel et al. *1990*). Two possible scenarios are envisaged in *Sinosauropteryx*: either the bundles of tightly strung ligaments broke contact with the vertebrae during post-mortem decay and came to lie alongside the caudal vertebrae, or the skin possessed masses of strengthening fibers or rays vertically orientated to the long axis of the body. For instance, Richard Owen (*1840–1845*) illustrated an ichthyosaur paddle in which fine rays, reminiscent of those of *Sinosauropteryx*, bordered the fleshy (non-skeletonized) edges of the paddle, presumably for support or stiffening.

It was not so long ago that pterosaurs covered in hair pervaded reconstructions (e.g., see Wellnhofer *1991*), an unfortunate interpretation of Sharov's (*1971*) description of hair-like structures in *Sordes pilosus*. More recently, however, the structures were shown to be fibers supporting the wings (Unwin and Bakhurina *1994*), straight, closely packed fibers on the outer half of the wing and shorter, loosely packed fibers close to the body. This fibrous architecture was construed to provide increased elasticity close to the body and greater rigidity further away. I would add that the structures show characteristics of collagen fibers. The outer fibers were apparently pre-stressed and laid down under tension as, for instance, in cat skin (Veronda and Westman *1970*) and mineralized before loss of tension (and curvature). Proximally, the bent fibers also resemble collagen fibers in a different form, in presumably a matrix of elastin, which has a low modulus. Thus elastin provides the elasticity. However, as this composite material stretches, the bent collagen material would straighten and become taut (see Gordon *1978*). Thus in the extended state of the pterosaur wing the modulus of the material throughout is that of collagen, providing an overall rigid wing surface in flight. Interpretations of fibers in fossils (e.g., Currie and Chen *2001*) that fail to take account of the complexity of integumentary fibers in living systems are regrettable.

Investigation of dermal collagen fibers, for example in sharks (see Fig. 1i), dolphins, snakes, and turtles have shown that the fibers are grouped in bundles of varying sizes. Examination of decomposed dolphin integument shows a breakdown of the fiber bundles and formation of myriad patterns of the disrupted fibers, many distinctly feather-like (unpublished data).

We still have some way to go before we understand how ubiquitous and complex integumentary fiber structures are in living animals (Fig. 2h), how similar they are in disparate groups of animals, how they function, and how they preserve. It is impossible to say that the famous Chinese dromaeosaurs did not possess feathers, or that they are not collagen fibers, which has been suggested as the biological material preserved in these dinosaurs (Feduccia *1999*). Each needs to be scrutinized on its own merits with scientific rigor. Progress in understanding feather evolution awaits clarification of the structure of the integument from which it evolves.

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References

Allison PA, Briggs DEG (1991) The taphonomy of soft bodied animals. In: Donovan SK (ed) The process of fossilization. Belhaven, London) pp 120–140

Broili F (1942) Verfestigungen im Integument der Ichthyosaurier. Sitzungsberichte Bayer Akad Wiss Math Nat 37–52

Chen P-J, Dong Z-M, Zhen S-N (1998) An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. Nature 391:147–152

Currie PJ, Chen P-J (2001) Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. Can J Earth Sci 38:1705–1727

Delair JB (1966) Unusual preservation of fibrous elements in an ichthyosaur skull. Nature 212:575–576

Feduccia A (1999) The origin and evolution of birds, 2nd edn. Yale University Press, New Haven, Conn.

Gordon JE (1978) Structures. Penguin Books, Harmondsworth, UK

Hebrank R, Hebrank JH (1986) The mechanics of fish skin: lack of an 'external tendon' role in two teleosts. Biol Bull 171:236–247

Ji Q, Norell MA, Gao K.-Q, Ji S-A, Ren D (2001) The distribution of integumentary structures in a feathered dinosaur. Nature 410:1084–1088

Kukhareva LV, Ileragimov RK (1981) The young mammoth from Magadan (in Russian). Nauka, Leningrad

Lingham-Soliar T (1999) Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England. Proc R Soc Lond B 266:2367–2373

Lingham-Soliar T (2001) The ichthyosaur integument: skin fibers, a means for a strong, flexible and smooth skin. Lethaia 34:287–302

Mayr G, Peters DS, Plodowski G, Vogel O (2002) Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. Naturwissenschaften 89:361–365

[SpringerLink]

Norell M, Ji Q, Gao K, Yuan C, Zhao Y, Wang L (2002) Modern feathers on a non-avian dinosaur. Nature 416:36

[SpringerLink] [SpringerLink] [SpringerLink]

Owen R (1840–1845) Odontography (2 volumes)

Pabst DA (1996) Morphology of the subdermal connective sheath of dolphins: a new fiber-wound, thin-walled, pressurized cylinder model for swimming vertebrates. J Zool 238:35–52

Prum RO (1999) The development and evolutionary origin of feathers. J Exp Zool 285:291

[SpringerLink] [SpringerLink] PubMed

Sharov AG (1971) New flying reptiles from the mesozoic deposits of Kasakhstan and Kirgizia (in Russian). Tr Paleontol Inst Akad Nauk SSSR 130:104–113

Unwin DM, Bakhurina N (1994) *Sordes pilosus* and the nature of the pterosaur flight apparatus. Nature 371:62–64

Veronda DR, Westman RA (1970) Finite deformations of skin. J Biomech 3:111–124

ChemPort PubMed

Wainwright F, Vosburgh F, Hebrank JH (1978) Shark skin: function in locomotion. Science 202:747–749

Wang X, Zhou Z, Zhang F, Xu X (2002) A nearly complete articulated rhamphorhynchoid pterosaur with exceptionally well preserved wing membranes and hairs from Inner Mongolia, northeast China. Chin Sci Bull 47(3):226–230

PubMed

Weishampel DB, Dodson P, Osmolska H (1990) The *Dinosauria*. University of California Press, Berkeley, Calif.

Wellnhofer P (1991) The illustrated encyclopedia of pterosaurs. Salamander, London

Wiman C (1946) Über Ichthyosaurier und Wale. Senckenbergiana 27:1–11

Xu X, Zhou Z-H, Prum RO (2001) Branched integumental structures in *Sinornithosaurus* and the origin of birds. Nature 410:200–204

Zhang F, Zhou Z (2000) A primitive Enantiornithine bird and the origin of feathers. Science 290:1955–1959