

Do Feathered Dinosaurs Exist? Testing the Hypothesis on Neontological and Paleontological Evidence

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ABSTRACT The origin of birds and avian flight from within the archosaurian radiation has been among the most contentious issues in paleobiology. Although there is general agreement that birds are related to theropod dinosaurs at some level, debate centers on whether birds are derived directly from highly derived theropods, the current dogma, or from an earlier common ancestor lacking suites of derived anatomical characters. Recent discoveries from the Early Cretaceous of China have highlighted the debate, with claims of the discovery of all stages of feather evolution and ancestral birds (theropod dinosaurs), although the deposits are at least 25 million years younger than those containing the earliest known bird *Archaeopteryx*. In the first part of the study we examine the fossil evidence relating to alleged feather progenitors, commonly referred to as protofeathers, in these putative ancestors of birds. Our findings show no evidence for the existence of protofeathers and consequently no evidence in support of the follicular theory of the morphogenesis of the feather. Rather, based on histological studies of the integument of modern reptiles, which show complex patterns of the collagen fibers of the dermis, we conclude that “protofeathers” are probably the remains of collagenous fiber “meshworks” that reinforced the dinosaur integument. These “meshworks” of the skin frequently formed aberrant patterns resembling feathers as a consequence of decomposition. Our findings also draw support from new paleontological evidence. We describe integumental structures, very similar to “protofeathers,” preserved within the rib area of a *Psittacosaurus* specimen from Nanjing, China, an ornithomimid dinosaur unconnected with the ancestry of birds. These integumental structures show a strong resemblance to the collagenous fiber systems in the dermis of many animals. We also report the presence of scales in the forearm of the theropod ornithomimid (bird mimic) dinosaur, *Pelecanimimus*, from Spain. In the second part of the study we examine evidence relating to the most critical character thought to link birds to derived theropods, a tridactyl hand composed of digits 1-2-3. We maintain the evidence supports interpretation of bird wing digit identity as 2,3,4, which appears different from that in theropod dinosaurs. The phylogenetic significance of Chinese microraptors is also discussed, with respect to bird origins and flight origins. We suggest that a possible solution to the disparate data is that Aves plus bird-like maniraptoran theropods (e.g., microraptors and others) may be a separate clade, distinctive from the main lineage of Theropoda, a remnant of the early avian radiation, exhibiting all stages of flight and flightlessness. *J. Morphol.* 266:125–166, 2005. © 2005 Wiley-Liss, Inc.

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“When I use a word,” Humpty Dumpty said in rather a scornful tone, “it means just what I choose it to mean — neither more nor less.” “The question is,” said Alice, “whether you can make words mean so many different things.” “The question is,” said Humpty Dumpty, “which is to be master — that’s all.” —Lewis Carroll, 1871.

Prior to the 1970s birds and dinosaurs were thought to have shared a common ancestry through Triassic basal archosaurs, often collectively termed thecodonts, characterized by the Triassic *Euparkeria*. But with John Ostrom’s discovery of the bird-like Early Cretaceous *Deinonychus*, the dinosaurian origin of birds gained ascendancy as the reigning dogma, based on overall similarity of this newly discovered dromaeosaur to birds and *Archaeopteryx*. Much of the heated debate that ensued has been hyperbolic, as everyone agrees that birds are derived from within the archosaurian assemblage: whether birds are derived from “dinosaurs” depends largely on how one defines the Dinosauromorpha (Feduccia, 1999a). However, following Ostrom’s dramatic discovery, the new version of the theropod origin of birds was formalized and codified by various cladistic analyses (beginning with Gauthier, 1986). Because *Deinonychus* and its allies were considered close to the origin of birds and nested deep within Theropoda, birds were thought to have evolved from obligate bipedal theropods, with highly derived (apomorphic) anatomical characters. With this new view of avian evolution came a series of cladistic inferences or corollaries, ranging from feathers evolving to insulate endothermic dinosaurs, to flight evolving from the ground up.

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At the extreme, *Archaeopteryx* became an earth-bound, predatory dromaeosaur that could not fly (Bakker, 1975), despite its obvious arboreal and flight capabilities and near absence of dromaeosaurid anatomy, lacking salient features including a pedal 2nd sickle claw and stiffened “ramphorhynchoid-like” tail. Instead of an early bird origin and a likely and facile trees-down flight origin, birds evolved later in time, directly from highly specialized theropods, and would have to fight gravity to gain ascendancy by a biophysically untenable cursorial origin (Feduccia, 1999a; Long et al., 2003). Numerous, often bizarre and intricate theories have thus been advocated to explain flight and feather origins in a non-aerodynamic context, the earliest being Ostrom’s (1979) “insect net theory” by which feathers elongated on the hands of terrestrial theropods to capture insects, and were later preadapted for flight. Despite its complex, unparsimonious nature, and apparent absurdity, the “insect net theory” appears to have been renewed and applied to the Lower Cretaceous arboreal, volant bird *Confuciusornis* (Padian and Chiappe, 1998). The latest theories involve a shift from one to three locomotor modules (Gatesy and Dial, 1996), and a truly bizarre model based on highly derived hill-running quail, running up tree trunks (Dial, 2003). Typical of modern paleontologists, Dingus and Rowe (1998, p. 192) linked the theropod ancestry of birds with the origin of flight from the ground up, and the so-called thecodont (basal archosaur) hypothesis with the origin of flight from the trees down. “Our map [of avian relationships] suggests that flight evolved from the ground up, but exactly how this happened is another question altogether.” But as evolutionary biologist Walter Bock (1999, p. 508) commented, “If the origin of birds and the origin of flight are tightly linked in this fashion, then the available discussion of all specialists in vertebrate flight is that the origin of avian flight from the ground up is exceedingly improbable, which would fatally weaken the dinosaur ancestry of birds.”

While all classes of land vertebrates have evolved some level of flight, it has demonstrably always been achieved in accordance with the extremely simple trees-down model, utilizing small size coupled with cheap energy provided by gravity, that is, high places (Norberg, 1990). The same untenable ground-up model was invoked for pterosaurs, and despite several decades of attempted imaginative explanations (beginning in Padian, 1983), the theory is now discredited by new discoveries of quadrupedal trackways, membranes binding the hindlimbs, and a basal Triassic flat-footed pterosaur (Feduccia, 1999a, 2002; Unwin and Henderson, 2002). Finally, the discovery of arboreal Lower Cretaceous flying, four-winged microraptors with pennaceous feathers, thought to be theropod dinosaurs (dromaeosaurs), appears to have validated an arboreal origin of flight regardless of the ancestry (Zhou, 2004).

It would not tax the imagination to engender a long list of obstacles for the now dominant model of a theropod origin of birds, including, but not limited to: the fact that early theropods (e.g., Triassic *Herrerasaurus*) are highly specialized obligate bipeds (with arms reduced to 1/2 the length of the hindlimbs); the fact that the stratigraphic sequence of bird-like theropods has been almost the reversal of the expected evolutionary sequence leading to birds; the fact that the earliest described “feathered dinosaur” is the unbird-like compsognathid *Sinosauropteryx*, devoid of any preserved structures that can be shown to be feather-like; the fact that any downy-like integumentary covering in a terrestrial theropod would be maladaptive; the fact that flight feathers arranged precisely on the hand as in modern birds are present in microraptors and the basal oviraptorosaur *Caudipteryx*; the fact that many of the derived characters or synapomorphies linking birds and theropods are in question, including notably but not limited to: the sliding lower jaw joint of theropods (absent in birds), the theropod ascending process of the astragalus (distinctive from the avian pretibial bone), and the digital mismatch (1,2,3 theropod vs. 2,3,4 bird hand), etc., to mention a few.

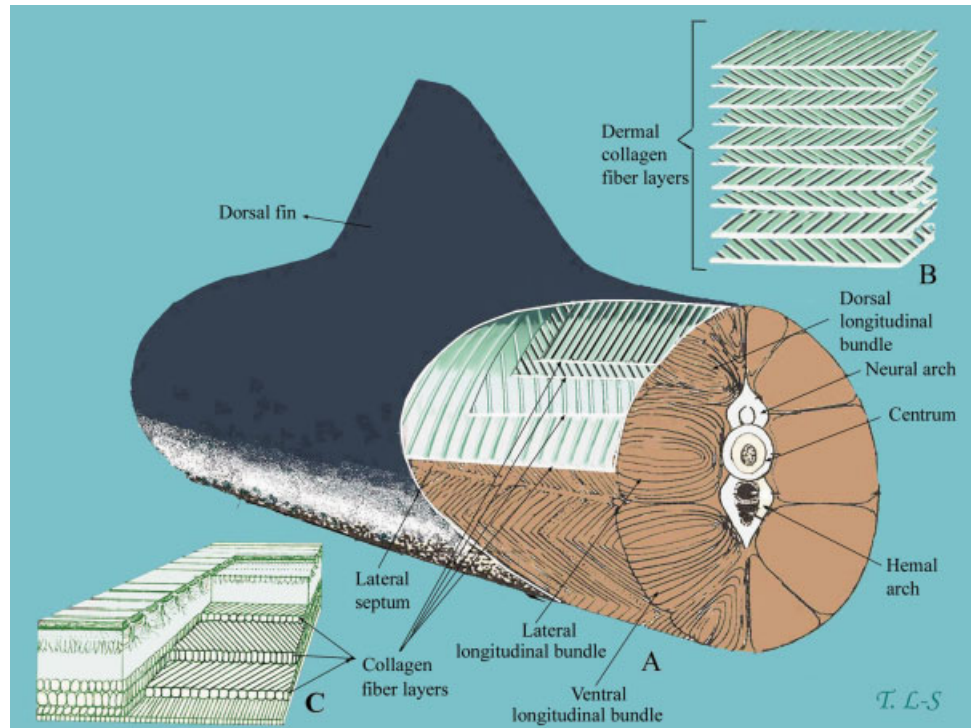
Here we focus on two paramount issues. First, one of us (T.L-S) examines the evidence for the assertion that the so-called “dino-fuzz” filaments preserved from lacustrine deposits from Early Cretaceous theropods of China represent protofeathers, and the confused interpretations caused by association of the preservation of “dino-fuzz” with true pennaceous feathers. Part of the confusion involves Chinese microraptors, which are most probably birds, remnants of the early avian radiation. This part of the study includes a reexamination of the follicular theory of the morphogenesis of the feather against the alleged fossil evidence (T.L-S) and lastly the thesis of downy dinosaurs (T.L-S and A.F.). Second, we (R.H. and A.F.) explore the paradox of the digital mismatch between birds and theropods. Although the vast majority of developmental evidence supports a 2,3,4 digit identity for the wing of birds, it is assumed that birds must be 1,2,3, because birds are thought to be “living dinosaurs” and the known digital morphology in Triassic theropods, from which birds are thought to have evolved, shows a hand preserved with 1,2,3 digit identity, with digits 4 and 5 greatly reduced.

REVISITING THE FEATHERED DINOSAUR HYPOTHESIS

Integumentary Structures in Basal Theropod and Dromaeosaurid Dinosaurs: Protofeathers or Collagen?

Proposals that integumentary structures found on a variety of non-avian dinosaurs are homologs of

Fig. 1. Integumental collagen architecture—from white sharks to worms. **A:** A schematic view of the collagen fiber architecture of the dermis in the white shark *Carcharodon carcharias*. **B:** An exploded schematic view of 10 layers of helically arranged collagen fibers in the stratum compactum of the dermis (varies from 12–20 layers) of *C. carcharias*, which form a complex architecture (as opposed to random networks of collagen that characterize the dermis of some animals). Note: The fiber bundle thickness gets progressively thicker deeper into the dermis, as previously hypothesized for those in the skin of the ichthyosaur, *Stenopterygius* (Lingham-Soliar, 2001). **C:** The cuticle of the worm, *Ascaris lumbricoides*, showing collagen fiber layers (after Clark, 1964).



true feathers (Chen et al., 1998; Xu et al., 1999; Currie and Chen, 2001), commonly referred to as protofeathers, are controversial (Maderson and Homberger, 2000; Xu et al., 2001; Lingham-Soliar, 2003a,b). It has been claimed that these varied integumentary structures are homologous with stages or levels of morphological complexity in feather morphogenesis (Prum, 1999; Xu et al., 1999; Sues, 2001; Prum and Brush, 2002). An alternative interpretation is that some of the integumentary structures represent fossilized collagen (Feduccia, 1999a; Ruben and Jones, 2000; Lingham-Soliar, 2003a,b). The response to this from advocates of the protofeather hypothesis has been largely negative (see, e.g., Norell and Xu, 2005; Norell, 2005). In our view this is a consequence of a lack of understanding of the complexity of collagen architectures, in particular, that of integumental collagen. Studies that show some of these complexities pertain, e.g., to dolphins and sharks (Pabst, 1996; Lingham-Soliar, 2005a,b) but, to our knowledge, there are none that illustrate comparable complexities in modern day reptiles, which may be construed by some to have more relevance to dinosaurs. We address this here. Collagen fibers are investigated in a number of reptiles in the present study.

Collagen is the basic structural material of the animal kingdom. Type I collagen is found in virtually all of the animal phyla, usually as a component of a complex, pliant connective tissue, but it is also found in a number of pure tensile structures, such as tendon, where it is present as parallel arrays of nearly pure collagen fibers (Wainwright et al., 1976). The dermis of

taxa across a broad phylogenetic range, from worms (Alexander, 1987) to the white shark, *Carcharodon carcharias* (Lingham-Soliar, 2005a,b; Fig. 1), may also consist of predominantly collagen fibers, densely compacted and either noncrossed-helically arranged or crossed-helically arranged in layers (for the functional significance, see Lingham-Soliar, 2005a,b). These fiber bundles are analogous to muscle fascicles. Collagen fiber bundles may be <0.05 mm to >1 mm thick (individual fibers range from ~0.004–0.02 mm thick). This ability to form fiber bundles in varied architectural constructions plays a crucial role in the tensile stiffness of skin. For instance, biomechanical tests on the caudal fin of *C. carcharias*, show that stiffness or shear modulus G (similar to Young's modulus) is high, the skin providing as much as 40–50% the total stiffness of the control surface despite its low percentage thickness in the element; virtually all this stiffness is contributed by the collagen fiber bundles (Lingham-Soliar, 2005b). In fossil animals such as ichthyosaurs (Lingham-Soliar, 1999, 2001) and dinosaurs, the stiffness of the skin may be functionally important for different reasons, e.g., swimming performance and protection, respectively.

Given the wide distribution of collagenous tissue throughout the animal kingdom, collagen should, in principle, be one of the most commonly preserved organic materials in fossil vertebrates, although in practice it would depend on its fossilization potential. The potential of collagen to preserve in fossils seems well supported in soft tissue preservations of several vertebrate taxa in the fossil record. This potential is furthermore significant in the ability of

collagen to preserve in a variety of sediments, from marine (Lingham-Soliar, 1999, 2001) to diverse terrestrial environments (Kukhareva and Ileragimov, 1981; Unwin and Bakhurina, 1994). Of importance, too, is the variety of forms collagen may take in the integument of animals since these forms may preserve in both normal and idiosyncratic ways depending on the complex processes of decomposition and fossilization.

The present study, therefore, is an attempt to understand what “protofeathers” are and their possible composition. The question we ask is, Could the alleged protofeathers be visual aberrations of some other form of organic material, principally collagen? We attempt to answer this question in two ways. First, we examine the skin of extant terrestrial and marine reptiles for the presence of collagen, using standard histological techniques. Second, we examine existing fossil material in theropod dinosaurs that are thought by some to include protofeathers, as well as new fossil soft tissue remains in an ornithopod and ornithomimid dinosaur.

MATERIALS AND METHODS

The skin of six reptiles (encompassing two suborders, Serpentes and Sauria, and two orders, Chelonia and Crocodylia), the Natal black snake, *Macrelaps microlepidotus* (0.75 m long), Burmese python, *Python molurus bivittatus* (3.0 m long), agamid, *Agama atricollis* (body 15 cm long), loggerhead turtle, *Caretta caretta* (shell length 65 cm, weight, 35.1 kg), juvenile, newborn crocodile, *Crocodilus niloticus* (body 15.4 cm long), and the crest of the Jesus lizard, *Basiliscus plumifrons* (body 10.1 cm long) were examined. Tangential sections (terminology after Hebrank, 1980, fig. 2), i.e., on a plane parallel to the skin surface, as opposed to transverse sections that are perpendicular to the skin surface (minimum $n = 4$, in each area), of 30–40 μm thickness were made using standard cryostat sectioning techniques. Sections were obtained from the lateral surface of the body of the snakes (at mid-body length), the neck of the loggerhead turtle, and ventral surface of the body or underbelly (between anterior and posterior legs) and anterodorsal surface of the tail of the agamid and dorsolateral surface of the neck of the crocodile (Fig. 2A–H). Tangential sections were also made of the comb of the domestic chicken, *Gallus domesticus* (Fig. 2I). The sections were

examined and digitally photographed using a Zeiss Axiophot light microscope under polarized light (DIC). Measurements were made by means of a Panasonic Biomed Analyzer.

Methods of investigating the integument of living animals via histological preparations are clearly not available to fossil animals. Nevertheless, the principles of study of fossilized soft tissue may closely follow those of extant animals. In a study of the ichthyosaur integument it was noted that the vagaries and variability of fossil preservation, rather than being thought of as negative, could have positive value “in the exposition of the different areas and levels of the integument,” in effect serving “as a laboratory dissection” (Lingham-Soliar, 2001, p. 289) or microtomy. A careful examination of material on the theropod dinosaur, *Sinornithosaurus*, shows that the substrate around the animal represents different organic layers. The variable preservation of the organic material in the substrate was used, as with the ichthyosaur (Lingham-Soliar, 2001), to understand different levels of the integument. Discerning different layers in the fossilized soft tissue and attempting to understand their nature may contribute to a better understanding of the material. We also applied these same principles of investigation to a new study of fossilized soft tissue material of the ornithopod dinosaur, *Psittacosaurus*.

This principle of treating the vagaries of fossilization to advantage included an examination of the most peripheral and most poorly preserved fossilized soft tissue in the hope that there might be insights into the degradation processes and consequently into the nature of the soft tissue of the animals concerned. In this respect some understanding of organic tissue in different states is useful: 1) in its normal state, i.e., in the living body; 2) in a state of decomposition; and 3) in a fossilized state. Of these three states perhaps least is known of the breakdown of tissue in a decomposing animal (with the possible exception of humans in forensic studies), with particular respect to the integument and collagen. An attempt to shed some light on this problem was made recently in a study of a decomposing dolphin (Lingham-Soliar, 2003b), an animal known to have large quantities of collagen in its integument. In that study a dolphin was buried and allowed to decompose for a year. At the end of that period the decomposing integument was examined using polarized light microscopy. The results of that study will be mentioned briefly below.

Note: Although the term “taphonomy” is applied to the processes by which animals become fossilized, strictly speaking, everything that happens to an animal after it dies, it is generally a term used by paleontologists and not, e.g., by biologists nor in forensics. Generally, too, the term taphonomy may include gross changes that occur to animal remains after death but not some of the more subtle changes described here. For this reason we separate here the decomposition processes or degradation of tissue

Fig. 2. Collagen in vertebrate (mainly reptile) integument (see Materials and Methods for sectioning techniques, sample areas, microscopic examination, and photography). **A:** The agamid lizard, *Agama atricollis*. Thick bundles of collagen fibers in the dermis overlying the anterodorsal part of the tail near its union with the body; above some of the component fibers (arrows) comprising a thicker bundle are seen; below some fiber bundles have separated as a consequence of mechanical abrasion (microtomy) to form an aberrant branched structure (arrow). **B:** *Agama atricollis*. Collagen fiber bundles (arrows) in the dermis in the ventral surface of the animal, approximately mid-point between the anterior and posterior legs (arrows show some collagen bundles). **C:** Part of the semitransparent head crest of the Jesus lizard, *Basiliscus plumifrons*, showing translucent scales and thick fibers (arrows), probably collagenous, within a dense matrix of connective tissue (tangential section of crest, ~ 0.25 mm thick, includes the scaly surface). **D:** The loggerhead turtle, *Caretta caretta*. Collagen. Fiber bundles in the dermis in the neck show alternating layers of fibers in left- and right-handed orientations (arrows); on the left can be seen traces of the overlying layer of left-handed fiber bundles (left arrow). **E:** The Natal black snake, *Macrelaps microlepidotus*. Dermis on the lateral surface of the body (mid-length) showing slightly wavy bundles of collagen fibers (arrows); waviness is probably a consequence of loss of muscle tone or dehydration of the tissue (Lingham-Soliar, 2003b); all sections showed the same orientations. **F:** Detail of some fiber bundles in **G** shows fine fiber components breaking off from the thick bundles. **G:** Burmese python, *Python molurus bivittatus* (3 m long). Unusual cross-weaving of layers of oppositely oriented helical fibers in skin at body mid-length (lateral surface); this architecture probably achieves increased strength with possibly a slight reduction in skin flexibility (see Lingham-Soliar, 2005b, for further discussion on different functional types of collagenous architectures of the dermis). **H:** *Crocodilus niloticus*, newborn juvenile (body 15.4 cm long). Collagen fibers in the skin in the lateral surface of the neck. On the right can be seen the edge of a scute. **I:** Domestic chicken, *Gallus domesticus*. A matrix of collagen fiber bundles reinforces the dense adipose tissue making up the comb. For further details, see Materials and Methods.

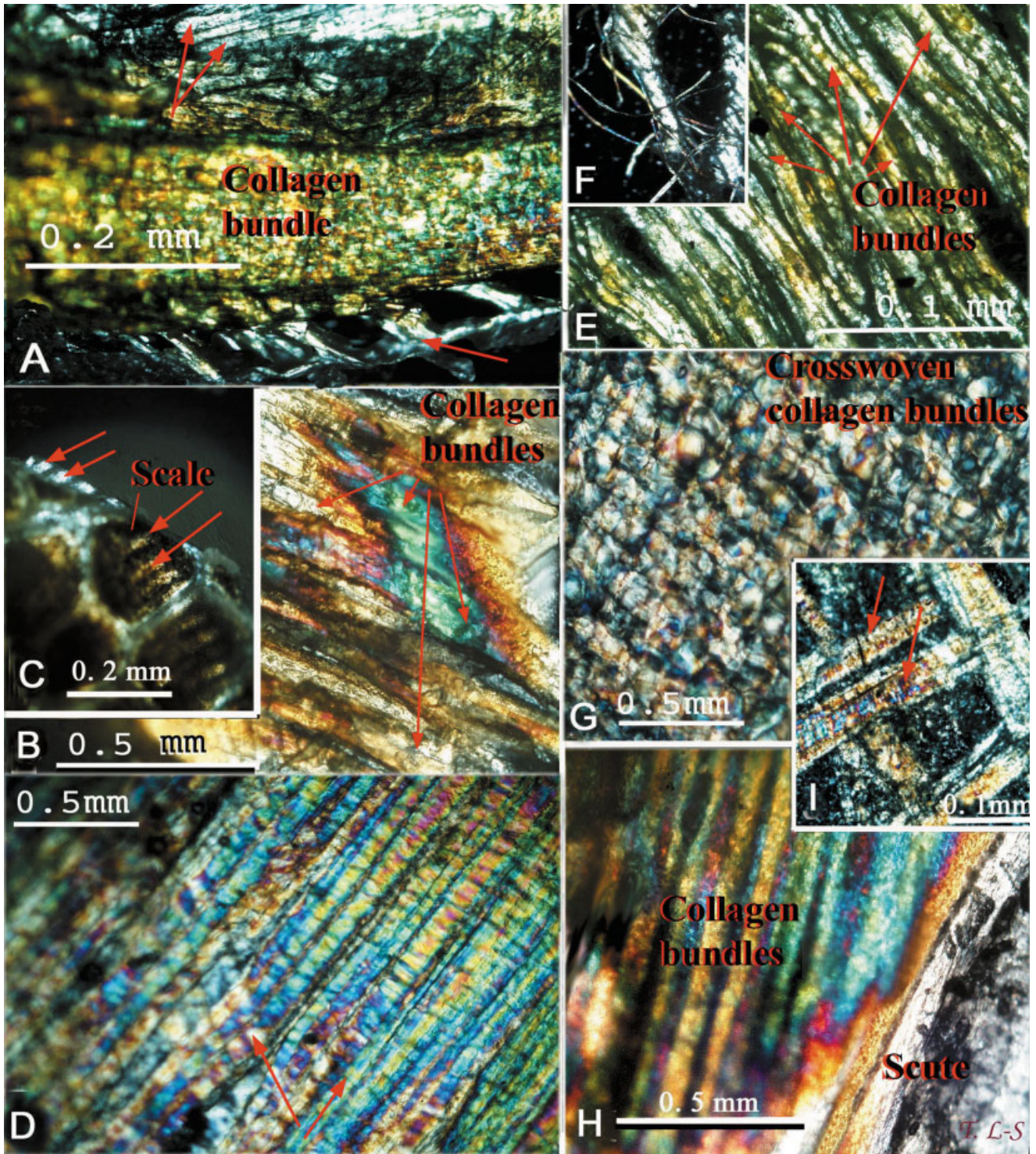


Figure 2

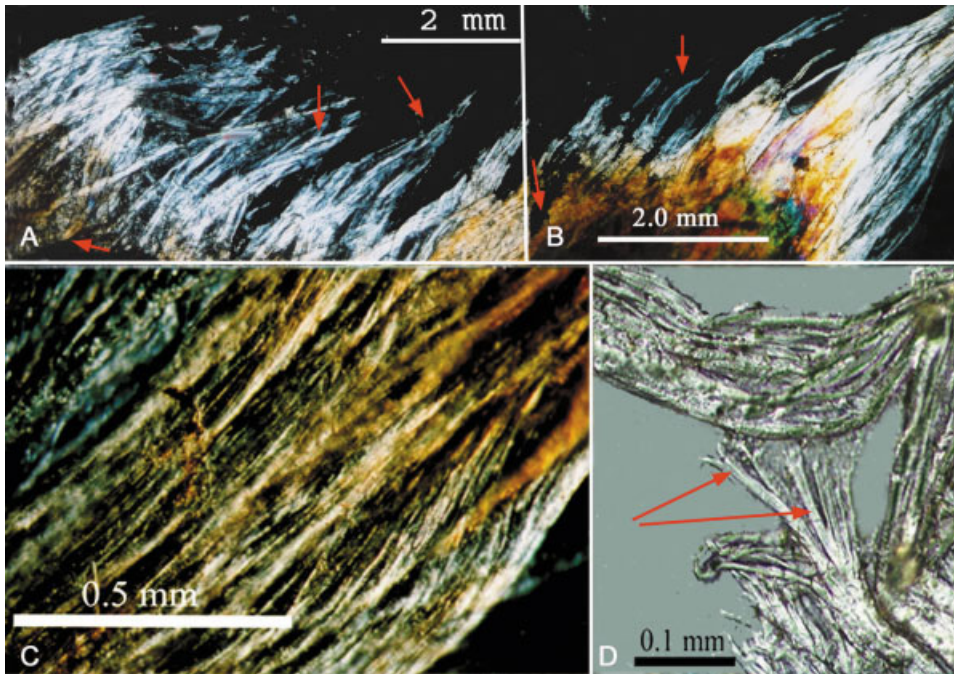


Fig. 3. Decomposing collagen fiber bundles in the hypodermis of a dolphin, *Tursiops aduncus* (formerly *truncatus*). **A,B**: Plume-like patterns of some of the fibers along the edges of the decomposing tissue, many groups of fibers have narrow points of attachment (bottom arrow) that broaden before tapering again (due to degradation) giving the flame-like shape (top arrows). **C**: Thick fiber bundles showing disorganization of the finer fibers and bundles to produce overlapping feather-like patterns. **D**: Detail of large fiber bundles showing component fibers during degradation, producing branching patterns among the filaments (after Lingham-Soliar, 2003b).

from the fossilization processes or petrification of organic remains, commonly referred to as taphonomy.

RESULTS

Microscopic Analysis of the Integument in Living Vertebrates and Examination of Soft Tissue Fossil Material

It is important to understand that collagen in the integument of many animals does not appear as simple interlacing strands dispersed in a matrix of other tissues, but rather that collagen may form highly organized complex architectural systems, frequently providing specific forms of reinforcement (Wainwright et al., 1976; Lingham-Soliar, 2005a,b). The reptiles studied here provided no exception to the complexities of collagen architectural systems found in other animals. It would therefore not be unexpected for such morphologically complex organic material to be manifested in fossilized soft tissue, bearing in mind the idiosyncrasies associated with the processes of decomposition and fossilization.

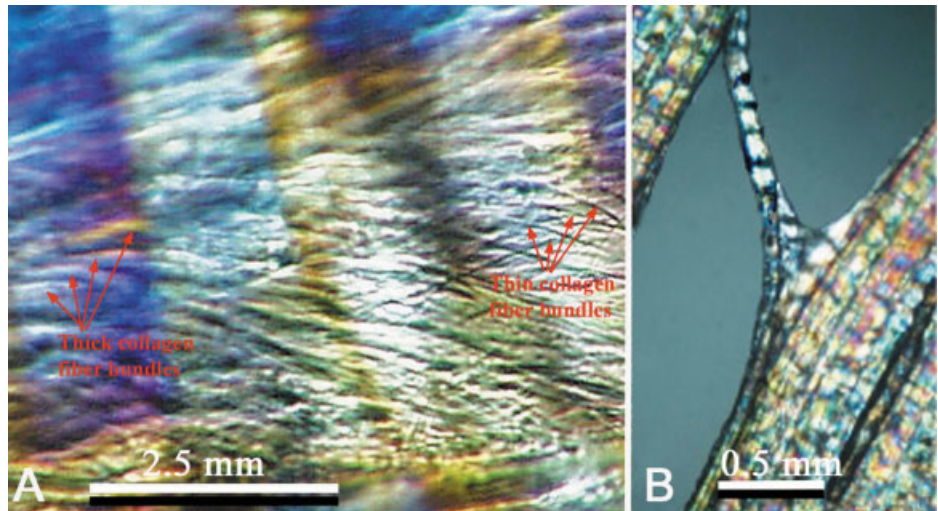
Figures 1 and 4 show collagen fiber bundles in the white shark, *Carcharodon carcharias* (Lingham-Soliar, 2005a,b). As opposed to more random networks of collagen in the dermis of some animals, the more complex patterns or architectures are shown, which may have profound functional implications.

Figure 2 shows collagen fiber bundles in the animals (six reptiles and one bird) examined. The collagen fiber bundles extend throughout most of the depth of the dermis in numerous layers, as indicated by several sections ($n = 4$). Thick collagen bundles occur in the dermis in the tail of *Agama utricolis* and

slightly thinner bundles in the skin on the reptile's ventral surface (belly region) (Fig. 2A,B). Fiber bundles in several sections ($n = 4$) showed orientation in the same direction (left-handed). A crossed-helical pattern of the fiber bundles is present in *Caretta caretta* and *Python molurus bivittatus* (Fig. 2D,G). The smaller snake, *Macrelaps microlepidotus*, shows fiber bundles in layers oriented in a single direction, left-handed (Fig. 2E). The crest in *Basiliscus plumifrons* extends from the longitudinal midpoint of the skull to the tail, progressively diminishing in height. The crest is covered by translucent scales, is almost entirely cartilaginous, and is strengthened along its length by dense fibrous structures (Fig. 2C). The comb of the domestic chicken, *Gallus domesticus*, is very different in structure from the crest of a lizard such as *B. plumifrons* or the skin generally; stiffness is achieved by dense adipose tissue reinforced by a matrix of collagen fibers (Fig. 2I), very similar to stiffening of the caudal peduncle in dolphins (Hamilton et al., 2004) and lamnid sharks (Lingham-Soliar, 2005b).

Figure 3 shows decomposing collagen fiber bundles from a dolphin, after a year's burial (see Lingham-Soliar, 2003b). The peeling apart of the fibers and fiber bundles was interpreted to be a consequence of degradation (probably from bacterial activity) of a glue-like substance. The "glue" was less evident along the edges of the sections where more of the fibers had been released from their bundles. A feature widely observed in decomposing dolphin tissue was a bead-like structure of the collagen fibers (Lingham-Soliar, 2003b, fig. 2a,b). A similar condition was noted in fossilized integumental fibers in

Fig. 4. Tracts of collagen fiber bundles in the skin of the white shark *Carcharodon carcharias*. **A:** Fiber bundles in this section have been distorted (fanned out) during microtomy. Note how the fiber bundles open out, thick at one end (arrows) and unraveling and becoming thinner further from it right (arrows). Scale bar = 2.5 mm. **B:** A few fibers teased from the main bundle show a beaded appearance as a consequence of dehydration (described in text and Lingham-Soliar, 2003b). Scale bar = 0.5 mm.



ichthyosaurs (Fig. 5C, arrows). Under polarized light at different azimuths, tangential sections of dolphin blubber and shark skin (cover, Lingham-Soliar, 2003b, and our Fig. 4B) showed peaks and troughs of the fibers, a consequence of regular, short waves (at about 50- μ m intervals), which coincided with the observed bead-like structure and confirmed that they were not breaks in the fibers. The feature was an artifact of preparation, i.e., dehydration. All sections were air-dried to increase transparency and birefringence during transmission microscopy, which resulted in slight contraction of the fibers (Lingham-Soliar, 2003b). In fossils, rippling of the skin would probably occur with dehydration and the peaks of the “waves” in collagen bundles would fossilize as beads.

Given that degrading collagen fibers of the dolphin demonstrate a striking resemblance to feathers (Fig. 3C), the readers may get a better idea of why two such different structures as feathers and collagen fibers may produce visually similar morphologies in fossils.

Figure 4A shows tracts of collagen fiber bundles in the skin of *Carcharodon carcharias*. Fiber bundles in this section have been distorted (fanned out) during microtomy. The fiber bundles open out, thick at one end (arrows) and unraveling and becoming thinner further from it (arrows). Figure 4B shows a few fibers teased from the main bundle and showing the beaded appearance resulting from dehydration (see below).

Figures 5 and 9–14 include fossilized integumental structures. Figure 15 shows scales in an ornithomimid (bird mimic) dinosaur.

DISCUSSION

Previous studies demonstrating similarities between collagen fiber tracts and dinosaur “protofeathers” (Lingham-Soliar, 2003a,b) involved the

extinct ichthyosaur, *Stenopterygius*, and extant bottlenose dolphin, *Tursiops aduncus* (formerly *T. truncatus*). Such comparisons were reasonable in view of the ubiquitous occurrence of collagen and collagenous architectural systems in a wide range of animals regardless of phylogeny (Fig. 1). To eliminate any doubts regarding the widespread occurrence of complex collagenous systems of the integument in the animal kingdom (i.e., that such fiber systems are not restricted to fishes and dolphins) we concentrate our investigation here on a number of species of extant, predominantly terrestrial reptiles. We report that the two major types of architectures of collagen fibers, namely, crossed helical (left- and right-handed orientations) and noncrossed helical (fibers oriented in a single direction), both of which were found in the skin of *Carcharodon carcharias* (Lingham-Soliar, 2005a,b), are represented in the reptiles studied here. Furthermore, a novel adaptation of the crossed-helical fiber architecture is observed in the dermis of the Burmese python (Fig. 2G), wherein the fibers of one layer cross-weave with the next in left- and right-handed orientations. The functional interpretation of this unusual architecture is that it probably provides greater stiffness to the skin. This may be useful in protection of the body and may also provide more support in regions that are likely to experience considerable stress, e.g., during the ingestion of large prey (cross-weaving of fibers was noted in some dermal layers of certain sharks [Motta, 1977]). These differences in structure or pattern could reflect different ways in which collagen might fossilize, e.g., cross-woven fiber layers may not disorganize as readily during tissue degradation as “free” fiber layers. However, regardless of the different architectures and functional strategies involving collagen, of great interest to the present discussion is the widespread occurrence of tracts

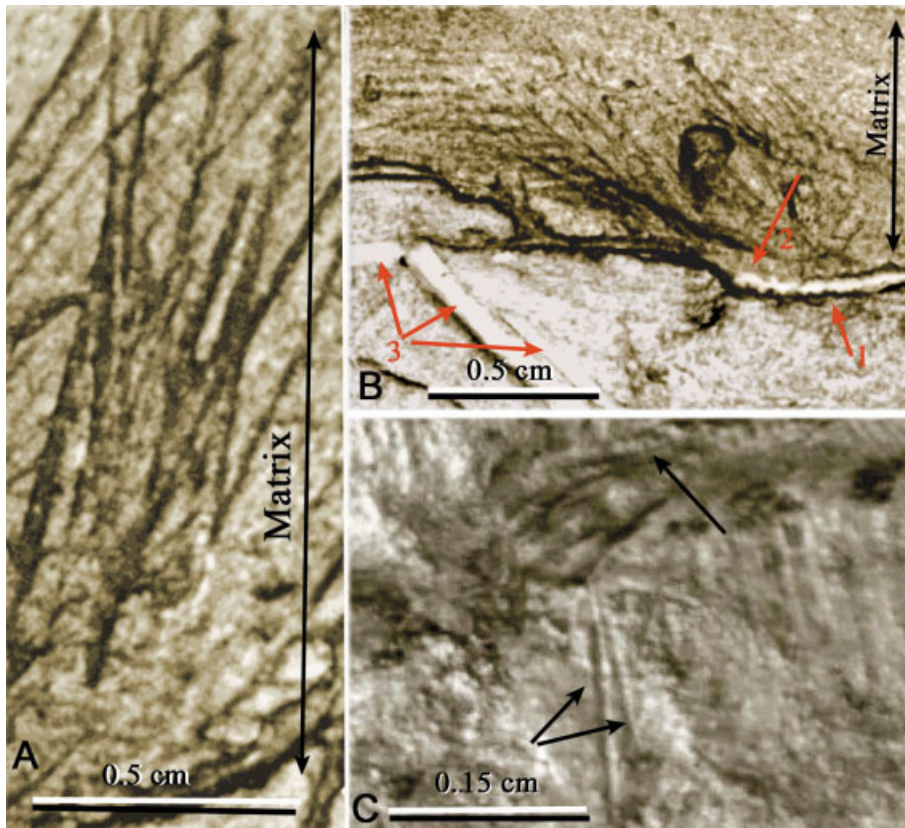


Fig. 5. The ichthyosaur, *Stenopterygius quadricissus*, SMF 457 with integumentary structures (probably collagen). **A:** Integumentary fibers on the matrix or substrate (i.e., around the body outline) near the anterodorsal surface showing straight thick filaments. **B:** Matrix above posterodorsal surface showing fibers resembling rachis and barbs (above dorsal body outline); arrow 1 shows an integumental structure in which there are differences in brightness between the inner and outer parts; arrow 2 shows a transition in brightness from dark along one region of the edge to entirely white along another; arrow 3 shows completely whitened integumental structures. **C:** Arrows show integumental structures in a part of the dorsal fin exhibiting the beaded condition, probably a consequence of tissue dehydration before fossilization.

of collagen fiber bundles in the skin of all the reptiles examined here.

Collagen fibers/fiber bundles disrupted either during degradation (Fig. 3) or by mechanical abrasion (Fig. 4A) are capable of forming aberrant patterns. Almost invariably, fibers open up such that the most compact are where they are attached to the tissue mass (“glued,” see above), unraveling and spreading out further away, and finally becoming frayed and narrow at the tips of the structure (comparable to the shape of a flame) (Fig. 3A,B, arrows). These characteristics of collagen are considered in the context of certain fossilized integumental structures that have been interpreted by some workers as protofeathers. Below we examine: 1) general arguments and interpretations concerning feathered dinosaurs, 2) the new thesis on the morphogenesis of the feather from follicles and its alleged support from the Chinese dinosaur fossils, and 3) the feathered dinosaur hypothesis in the light of modern investigative techniques and new fossil evidence from *Psittacosaurus* and *Pelecanimimus*.

General Arguments and Interpretations Concerning the Hypothesis of Feathered Dinosaurs

Sinosauropteryx (Chen et al., 1998; Currie and Chen, 2001) was the first dinosaur to be described

with “feather-like structures.” In view of its basal theropod status, *Sinosauropteryx*’s importance in questions relating to the origin of the feather, in particular the alleged presence of protofeathers, needs to be accepted or rejected on incontrovertible evidence.

Currie and Chen (2001, p. 1723) speculated that the integumentary structures “probably covered most of the body of living *Sinosauropteryx*” despite the occurrence of only coronal preservations in all specimens examined. Given the description of only coronal preservations by the authors, the comment by Norell and Xu (2005, p. 292) that “careful observation of the *Sinosauropteryx* specimens shows [my italics] that the integumentary fibers were distributed over the entire body and were not just a Mohawk-like crest (Currie and Chen, 2001)” is misleading in its misrepresentation of the cited data. There are other points that Norell and Xu (2005) misinterpret both from the literature (Lingham-Soliar, 2001, 2003a,b) and, presumably, as a consequence of an unusual perception of animal decomposition and taphonomic processes. Norell (2005) states that there are flaws in Lingham-Soliar’s (2003a,b) argument, the two most notable in his view are considered here. The first “flaw” Norell (2005, p. 233) states is that “...the integumental structures in the Liaoning animals are clearly not internal and extend far from the body.” This presumably means that in soft tissue preservations it is

only feathers or their alleged progenitors, protofeathers (or at least not collagen), that may lie outside the boundary of the animal's body. However, it should not in our view be surprising to anyone dealing with death, decomposition, and degradation (our job as paleontologists) that rotting flesh and skin should come to lie around the animal, aided by the elements, e.g., wind and rain and even by scavengers. The picture presented (Norell and Xu, 2005; Norell, 2005) that every piece of flesh will lie pristinely over the body is quite unrealistic and is a simplistic attitude to the complex subject of taphonomy, which includes paleopathology (the study of disease in fossil animals, e.g., see Lingham-Soliar, 2004). Furthermore, the interpretation that in ichthyosaurs the integumental structures had to be internal to the body outline (Norell and Xu, 2005) is not only a constricted view of decomposition and taphonomic processes, but also a misrepresentation of Lingham-Soliar's (2001, figs. 5, 8, 9) study in which collagenous fibers from the skin were shown to be excellently preserved on the matrix, frequently several centimeters above the outline of the animal (see our Fig. 5A,B). These fibers were clearly described as part of "the remains of flayed skin displaced onto the sediment" (Lingham-Soliar, 2001, p. 290). Norell and Xu's (2005, p. 292) use of the term "interstitial" for collagen described in a dolphin is also confusing and is really better described, as in the article (Lingham-Soliar, 2003b), as the deeper dermis or hypodermis. Their (Norell and Xu, 2005, p. 292) contention that "interstitial collagen fibers would not exist on the top of the head where the skin would have clung tightly" is again based on their misunderstanding of the term integumental collagen. Fibers at the top of the head could emanate from flayed skin or even a crest similar to that of modern day lizards.

The second alleged flaw in Lingham-Soliar's (2003b) argument, according to Norell (2005, p. 233), is that "the sort of collagen fibers found in the dolphin are associated with aquatic skin types." The flaw in the argument, rather, is Norell's (2005). His definition of collagen of "aquatic skin types" does not, and should not, exist, and shows a total lack of understanding of collagen fibers in the animal kingdom. Complex, comparable collagenous architectural systems were found in the cuticle and skin of animals from worms (Clark, 1964; Wainwright et al., 1976; Alexander, 1987) to the white shark (Lingham-Soliar, 2005a,b; Fig. 1). Reptiles, as we have shown in the present study, are no exception (Fig. 2).

The following points made by Currie and Chen (2001), which in our view summarize many of the arguments for the feathered dinosaur hypothesis, and our comments, will, we believe, help as a prelude to the more detailed discussions that follow.

1) "The distances separating the integumentary structures from the underlying bones are directly

proportional to the amount of skin and muscle that would have been present" (Currie and Chen, 2001, p. 1719). According to Currie and Chen (2001, p. 1719), in regions with large proportions of skin and muscle the overlying integumentary structures would have been destroyed when the soft tissue was destroyed. While this is reasonable, such decomposition would apply to most organic material, including feathers and collagen. It does, however, fail to take note of how tough vertebrate skin may be, which, after all, is the first line of defense of the body. There are also many imponderables with respect to soft tissue preservation. For instance, in ichthyosaurs the preservation of collagen is rare, and indeed the fibers are better preserved on the matrix surrounding one specimen of *Stenopterygius* (SMF 457) than on the body, while the opposite was true in another specimen (PMU R435). Also, preservation of fibers over bone is noted over much of the vertebral column in SMF 457 but not in PMU R435 (Lingham-Soliar, 2001, figs. 1, 7A). Integumental structures might quite possibly have occurred over the entire body of *Sinosauropteryx* and the argument that they preserve better as coronal features is reasonable but not conclusive. The vagaries of fossilization must be given serious consideration. For example, large robust integumental filaments were recorded as coronal preservations in a specimen of the dinosaur *Psittacosaurus* (Mayr et al., 2002) and yet in another *Psittacosaurus* specimen (described in the present study), very similar in skeletal preservation, there is not a trace of these coronal structures; in striking contrast, integumental structures are preserved within the area of the ribs (i.e., non-coronal), which are absent in the specimen of Mayr et al. (2002). We believe that interpretations of a complete covering of integumental structures based on coronal preservations (Currie and Chen, 2001) requires more study regardless of the nature of the integumental structures.

2) "Integumentary structures probably covered most of the body of living *Sinosauropteryx*" (Currie and Chen, 2001, p. 1723). Currie and Chen (2001) present birds found at the same site, which show coronal preservations (and all *Archaeopteryx* specimens, which also show preservation of the feathers restricted to a corona), as support that the restricted preservations in *Sinosauropteryx* were part of a complete covering of integumental structures. This response is very similar to Norell's (2005, p. 233) in which he shows bewilderment that only the "fluffy body covering in *Sinosauropteryx*" and other theropod dinosaurs was questioned by certain workers and yet "the veracity of the feathers on the avian specimens never raised an eyebrow." The reason for the differences in attitude seems simple—both these authors' support for the speculation of a completely feathered dinosaur begs the question. The question is whether certain theropod dinosaurs or some other group of reptiles directly gave rise to birds. For

instance, *Archaeopteryx* is generally accepted as a bird (Currie et al., 2004). Given this, an extrapolation of a complete feather coating from modern to birds to *Archaeopteryx*, preserved with just a coronal preservation of feathers, is probably the most parsimonious explanation (applying the principle of “Occam’s razor”), i.e., we are making the connection from bird to bird, and understandably it may “not raise an eyebrow.” On the other hand the relationship of *Sinosauropteryx*, and certain other theropod dinosaurs, with respect to birds is precisely what is in question. Thus, the extrapolation of a complete covering in birds to an animal of questionable direct relationship with respect to birds does not have the same logical rationale. Put another way, consider finding a fossil iguanid with a preserved nuchal fringe. Comparing it with living iguanids and extrapolating from them that the nuchal fringe was coronal only is reasonable. However, it would be just as illogical as using a bird’s external covering as a rule for other taxa found in the same deposits as it would be to use an extant iguanid’s, even for other reptiles. If such extrapolations are to be more than speculations, like must be compared with like.

3) “The integumentary structures were soft and pliable.” This comment by Currie and Chen (2001, p. 1719), based on somewhat sinuous-looking integumentary structures, is highly speculative given that the biological composition of the fibers is in question. For instance, fibers composed of collagen have different forms (e.g., straight or bent), which are affected by various conditions including decay (Lingham-Soliar, 2003b, p. 564, and fig. 2). Collagen fiber bundles in the Natal black snake (Fig. 2E) show a wavy appearance, which if fossilized could be incorrectly interpreted as being “soft and pliable” if appearance alone is considered. Due regard is required with respect to changes, e.g., loss of muscle tension, that occur in soft tissue with the onset of death and degradation.

4) “Under magnification, the margins of the larger structures are darker along the edges but light medially [middle]” (Currie and Chen, 2001, p. 1719). In their view, these changes in brightness suggest that the larger structures may have been hollow. This highly speculative interpretation in support of a fundamental characteristic of the feather has now been widely accepted by the proponents of the protofeather hypothesis (Xu et al., 2001; Prum and Brush, 2002; Norell and Xu, 2005). This interpretation of hollow integumentary structures will be discussed further below in the section on feather morphogenesis.

5) “Thick and thin strands close to the body, the increased presence of thinner strands distally. . .” suggest feather-like structures (Currie and Chen, 2001, p. 1721). This speculation was considered against an examination of decomposing collagen fibers; the collagen fibers were found to produce very similar patterns (Lingham-Soliar, 2003b, fig. 2; Fig.

3 herewith). The tendency to produce feather-like patterns is also shown here in fresh tissue (Fig. 4A).

The major, and most worrying, problem of the feathered dinosaur hypothesis is that the integumental structures have been homologized with avian feathers on the basis of anatomically and paleontologically unsound and misleading information. We have demonstrated this with extant vertebrates and some key fossils. It is true that many non-avian dinosaurs have been found with unusual-looking integumental structures, but the expression *abusus non tollit usum* is pertinent (abuse [of data] does not nullify proper use).

The flimsiness of the arguments with respect to the thesis of feathered dinosaurs extends most recently to tyrannosauroids (Xu et al., 2004). The authors allege that one of the specimens (IVPP V12811) “preserves a filamentous integumentary covering” and “that it provides the first direct fossil evidence that tyrannosauroids had protofeathers” (Xu et al., 2004, p. 680). What is the evidence for this major reconstruction of tyrannosauroids to include protofeathers with all of the controversial physiological implications (see Xu et al., 2004, p. 683)? On the tail there are traces of filamentous structures over a pair of distal caudal vertebrae (Xu et al., 2004, fig. 3) and, allegedly, close to the posterior left mandible (not figured). The authors state that the filaments are branched and “seem to be composed of a series of filaments joined at their bases along a central filament as in *Sinornithosaurus*” and that “many of these structures seem to be distally branched, as can be observed in some cases in *Sinornithosaurus*” (Xu et al., 2004, p. 682). The weaknesses of such arguments based on the *Sinornithosaurus* specimens will be shown in a reexamination of the material below. Nevertheless, we consider these arguments on their own merits. While the authors interpret the ‘V’ or ‘Y’ shapes made by the fibers as a simple branching pattern, it would be interesting to know how they would interpret all the ‘+’ or ‘X’ shapes present. Could a reasonable interpretation be that these are all randomly arranged (or preserved) filaments, like matchsticks thrown onto a board (Fig. 6) falling to the laws of chance, some overlying others to form ‘X’ shapes, others adjacent to form ‘V’ and ‘Y’ shapes and a few, isolated ‘I’ shapes? The randomness of such shapes would apply to rearrangement of fragments of fibers or filaments in dinosaurs or the idiosyncratic preservation of integumental structures as a consequence of the degradation of tissues and geological erosion of fossils (see Lingham-Soliar, 2001, fig. 8). The meaninglessness of simple feather-like branching shapes in “external” (by “external” it is meant on the substrate around the animal) ichthyosaur fibers was previously demonstrated (Lingham-Soliar, 2003a) and there are unquestionably better feather-like branching structures preserved on the substrate adjacent to the dorsal surface of the ichthyosaur, *Stenopterygius* SMF 457

Fig. 6. Matchsticks randomly thrown onto a board. Given that all patterns are created by chance, some show branching patterns similar to those of integumental structures preserved in the skin of ichthyosaurs and theropod dinosaurs.



(Fig. 5B) than those in the tyrannosauroid (Xu et al., 2004). A model on how some taphonomic aberrations (i.e., unnatural associations or patterns as a result of decomposition and fossilization whereby distant fibers or patches of skin come together) occur in preserved fossilized integuments was proposed in an earlier study (Lingham-Soliar, 2003a; Fig. 7 here-with).

The above discussion raises serious doubts concerning interpretations that the integumentary structures in *Sinosauropteryx* are homologous with feathers. We have shown that the arguments are faulty and lack scientific rigor, not least in the almost complete absence of considerations of possible alternative scenarios.

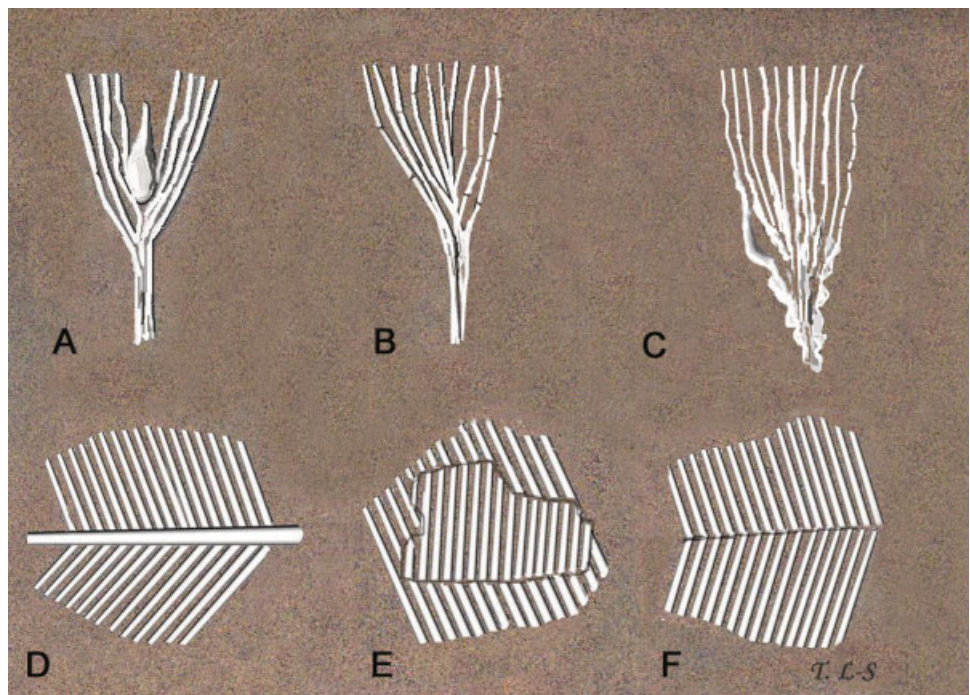
Feather Morphogenesis

Xu et al. (2001, p. 200) state: “Confirmation of the theropod origin of feathers requires documentation

of unambiguously feather-like structures in a clearly non-avian theropod.” We agree implicitly with this statement, and it is precisely this claim of “unambiguously feather-like structures” that we shall examine in their hypothesis (also see Prum, 1999; Prum and Brush, 2002) of feather morphogenesis.

Prum and Brush’s (2002) model on feather morphogenesis proposes that the first feather was a hollow conical structure that evolved with the first follicle (Prum, 1999). In our view, strictly speaking it is not a model but rather a function independent evolutionary hypothesis of feather evolution. The crux of this view is that feathers are novel structures, contra the classical view that feathers evolved from reptilian scales (Maderon, 1972; Feduccia, 1999a; Maderon and Homberger, 2000; Sawyer et al., 2003a,b; Zhang and Zhou, 2000; Martin, 2004). It is important to state explicitly here that Maderon (1972) is the first publication that used paleontological data in conjunction with neontological data

Fig. 7. Models of how some taphonomic aberrations (i.e., artifacts rather than primary features) occur in preserved integuments. **A:** Impressed objects cause fibers to diverge before fossilization. **B:** False joins (i.e., when two dissociated integumental structures come together) that give the impression of a continuous structure or of branching structures. **C:** Creasing of skin at the base results in fluting (like an open fan) of the fibers. **D-F:** Herringbone patterns can result from: **D:** Two flaps of skin being overlain or underlain by thicker fiber or adjacent to it. **E:** Loose flap of skin overlying another. **F:** Two opposing flaps of skin joining as pages in a book. Such aberrations were found in ichthyosaur integuments (Lingham-Soliar, 2001).



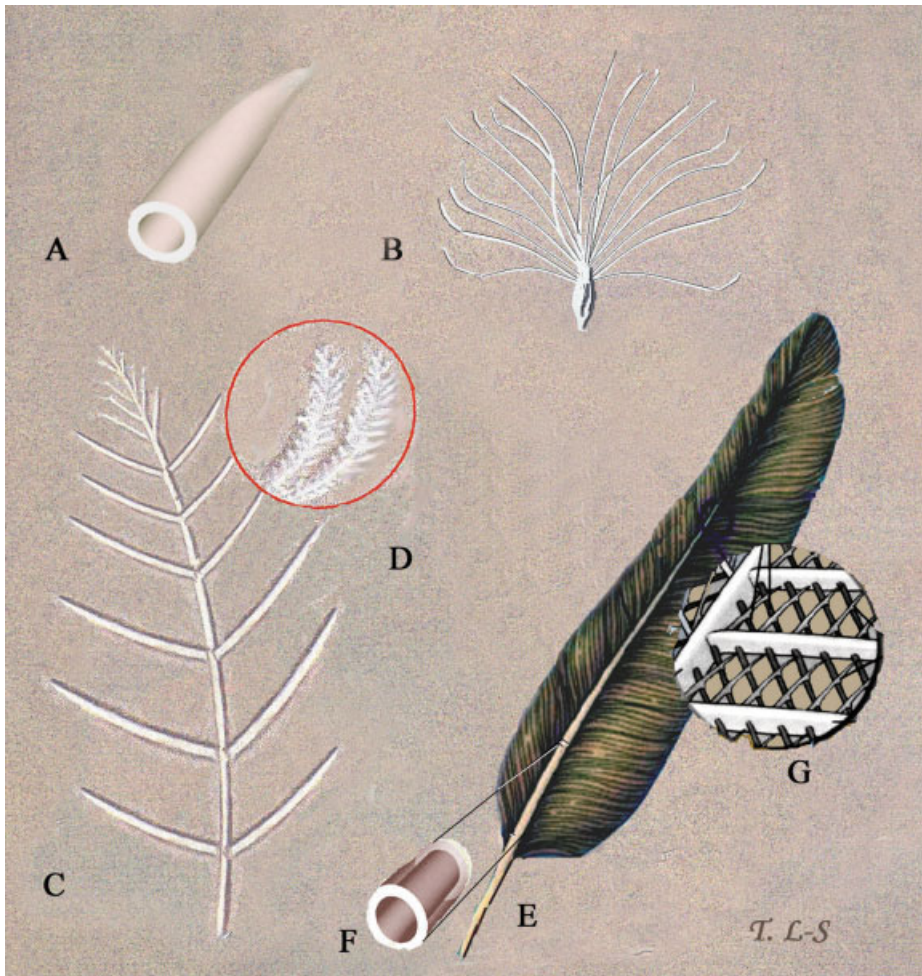


Fig. 8. Our figure representing the hypothetical evolution of the feather according to Prum and Brush (2002) based on non-avian dinosaur fossils. **A–D:** Stages I–IIIA based on *Sinosauropteryx*, *Sinornithosaurus*, and an indeterminate theropod. **A:** Stage I, a hollow unbranched filament. **B:** Stage II, a tuft of filaments fused at the base. **C:** Stage IIIA, a central rachis and serially fused barbules. **D:** Stage IIIB, addition of secondary barbules (barbules) to IIIA. **E:** Stages IV, bipinnate feather with closed vane, and V, asymmetrical modern flight feather, are incorporated in this figure. **F:** Section of the hollow rachis. **G:** Detail of closed vane showing barb and barbule structure.

to propose a sequential series of steps possibly involved in feather evolution. Prum and Brush's (e.g., 2002) reference to "classical models" are no more than numerous ad hoc speculations based solely on avian scales and feathers, since the only pertinent fossil, prior to Sharov's (1971) *Longisquama*, was *Archaeopteryx*.

The view presented in some detail in the present study is that the integumentary structures described in non-avian dinosaurs are aberrant tracts of collagen fibers. In the following part of the discussion we examine the hypothesis of the follicular development of the feather (Prum, 1999; Xu et al., 2001; Prum and Brush, 2002; Harris et al., 2002; Fig. 8 herewith) from the following authors' (Xu et al., 2001; Prum and Brush, 2002) perspective that theropod dinosaur fossils support their thesis of feather morphogenesis.

Prum (1999) and Xu et al. (2001) propose five stages in feather evolution (see Fig. 8 herewith). Each of their predictions they claim receives support from non-avian dinosaur fossils from Liaoning in China (Xu et al., 2001). The ramifications of the claims may best be understood in Prum and Brush's (2003, p. 92) own words: "The heterogeneity of the

feathers found on these dinosaurs is striking and provides strong direct support for the developmental theory. The most primitive feathers known—those of *Sinosauropteryx*—are the simplest tubular structures and are remarkably like the predicted stage 1 of the developmental model. *Sinosauropteryx*, *Sinornithosaurus* and some other non-avian theropod specimens show open tufted structures that lack a rachis and are strikingly congruent with stage 2 of the model. There are also pennaceous feathers that obviously had differentiated barbules and coherent planar vanes, as in stage 4 of the model. These fossils open a new chapter in the history of vertebrate skin. We now know that feathers first appeared in a group of theropod dinosaurs and diversified into essentially modern structural variety within other lineages of theropods before the origin of birds *Caudipteryx*, *Protopteryx* and dromaeosaurs display a prominent 'fan' of feathers at the tip of the tail, indicating that even some aspects of the plumage of modern birds evolved in theropods."

We examine the alleged support from the fossils *Sinosauropteryx* (Currie and Chen, 2001), *Sinornithosaurus*, an indeterminate theropod (Ji et al., 2001), and *Caudipteryx* (Qiang et al., 1998) with

respect to the key features in stages 1–4 of Prum and Brush's (2002) developmental theory on feather morphogenesis. Stage 5, which involves the feature of the asymmetrical feather, is not considered because of controversy concerning the fossils in which they occur (below).

Prum and Brush's Stage 1. Prum and Brush (2002) state that the feather follicle originates as a hollow cylinder that resembles the calamus of a modern feather, which they claim receives support from the fossil theropod dinosaur, *Sinosauropteryx* (Fig. 8A). The feather follicle is a tubular or hollow structure and a critical part of fossil support of Prum and Brush's stage 1 would be the reliability of the evidence from *Sinosauropteryx* to support hollowness. Currie and Chen's (2001) speculation in support of a hollow structure is that the larger integumentary structures under magnification are darker along the edges but "light medially" [?middle]. The weakness of the above speculation was noted in a recent study (Lingham-Soliar, 2003a) but the arguments therein were nevertheless ignored in subsequent studies and reviews (e.g., Norell and Xu, 2005; Norell, 2005). We elaborate here on Lingham-Soliar's (2003a) refutation.

Under exceptional circumstances the taphonomic history of a fossil may include mineralization of soft tissue. The latter is a complex process, which we will consider with reference to a group of marine reptiles, ichthyosaurs. Ichthyosaurs from the Toarcian, Posidonia Shale of Baden-Württemberg, southern Germany, have long been known to show soft tissue preservations. Martill (1993) suggested that some of the exceptional soft-tissue preservation in Jurassic ichthyosaurs was the result of critical timing of diagenetic phosphatization. On the other hand, frequently so-called preserved skin is in fact often decayed and transformed soft tissue that may outline the body as a black carbonaceous film (Wild, 1990; Martill, 1993). It is easy to understand why the preserved material might show variations in color (light or dark) depending on the type of preservation. For example, the dark and light areas that Currie and Chen (2001) refer to probably reflect part of the process of decay and diagenetic phosphatization. The ichthyosaur SMF 457 provides an excellent example of mineralization and color changes (Fig. 5B, arrows). During the degradation of the collagen fibers (Lingham-Soliar, 2001, 2003a) mineralization appears to progress in stages from the inner part of the fiber bundles to the outer, reflected by lighter and darker regions, respectively (Fig. 5B, arrow 1). In many instances, the thick fiber bundles are entirely whitened (Fig. 5B, arrow 3). Interestingly, in this figure, within a single integumental structure, the whitening transition can be seen both in a partial and complete stage (Fig. 5B, arrow). The complex process of mineralization of muscle fibers was demonstrated in laboratory controlled experiments (predominantly calcium phosphate, i.e., >80%)

(Briggs et al., 1993). Areas of partial or complete phosphatization (whitened) from within the collagen bundles in SMF 457 appear consistent with Briggs et al.'s (1993) remarks that a primary source of phosphate may be the organism [or tissue] itself. During taphonomic processes mineralization (including the rate at which it proceeds) is a complex process and dependent on numerous conditions. For instance, lowering or increasing the pH in the vicinity of the fossil may inhibit or enhance carbonate precipitation (Briggs et al., 1993). Hence, in view of the chemical changes, color changes from the center of the organism or structure to its surface may not only be reasonable but predictable, e.g., connected with different levels of phosphatization and carbonization. The most parsimonious explanation, in our view, is that the light center and dark margins reflect aspects of the complexities of the mineralization process of fossils (Briggs et al., 1993).

Sinosauropteryx no more provides evidence of hollowness of integumental structure than does the ichthyosaur (indeed, the collagen fibers in the latter show an even more striking lightening and darkening process). Hence, in our view, support from a theropod dinosaur for a hollow conical structure in the follicular evolutionary model of the feather (Prum and Brush, 2002, 2003) is absent.

Prum and Brush's Stage 2. Xu et al. (2001, p. 200) concede that two taxa with true feathers, *Caudipteryx* and *Protarchaeopteryx*, are controversial insofar as they have been proposed to be flightless birds rather than dinosaurs and that confirmation of the theropod origin of feathers requires documentation of unambiguously feather-like structures in a clearly non-avian theropod. *Sinornithosaurus millenii*, a basal dromeosaurid dinosaur, they (Xu et al., 2001, p. 200) postulate, fulfills just such a role in its possession of filamentous integumental appendages "indistinguishable from the contour feathers of birds preserved in the same deposits."

These "appendages" according to Xu et al. (2001, p. 200) exhibit two types of branching structure that are unique to avian feathers: filaments joined in a basal tuft, and filaments joined at their bases in series along a central filament—both conditions in their view supporting the theropod ancestry of birds. They also characterize the integumental structures as being dissociated, compound integumental appendages. Furthermore, they state (Xu et al., 2001, p. 200) "The plesiomorphic feathers of *Sinornithosaurus* also conform to the predictions of an independent, developmental model of the evolutionary origin of feathers."

Given the serious implications of these claims concerning the integumental appendages in *Sinornithosaurus*, they are examined in detail below.

In the precise area in which the "tuft" of filaments is alleged to converge (Xu et al., 2001, fig. 3) there is severe erosion of the matrix (Fig. 9A, arrow 1 and detail 1). The authors neither show nor mention the

eroded matrix nor do they take account of fibers to the left of the damaged area. Hence, not only are fibers that allegedly converge missing because of erosion, the fibers to the left of this area (Fig. 9A, arrow 2; arrows in detail 1) indicate, if anything, a broad base. Perhaps of greatest significance is the eroded area itself. In Figure 9A, despite the eroded area being small, the damage has exposed a deeper level of the integument in which a narrow strip of “fibers” can be seen preserved diagonally to the main “surface” integumental structures (see fine white pointer lines in Fig. 9A, detail 1). Examination of the alleged integumental appendages (Xu et al., 2001, fig. 3) shows that they are not isolated structures at all, but rather they are part of integumental structures present throughout the substrate (Fig. 9A, detail 2). The alleged appendages appear to lie in a slightly deeper tract/layer and to be better preserved than those surrounding them and are highlighted by patchy carbonization of the fibers.

Xu et al.’s (2001) figure 2 shows integumental “appendages” aligned at various angles (part of which seen in Fig. 9B). Details (Fig. 9B, circle 1 and 9C) show that there is barely a space between the alleged appendages that is not replete with integumental structures, comparable to the condition in Figure 9A. A hazy preservation of horizontal integumental structures is seen apparently overlying an “integumental appendage” in Figure 9C (detail 1).

What is wholly inconceivable is that Xu et al.’s (2001) “integumental appendages” are assessed without even a passing comment on the surrounding integumental structures or a single figure depicting them.

Prum and Brush’s Stage 3a. Xu et al. (2001, p. 202, fig. 4) describe another “integumental appendage” as comprised of a bundle of filaments with secondary branching filaments “in a manner similar to a pennaceous feather vane.” While other explanations for such a condition are possible, albeit not considered by Xu et al. (2001), e.g., thick collagen fiber bundles may unravel in this way to give the impression of branches (see Figs. 2F, 3, 4A; also Lingham-Soliar, 2003b), there is a more obvious explanation for this condition here. Our own study shows that Xu et al.’s (2001, fig. 4a,b) branching structures appear to be no more than a few integumental structures lying coincidentally (see Fig. 6 for the laws of chance) adjacent to the “integumental appendage.” Our view is based on the presence of numerous other integumental structures across the surrounding substrate, aligned at similar angles and similarly preserved (Fig. 10A, and detail 1, white arrows show alleged branches, red arrows show numerous integumental structures similarly aligned both above and below the “integumental appendage”). It is also based on our assessment that these numerous integumental structures along with Xu et al.’s (2001) “secondary branching filaments” belong to the topmost layer and not to that of the

“integumental appendage.” There are signs that the curved “integumental appendage” may be part of a broader curved tract of integumental fibers (a small exposure below it shows a similar curvature of integumental structures; see Fig. 10, detail 2, black arrow). We see another interesting phenomenon in this part of the material (Fig. 10A, detail 3): the “integumental appendage” comprising longitudinal filaments is apparently traversed by vertical filaments, producing a matrix-like pattern (consistent with stiffening fiber architectures seen in the dermis of many animals; some isolated vertical fibers also occur further above as shown by the red arrows in Fig. 10, detail 3).

Xu et al.’s figure 5a,b (2001) with alleged rachis and barbs is equally unconvincing as the material discussed in the foregoing sections and we feel we will add nothing more to the present debate by further discussions on the material of *Sinornithosaurus*.

The preservation of integumental structures in tracts or bundles of filaments that appear to visually dominate those of the surrounding substrate is not unusual (Lingham-Soliar, 2001, 2003a). Thick fiber bundles oriented in varying directions were noted in the ichthyosaur, *Stenopterygius*, many of the larger bundles considered to be severely disorganized during decomposition and fossilization (Lingham-Soliar, 2001, fig. 8). Although the component fibers of the thick integumental structures noted in that study could not be distinguished, as, e.g., in *Sinornithosaurus*, this can safely be assumed to be the case with our understanding of dermal collagen fibers. Random orientation of fiber bundles may be a natural condition of skin (Wainwright et al., 1976) or it may arise as a consequence of displacement during decomposition (Lingham-Soliar, 2001, 2003a,b). Patches of filaments overlying the carbonized filaments/fibers (Fig. 9C, detail 1; Fig. 10, detail 3) strongly suggest that the latter belong to a slightly deeper layer than the less well-preserved fibers pervading the material (Figs. 9, 10). A similar preservation of finer fiber bundles imprinted over thicker bundles permitted delineation of fiber layers in the ichthyosaur SMF 457 (Lingham-Soliar, 2001, fig. 9B). A more recent uncovering of the narrow tracts of carbonized filaments (Figs. 9C, 10) would account for their better preservation. Their exposure we suggest is probably a consequence of preparatory techniques or of natural erosion propagating by “tramlining” along the more robust bundles of fibers below. In several areas it is possible to see that exposure of the underlying fibers occurred as a consequence of flaking of the substrate in their immediate vicinity (e.g., Fig. 9C, white arrow). It would not be surprising to find that there are more such bands of fibers below the surface, while others possibly decomposed before fossilization.

Significantly, in the present study some remarkably preserved tracts of integumental structures, in

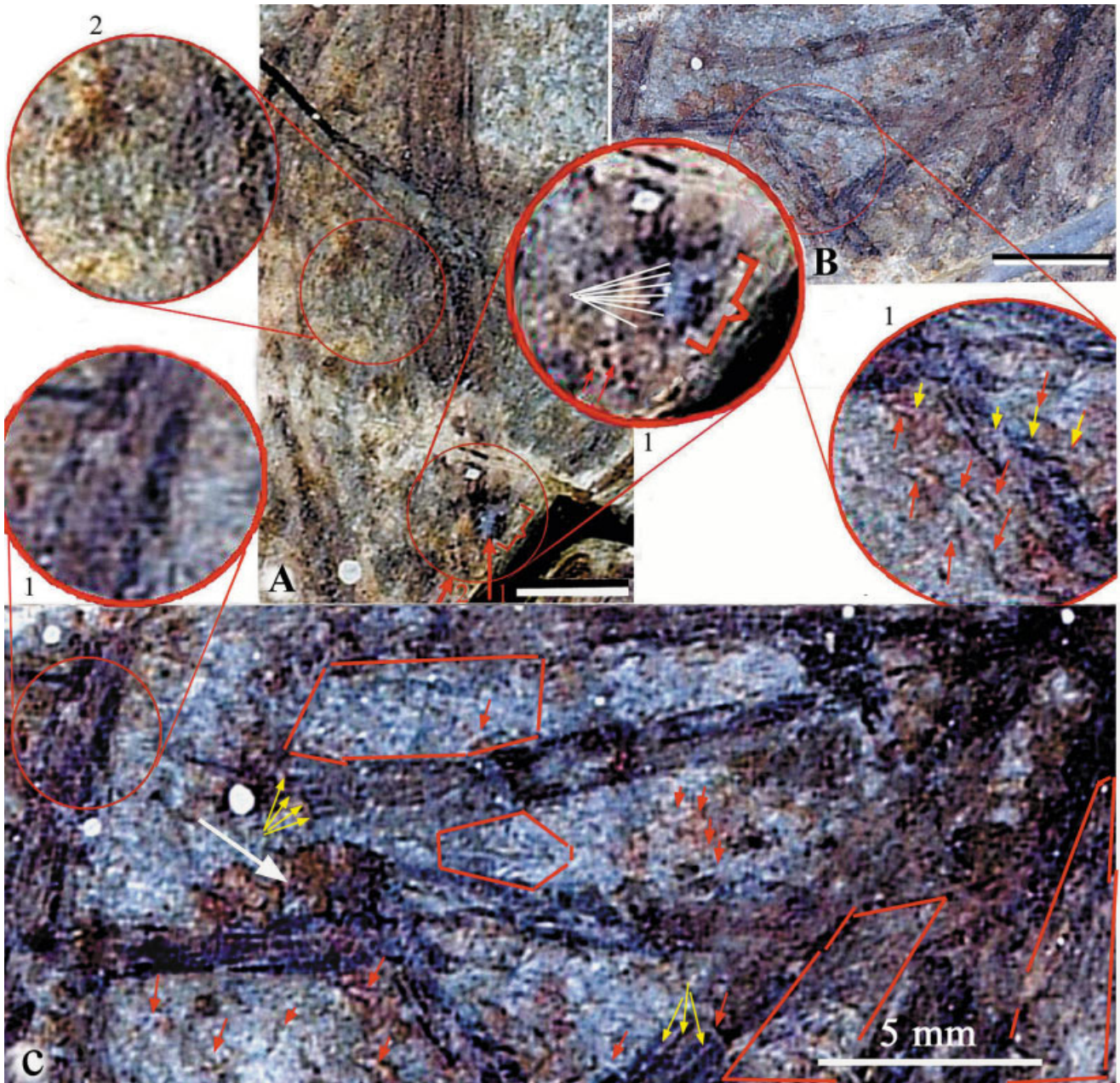


Fig. 9. Integumental structures in the theropod dinosaur *Sinornithosaurus millenii* (holotype IVPP 12811). **A:** The dark lines are eroded tracts of the underlying layer of the sediment that includes carbonized integumental structures, which are similar but somewhat better preserved and possibly thicker than those on the surface of the substrate. Detail (circle 1) shows an even deeper erosion of the sediment (arrow 1) not seen in the published figure (Xu et al., 2001, fig. 3). It shows eroded but definable short segments of integumental structures within the eroded area (see white pointer lines), which are diagonal to the long vertical integumental structures; arrow 2 shows short segments of integumental structures that indicate a broad base of the alleged filamentous appendage. Detail (circle 2) shows area between two alleged “filamentous integumental appendages,” apparently the surface layer, which is replete with eroded integumental structures. **B:** Another area of preserved integumental structures which is also figured by Xu et al. (2001, fig. 2). Here also the alleged “filamentous appendages” are actually tracts in the substrate that reveal an underlying layer in which integumental structures occur. Detail 1 shows some integumental structures in the vicinity of an eroded tract (red arrows). The yellow arrows show traces of an integumental structure that apparently overlies an eroded tract of filaments diagonally. **C:** Detail of **B**. The demarcated areas (in red) show areas between the dark eroded tracts replete with integumental structures, which were not figured nor reported by Xu et al. (2001). These integumental structures probably reflect a higher layer than that of the tracts (this would account for the more eroded appearance of the integumental structures in this layer). Lower half of detail 1 shows hazy view of horizontal integumental structures apparently overlying those in the underlying tract. Scale bar = 5 mm (modified after Xu et al., 2001).

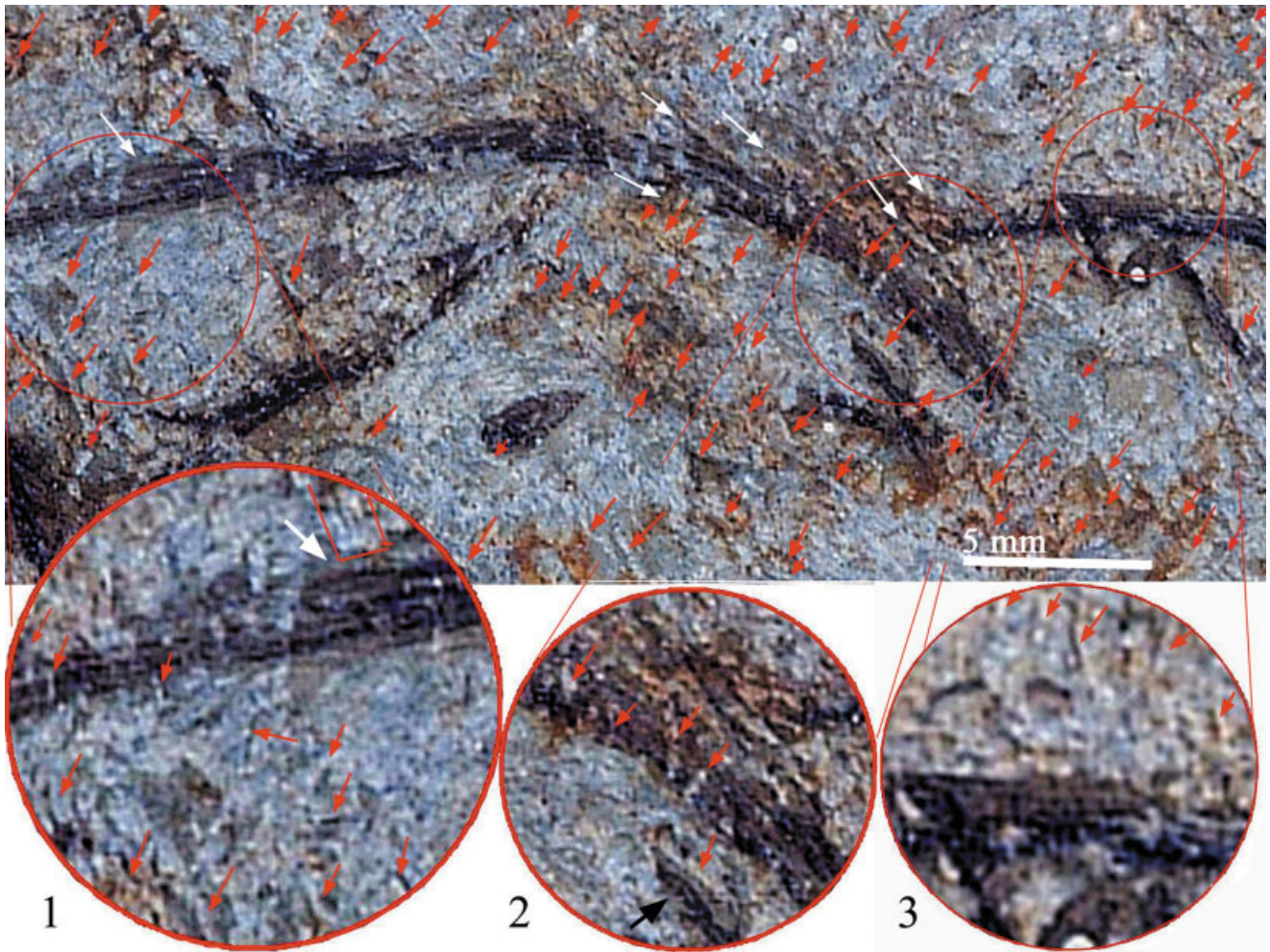


Fig. 10. Integumental structures in the theropod dinosaur *Sinornithosaurus millenii* (holotype IVPP 12811) described by Xu et al. (2001, fig. 4) as a second form of branched structure. The white arrows show the alleged branches from the central filament or shaft. The latter probably represents tracts of the lower layer as in Figure 9. Red arrows show numerous similar structures to the alleged branches (white arrows), and similarly oriented, throughout the substrate (also in details 1–3), which are probably eroded integumental structures of the surface layer. Detail 1 shows area near the tip of the dark “tract,” which comprises fiber-like filaments. Red demarcated area incorporates three integumental structures at right angles to a tract. Detail 2 shows numerous integumental structures including some overlying the “tract.” Detail 3 shows part of the tract in which there are longitudinal filamentous structures, apparently overlain by vertical filamentous structures, to form a matrix-like pattern. These vertical integumental structures, similar to fibers toward the top of the detail (red arrows), seem to have been impressed from the overlying layer onto the longitudinal integumental structures in the underlying layer (observed as eroded tracts). Scale bar = 5 mm (modified after Xu et al., 2001).

varying orientations not unlike those in *Sinornithosaurus* (Xu et al., 2001, fig. 2; Fig. 9C herewith), are recorded in *Psittacosaurus* from Nanjing, China (Figs. 11, 12), an ornithomimid dinosaur clearly unconnected with the theropod origin of birds or feathers (see section on *Psittacosaurus* below).

It is impossible to predict how integumental structures might preserve and fossilize, although in cases of unusual soft tissue preservations, e.g., in *Sinornithosaurus*, certain points with respect to the soft tissue preservations and our understanding of such structures in living animals is worth a brief mention at this point.

Integumental fibers in fossils are frequently observed oriented predominantly in a single direction.

Careful examination, however, may reveal patches of oppositely oriented fiber layers. This is usually noted along the edges of the fossilized material as, e.g., in *Psittacosaurus* (see Fig. 13A, top right, and detail in Fig. 14). Similarly, in histological studies of dermal fiber layers it is difficult to see more than one layer of fibers when the section is cut on the same plane as the skin surface (tangentially), although occasionally a partial “ghost” layer of oppositely oriented fibers is seen (e.g., Fig. 2D; also Lingham-Soliar, 2005b, figs. 10, 11; and Lingham-Soliar, 1999, fig. 2a, for fossilized fibers). In *Sinornithosaurus*, numerous integumental structures in the substrate around it show predominantly left-handed orientations (Fig. 10, red arrows show examples of

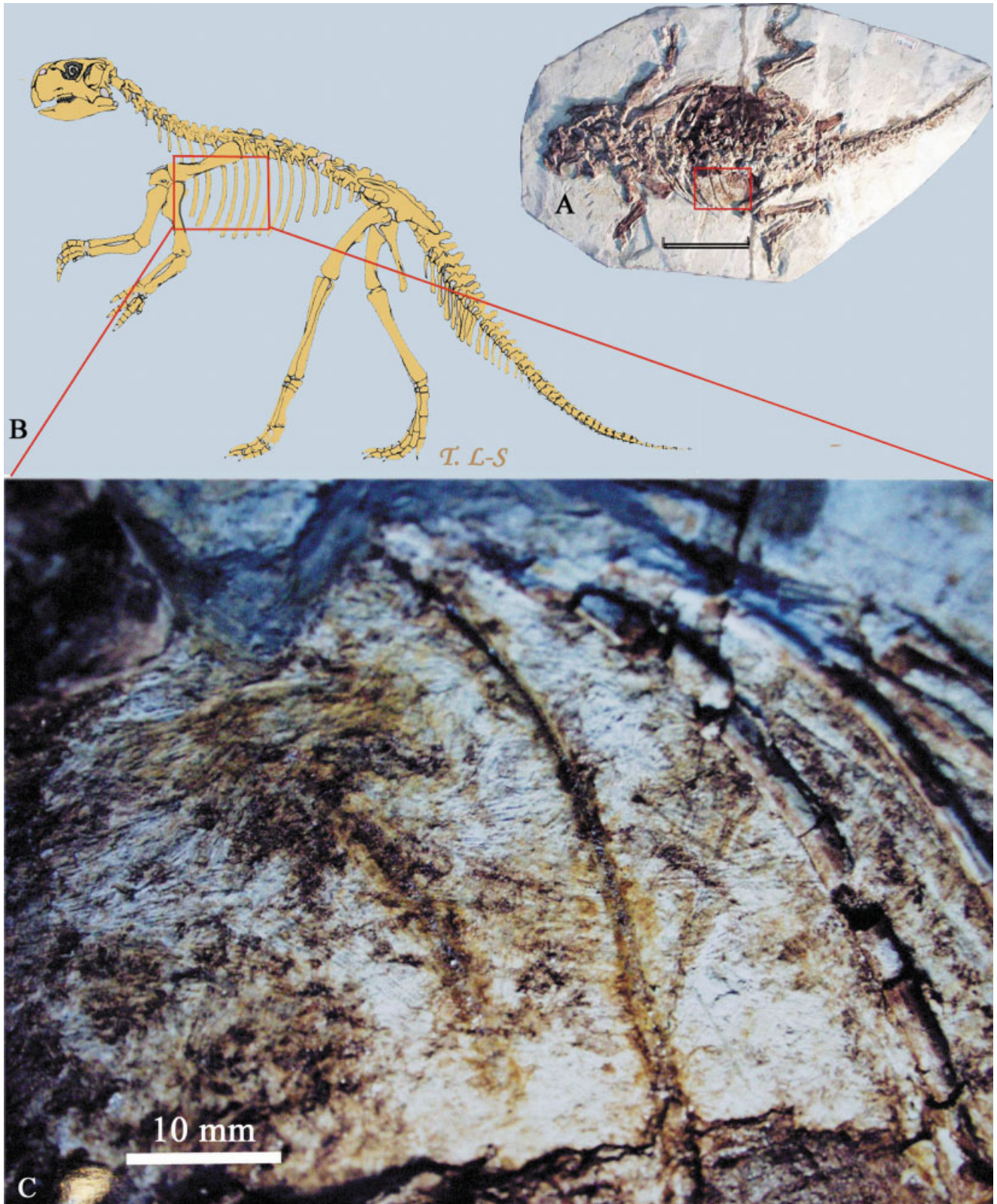


Fig. 11. The ornithomimid dinosaur *Psittacosaurus* (Nanjing specimen). **A:** Dorsolateral view of *Psittacosaurus* (Scale bar = 10 cm). **B:** Restoration modified after Osborn (1924). **C:** Integumental fibers preserved in the rib area (approximately area demarcated by red rectangle in A). Large structures to the right are ribs. See detail in Figure 12A. Scale bar = ~10 mm. (Photos: **A**, courtesy Profs. John Ruben and Jaap Hillenius; **C**, courtesy of Dr. H. Pfretzschner (Tübingen University [TU]).)

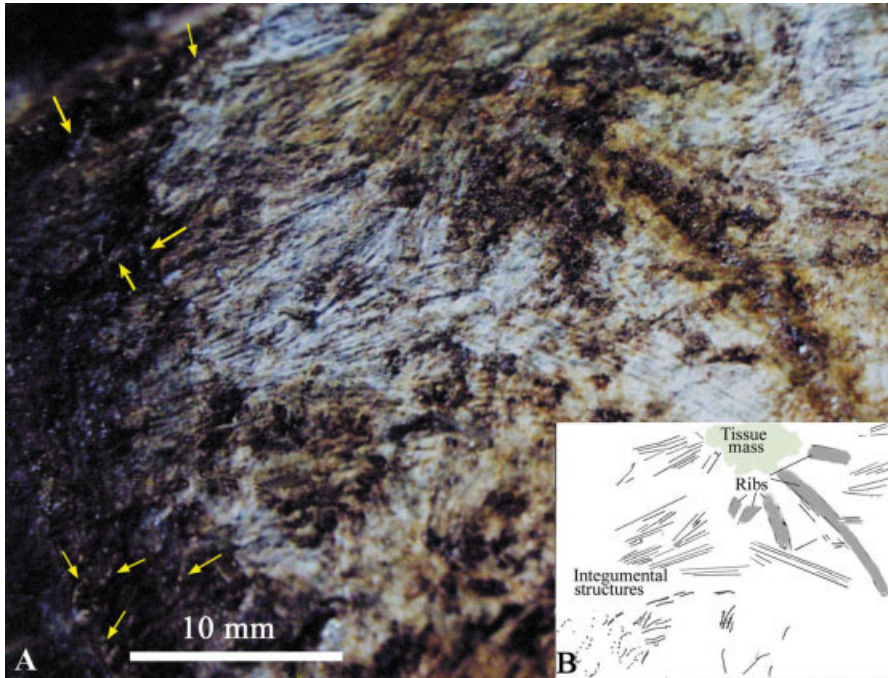


Fig. 12. The ornithomimid dinosaur *Psittacosaurus* (Nanjing specimen). **A:** Bands of integumentary structures are seen oriented in various directions (approximate area 4×3 cm). **B:** A diagrammatic representation of the orientations of the bands of integumentary structures. Scale bar = ~ 10 mm. (Photo **A** courtesy of Dr. H. Pfretzschner.)

the better-preserved fibers). However, there are a small number of fibers with right-handed orientations (e.g., bottom right corner), which possibly represent traces of another layer.

Xu et al. (2001) postulate that different fiber orientations in the *Sinornithosaurus* material preclude them from belonging to a single piece of skin. This suggests some confusion on how they perceive integ-

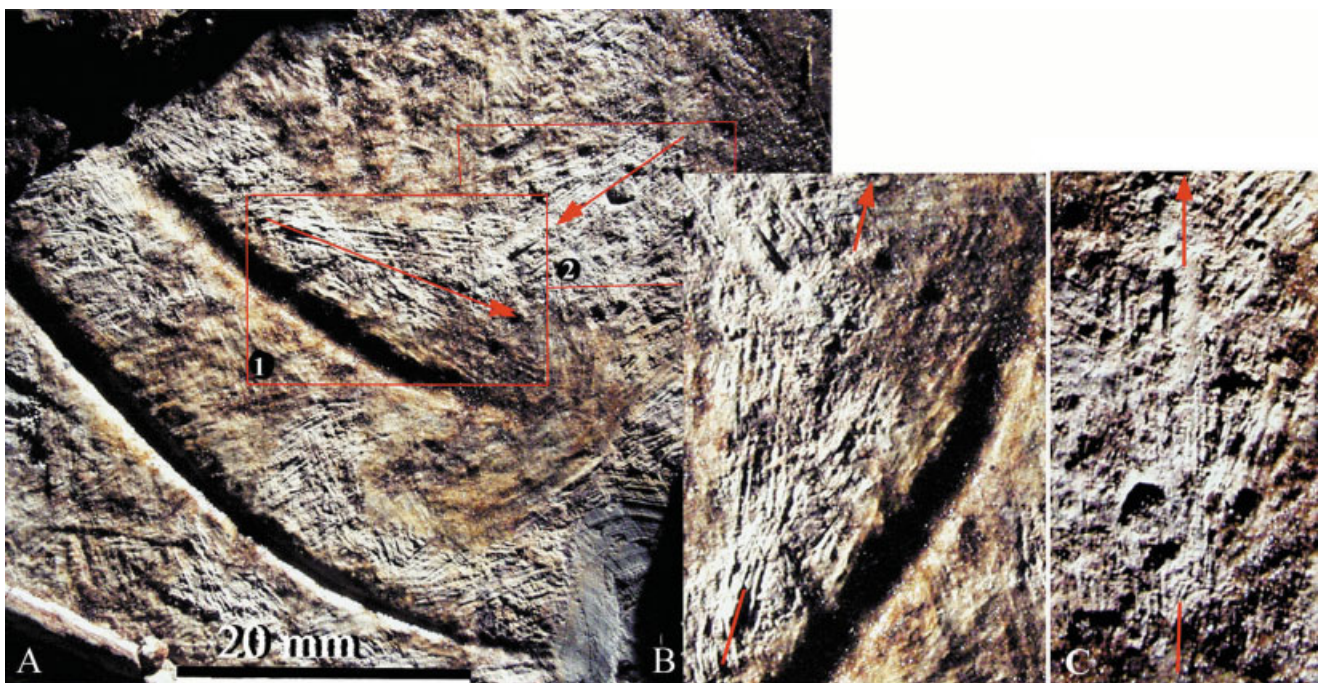


Fig. 13. The ornithomimid dinosaur *Psittacosaurus* (Nanjing specimen). Preserved integumentary structures lower down the rib area (approximate area 6×4 cm) (see Fig. 11A for the approximate location shown by the inset rectangle). Herringbone patterns made by the integumentary structures (arrows show direction of the pattern), delineated within the inset rectangles 1 and 2, are shown in detail in **B** and **C**, respectively. Note details **B** and **C** have been rotated for ease of viewing (see **A** for actual positions). Scale bar = 20 mm. (Photo courtesy John Ruben and Jaap Hillenius.)

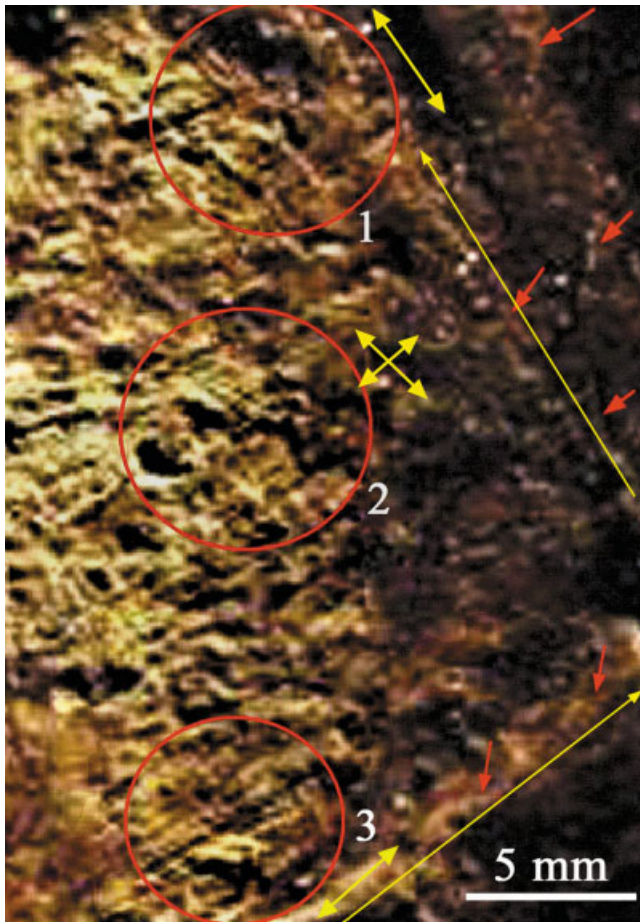


Fig. 14. The ornithomimid dinosaur *Psittacosaurus* (Nanjing specimen). Detail of area of integumental structures from top right-hand corner of Figure 13A. The circled areas show a matrix of the integumental structures that is reminiscent of the helical fibers of many vertebrates. Along the edges of the section the integumental structures are more beaded-like and curved as a consequence of decomposition of the tissue prior to fossilization. The latter features reflect the behavior of collagen (Lingham-Soliar, 2003b). Long yellow arrows show left- and right-handed orientations of integumental structures in the eroded part of the material. Scale bar = 5 mm.

umental structures might preserve. For instance, during decomposition fragments of skin or skin folded/creased (Fig. 7C) or overlying or lying adjacent to others (Fig. 7E,F, respectively) would account for different orientations of the integumental structures. In other instances, as mentioned above, such diverse orientations may be part of a natural structure for the purpose of strengthening.

The discussion above shows that there is no scientific evidence to uphold the view that the integumental structures in *Sinornithosaurus* are congruent with stage 3a of the hypothesis (Xu et al., 2001: 202, figs. 4a,b, 5a,b) (see our Fig. 8C), i.e., a pennaceous feather (Xu et al., 2001, stage 3a in their fig. 6). Hence, this part of fossil evidence in support

of their thesis must be wholly dismissed. Xu et al.'s (2001) simplistic treatment of unquestionably complex material with tenuous arguments and interpretations that do not sustain scrutiny are shown by a reexamination of the *Sinornithosaurus* material above. Furthermore, it is necessary to underscore the present examination with concern that the conclusions arrived at by Xu et al. (2001) are not only seriously flawed and technically unsound but misleading to the reader both by the extremely poor quality of their figures (uninformative in vital respects) and by descriptions that omit important details of the preserved soft tissue.

Prum and Brush's Stage 3b. Stage 3b is referred to as the herringbone pattern of the pinnate feather and derives its alleged support from an indeterminate theropod (Ji et al., 2001). Some of the best-preserved integumental structures are those described as having a herringbone pattern (Ji et al., 2001, fig. 6). Nevertheless, despite excellent preservation, a herringbone pattern is unconvincing. There are some angled groups of fibers, but these are consistent with the way in which fibers strengthen skin or become displaced during decomposition. Our specimen of *Psittacosaurus* shows tracts of integumental structures in the region of the ribs even more reminiscent of a herringbone pattern (Fig. 13; see description below) than those described by Ji et al. (2001, fig. 6). This new specimen of an ornithomimid dinosaur must seriously throw doubt on the narrowly focused interpretations that the integumental structures are feathers or feather progenitors in theropod dinosaurs (Ji et al., 2001; Sues, 2001; Xu et al., 2001; Prum and Brush, 2002)

Prum and Brush's Stage 4. This stage is not represented by non-avian dinosaur fossils or at the least is not without controversy, as acknowledged by Xu et al. (2001). *Caudipteryx* (Qiang et al., 1998), a primary candidate for these stages, has, in our view, been fairly conclusively shown to be a secondarily flightless bird. Wellnhofer (2004; see James and Pourtless, 2004, for review) confirmed that *Archaeopteryx* was a true bird while *Caudipteryx* as non-avian is more controversial. Wellnhofer (2004, p. 294) also cautiously stated with respect to "dino-fuzz" that "it could be that these filamentous structures of the integument have nothing to do with protofeathers at all." Furthermore, exhaustive cladistic analyses (Maryńska et al., 2002), place *Caudipteryx* and other taxa that belong to Oviraptorosauria as flightless birds.

Prum and Brush's Stage 5. Stage V concerns fossil evidence with respect to the asymmetrical feather and is equally controversial with respect to whether or not the specimens represent non-avian dinosaurs or flightless birds. If, as we believe, they are flightless birds, then they have no place in the discussion on the dinosaurian origin of feathers.

Fossil Discoveries and Experimental Findings that Question the Feathered Dinosaur and Follicular Feather Morphogenesis Hypotheses

It was shown in some detail above that interpretations of branching integumental structures in two-dimensional fossil preservations need to take account of the physiological and anatomical make-up of integumental structures in living animals, of decomposition, and of the processes of fossilization. Within the framework of such considerations the viability of the integumental structures found in *Sinosauropteryx* (Currie and Chen, 2001) and *Sinornithosaurus* (Xu et al., 2001) being protofeathers is seriously challenged. Nevertheless, let us accept, for the moment, Xu et al.'s (2001, p. 200) argument, if somewhat circular, that "combined with independent phylogenetic evidence supporting the theropod ancestry of birds, these observations [alleged branching filaments] strongly corroborate the hypothesis that the integumental appendages of *Sinornithosaurus* are homologous with avian feathers." Implicit in the proposition of a homology of these appendages with the avian feather are two interlinked criteria: 1) they look like feathers, and 2) they are found in a theropod. Quid pro quo, all other things being equal (or unequal), the discovery of identical fibers in a non-theropod would suggest that such appendages have no prior claim to feather homology. In the latter case we would have to remove from the entire equation the integumental appendages, as they could apply equally to a theropod or non-theropod ancestry of birds, i.e., they do not constitute prima facie evidence either way for the origin of birds since they lack exclusivity. With this in mind, we next consider other integumental structures resembling those found in theropod dinosaurs. These structures are described below in an ornithomimid lineage of dinosaurs thought to have no close affinity with birds, and separated from theropods since the Triassic Period, at least some 220 million years ago (see Sereno, 1999).

Mayr et al. (2002) reported integumental filaments along the tail of an ornithomimid dinosaur, *Psittacosaurus*. We abide by the authors' comments that in their view the filaments described were not identical to those found in theropod dinosaurs to date (the main difference is that the filaments are much thicker in the psittacosaur). In striking contrast, another specimen of *Psittacosaurus*, from Nanjing, China, provides evidence of integumental structures of a different nature, which we discuss below.

Psittacosaurus. Integumental structures in the Lower Cretaceous ornithomimid dinosaur, *Psittacosaurus*, were brought to our notice recently (Profs. John Ruben and Jaap Hillenius, pers. commun., 2005). Our own examinations concern the preservation of integumental structures in the vicinity of the ribs (Figs. 11–14). The thickness of each integumen-

tal structure is ~ 0.4 mm. The most dorsal filaments are preserved in a clump, so that details of orientations are difficult to assess. However, in a clearer area below this clump bands of fibers are observed oriented in several different directions (Fig. 12A,B). This possibly represents natural orientations in the way collagen fibers may strengthen the dermis or may be a consequence of decomposition and geological disturbance. This pattern is very similar to that of integumental structures figured by Xu et al. (2001, fig. 2) in *Sinornithosaurus* (our Fig. 9B,C). In *Sinornithosaurus* the integumental structures were preserved on the substrate around the animal. This "external" position of preserved structures, Xu et al. (2001) suggest, would only be possible for dissociated feather-like structures. However, as we have shown above, it is very easy to see how patches of skin containing such integumental structures could as a consequence of decomposition become detached and come to lie and be preserved around the animal. Furthermore, some integumental structures also form herringbone patterns reminiscent of those described by Ji et al. (2001, fig. 6) in a theropod dinosaur. With respect to the herringbone patterns of some integumental structures noted in our specimen (Fig. 13A; details Fig. 13B,C reoriented for convenience), we consider them, as we do those described by Ji et al. (2001), as no more than artifacts resembling feather-like patterns resulting from decomposition (Fig. 8A–F) and taphonomic processes.

Our specimen of *Psittacosaurus* is also interesting from another important perspective, namely, the way in which organic tissue decomposes, preserves, and fossilizes. In an area of severe tissue degradation (top right, Fig. 13; detail in Fig. 14) the integumental structures appear as beaded, curved filaments. In the fossilization process this condition represents a high degree of degradation, unlike the straight "healthy" state of the fiber seen elsewhere (Figs. 12, 13). The wavy condition reflects the behavior of collagen when tension is lost via loss of molecular tone or tissue dehydration (see above and Lingham-Soliar, 2003b). As the prominent beads erode, gaps appear in the "chain" to produce wider spaces between beads. These conditions are frequently found at the edges of preserved soft tissue (e.g., Figs. 12A, 14, arrows in both). Closely spaced beads may indicate little erosion of the integumental structures (e.g., see integumental structures in Fig. 14, circled areas). The patterns of regularly aligned integumental structures (Fig. 14, the circled areas 1–3 and adjacent arrows indicating orientation of the integumental structures) in left- and/or right-handed orientations, which can even be seen in the poorly preserved area on the right of the figure (Fig. 14, long yellow arrows), are strongly reminiscent of well-organized collagen fiber bundles in different layers in the dermis of living animals. On the other hand, just to the left of this area are the herringbone patterns preserved (Fig. 13), providing reasonable

confirmation that they are aberrant, a probable consequence of tissue decomposition and taphonomic processes. Both the curvature and beaded condition have been demonstrated as features of decomposing collagen (Lingham-Soliar, 2003b) and may provide a clue to the nature of the integumental structures preserved in *Psittacosaurus* and *Sinornithosaurus*. A similar condition was expressed in some fibers of collagen in the ichthyosaur SMF 457 (Fig. 5C). The structure of keratin in sheaths rather than bundles (the latter a feature of collagen) is clearly very different. We cannot comment on whether or not keratin may decompose in a similar way to collagen, but certainly the beaded condition is not precluded if rippling of the keratin layer, perhaps as a consequence of dehydration, takes place during decomposition.

While we interpret many examples of preserved integumental structures as collagen fibers or fiber bundles, we do not preclude alternative explanations. Sawyer et al. (2003b, p. 30) suggest the integumentary structures of theropod dinosaurs “may more closely resemble the bristles of the wild turkey beard and may not depict intermediate stages in the evolution of feather.” It would be reasonable to envisage such structures constituting peripheral or coronal appendages, e.g., along the dorsal surface of the tail (see Mayr et al., 2002), neck, and back of certain dinosaurs. Could any of the integumental structures preserved in theropod dinosaurs be feathers? On the basis of current evidence this seems unlikely. Nevertheless, we underwrite this comment with the view that it would be foolhardy and dogmatic for either side of the debate on the origin of birds (dinosaurian or non-dinosaurian) to proclaim that the subject is closed. Further attempts to resolve this interesting debate will depend on careful, objective studies of existing and new material.

The classic theory of the evolutionary development of the feather has been eloquently expressed using traditional investigative techniques (Maderison, 1972; Maderison and Alibardi, 2000) as well as most recently on the basis of DNA sequencing, histochemical and antisera analysis, and immunofluorescence techniques (Sawyer et al., 2003a,b). In the complex question of the evolution of the feather, only with a better understanding of the molecular and developmental mechanisms responsible for the evolution of integumental appendages should a clearer picture emerge (Sawyer et al., 2003b). However, with regard to Prum and Brush’s (2002) thesis of feather morphogenesis, our findings here suggest that there is not a shred of evidence from fossils that may reasonably be construed to support it.

Sawyer et al.’s (2003b, p.32) proposal that the initial embryonic cell populations, which form during scale morphogenesis, are homologous with those of the embryonic feather filament is interesting, especially in light of the discovery of metatarsal feathers in *Microraptor gui* (Xu et al., 2003). It raises the

possibility that the ancestors of modern birds had feathers on their metatarsus rather than scutate scales. Indeed, the idea of scales in dinosaurs and the timing of the possible transition to feathers is a very important question, of which we know very little. In this context, we examine a new specimen of the dinosaur, *Pelecanimimus*, which came from the Lower Cretaceous of Spain (Briggs et al., 1997).

Pelecanimimus. A specimen of the ornithomimid theropod, *Pelecanimimus*, specimen LH 7777 (also Briggs et al., 1997; our Fig. 15), is especially interesting in the light of scales found on the forearms (Profs. John Rubin and Jaap Hellenius, pers. commun., 2005). It is noteworthy that in this region of the forelimbs of a cursorial theropod, one would expect to find some form of protofeathers rather than scales, if the prevailing view of many paleontologists holds good (e.g., Currie and Chen, 2001; Xu et al., 2001). Yet these are indisputable scales. The detail (Fig. 15D, arrow) shows on the left small scales lying adjacent to one another and possessing little finger-like projections along the edges, which presumably initiate overlapping of the scales during growth; on the right (numbered 1–5) can be seen large scales with the typical overlapping formation. We believe that *Pelecanimimus* did not possess feathers, but certainly possessed scales over at least some parts of the body.

Skin impressions are fairly commonly preserved in diverse dinosaurs, including sauropods, ornithomimids, stegosaurs, ankylosaurs, ceratopsians, and theropods. Aside from the Lower Cretaceous Chinese fossils, in no case is there any evidence of feather-like structures. The typical dinosaur skin has the “pebbly” texture of tuberculated skin (particularly well-preserved in hadrosaurs), and there are no known integumentary appendages. Other exceptionally well-preserved theropods with integument have been discovered in recent years, including an unnamed theropod from Brazil, and as noted above, the Lower Cretaceous Spanish ornithomimosaur *Pelecanimimus*, and there is nothing remotely resembling feathers (Feduccia, 1999a, p. 377). Kellner (1996) reported preserved skin from the Brazilian theropod that under SEM showed a thin epidermis, formed mostly by irregular quadrangles bordered by deep grooves in a criss-cross pattern. “No evidence was found of any structure covering the skin, such as dermal ossicles, scales or feathers, which should be preserved if they were originally present” (Kellner, 1996, p. 32). Another Lower Cretaceous Italian small theropod, *Scipionyx*, that even preserved the detail of the internal organs (Dal Sasso and Signore, 1998), shows perhaps better preservation than any other known dinosaur, including patches of muscle, but no evidence of feather-like structures.

The taxonomic distribution of “dino-fuzz” fibers also does not lend confidence to the assertion that they have any relation whatsoever to protofeathers.

lation. The down-like form of Prum's (1999) protofeather seems improbable for the roles of water repellence and insulation. Down is a good thermal insulator but loses its insulatory qualities when wet. Hence, down in adult birds can only function effectively under the regular feathers which form a waterproof coating or in juveniles if there was some effective mechanism for preening the down (as, e.g., in ducklings), for which there is absolutely no evidence in dinosaurs. The feathers in, for example, penguins, require complete reorganization as adaptations to extremes in cold and as demonstrated by Bonser and Dawson (2000, p. 547) "despite profound differences in function, the mechanical properties of specialized insulatory feathers (afterfeathers) are remarkably similar to those used as aerodynamic surfaces."

Adult dinosaurs, like young birds possessing only downy feathers (lacking afterfeathers, which are only in stage 5 of Prum's [1999] hypothesis), would lack the insulation provided by the afterfeather (entirely responsible for the insulation in penguins; Dawson et al., 1999) and waterproofing provided by the pennaceous feathers of adult birds. To avoid getting wet, young birds rely on the protection of their mother, but this provides no solution for adult dinosaurs covered in downy feather-like structures. In particularly dry climates, e.g., Outshoorn in South Africa, down-covered ostrich chicks may forage without parental protection and become wet but drying-out is rapid. Nevertheless, they do not survive prolonged periods of being wet greater than 2–3 days. For instance, young downy ostriches if not protected by their parent's wings in rain become soaked and chilled, from which they frequently die (Feduccia, 1999a). This ineffectiveness of down feathers is underpinned by the biomechanical studies on the penguin afterfeather (Dawson et al., 1999; Bonser and Dawson, 2000), which point to the high probability that the insulatory capabilities of the feather stem from an advanced feather structure (Feduccia, 1999a) rather than from a primitive feather or protofeather (Prum, 1999). Given the above, one can only conclude that it would be maladaptive for a terrestrial theropod to have an integumentary coat of downy feathers. Despite the lack of evidence and a satisfactory explanation as to how a downy coat would be adaptive, the cover of *The Encyclopedia of Dinosaurs* (Currie and Padian, 1997) features *Sinosauropteryx* with a complete downy coat, like a precocial avian chick.

With respect to both questions, namely, feathered non-avian dinosaurs (theropods) giving rise to birds and the follicular origin of the feather, a careful analysis of the component evidence here shows extensive and serious weaknesses, which include weak paleontological methodology (for instance, the concepts of decomposition, taphonomy, and the laws of chance have been almost entirely disregarded). Clearly, the purported "overwhelming" evidence for

the origin of birds from dinosaurs is filled with a good deal of emotion as, e.g., illustrated by Sues' (2001, p. 1036) comment: "Most paleontologists accept this evidence [close morphological relationship between theropod dinosaurs and birds]. Only a small (if vocal) group continues to argue that birds have no clear relationship to dinosaurs." Numerous statements by Prum (2002, p. 4), such as "it is universally agreed," and "conclusive evidence of the strongest possible," and "wealth of and increasing strength of the evidence," characterize comments by the advocates of the dinosaurian origin of birds. It is necessary to try to avoid such emotive comments including arguments as to how many people may agree or not agree with a particular hypothesis since the argument could degenerate further into an equally nonconstructive response that most ornithologists support a non-dinosaurian origin of birds. This article, if anything, is to urge that scientific equanimity prevails.

Paradox of the Digital Mismatch Between Birds and Theropods

Problem of digit identity in the bird wing.

I. Developmental Biologists and Paleontologists Disagree. Embryologists and paleontologists have disagreed over bird wing digit identity (Hinchliffe and Hecht, 1984; Burke and Feduccia, 1997; Feduccia, 1999a). Paleontologists have usually identified bird wing digits as 1,2,3—homologous with the three forelimb digits of theropod dinosaurs. Their evidence is that in the archetypal 5-digit reptile hand, the phalangeal formula for digits 1,2,3 is the same as in both the surviving 3 digits of the forelimbs of theropods and those in *Archaeopteryx* (Vargas and Fallon, 2005). Most arguments of this nature, however, fail to point out that the phalangeal formula (P) of P2-3-4-x-x (x = absence), for digits 1,2,3 in theropods is the same as for basal archosaurs, and is therefore not phylogenetically informative. For example, basal archosaurs begin with an ancestral formula, P2-3-4-5-3, which is reduced to P2-3-4-3-2 in basal theropods, to P2-3-4-1-x, and ultimately to P2-3-4-x-x, with even more reduction in tyrannosaurids. Theropod digits are also identified as D1,2,3 from the fossil record showing progressive reduction and loss of digits 4 and 5 (e.g., *Herrerasaurus*, Sereno, 1993—see Fig. 16) during evolution. The theropod hand, with its retention of digit 1 and loss of digits 4 and 5, is therefore unusual in digital reduction in vertebrates, violating the normal pattern of symmetrical reduction known as Morse's law. There appears to be little question that the hand of theropods represents D1,2,3, and in fact it has been suggested that it is the primary synapomorphy for "dinosaurs" (Fig. 17; Feduccia, 2002). The trend in dinosaurs is for the combined reduction of the medial and lateral pedal digits, but only the lateral manual digits. Thus, the postaxial reduction

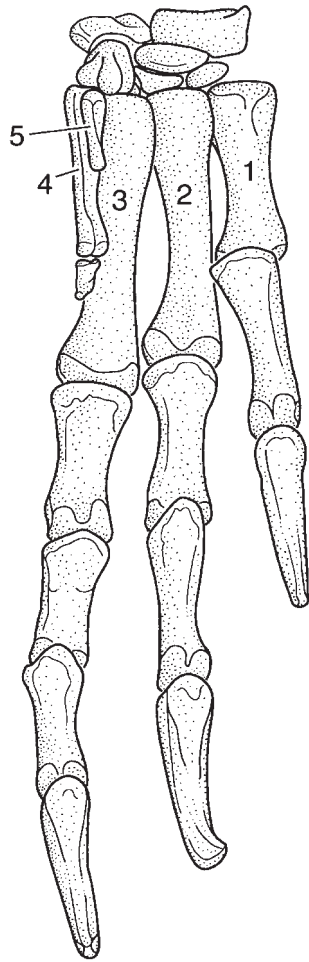


Fig. 16. The left hand of the Late Triassic basal theropod *Herrerasaurus*, typical of many Late Triassic theropods, illustrating a pentadactyl hand but with digits 4 and 5 greatly reduced. Note that the longest finger in primitive theropods is not the middle finger, as in *Archaeopteryx* (and birds), and dromaeosaurs (microsaurs, *Deinonychus*, etc.), and most tetrapods including man, but finger 3, which is what one would expect. Note also the primitive nature of the carpal elements, with nothing remotely resembling a semilunate carpal or any bird-like features (modified after Sereno, 1993).

of digits 4 and 5 may be the most salient synapomorphy for the monophyly of Dinosauria (Feduccia, 2002:1190).

Similarities have been cited in the detailed morphology of the carpus and phalangeal elements of *Archaeopteryx* and dromaeosaur theropods (Ostrom, 1977). In this view, the three wing digits of *Archaeopteryx* are thus identified as D1,2,3, but this assumes that dromaeosaurs are indeed dinosaurs and not derived flightless birds. But to embryologists the modern bird wing digits appear to be D2,3,4 on the basis of comparison with the stereotyped pattern of limb skeletal development in other amniote limbs (Hinchliffe, 2002). This identification is based on classical homology criteria: timing (e.g., D4 the first forming digit), position (D4 postaxially positioned as

in the leg bud), and connections (ulnare at base of D4) (Shubin and Alberch, 1986).

Using these criteria, comparison was made first by Müller and Alberch (1990) and then in more detail by Burke and Feduccia (1997) of digit development in the wing with that in the chick leg bud and also in the limb buds of alligator and turtle (Figs. 18, 19). These two reptiles both generate all five digits in the adult, making their digit identity certain. Comparison of timing, position, and connections supports homology of the postaxial avian wing bud condensation with the digit 4 condensation in the other two species.

The wing skeleton precartilaginous condensations and early cartilages are clearly revealed in autoradiographs of $^{35}\text{SO}_4$ uptake into chondroitin-6-sulfate (a major cartilage matrix component) in chick wing buds (Fig. 20; see also fig. 2, Hinchliffe, 1977, and figs. 1–4, Hinchliffe, 1985). This method shows the early skeletogenic pattern more clearly than older classical histological methods (e.g., Montagna, 1945; Holmgren, 1955). Timing, position, and connections supported the D2,3,4 (plus a reduced D5) interpretation of the main digit rays (detail in Figs. 20, 21).

How should we interpret the similar phalangeal formula (P2,3,4) of D1,2,3 in (some) theropods and in the first three digits in *Archaeopteryx*? On the basis of parsimony it can be argued that since *Archaeopteryx* retains the primitive reptile phalangeal formula for D1,2,3, it must therefore (like theropods) have retained these but lost digits 4 and 5. This is seen as only one change, originally evolved in theropods. However, the *Archaeopteryx* pattern need not necessarily be inherited from theropod ancestors. Studies on limb buds in other species have shown that when mitosis is experimentally reduced, all digits may each lose a terminal phalange—this can equally be regarded as a single change. In fact, this was the exact result of Raynaud and Clergue-Gazeau (1986) and Raynaud (1980) in studies on limb development in the lizard, *Lacerta viridis* (Raynaud, 1980; Raynaud and Clergue-Gazeau, 1986). At a specific level of reduced cell division in *Lacerta* limb buds they found that each of the three middle digits lost its terminal phalange. Thus, in the foot a normal phalangeal formula of 2,3,4,5,4 became a formula of 0,2,3,4,3, with a similar reduction pattern for the forelimb (P2,3,4,5,4 becoming P 0,2[or1],3,4,3). Applying the basal reptile phalangeal formula to such experimental limb buds in *Lacerta* would identify their three middle digits as D1,2,3, whereas in fact we know them from other evidence to be D2,3,4. Thus—returning to the question of bird evolution—loss of a terminal phalange from each D2,3,4 of the basal reptile digits would produce the same phalangeal formula as in the three digits of *Archaeopteryx* and be consistent with a D2,3,4 identity for them. The *Lacerta* experiments provide an instructive model, showing such transformation is feasible and not simply theoretical.

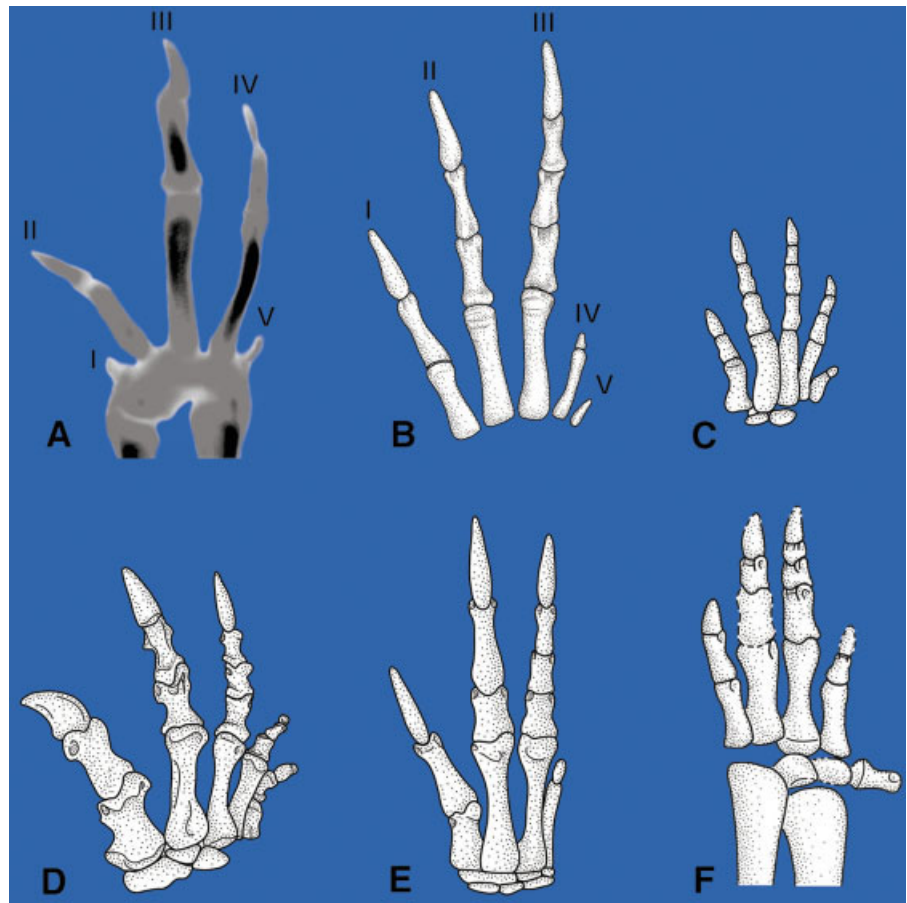


Fig. 17. The pentadactyl hand of a 14(–15)-day-old ostrich (A), showing the anlagen for digits I, “thumb” (left) and V (right), compared to the hands of various dinosaurs illustrating the reduction of digits IV and V (disappearance of V in E). **B:** *Herrerasaurus* (putative basal theropod, Late Triassic). **C:** *Lesothosaurus* basal ornithischian, Late Triassic. **D:** *Plateosaurus* (basal sauropodomorph, Late Triassic). **E:** *Syntarsus/Coelophysis* (theropods, Late Triassic). **F:** *Hysilophodon* (ornithopod, Early Cretaceous). (Drawn to the same scale, modified from a variety of drawings (primarily modified from drawings in Weishampel, 1990; ostrich embryo from Feduccia and Nowicki, 2002).)

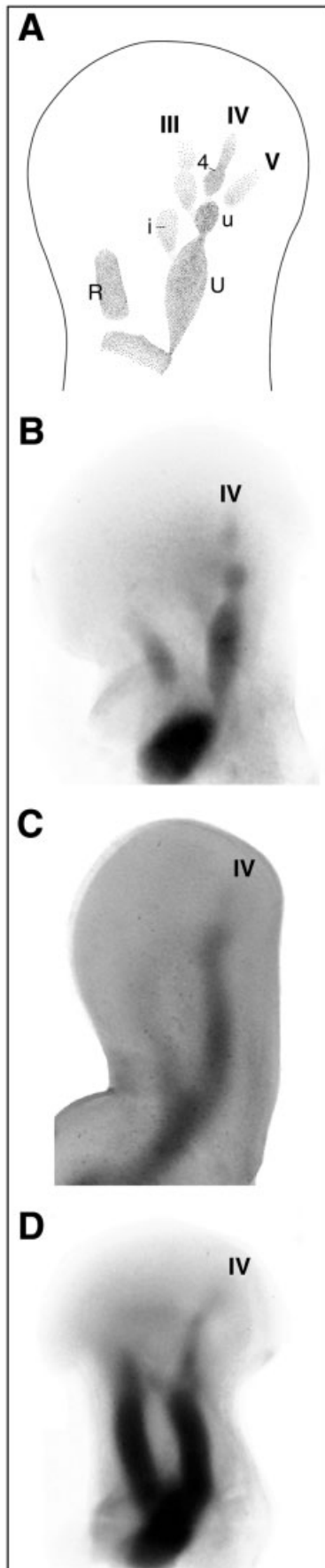
Phalangeal formulae are in any case quite labile: for example, in the foot of *Archaeopteryx* where individual specimens have differing formulae and in the relatively rapid reduction of wing phalangeal formulae to 2,3,2 in the Lower Cretaceous primitive toothed bird *Sapeornis*, as well as in the flightless bird (sometimes termed a feathered theropod) *Caudipteryx*. This reduction continues in modern birds, with P2,2,1 (*Gallus*; sometimes reduced to P1,2,1), and P2,3,1 in *Struthio*. The phalangeal formula for the South American Hoatzin *Opisthocomus* is P2,3,1 in the juvenile, but reduces to P1,2,1 in the adult. In Cretaceous enantiornithine birds, phalangeal formulae are varied: P2,3,3 (*Eoalulavis*), P2,3,1 (*Concornis*), and P2,3,2 (*Protopteryx*).

Traces of this reduction in D4 (where three of the original four phalanges are lost in modern birds) are probably represented by the massive cell death in the prospective D4 area of the distal digital plate mesenchyme (Figs. 22, 23; also see fig. 1 in Hinchliffe, 1982). Such a reduction of distal phalanges simultaneously in all digits can be accomplished by experimental blockage of bone morphogenetic protein 4 (BMP4) signaling, which mediates apoptosis in the avian limb bud (Zhou and Niswander, 1996).

But it is clear that clinching embryological evidence would be the presence of an atavistic anterior

D1 in modern birds. Recently, such evidence (Figs. 24, 25) was obtained by Feduccia and Nowicki (2002) and by Welten et al. (2005), respectively, at the descriptive and molecular levels. First, Feduccia and Nowicki reported that D1* appears briefly and reaches early chondrogenesis in the ostrich wing bud, and second, Welten et al. (2005) reported the appearance of a prechondrogenic molecular domain (Sox9, specific for condensation and expressed briefly in subridge anterior mesenchyme in a position appropriate for D1—see Fig. 25) in the chick wing bud. Sox 9 expression in this D1 position is not followed by cartilage matrix synthesis. Thus, the wing is (briefly) pentadactyl, confirming the embryologists’ allocation of D2,3,4 identity to the main digits (Fig. 24).

*Vargas and Fallon (2004) in supporting their 1,2,3 wing digit theory (see below) as an alternative to the FS hypothesis identify the vestigial ostrich digit 1 as a prepollex. This interpretation can be discounted on the grounds of position that if it is a prepollex then (in comparison with the leg bud digit rays) the remaining wing digit rays would be dramatically skewed forwards, with D3 (Vargas and Fallon interpretation) postaxial rather than midline (our interpretation).



II. Frame Shift Hypothesis: An Unsatisfactory Compromise. The embryologists' view that the avian wing digits are 2,3,4 raises considerable problems for the "bird ancestry from dinosaurs" hypothesis that arises from a cladistic analysis in which apparent homology of the digits of *Archaeopteryx* wings and of the forelimbs in some theropods represents critical evidence (see discussion in Martin, 1991; Feduccia, 1999a,b; Wagner and Gauthier, 1999). A new theory accepts the 2,3,4 interpretation of avian wing digits but attempts to resolve the paradox by separating condensation identity (C2,C3, etc.) from the later specification of its definitive morphology (D2,D3, etc.). This highly original approach attempts to integrate paleontological and molecular data within a single hypothesis.

According to Wagner and Gauthier's "frame shift" (FS) hypothesis (1999) of molecular identity transformation, there could be a repositioning within the limb bud of the expression domains of genes such as the Hox d group, regarded as having a role in control of digit identity. Wagner and Gauthier argue that in bird evolution through frame shift (= "homeotic shift") the theropod identities for D1,2,3 have become shifted in evolution of birds to digit blastemas or condensations, C2,3,4. In this view, avian digit condensations have been correctly identified by embryologists as C2,3,4, but the developmental mechanism that specifies the morphological identities has become shifted so that condensation C2 generates the theropod digit 1 morphology, C3 generates D2 morphology, and C4 forms D3. If this hypothesis were true, it would be an argument for nesting birds in the same clade as maniraptoran theropods.

Possible general objections to the FS hypothesis are (see also Feduccia, 1999b):

- i) The proposed FS or homeotic shift would have occurred not in the lineage leading to theropods or the earliest bird, but within the theropod lineage leading to birds (at about the *Allosaurus* level in the view of Wagner and Gauthier, 1999). Galis et al. (2003, p. 8) note, "A homeotic shift ... in theropods without any further anatomical changes does not appear to lead to an adaptive advantage." And, there is none: "there is as yet no adap-

Fig. 18. Illustrations showing the developing primary axis. **A:** Diagrammatic illustration of developing turtle limb bud to show general topography (precondensations) of: R, radius, U, ulna, u, ulnare, I, intermedium, 4, carpal four, and digits 3–5). **B–D:** Illustrations of developing limb buds in turtle, bird, and alligator, respectively, illustrating the conserved developmental pattern of the primary axis. (The postaxial distal extension of the Y condensation (rt.) is termed the "primary axis"—a linear array extending distally through the ulnare into distal carpal 4, metacarpal 4, and ultimately through digit 4, with fidelity in all amniotes.) The primary axis is therefore highly conserved developmentally in amniotes and invariably identifies digit 4. (**A** modified from Burke and Alberch (1985); **C,D**, photos from specimens prepared by A.C. Burke; from Feduccia (1999b).)

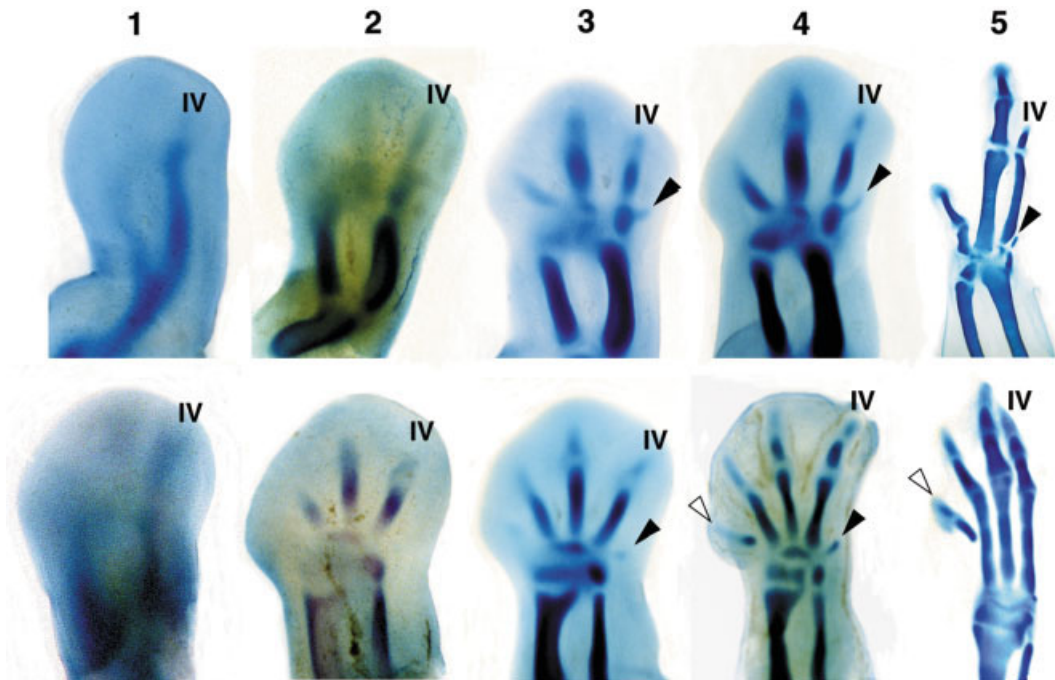


Fig. 19. Comparison of right manus (top row) and pes (bottom row) development in the chicken, dorsal views. The stages in the left column represent the early appearance of the primary axis. Column two shows the digital arch. Note the transient appearance of digit 5 (dark arrows to right on last three columns), and the eventual appearance of digit 1 in the pes (open arrows to left), which persists in adult birds as the reversed hallux. Digit 1 fails to appear in most avian species. (Reprinted with permission from Burke AC, Feduccia A. Developmental patterns and the identification of homologies in the avian hand. ©1997, AAAS.)

tive significance that would overcome the evolutionary constraint” (p. 9).

- ii) The shift would have to be confined to the forelimb digits without effect on the homologous hindlimb digits. (Most limb mutants have similar effects on both fore- and hindlimbs.)

- iii) FS assumes that theropods in fact would have had an embryonic C4 condensation (it should be remembered that their D4 is reduced or lacking, implying C4 was also small or missing) on which to impose the identity of D3. The C4 condensation would have had to be sufficient to generate a long metacarpal element plus four phalangeal elements for a posterior digit of *Archaeopteryx* type (even in modern birds there is a substantial wing digit 4, especially in the embryo—see Figs. 22, 23). Alternatively, a supplementary theory additional to the FS of formation of a greatly increased C4 condensation size is required.
- iv) FS must explain not only the change in digit identity but also necessary integrated changes in the carpus. Thus, the distal carpal semilunate (a key synapomorphic element of [some] theropods

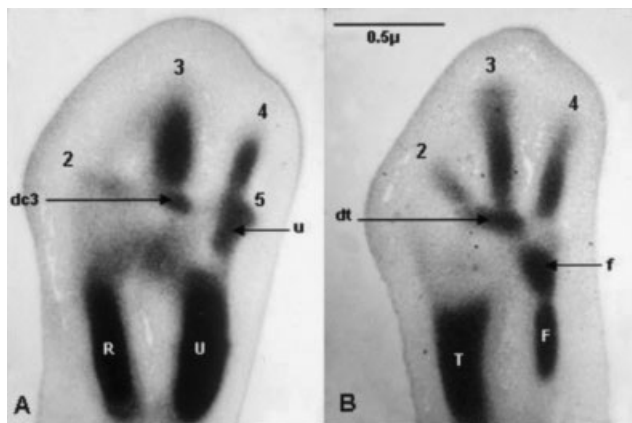


Fig. 20. Autoradiographs of chondroitin sulfate synthesis in chick stage 27/28 wing bud (A) and stage 26/27 leg bud (B) (technique detail in Hinchliffe, 1977). The wing bud (A) clearly shows the primary axis (U, u, 4—compare with Figs. 18 and 19). Digit rays numbered (for identity criteria, see text); note postaxial position of D4 in both limb buds. dc3, distal carpal; dt, distal tarsal; F, fibula; f, fibulare; R, radius; T, tibia; U, ulna; u, ulnare.

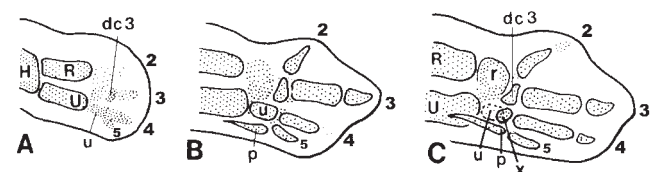


Fig. 21. Pattern of skeletogenesis in chick wing bud. A: Stage 27. B: Stage 28. C: Stage 30. Note the ulnare regression and replacement by the more ventral element x. Abbreviations as in Figure 20. p, pisiform; r, radiale.

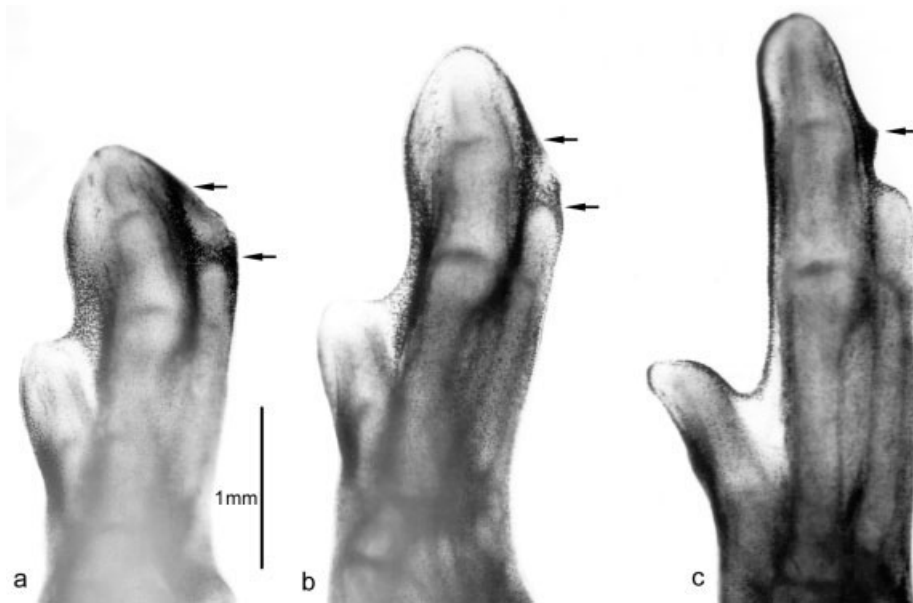


Fig. 22. The chick embryo wing shortens digit 4 relative to digit 3 through controlled cell death that eliminates the mesenchyme distal to the D4 phalange. Intense staining marks areas of cell death (arrowed). Vially stained with Neutral Red (Hinchliffe and Griffiths, 1986). Hamburger-Hamilton Stages 32 (a), 33 (b), 35 (c).

and *Archaeopteryx*) would have to be shifted posteriorly so that it retained its position at the base of theropod metacarpals 1 and 2, now according to FS formed from bird C2 and C3. This would have involved identity changes in, or other modification of, the distal carpal elements of the embryo limb, implicating even greater morphological reconstruction of the limb by FS than has been assumed. At present no study has been carried out of Hox control of normal carpal structure, never mind its molecular transformation.

- v) The mechanism for such a shift (which would have to simultaneously affect four digit condensations) is unknown.
- vi) Such a homeotic shift would be the only known such shift across a broad embryonic field in any amniote.

Molecular evidence is now central to any understanding of limb evolution and development (Sordino et al., 1996; Wolpert et al., 2001) and specifically of determination of digit identity. Thus, the FS hypothesis must be compatible with such evidence and this is claimed in recent work on limb development for the FS hypothesis by Vargas and Fallon (2004), who argue that in both mouse fore- and hind-buds and chick hindlimb buds, prospective digit 1 is characterized by Hox d 13 expression alone while prospective digits 2–5 express both Hox d 13 and Hox d 12. Since the anterior wing bud digit expresses only Hox d 13, they argue it is digit 1 on the grounds of molecular homology. However, in a review of this hypothesis Gallis et al. (2005) argue cogently that the molecular evidence cited is unconvincing as these mutants (e.g., talpid and Hox d deletion mutants) show only a weak correlation of Hox d 12/13 expression with digit identity (Kmita et al., 2002; Galis et al., 2005).

We need to examine critically evidence for the claim that specific molecular domains represent signatures for particular digits and that these specific domains can be shifted from one prospective area or anlage to another as the basis for evolutionary transformation, as in the FS hypothesis of Wagner and Gauthier (1999) and of Vargas and Fallon (2004). Vargas and Fallon propose that their molecular studies on the polydactylous talpid 2 mutant provides key support. Talpid 2 embryo limb buds demonstrate uniform Hox d 12/13 expression, even in the prospective anterior digit position, and Vargas and Fallon (2004) correlate this with the supposed absence of digit 1 and the appearance only of numerous digits that they identify as posterior or posteriorised. But talpid digit morphology is so bizarre as to defy classification in terms of normal limb identity. Ill-defined or fused talpid phalanges make their scoring for calculating the phalangeal formula of the polydactylous digits difficult (e.g., in talpid 3, described by Ede and Kelly, 1964; Hinchliffe and Ede, 1967), and in fact Goetinck and Abbott (1964, p. 162) state that “in talpid 2 the entire leg pattern is so completely distorted that none of the 8 to 10 digits can be recognized as a specific toe.” Talpid 2 and 3 wing buds have 7–8 digits equally unrecognizable, often comprising single cartilages (Goetinck and Abbott, 1964; fig. 1, Ede and Kelly, 1964; Fallon et al., 1991). Fallon et al. (1991, p. 378) state that “The [talpid 2] wing digits were disorganized showing variable fusion of the one or two phalanges present. None of the phalanges resembled normal digits.” Moreover, since the Hox d 12/13 anomalous expression appears late, after the abnormal talpid 2 digit patterning is already clearly recognizable, a causative Hox d 12/13 role in initiating control of digit identity here is not clearly estab-

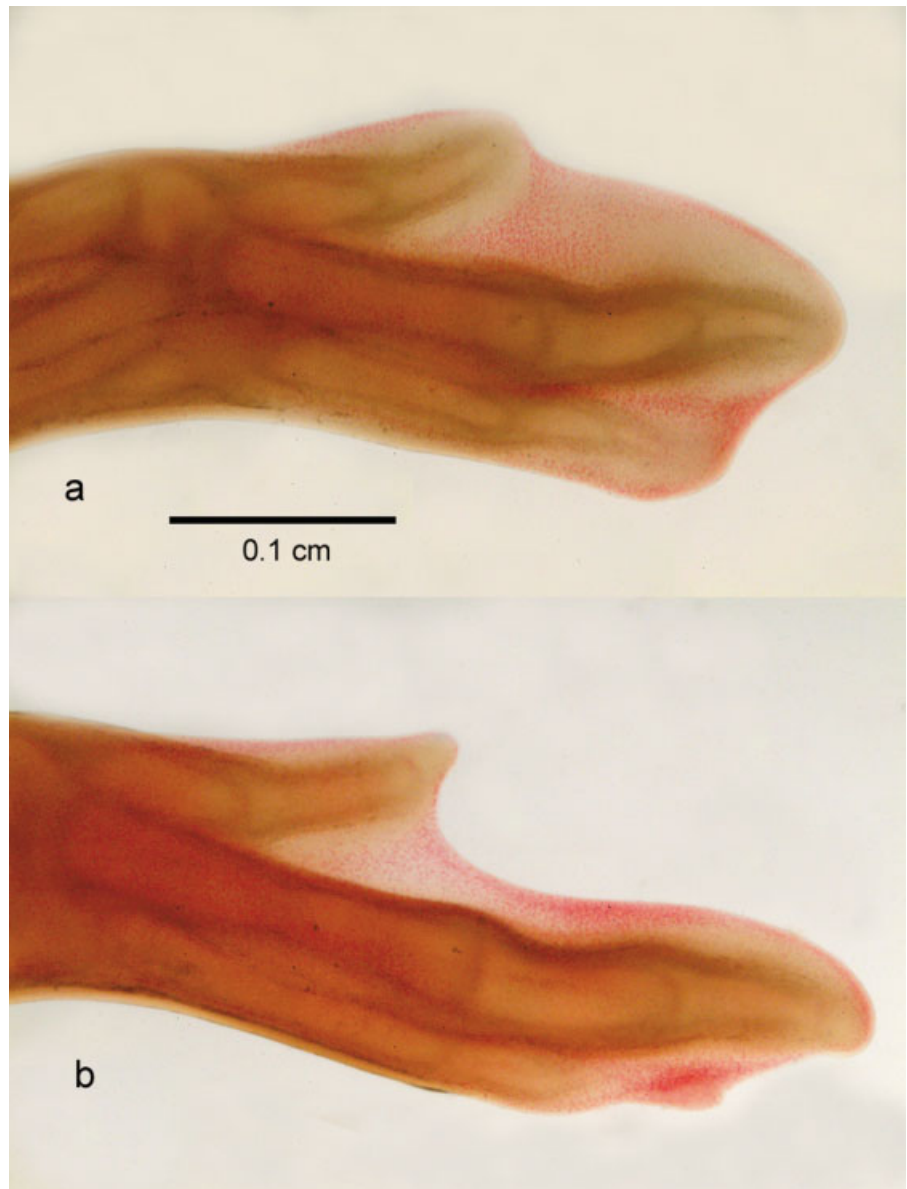


Fig. 23. Like the chick (Fig. 22), the duck embryo also shortens D4 (bottom right in both photographs) relative to D3 (middle right) by controlled cell death of mesenchyme distal to the proximal D4 phalange, again demonstrated by red vital staining with Neutral Red. Stages are approximately similar to chick embryo Stages 32 and 34.

lished. These considerations bring into question any attempt to correlate causally the altered Hox domains in talpid 2 limb buds with digit identity specification.

The gene networks of the limb bud are complex (Fig. 24—Zákány et al., 2004) and molecular developmental biologists are far from agreed that digit identity can be assigned by, for example, simple combinations of Hox gene expression. An earlier assignment by Tabin (1992) of a digit identity control role to five spaced expression domains of the five Hox d 9–13 genes with each domain controlling one of pentadactyl digits 1–5 (e.g., Hox d 13 specifying D5) has been abandoned, as later study showed that all the domains overlapped in the distal limb bud well before digit differentiation. Hox d genes were instead allocated a role in regulating rate and timing of cartilage proliferation and differen-

tiation, and therefore had only indirect effects on digit identity (Tabin, 1997). In a study of digit reduction patterns in skinks by Shapiro et al. (2003), variance in Shh (sonic hedgehog) expression was considered to control digit identity, rather than Hox d expression. Sanz-Ezquerro and Tickle (2001) discuss a critical role for BMPs (bone morphogenetic proteins) possibly acting in concert with Shh in control of digit identity. At present, there seem to be too many unknowns to accept the “Frame Shift” as a well-established and convincing theory. Several new assumptions and factors have been introduced without real evidence. Parsimony appears to favor the 2,3,4 identity for bird wing digits and 1,2,3 for theropod forelimb digits.

In summary, recent findings from embryology consistently support identification of the avian digits as

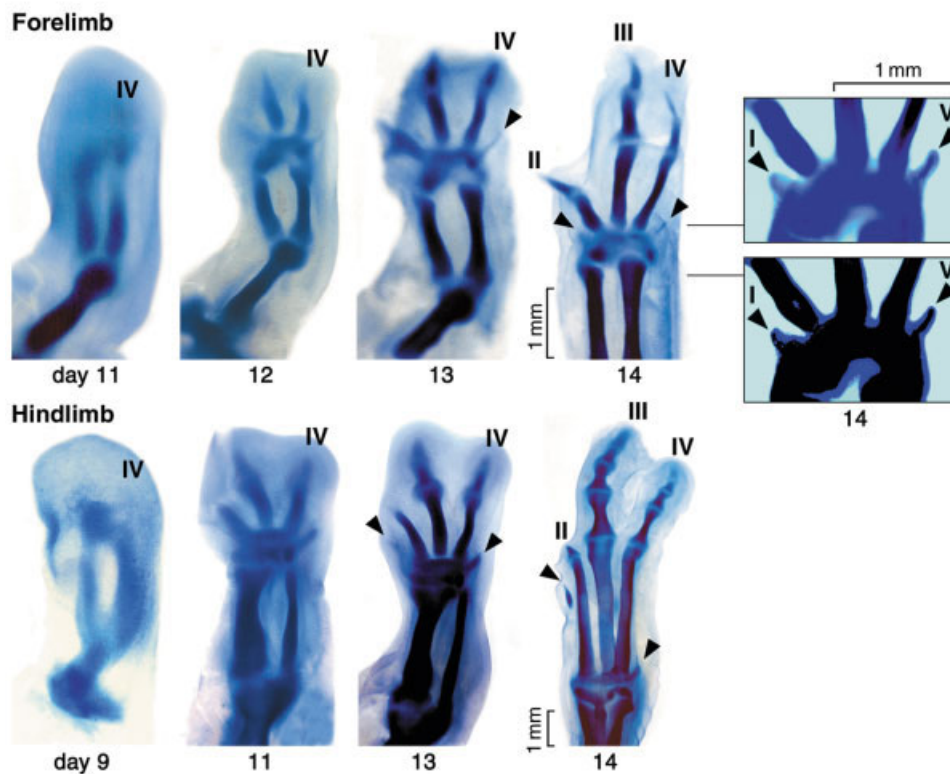
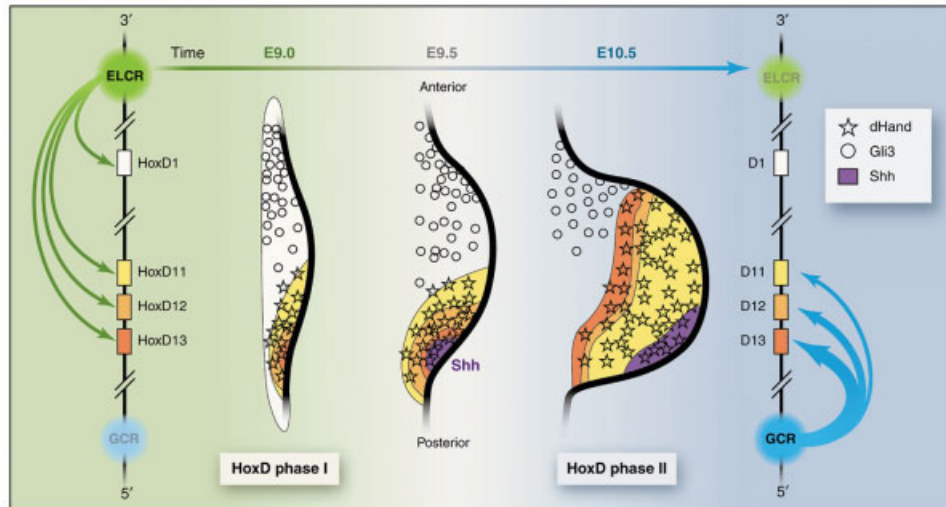


Fig. 24. Upper: Patterning the budding limb. Biphasic regulation of the 5' *HoxD* gene cluster during limb bud outgrowth. Left: The early overlapping expression of domains of *HoxD* genes. Right: *Shh* expression domain subsequently extends and is displaced distally. Note that the second phase initiates morphogenesis of the most distal limb structures, the digits. *Shh* and *Gli3* are dispensable for generating limb skeletal development, but are required for specifying digit identity; yet their activation is during phase 2, which is still limb bud stage (Zákány et al., 2004; Deschamps, 2004). Lower: The pentadactyl hand of birds illustrated by a 14-day ostrich embryo. Phase 2 (in which digit identity is regulated) in the ostrich would be at ~day 7, long before the display of the pentadactyl condensations. (Upper, reprinted with permission from Deschamps J. *Hox* genes in the limb: a play in two acts. ©2004, AAAS; lower from Feduccia and Nowicki, 2002.)

2,3,4, and show that the primitive avian hand was pentadactyl. "The presence of a first digit in the early embryo argues for a primitive avian pentadactyl hand, with adult digits II, III, IV ... unlike the highly derived I, II, III hand of theropods" (Feduccia and Nowicki, 2002, p. 393); "The direct avian ancestor is predicted to have been five-fingered with dominant digits ... II, III, IV" (Kundrát et al., 2002, p. 294); and "a full pentadactyl prechondrogenic digital anlage has been maintained in the bird lineage for at least 220 million years since the last known pentadactylous ancestor of the lineage" (Larsson and Wagner, 2002, p. 146). In fact, Larsson and Wagner

note that this age is congruent with *both* a dinosaurian and non-dinosaurian origin of birds.

However, if the bird ancestor were a dinosaur, then the only known theropods of that age are forms like the late Triassic *Herrerasaurus* and *Coelophysis*, which are already committed to a highly derived pattern of postaxial reduction, the former clearly preserving vestigial digits (metacarpals) 4 and 5. In order for there to be a pentadactyl ground plan one would have to invoke a basal archosaur that had an undifferentiated hand, a form such as the Triassic *Lagosuchus*, considered by many to be close to the ancestry of dinosaurs (Feduccia, 1999a), and

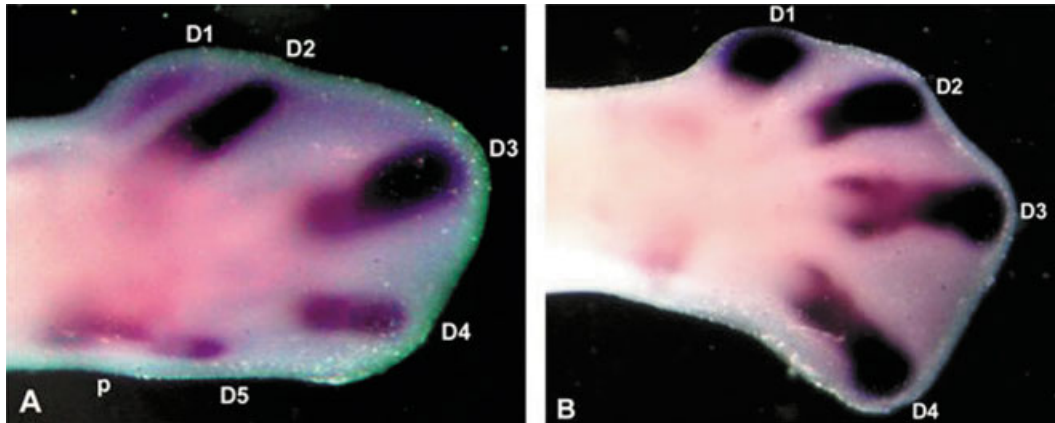


Fig. 25. Chick wing (A) and leg (B) buds at Stage 30 showing expression domains for *Sox9*, a precondensation marker. Note small *Sox9*-positive D1 in the wing, showing that the prechondrogenic pattern is pentadactyl. Prechondrogenic digital rays are labeled D1–D5 (p = pisiform). In the leg bud, although absent here, D5 is present at earlier Stages 26 and 27. The precondensation process is normally followed by chondrogenesis (e.g., in D2–5 and also D1 in the leg bud) and is therefore the first stage at the cell level of the skeletogenic patterning process. Other details of *Sox9* patterns and of technique are in Welten et al. (2005). (Courtesy of the authors and Blackwell Science Publishers.)

whether or not it is considered a “dinosaur” is anyone’s opinion. In any case, the Triassic is an entire geologic period before the appearance of anything that could be called a dromaeosaur.

The “Feathered Dinosaur” Is a Secondarily Flightless Bird

That phylogenetics has become an assumption-laden field is best illustrated by the insistence that the avian wing of *Caudipteryx*, with its intricate detailed flight anatomy and avian arrangement of primary and secondary feathers on the hand and arm (Fig. 26), evolved in a context other than flight (Sereno, 1999; Norell and Xu, 2004). It is argued that because *Caudipteryx* was an earthbound oviraptorosaur dinosaur, and its primaries and secondaries had no flight function, “vaned feathers and their arrangement as primaries, secondaries and rectrices therefore must have originally evolved for other functions (such as thermoregulation, brooding, or display)” (Sereno, 1999, p. 2143; Norell and Xu, 2004), and the same argument is made for a “down-like body covering, and even the enlargement of the forebrain.” According to recent paleontological theory, everything related to the lineage of avian origins must be developing flight from the ground up and all aerodynamic adaptations, regardless of their aerodynamic precision, must have evolved in a context other than flight, as preadaptations. “Non-avian theropods such as *Velociraptor*, *Compsognathus*, and *Tyrannosaurus* were clearly terrestrial cursors. Thus, the ancestral mode of life of birds was that of a cursorial biped. Inferences about the habits of *Archaeopteryx* should be made within this framework and not the inverse” (Chiappe, 1997, p. 110). This line of reasoning completely ignores the obvi-

ous bird-like features of *Caudipteryx*, the fact that oviraptorosaurs are likely secondarily flightless birds (with *Caudipteryx* as a basal member), and the fact that it is not parsimonious to assume that the intricate aerodynamically designed detail of the positioning of the remiges of the avian wing evolved in a nonflighted theropod (Fig. 26). *Caudipteryx* has a manual digital formula of 2,3,2, as in advanced birds, an avian hand, an avian-like skull with a ventral foramen magnum and avian-like teeth, and a partially reversed hallux, compelling Zhou et al. (2000, p. 243) to note that “the ancestor of *Caudipteryx* had probably possessed the arboreal capability.”

The most parsimonious explanation is that the Oviraptorosauria and *Caudipteryx* are secondarily flightless birds (Jones et al., 2000; Maryańska et al., 2002; Lu et al., 2002). Despite the fact that the cladistic analysis of Maryańska et al. (2002) utilized 195 coded characters and is “unassailable from the standpoint of strict cladistic orthodoxy” (Olson, 2002, p. 1204), Dyke and Norell (2005), noted for strict adherence to cladistic methodology, cannot accept that *Caudipteryx* could be a flightless bird. Yet the wing anatomy of *Caudipteryx* cannot be logically explained other than having evolved its flight adaptations in an aerodynamic context, still retaining the anterior center of mass and hindlimb proportions resembling those of cursorial birds (Jones et al., 2000). Flight adaptations thought to have evolved in earthbound theropods are the result of an assumption-laden hypothesis that dictates that unparsimonious scenarios be “shoe-horned” into the phylogeny, no matter how difficult. Thus, *Science News* (1998, 153, p. 404) noted that feathers “must have originally served some purpose unrelated to flight.”

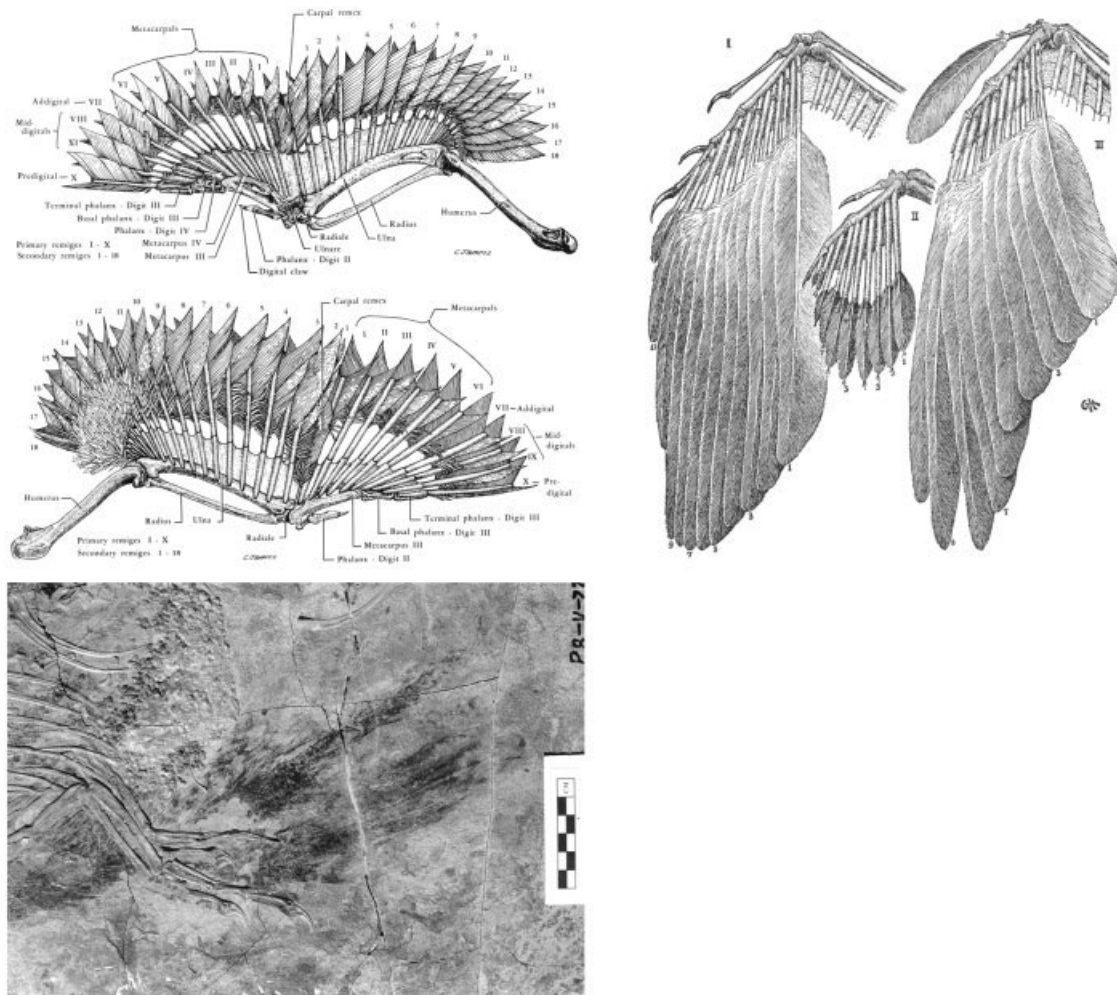


Fig. 26. Drawings (ventral view, upper; dorsal view, lower) showing the precise attachment of primary and secondary feathers in the avian wing (*Gallus*). Right (left to right), dorsal views of the wings of *Archaeopteryx*, baby hoatzin (*Opisthocomus*), and adult hoatzin. Note that the arrangement in *Gallus* is virtually the same as in *Archaeopteryx* and the hoatzin. Lower, the wing of the Lower Cretaceous flightless bird *Caudipteryx*, showing feather attachment as in a typical flighted bird. (Upper left, from Lucas and Stettenheim, 1972; upper right, from Heilmann, 1926; lower photo courtesy Zhonghe Zhou.)

Interestingly, the discovery of *Caudipteryx* (cover article in *Nature*, Ji et al., 1998) was the first announcement of a “feathered dinosaur” despite its myriad bird-like features, which were completely ignored. The article was followed quickly by *Nature* paleontology editor Henry Gee (1998) proclaiming that “the debate is over”! Paleontologists are still trying to return *Caudipteryx* to theropod status (Dyke and Norell, 2005), but Maryańska et al.’s (2002) exhaustive cladistic analysis remains undisputed and cannot be breached; *Caudipteryx* is a flightless bird. One thing is axiomatic: all living and extinct birds, including flightless forms, evolved from flying ancestors.

Flightlessness in birds is a pervasive phenomenon, occurring in terrestrial birds as diverse as geese and passerines, and on continents, archipelagos, and oceanic islands. Flightlessness is also a common phenomenon in aquatic forms, having ap-

peared in orders ranging from penguins, pelicans, and ducks, to ancient hesperornithiforms. Flight is a taxing and energetically expensive ability to maintain, both developmentally and metabolically, so there must be continual selective pressure to maintain it, or flight will disappear in favor of the flightless condition. The fact that some 35 families of living birds have produced flightless species is a testament to the penchant of birds to become flightless. Because flightlessness can be achieved very quickly by the process of neoteny or arrested development (Feduccia, 1999a), flightless birds can attain large size and bizarre morphologies very quickly, and are often almost unrecognizable as to their order of origin. Thus, it is not surprising that there is still debate as to what order the giant Eocene bird *Diatryma* belonged. More recently described flightless goose-like ducks (moa-nalos) from Hawaii would have clearly been unrecognizable as to order if the

skulls had not been recovered, and the enormous, extinct Australian mirhings, the dromornithids, were long thought to be ratites until their recently discovered skulls showed that they were of anseriform derivation. Given this background, it would be extraordinarily surprising if flightlessness were not almost as old as flight itself, and the appearance of flightlessness by the Early Cretaceous is certainly not surprising. It would be surprising if it had not occurred.

In a series of articles, Lowe (last article, 1944), proposed that ratites and small coelurosaurian dinosaurs shared a common ancestor, and that the ancestors of ratites never acquired flight; the *Nature* description (Ji et al., 1998) of *Caudipteryx* as a feathered dinosaur appears as déjà vu, given Lowe's (1944) assertions. The preponderance of evidence points to *Caudipteryx* being a flightless bird (Feduccia, 1999a), but one can only ponder how the postcranial remains of any ratite would be identified if recovered from the Early Cretaceous of China. Furthermore, given the view that "the smallest dinosaur is the bee hummingbird ... found only in Cuba" (Norell et al., 1995, p. 25), it follows logically that any bird, flighted or flightless, discovered in Mesozoic deposits would be classified as a dinosaur.

***Confuciusornis* Provides Another Example**

Another example of the constrained thinking produced by cladistic analyses is illustrated by reconstructions of the abundant Early Cretaceous bird *Confuciusornis* as a terrestrial bird. Although primitive in a number of anatomical features related to the flight apparatus, this bird nevertheless possessed long, pointed wings, remiges with asymmetrical vanes, and an alignment of primary and secondary feathers virtually identical to those of modern birds. In addition, it had a modern avian foot (coraciiform-like), with highly recurved, arboreally adapted claws, and two elongate rectrices, which can only be adaptations for a highly refined flying bird. Yet *Confuciusornis* is consistently reconstructed by paleontologists as an earthbound predator, using its hands in raptorial fashion (Padian and Chiappe, 1998; Chiappe et al., 1999). It is as though these paleontologists can only envision these early birds as terrestrial, somehow adding strength to the now nearly abandoned theory of a cursorial origin of flight in both birds and pterosaurs. Chiappe et al. (1999) argue not only that *Confuciusornis* was terrestrial, but that it was not arboreal, when even the most casual analysis suggests that it was a competent flier and tree-dweller. Their reconstruction (Padian and Chiappe, 1998), which appeared on the cover of *Scientific American*, depicts the arboreal, volant *Confuciusornis* as a cursorial predator, in theropod fashion, with a vertical, "theropod" pubic boot (*Confuciusornis* has a typical avian retroverted pubis). And there is further misinterpretation: the

hand is anatomically incorrect, showing the fingers free to kill and capture prey—yet its avian wing is tightly bound up by primary feather attachments and would have been useless for such a predatory function. The remiges of this bird are attached, as are those of the earlier *Archaeopteryx* and modern birds (Fig. 26). It was not a creature with a theropodan lifestyle. The problem in reasoning is clear: Chiappe (1997) argued that non-avian theropods were terrestrial cursors, and therefore the ancestral mode of life for birds was that of an earthbound predator, and Padian and Chiappe (1998) further argued that the cursorial hypothesis for flight origins was strengthened by the fact that the immediate theropod ancestors of birds were terrestrial. Similarly, Padian (1983, and subsequent decades) argued equivalently that pterosaurs were the sister-group of dinosaurs and were therefore bipedal cursors that evolved flight from the ground up. As noted earlier, this hypothesis can now be discarded.

Dinosaurs and Early Birds Were Not Hot-Blooded

The basic themes of the new theropodan dogma are that birds are living dinosaurs, that flight originated from the ground up, and that feathers arose as a downy insulative covering to insulate small endothermic dinosaurs. Yet there has never been, nor is there now, any clear evidence that dinosaurs were endothermic (Feduccia, 1973, 1999a). Based on the biology and physiology of extant birds and mammals, there are simply no reliable data consistent with dinosaurs or even early birds having attained the metabolic status of living endotherms. To the contrary, the absence of respiratory structures causally linked to enhanced lung function in extant birds and mammals (e.g., respiratory turbinates, specialized rib cage anatomy) suggests that metabolic rates in dinosaurs and early birds may have differed little from those in many extant reptiles (Ruben et al., 2003).

Notwithstanding the dearth of relevant data, many authors have tried to make specimens conform to the hot-blooded theropod dogma. A recent example is the interpretation of a late-developed Early Cretaceous enantiornithine bird within an egg as being precocial, thus allegedly providing evidence that precociality is primitive for birds and like that of their putative dinosaurian ancestors (Zhou and Zhang, 2004). Yet another juvenile enantiornithine from the same deposit (*Liaoxiornis*) appears to have been altricial. Zhou (2004, p. 456) correctly states earlier that "all known enantiornithines appear to be perching forms," which would seem to all but preclude a precocial state for their young. Yet Zhou and Zhang (2004, p. 653) conclude that "the precociality of birds might represent a feature derived from their dinosaurian ancestor." Given the morphological and hence ecological diversity of Cretaceous

enantiornithines, it may well be that they had an altricial–precocial spectrum of chick types, as in modern birds.

At the opposite end of the spectrum, the dinosaurologists have attempted to show that many ornithischian dinosaurs had altricial young to bolster the argument that dinosaurs were intelligent, possessed advanced parental care, and they inappropriately attempt to associate brooding with endothermy (Horner and Weishampel, 1988). This view, however, has been challenged by Geist and Jones (1996), who found that the state of fossilization of long bone epiphyses cannot be considered indicative of the mode of development. They concluded that all known dinosaur young are precocial. It should be noted that there is no theropod brooding behavior not also known in crocodylians or other reptiles, and there are over 100 species of reptiles and amphibians that practice some form of nest brooding.

In reality, the altricial–precocial spectrum is extraordinarily complex, and although parent crocodylians care for their young in a variety of ways, the hatchlings are clearly precocial. As Starck and Ricklefs (1998) appropriately note, it is impossible to determine whether precocial development is ancestral or secondarily and independently derived, and certainly the degree of ossification is a poor predictor of developmental mode. And (p. 13), “Regardless of whether precocity or altriciality was the ancestral state, the other would have evolved independently in at least two lineages.”

Confusing Issues of Definition

The debate on bird origins has centered not only on the reptilian ancestors of birds, but the origin of flight. At least in the latter case, given the discovery of four-winged microraptor dromaeosaurs, no one can continue to take the ground-up scenario seriously, regardless of the nature of the true ancestors of birds. However, answers to the question of the immediate ancestor of birds remains elusive, as does the overall early radiation of the Dinosauromorpha. As noted earlier, the question of whether birds are derived from dinosaurs depends on what one defines as dinosaur, or the Dinosauromorpha (Feduccia, 1999a, p. 91). We know little about the origin of dinosaurs, and we know little about the interrelationships. To illustrate the difficulty of defining the various dinosaur groups, Carroll (1988, p. 290) pointed out that “The ‘carnosaur’ families may each have evolved separately from different groups that have been classified as coelurosaurs.”

Thus, Gauthier (1986, p.15) defines Saurischia as comprising “all dinosaurs that are closer to birds than to Ornithischia,” and Currie (in Currie and Padian, 1997, p. 731) defines Theropoda as including “birds and all other theropods more closely related to birds than to Sauropodomorpha.” And Holtz et al. (2004, p. 104) define Coelurosauria as: “*Passer do-*

mesticus and all taxa sharing a more recent common ancestor with it than with *Allosaurus*.” Such meaningless phylogenetic definitions make any reasonable discussion of this complicated nexus next to impossible, and discussion is further complicated by the tendency to gloss over major problems of phylogenetics in the field. For example, in the new, 861-page 2nd edition of *The Dinosauria* (Weishampel et al., 2004), the chapter on dinosaur origins (Benton, 2004, p. 16) devotes only two paragraphs to the monophyly of Dinosauria! (Larsson, 2005). While many of us are in search of meaningful morphological characters to delineate lineages, De Queiroz and Gauthier (1990, p. 310) note that “The use of phylogenetic definitions liberates biological taxonomy from a 2,000-year-old tradition of basing the definitions of taxon names on characters.” These definitions may be liberating to some, but their implementation is difficult, and they are devoid of information or utility, and are exceptionally misleading.

New Arboreal “Feathered Dinosaurs” May Hold the Key

The discovery of the so-called four-winged microraptor theropods that occur some 25 million years after *Archaeopteryx*, such as *Microraptor zhaoianus* and *M. gui* with pennaceous feathers, has broken the field of avian origins wide open (Xu et al., 2003; Zhou, 2004). First, the projection of feathers from the hindlimbs along with small curved claws could only be interpreted as arboreal adaptations, and precludes their having been capable cursors, particularly since the hindlimb remiges came off the tarsometatarsus, and the femora are unusually long and must have extended somewhat laterally (Martin, 2004). Zhou (2004) envisioned a “dinosaurian-trees-down” hypothesis to account for flight origins in birds. Too, the more recent discovery of early enantiornithine birds with pennaceous leg feathers, and the revelation that *Archaeopteryx* probably had hindlimb feathers (Longrich, 2003; Christiansen and Bonde, 2004; also in an enantiornithine, Zhang and Zhou, 2004), has led to the inescapable conclusion that it is probable that hindlimb wings were primitive within Aves, and that Beebe’s (1915) famous missing “tetrapteryx stage” in the evolution of avian flight has been validated.

The solution of a flight origin scenario, however, in no way resolves the problem of avian ancestry. The problem also seems further complicated by the fact that a number of bird-like theropods occur some 80 million years after the appearance of *Archaeopteryx*. Feduccia (1999a) used the term “temporal paradox” to allude to the fact that the most truly bird-like dinosaurs (excluding microraptors, which were discovered later) occur some 60–80 million years after the earliest known bird, *Archaeopteryx*, which could be interpreted as an indication of convergent evolution. If birds are derived from theropods, then one

would expect to see bird-like dinosaurs abundant in the fossil record prior to the Late Jurassic *Archaeopteryx*: no such specimens have been described. When one examines today's generally accepted cladograms, they show a striking trend toward a reversal of the evolutionary sequences indicated by stratigraphy. Vertebrate history, as interpreted in all other major groups except birds, follows the stratigraphic sequence almost without exception. As Romer (1970, p. 30) noted years ago, "In discussing fossils, some notion of the geologic time scale is necessary."

Sinosauropteryx (a compsognathid allegedly possessing down-like protofeathers, or dino-fuzz) is normally near the base of the cladogram, followed by the flightless *Caudipteryx* (with a precise avian arrangement of wing feathers), followed by such Early Cretaceous Chinese forms as *Beipiaosaurus* and *Protarchaeopteryx*, and finally at the end is the advanced early avian *Archaeopteryx* (Upper Jurassic bird in the modern sense). The cladistic inference is that flight evolved from the ground up, down-like feathers or "dino-fuzz" are protofeathers and evolved to insulate endothermic dinosaurs, and none of these early feathered forms went through an arboreal stage of flight. In addition, the volant arboreal *Archaeopteryx* is nowadays always reconstructed as a terrestrial predator (Serenó, 1999), to accommodate the dogma of a theropod, ground-up origin of birds and avian flight.

The preponderance of evidence, however, indicates that all living and extinct birds evolved from flying forms, the compsognathid *Sinosauropteryx* has nothing to do with avian origins, the filamentous structures of this compsognathid are not protofeathers, *Caudipteryx* and more advanced oviraptorids are secondarily flightless birds, and *Archaeopteryx* is still the basal bird, although with a fairly advanced flight architecture, including an avian brain (Alonso et al., 2004). In other words, as noted, the typical cladistic analysis for birds is generally and almost precisely reversed. Many students of dinosaur evolution have been trapped into the same dogma as Percy Lowe (1935), who proposed that the ratites had evolved directly from earthbound theropods that never went through a flight stage, but many workers, including notably Gavin de Beer (1954) of the British Museum of Natural History, demolished the Lowe hypothesis by showing that most ratite characters, including notably the cerebellum, fused carpometacarpus, and flight quills of cassowaries could only have evolved from flighted ancestors. Now, over seven decades later we have witnessed the resurrection of Lowe's ideas among paleontologists, but, like Lowe's, their arguments are certainly incorrect.

The bird-like nature of many maniraptoran theropods has not gone unnoticed over the years. Recently, studies by Paul (2002), Czerkas et al. (2002), and Czerkas and Yuan (2002) have attempted to cut

through the time-honored dogma and provide a possible starting point to a solution to the seemingly intractable problem of bird origins. They provide evidence that many of these early maniraptoran theropods are actually derived from the avian lineage and are therefore birds. This view was first proposed by Abel (1911), and developed by George Olshevsky (Paul, 2002), and since the 1980s the theory has been developed by Gregory Paul. Most recently in a book entitled *Dinosaurs of the Air*, in he argues that some theropods, including dromaeosaurids, troodontids, and oviraptorosaurids, are secondarily flightless birds. In addition, Stephen Czerkas (2002) has promoted an avian origin from basal dinosauromorphs rather than theropods by his museum exhibits, and also in a book edited by Sylvia Czerkas entitled *Feathered Dinosaurs and the Origin of Flight* (Czerkas, 2002).

Czerkas et al. (2002) describe *Cryptovolans* (= *Microraptor*) as an ancestral dromaeosaur of pre-theropod, or non-theropod status. It has the typical dromaeosaur features of a stiffened "ramphorhynchoid" tail, an enlarged second toe, and a retroverted pubis. However, given the probability that all microraptors had hindlimb wings attached to a short metatarsus, with long recurved pedal claws, they were probably precluded from being efficient ground-dwellers and would have been incapable of using the enlarged claw as a sickle claw for predation. It may, in fact, have been some type of climbing adaptation. Microraptors, unlike true theropods, also lacked a supra-acetabular shelf (Martin, 2004) for efficient bipedal locomotion, and had many avian features (Czerkas et al., 2002; Paul, 2002; Martin, 2004) (Figs. 27, 28), such as an avian hand and distal pubic spoon (hypopubic cup), as opposed to the dinosaurian pubic boot, to mention only a few. Most impressively, the hand bones of the wing are virtually identical to those of *Archaeopteryx*, if not more advanced (Fig. 27). Czerkas et al. (2002, p. 118) correctly note that "both camps have portrayed dromaeosaurs incorrectly as dinosaurs ... to support their ... opposing views." For example, Norell (2001), commenting on a small dromaeosaur with feather impressions, noted that non-avian theropods, such as this dromaeosaur, led toward the origins of true birds from the ground up. "Cladistics has presented a highly misleading interpretation of the evidence by arbitrarily insisting that the ancestral origins of avian flight must have been from an exclusively ground dwelling theropod dinosaur" (p. 120). Czerkas et al. (2002) further note, following Paul (2002), that it is probable that larger dromaeosaurs, such as *Deinonychus* and *Velociraptor*, were secondarily flightless. Czerkas et al. (2002, p. 122) conclude that "The origin of birds stems further back to a common ancestor of pre-theropod status that was arboreal. The proto-maniraptoran, *Scansoriopteryx* [= *Epidendosaurus*] and *Cryptovolans* [= *Microraptor*] are the only known members of such arboreal pre-



Fig. 27. Hands of microraptors, *Deinonychus*, and birds, with a focus on the development of a posterolateral flange on the proximal bone of the central finger (indicated by arrows). Top row, flightless examples; bottom row, flying examples. In both rows hands become increasingly avian progressing to the right. Note that the combination of a well-developed posterolateral flange and a strongly bowed outer metacarpal make the hand of the flightless microraptor *Sinornithosaurus* better suited for supporting primary flight feathers than was the hand of *Archaeopteryx*. (Paul, Gregory S. *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*. pp. 407, Fig. 19. © 2002 [Johns Hopkins Univ. Press]. Reprinted with permission of the Johns Hopkins University Press.)

theropods.” Interestingly, in a recent review, Zhou (2004, p. 462), writing on the possibility that “feathered dinosaurs” may be flightless birds, notes that, “These ideas have the advantage of explaining why some advanced avian features ... appeared in some feathered theropods but not in the most basal birds.”

Possible Solution to the Morphological Mismatches

In a sense, the controversy over the ancestors of birds has been grossly overstated. All the various

protagonists believe that birds are nested within the Archosauria, and the two views contrast an earlier origin of birds with a common basal archosaur ancestor of theropods, versus the more popular “dinosaurian” origin of birds, later in time, directly from highly derived theropods. As this interesting saga continues, at least for the time being it is obvious that most workers on both sides of the debate were at least in part wrong, but in many cases for the right reasons.

We believe it is time to focus on teasing out the avian lineage from that of “true” theropods. It should give one pause to realize that if a modern kiwi were discovered in the lacustrine deposits of the Early Cretaceous of China, it would most assuredly be considered a theropod dinosaur, illustrating an early stage in the evolution of flight from the ground up, and adorned with protofeathers and all stages of feather evolution. Yet most current evidence could be interpreted to indicate that the Chinese dromaeosaurs are an early remnant of the avian radiation, with species at practically all stages of flight and flightlessness, showing that the flightless state in birds is almost as old as birds themselves. Given the tendency of modern birds to become flightless, particularly on islands (one-fourth of living rails, many now extinct, are flightless or nearly so), the early evolution of flightlessness in birds is not surprising. Also not surprising is that early avians would closely resemble true theropods, just as modern ratites do, albeit superficially. Yet although birds, particularly the early forms, resemble theropods, their early evolution was from the trees down, and a “flight” morphology still resides deep within their morphology, even though many are flightless.

Little evidence exists for the existence of protofeathers, and therefore the best evidence for feather origins still resides with the study of living birds. It is also clear that the Chinese “dromaeosaurs” are derived, and not ancestral to, subsequent birds. If we use the stratigraphic sequence of the relevant fossils as a guidepost, we can begin to understand the evolutionary sequence in the early radiation of the class Aves. The questions are: 1) Where do microraptors fit in the evolution of birds? and 2) Are the later dromaeosaurs, such as *Deinonychus*, *Dromaeosaurus*, and *Velociraptor*, as well as *Troodon*, really secondarily flightless birds? Although they are quite different from earlier forms, they are no more distinctive than, say, a clapper rail and *Diatryma*. Certainly the inability of cladistic methodology to deal with convergence has been illuminated in this debate. It may well be that John Ostrom, as well as more recent workers on the Early Cretaceous Chinese fossils, have been looking at highly derived flightless forms (Fig. 29) rather than basal avian ancestors, as they have interpreted the fossils. By viewing these so-called maniraptorans as “derived” one is relieved of the burden of inventing



Fig. 28. *Microraptor gui*, a small Early Cretaceous microraptor from lacustrine deposits in China. Although described as an arboreal, four-winged “feathered dinosaur,” microraptors have a fairly typical suite of avian skeletal features, with a forward center of gravity. They are a remnant of an early avian radiation. (Photo courtesy of Zhonghe Zhou.)

unparsimonious models for everything from a ground-up flight origin to preadaptive scenarios for the evolution of the avian wing, and feathers evolving to insulate hot-blooded dinosaurs.

In 2002, a house sparrow-size, arboreal bird-like archosaur *Epidendrosaurus* (Zhang et al., 2002; =*Scansoriopteryx* Czerkas and Yuan, 2002), was de-

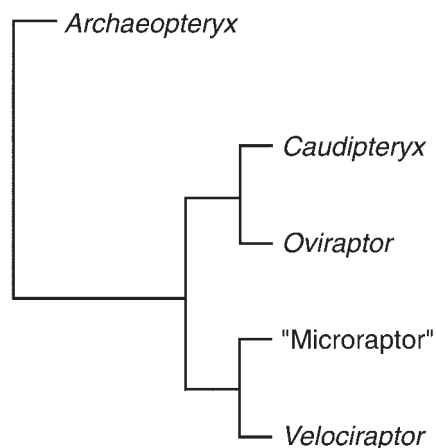


Fig. 29. Cladogram modified after Martin (2004) showing the relative position of *Archaeopteryx*, the primal urvogel, relative to oviraptorosaurs, and microraptors and dromaeosaurs. This view differs dramatically from that of most current cladistic paleontological dogma, in which the terrestrial oviraptorosaur *Caudipteryx* and terrestrial dromaeosaurs are basal to birds, and not derived as secondarily flightless forms as indicated here and supported by the preponderance of evidence, both morphological and temporal.

scribed from the Late Jurassic of China. It was described as an arboreal coelurosaur, but there are no definitive synapomorphies that link this creature to any specific group of theropods (and there is no satisfactory definition of coelurosaur), and Czerkas and Yuan (2002) considered it to be a pre-theropod, or basal archosaur. Like the term “thecodont,” a collective term to describe Triassic basal archosaurs, coelurosaur and carnosaur describe, respectively, small and large theropod dinosaurs. As Paul (2002, p. 179) correctly notes, “*Euparkeria* [Trias. S. Africa] is a suitable ancestral type for birds ... and ... *Euparkeria* is a good ancestral type for all archosaurs.”

Czerkas and Yuan (2002) argued that *Scansoriopteryx* showed that avian status was derived prior to the advent of theropods, and it certainly lacks characteristic theropod synapomorphies, even including the absence of a pre-acetabular shelf, but it has a reversed hallux. They note (pp. 91–92) that while it “represents an arboreal precursor of *Archaeopteryx*, in essence it also represents a ‘proto-maniraptoran’ ... and it represents ‘an arboreal lineage of theropods,’ or a ‘pre-theropod’ lineage of saurischian archosaurs [which the authors favor] which could climb.” Even Zhang et al. (2002, p. 396), who described it provisionally as an arboreal coelurosaur, note, “that *Epidendrosaurus* is very close to the transition to birds.” Likewise, Czerkas described *Cryptovolans* (= *Microraptor*) in an independent article (Czerkas et al., 2002), but at about the same time. He concluded, however, that the beast was a bird, not a theropod dinosaur, and that *Cryptovolans*

(p. 112) “is an ancestral dromaeosaur of pre-theropod, or non-theropod status.” Microraptors lack many of the typical theropod synapomorphies, including the pre-acetabular shelf characteristic of obligate bipeds, and have numerous avian features, including the diagnostic pubic spoon, partially reversed hallux, etc. As Zhou (2004, p. 462) notes, “If we simply compare the hands of *Archaeopteryx* and some maniraptoran theropods, such as *Microraptor*, they are almost the same in every detail, including the phalangeal formula (Fig. 27). If we accept the ‘II-III-IV’ for modern birds, and assume the same for *Archaeopteryx*, then why not accept the same conclusion for *Microraptor*?” Microraptors are, thus, **avian non-theropods**.

CONCLUSION

It should give one pause that while paleontologists employing cladistic methodology use a list of a hundred or more characters that link birds and theropods, most are simple binary designations, one step removed from the organisms. The vast majority are plesiomorphic, not qualifying as Hennigian synapomorphies, and in this view there is no accounting for acceptance of large groupings of the characters that are co-correlated. Thus, 15 or more characters may simply represent one character complex, diluting their phylogenetic resolving power. These facts have rendered modern cladistic methodology a form of “Sokalian” phenetics, which can be termed “cladophenetics.” Homology is usually ascertained in an a posteriori fashion to conform to the established cladogram, and embryonic connectivity and position are largely ignored. It should also be a matter of concern that bipedal reptiles first appeared in pre-archosaurian lineages as the Permian *Eudibamus* (Berman et al., 2000). Of further concern should be the fact that among basal archosaurs, most ornithomorphs (without the ankle) would easily reach the ceratosaur level in any cladogram. The inability of cladistic methodology to deal with convergence has been pointed out time and again (Carroll and Dong, 1991; Feduccia, 1999a). This methodology always groups as clades convergent avian pairs such as loons and grebes, which form the bones of their swimming feet by disparate means embryologically, and most recently the pelecaniform wing-propelled divers, the plotopterids, form a cladistic clade with penguins (Mayr, 2005), another convergent pair. Dodson (2000, p. 504) correctly notes that:

Cladistics systematically excludes data from stratigraphy, embryology, ecology, and biogeography that could otherwise be employed to bring maximum evolutionary coherence to biological data. Darwin would have convinced no one if he had been so restrictive in his theory of evolution.

What was once “Hennigian cladistics” has now turned into a distinctive methodology, nicely sum-

marized by Fisher and Owens (2004, p. 39): “The phylogenetic approach is a statistical method for analyzing correlations between traits across species.” And, like the earlier statistical approaches of the 1970s, this approach frequently groups ecological morphologies instead of clades: the methodology is incapable of discerning massive convergence.

If the proposals from the detailed anatomical analyses of Paul (2002) and Czerkas (2002), that dromaeosaurs are actually birds, at all stages of flight and flightlessness, turn out to be correct, then the question of bird origins is completely reopened. Also, if true, then both camps in the debate have portrayed dromaeosaurs incorrectly, and as Czerkas et al. (2002, p. 120) note, “Cladistics has presented a highly misleading interpretation of the evidence” and (p. 122), “the origin of birds stems further back to a common ancestor of pre-theropod status.”

The microraptors of China are birds, regardless of their ancestry. However, one must address the question of their relationship to Middle and Late Cretaceous deinonychosaurs. Is it possible that these forms, such as *Deinonychus*, *Dromaeosaurs*, *Velociraptor*, as well as the troodontids, are actually secondarily flightless birds masquerading as small theropods? These and other important questions will only be answered by keeping an open mind, and by not being bound to past concepts of relationships. Nevertheless, it has become clear that the flightless *Caudipteryx*, as well as the microraptors and possibly later dromaeosaurs, are not basal, as commonly portrayed by current paleontological theory, but rather derived from the basal avian radiation (Fig. 29); thus, cladistic methodology consistently reverses the true evolutionary sequence of dromaeosaurs and birds. Microraptors represent a remnant of an early avian radiation, exemplifying all stages of flight and flightlessness, and *Caudipteryx* and oviraptorosaurs are secondarily flightless birds, and in that sense derived, not basal. As Martin (2004, p. 989) notes of the paleontological cladists (see Hwang et al., 2002), “The cladograms were correct in embedding some putative dinosaurs within birds, but were incorrect in their relationship to the dinosaur radiation as a whole.... The common ancestor of such a grouping must have looked like a bird and lacked most salient dinosaurian features.”

In closing, we offer an interim attempt to define the most salient features of Aves morphologically. *Birds are mesotarsal bipedal archosaurs with pennaceous feathers, and a tridactyl avian hand composed of digits 2-3-4.* Other important features include: a proximal phalanx of middle digit forming a long, slender, distally tapering rod with a slightly expanded distal tip, primary feathers anchored to the terminal and basal phalanx of digit III and metacarpal III, secondary feathers anchored to the dorsal aspect of the ulna, reduced carpals, including a semilunate bone (or carpal trochlea equivalent in modern birds), a foot with a reversed digit I (hallux),

a pretibial bone analogous to the ascending process of the astragalus of true theropods, and a retroverted pubis with a pubic spoon (accommodating the suprapubic muscles).

It will only be through considering the totality of evidence from various branches of science that we can ever hope to solve the mystery of bird origins and the origin of avian flight. The frequently used phrase “birds are living dinosaurs” does little more than dampen research, because if it were true, then any fossil specimen with feathers in the Mesozoic would automatically be both a bird and a dinosaur. With the recent spectacular discovery of bird-like fossil footprints with a clearly preserved hallux from the Late Triassic (Melchor et al., 2002), Zhonghe Zhou (2004, p. 463) correctly notes, “it is probably too early to declare that ‘it is time to abandon debate on the theropod origin of birds’ (Prum, 2002). Abandoning debate may succeed in concealing problems rather than finding solutions to important scientific questions.” The problem of avian origins is far from being resolved.

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We dedicate this study to the memory of an outstanding paleontologist and inspiring teacher, Prof. Beverly Lambert Halstead, whose belief that attempts to resolve problems in the evolution of life on earth “require cold, clear logic, and buckets of it” is as true today as ever. We also dedicate this paper to the memory of Max Hecht, paleontologist and evo-

lutionary biologist, energizer of many a conference and debate, with his consuming interest in developing an integrated view of evolution, fact, and theory.

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