In retrospect

25th anniversary of first feathered-dinosaur finds

Kevin Padian

Our understanding of the origin of birds took a major step forward in 1998, thanks to the reported discovery of a remarkable fossil that unveiled the existence of feathered dinosaurs. Fossil publications that year caused a sensation.

It was the annual meeting of the Society of Vertebrate Paleontology in 1996, held at the American Museum of Natural History in New York City. I was talking to John Ostrom, my former PhD thesis adviser from Yale University in New Haven, Connecticut. John's work had shown that birds evolved from small carnivorous dinosaurs called theropods[1]. I don't remember what we were talking about, but it didn't matter. The world shifted when we were approached by our colleague Pei-ji Chen from the Nanjing Institute of Geology and Palaeontology in China.

Chen graciously offered us a sheaf of colour photos the size of index cards, explaining that they were images of fossils recently found in China's Liaoning province (approximately 500 kilometres from Beijing). As John leafed through the photos, his eyes widened and his jaw began to drop. "I need to sit down," he said. "This is unbelievable."

It turned out that disbelief was not an option. Chen had handed us the first photos of a fossil of a small, carnivorous dinosaur, flattened, with all the bones exposed and a dark eyespot (Fig. 1). But what caught the viewer's eye was the outline of the specimen, which was rimmed with hair-like structures that were undeniably feather-like. They were unbranched, lacked vanes (feather components attached to a central shaft) and were unsuitable for flight. In short, this was a rudimentary form of feather, similar to those of flightless birds such as the kiwi. No one had ever seen anything like these in dinosaurs before, and few had even dreamt of them.

When John had caught his breath, I reminded him that this discovery confirmed his hypothesis that some sort of proto-feathers had evolved in the theropod ancestors of birds. John had proposed[2] that feathers must have started as simple structures that would have immediately conferred the properties of insulation on their bearers, and that only later did feathers evolve the length and structural integrity needed to enable flight.

Chen and colleagues published[3] the first description of this amazing *Sinosauropteryx prima* specimen in *Nature* in early 1998. Months later, Ji Qiang at the National Geological Museum of China in Beijing and his colleagues described in *Nature* two more proto-feathered theropod species from the same geographical area[4]. Each of the three newly identified species had slightly different feather-like structures: some had simple stalks and some had branches, but none had feathers with the central shaft and vanes found in birds today.

Those discoveries would come later, as a variety of feather-like structures — some without representation in living birds — emerged from the Chinese fossil deposits[5]. Ornithologists Richard Prum and Alan Brush linked the evolution of complex feathers in these dinosaurs to the developmental process that produces the feathers of living birds[6]. They outlined an evolving sequence of different forms of feather, progressing from a hollow tube, to simple and then more-complicated branching structures, and finally to a central stalk and a flattened double vane of overlapping, interconnected tiny hooks called barbs. In a sense, the patterns of developmental processes in an individual feather mirrored the changes that occurred as the feathers themselves evolved (a situation sometimes described as ontogeny recapitulating phylogeny), with some inevitable dead ends. The evolution of feathers became almost fully understood.

What did these discoveries mean? First, for many people, they cemented the evolutionary link between dinosaurs and birds, because no other animals have feathers. But John Ostrom had already convinced most experts of this connection, thanks to his painstaking and detailed analysis of the unique skeletal similarities between the two groups[1]. Some people remained agnostic about the bird–dinosaur link until 1986, when Jacques Gauthier, a graduate student at the University of California, Berkeley, incorporated data from Ostrom and dozens of other sources into a true phylogenetic (cladistic) framework[7] — a method of

From the archive

Growing seeds by moonlight, and a star shower seen at sea.

100 years ago

During the summer of 1921 I investigated the effect of moonlight on the germination of seeds, and the results seemed to indicate a greatly increased velocity of germination. In order to determine whether this might be due to the effect of the moonlight on the [enzyme] diastase [which hydrolyses carbohydrates to produce sugar], a small quantity of mustard seed was crushed, and weighed quantities, after mixing with known amounts of water, were exposed to moonlight in Petrie dishes, controls set alongside being covered. Estimation with Fehling's solution of the sugar produced showed that there was an increased yield of about 15 per cent. caused by the moonlight. A possible explanation of these results is to be found in the fact that at certain periods moonlight is plane-polarised, and in order to test this suggestion the experiments with crushed mustard seed were repeated with daylight after polarisation, either by reflection or by a Nicol prism. Control experiments were also carried out both in darkness and in ordinary daylight ... A remarkable increase in the amount of hydrolysis was always noted when polarised light was used. Similar results were obtained with fresh oats, wheat, and cornflour, to which diastase had been added.

From *Nature* 13 January 1923

150 years ago

In case no other account should reach you of a meteoric shower witnessed by the officers and military passengers of H. M. troopship *Tamar* on the night of Wednesday, November 27, 1872, I send notes collected from several accounts. The vessel was at the time about 7° south and 4° west of the Bermudas ... Between 8 and 10 P.M. by one witness, between 10 and 12 P.M. by another ... there was a nearly uninterrupted succession of shooting stars — from all parts of the sky, says one, from about E.N.E. to W.S.W., says another ... Sunset would have been soon after 5; thus it was dark with no moon before the earliest hour named.

From *Nature* 9 January 1873

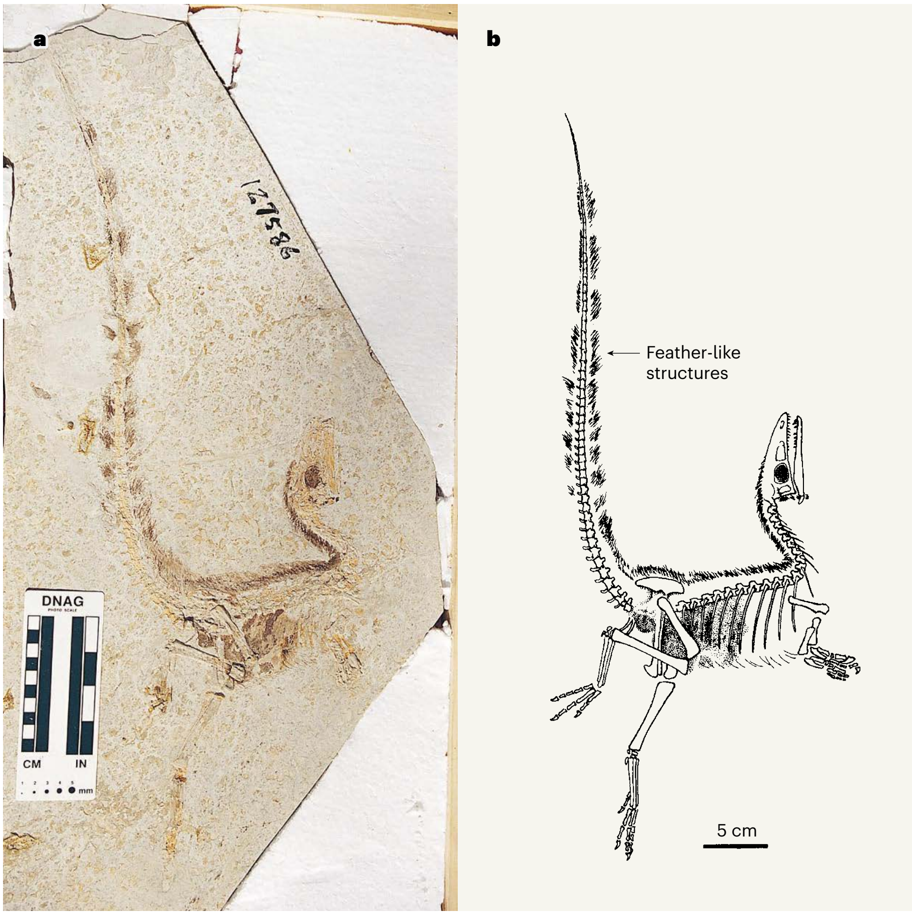

Figure 1 | *Sinosauropteryx prima*. In 1998, Chen *et al.*[3] presented this fossil (**a**) and reconstruction (**b**) of the first known non-avian dinosaur with a feather-like body covering. This covering is visible on its back and tail. Other evidence of dinosaurs with feather-like structures was also published that year[4].

P.J. CHEN *ET AL.*/*NATURE*

determining evolutionary relationships that was by that time widely accepted in vertebrate palaeontology. After that, there were few denialists.

Second, if these structures were indeed similar to bird feathers, then feathers could not have originated for flight. Flight was an example of what the palaeontologists Stephen Jay Gould and Elisabeth Vrba had termed an exaptation – a secondary function that evolved after the original one[8]. And this happened in only one feathered dinosaur lineage: birds. What was or were the original function or functions of these structures?

Although the proto-feathers were visible only around the periphery of the fossil that Chen and colleagues reported, they seemed to be thickly and continuously distributed, and would have provided the body with thermal insulation. The implication of this observation is that the animal's body temperature must have been relatively constant. This is because an insulating feature of this kind to aid temperature control would be of no advantage in an ectothermic animal such as a reptile, which can regulate its low body temperature to only a limited extent. Thus, the feathered dinosaur was probably able to regulate its body temperature, and is likely to have been an endothermic organism (one that produces most of its own body heat).

This line of reasoning is consistent with results from microscopic analyses of fossilized bone. Such studies can reveal the rate of bone deposition (high rates suggest sustained high metabolic rates, which are characteristic of endotherms) and the age of an individual when levels of bone deposition change or cease (termed skeletochronology)[9]. Birds seem to have inherited both high metabolic rates and high growth rates from their dinosaurian ancestors, but by the time the living groups of birds appeared, they had evolved the even-higher rates of growth and metabolism that are observed today[10]. The first birds took several years of development to reach skeletal maturity[11], but today's birds can do so within a year or less.

Given the various functions of display that feathers serve in living birds, it was natural to wonder whether these rudimentary feathers were coloured or patterned in some way. Zhang *et al.* provided some answers in a key 2010 paper[12] reporting the discovery of melanosomes (colour-bearing organelles) in the feathers of both early birds and non-avian dinosaurs. The authors inferred that the different melanosome shapes represented different colours and patterns in the feathers[12]. It could not be determined whether these colours aided camouflage, species recognition or mate attraction, or had other social functions (different colours in males and females were not detected). Then in 2013, Manning *et al.*[13] used synchrotron-based imaging to identify trace chemical elements that revealed the colour patterns on the feathers of the first known bird, *Archaeopteryx*.

After a serendipitous fossil find, in 1999 Clark and colleagues reported[14] the discovery of a nest of eggs of an oviraptorid, a type of dinosaur that is related to the lineage that led to birds. Amazingly, the parent was preserved sitting on its nest in a crouched position, like a chicken. Its forelimbs were spread over the eggs, suggesting that, if its limbs had borne somewhat elongated feathers, they could have helped to shelter and insulate the eggs. This would have been yet another exaptation of the proto-feathers.

Many more discoveries of the timing and modification of features in the theropod lineage have shed light on the evolution of the body plan we recognize in living birds. It seems a long time ago, but it is really only 25 years since Chen and colleagues published those remarkable photos. The discovery that birds evolved from small theropod dinosaurs, and therefore belong to the Dinosauria, is one of the great scientific revelations of the late twentieth century.

Kevin Padian is in the Department of Integrative Biology and the Museum of Paleontology, University of California, Berkeley, California 94720, USA.
e-mail: kpadian@berkeley.edu

1. Ostrom, J. H. *Biol. J. Linn. Soc.* **8**, 91–182 (1976).
2. Ostrom, J. H. *Q. Rev. Biol.* **49**, 27–47 (1974).
3. Chen, P., Dong, Z. & Zhen, S. *Nature* **391**, 147–152 (1998).
4. Qiang, J., Currie, P. J., Norell, M. A. & Ji, S.-A. *Nature* **393**, 753–761 (1998).
5. Padian, K., Qiang, J. & Ji, S. in *Mesozoic Vertebrate Life* (eds Carpenter, K. & Tanke, D. H.) 117–135 (Indiana Univ. Press, 2001).
6. Prum, R. O. & Brush, A. H. *Q. Rev. Biol.* **77**, 261–295 (2002).
7. Gauthier, J. A. *Mem. Calif. Acad. Sci.* **8**, 1–55 (1986).
8. Gould, S. J. & Vrba, E. S. *Paleobiology* **8**, 4–15 (1982).
9. Padian, K. & Lamm, E.-T. (eds) *Bone Histology of Fossil Tetrapods* (Univ. California Press, 2013).
10. Padian, K. & Woodward, H. N. in *Vertebrate Skeletal Histology and Paleohistology* (eds de Buffrénil, V., de Ricqlès, A., Zylberberg, L. & Padian, K.) 511–549 (CRC Press, 2021).
11. de Ricqlès, A. J., Padian, K., Horner, J. R., Lamm, E.-T. & Myhrvold, N. *J. Vert. Paleontol.* **23**, 373–386 (2003).
12. Zhang, F. *et al. Nature* **463**, 1075–1078 (2010).
13. Manning, P. L. *et al. J. Anal. Atomic Spectrom.* **28**, 1024–1030 (2013).
14. Clark, J. M., Norell, M. A. & Chiappe, L. M. *Am. Mus. Novit.* no. 3265 (1999).

The author declares no competing interests.