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The life and times of the dinosaurs

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Bright Horizons 10

10th October, 2011

Dinosaurs – how do we know?

- Movies like *Jurassic Park*, and science documentaries like the BBC's *Walking with Dinosaurs* raise questions about what we know and what we do not know
- Many viewers are rightly sceptical – "surely they don't know that?" This requires palaeobiologists to focus their efforts and clarify levels of confidence in their claims
- This is part of a more profound issue – namely what is science and what is not? Some would exclude the historical sciences (e.g. geology, palaeobiology, archaeology) because it is impossible to perform repeat experiments
- But, Karl Popper and others have argued strongly that such a strict view would exclude also cosmology and much of evolutionary biology as nonscientific

Colours of dinosaur feathers

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LETTERS

Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds

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Spectacular fossils from the Early Cretaceous Jehol Group[1–3] of northeastern China have greatly expanded our knowledge of the diversity and palaeobiology of dinosaurs and early birds, and contributed to our understanding of the origin of birds, of flight, and of feathers. Pennaceous (vaned) feathers and integumentary filaments are preserved in birds[4–5] and non-avian theropod dinosaurs[6–10], but little is known of their microstructure. Here we report that melanosomes (colour-bearing organelles) are not only preserved in the pennaceous feathers of early birds, but also in an identical manner in integumentary filaments of non-avian dinosaurs, thus refuting recent claims[11–16] that the filaments are partially decayed dermal collagen fibres. Examples of both eumelanosomes and phaeomelanosomes have been identified, and they are often preserved in life position within the structure of partially degraded feathers and filaments. Furthermore, the data here provide empirical evidence for reconstructing the colours and colour patterning of these extinct birds and theropod dinosaurs: for example, the dark-coloured stripes on the tail of the theropod dinosaur *Sinosauropteryx* can reasonably be inferred to have exhibited chestnut to reddish-brown tones.

Ever since they were first announced[6,7], the 'feathered' dinosaurs from the lacustrine sediments of the Jehol Group (Early Cretaceous, 131–120 Myr ago[1]) of China have been controversial. Pennaceous feathers—those with a central shaft and lateral vanes, such as the contour and flight feathers of modern birds—occur both in Jehol birds[4,5] and in non-avian theropods, primarily Maniraptora such as the oviraptorosaur *Caudipteryx*[7], the dromaeosaurid *Microraptor gui*[8], and the unclassified maniraptorans *Protarchaeopteryx*[7], *Pedopenna*[10] and *Yixianosaurus*[11].

Integumentary filaments occur both in non-avian theropods that possessed true pennaceous feathers (for example, *Caudipteryx*) and in those in which the latter are absent, such as *Sinosauropteryx*[6], *Sinornithosaurus*[9] and *Beipiaosaurus*[12]. The report of superficially similar unbranched filaments in the ornithischian dinosaurs *Psittacosaurus* and *Tianyulong*[17] suggests that such structures might be common to all dinosaurs. Many investigators have accepted that these various filamentous to feather-like structures are epidermal in origin and represent feathers[6–12,17,18]; others[13–16] have disputed this view, arguing, for example, that in the theropod dinosaur *Sinosauropteryx* they represent degraded dermal collagen fibres, part of the original strengthening materials of the animal's skin[16]. Resolving this fundamental difference in interpretation is important for our understanding of the biology of the taxa in which they occur, but also has wider implications; if epidermal in origin, these structures will inform models of the evolutionary origin of modern feathers[19,20], and the timing of steps in the acquisition of this evolutionary novelty.

Here we demonstrate, using scanning electron microscopy (SEM), that both the integumentary filaments of *Sinosauropteryx* and *Sinornithosaurus* and the pennaceous feathers of the Jehol birds contain sub-micrometre-sized bodies that are either highly elongate with rounded termini, or oblate to sub-spherical, in shape. We eliminate the possibility that these bodies represent fossilized bacteria or diagenetic minerals, and interpret them as fossilized melanosomes. Their morphology is identical to that of melanosomes in the feathers of extant birds. Melanosomes are lysosome-related organelles of pigment cells in which melanins are stored, and are responsible, in part, for the colours exhibited by the feathers of modern birds. The two most common types of melanin are the reddish-brown to yellow pigment phaeomelanin and the black-grey pigment eumelanin[21]. These melanosomes, the first examples reported from the Jehol Group, and the first fossil examples of phaeomelanosomes, are preserved in life position. Representative examples are shown from an isolated feather (Fig. 1), feathers from the bird *Confuciusornis* (Fig. 2), and integumentary filaments of the theropod dinosaurs *Sinosauropteryx* (Fig. 3) and *Sinornithosaurus* (Fig. 4).

The outline of fossil feathers is often defined by layers of closely spaced, aligned, micrometre-sized, oblate bodies that have been

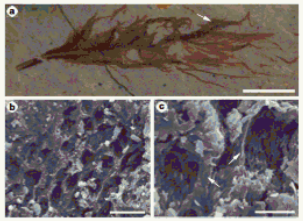

Figure 1 | Melanosomes in an isolated pennaceous feather (IVPP V15388). a, Optical photograph; position of area analysed by SEM indicated by arrow. **b**, **c**, SEM images (at lower and higher magnification, respectively) of eumelanosomes preserved as moulds inside small areas that are separated from each other by anastomosing ridges of degraded feather (at arrows in **c**). Scale bars: **a**, 5 mm; **b**, 20 μm; **c**, 5 μm.

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Sciencexpress Report

Plumage Color Patterns of an Extinct Dinosaur

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As long as dinosaurs have been known there has been speculation about their appearance. Fossil feathers can preserve the morphology of color-imparting melanosomes, which allows color patterns in feathered dinosaurs to be reconstructed. Here we map feather color patterns in a Late Jurassic basal paravian theropod dinosaur. Quantitative comparisons with melanosome shape and density in extant feathers indicate that the body was gray and dark and the face had rufous speckles. The crown was rufous, and the long limb feathers were white with distal black spangles. The evolution of melanin-based within-feather pigmentation patterns may coincide with that of elongate pennaceous feathers in the common ancestor of Maniraptora, before active powered flight. Feathers may thus have played a role in sexual selection or other communication.

Exceptionally preserved specimens from the Lower Cretaceous of China have shown that simple body contour feathers and elongate pennaceous forelimb and tail feathers, bearing both barbs and barbules, were present in basal maniraptoran dinosaurs before powered flight evolved (*1*–*3*). Discoveries of elongate leg and foot feathering in Paraves (*4*–*6*) have raised new questions about the evolutionary origin of aerodynamic feather function (*2*, *3*). Preserved color patterns have also been noted, such as the light and dark regions in the tail of *Caudipteryx (1)*, but there has been no evidence to indicate how such patterns, or color more generally, evolved.

Fossil avian feathers preserve the morphologies of melanosomes, the melanin-containing organelles, which determine key aspects of color (*7*, *8*). A recent study (*9*) reported melanosome impressions in Cretaceous feathers, but the limited sample of small regions of distinct animals and comparison based simply on gross melanosome shape prevented the interpretation of plumage color patterns. Here we analyze melanosome size, shape, density and distribution to reconstruct the plumage color patterns of a new specimen of a feathered dinosaur. The specimen, BMNHC PH828 (21) (Figs. 1 and 2 and figs. S3 and S4), comprises part and counterpart of a partial skeleton in three shale blocks, with elements of the forelimbs- and distal hind limbs in near-complete articulation. Preparation was minimal and most feathers are well preserved even to their insertions (fig. S4). Elongate pennaceous forelimb (primaries, secondaries, and coverts) and hind limb feathers are present, as are contour feathers associated with the skull and body (Figs. 1 and 2 and figs. S3 and S4). The new specimen is referred to *Anchiornis huxleyi* Xu et al., 2009 (*10*) and preserves morphologies consistent with the recovered placement of this species within Paraves as a part of Troodontidae (see SOM) (*6*). It was found in strata estimated to be Late Jurassic in age from the Daxishan site (Jianchang County, Liaoning Province), the same locality as a specimen recently referred to this taxon (LPM-B00169) (*6*).

We sampled proximal and distal parts of all feather types and all body regions preserved in BMNHC PH828 (Figs. 1 and 2 and table S4). Scanning electron micrographs of all 29 samples revealed impressions of spherical to oblate carbonaceous bodies or impressions 100 to 1908 nm in length (Figs. 1 and 2 and fig. S2) identified as melanosomes (*8*). Most samples revealed elongate eumelanosomes that varied slightly in morphology and distribution in different regions of the body. The distal crown feathers contained distinct sub-spherical phaeomelanosomes about ~500 nm in length (Fig. 2B). A posteroventral sample from the skull showed distinct regions of spherical and elongate melanosomes.

For the purpose of comparison we assembled a dataset on melanosomes from a phylogenetically diverse sample of extant bird feathers with black, gray, and brown melanin pigmentation, but lacking structural coloration [See material and methods in the supplementary online material (SOM)]. Other molecular pigments like carotenoids and porphyrins also produce plumage colors, but are not preserved

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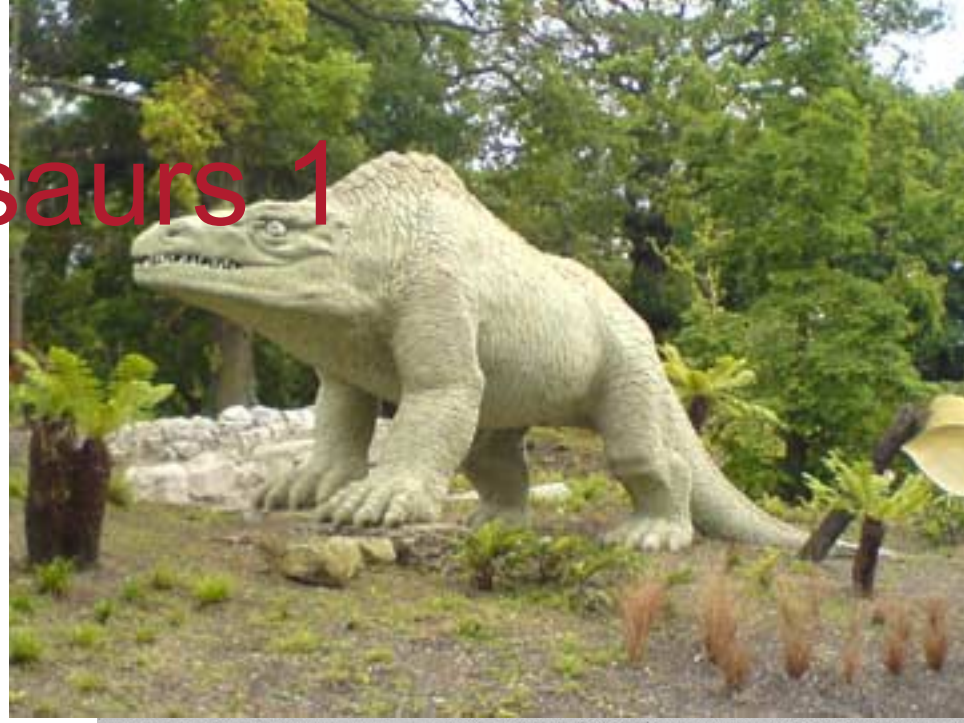
Picturing dinosaurs 1

- Owen's dinosaur reconstructions were part of the first wave of 'dinomania', in the 1850s
- Life-sized concrete models at Crystal Palace, London; posters; book illustrations
- Owen's dinosaurs were curiously mammalian in appearance

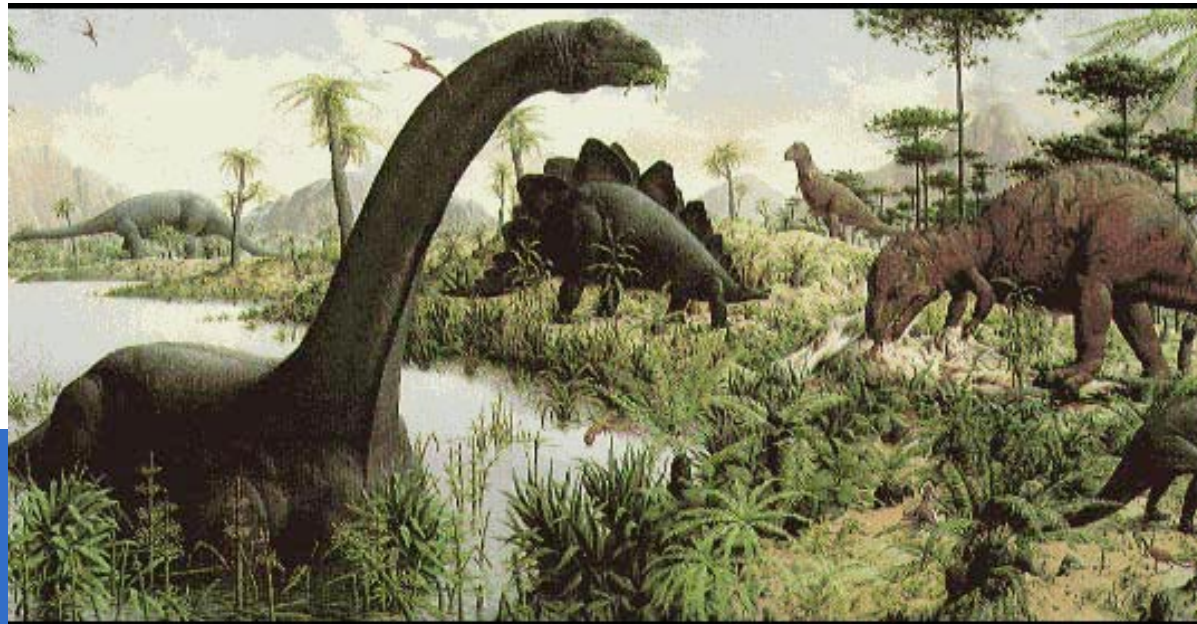


Picturing dinosaurs 2

- Thanks to work by Leidy, Cope, and Marsh, a new image of dinosaurs emerged by 1870-1900
- The key artist was Charles Knight at the AMNH - his images dominated from 1900-1950
- ‘Kangaroo pose’ for bipeds

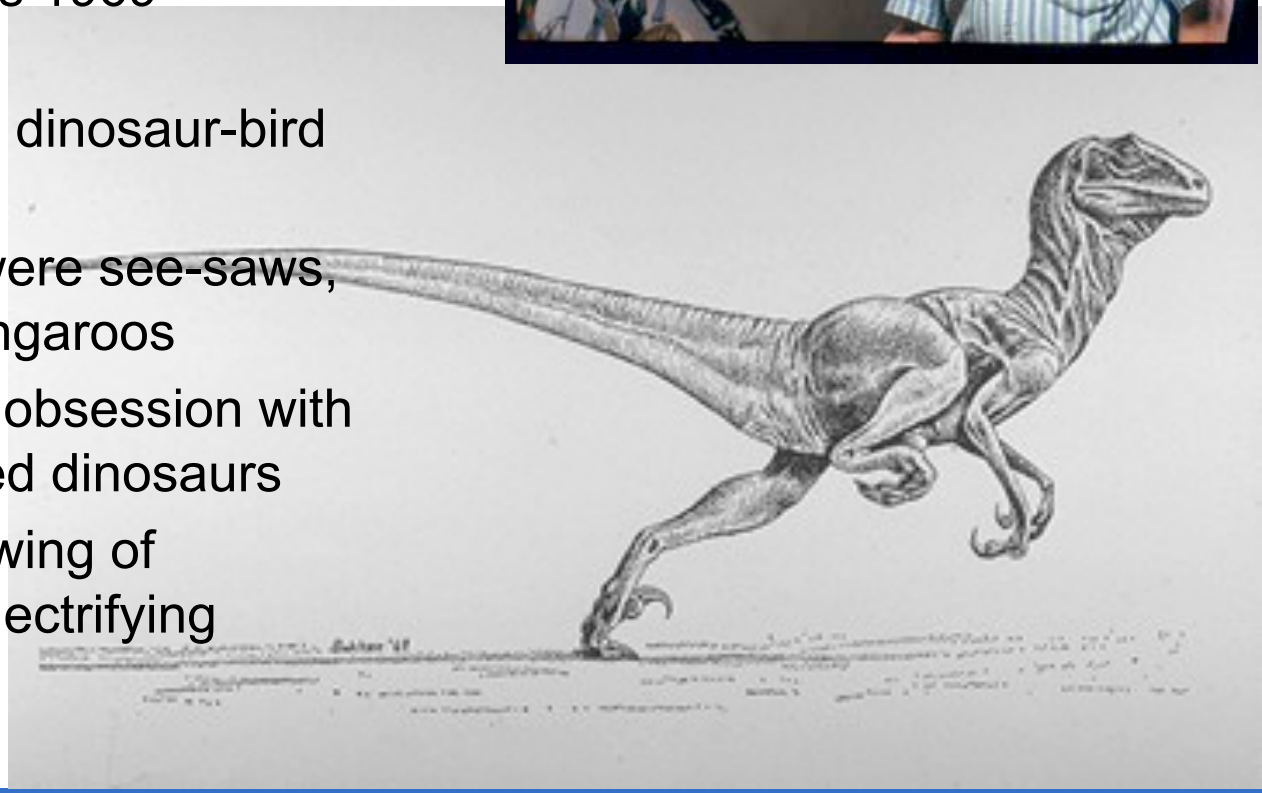
Picturing dinosaurs 3

- Iconic images in the Yale Peabody Museum Zallinger mural
- Widely reproduced in magazines and books
- The dominant view until the 1970s



Picturing dinosaurs 4

- John Ostrom's discovery of *Deinonychus* and his 1969 *Peabody Bulletin*
- Reawakening of the dinosaur-bird model
- Bipedal dinosaurs were see-saws, not tail-dragging kangaroos
- Bakker's irreverent obsession with active, warm-blooded dinosaurs
- His 1969 pencil drawing of *Deinonychus* was electrifying

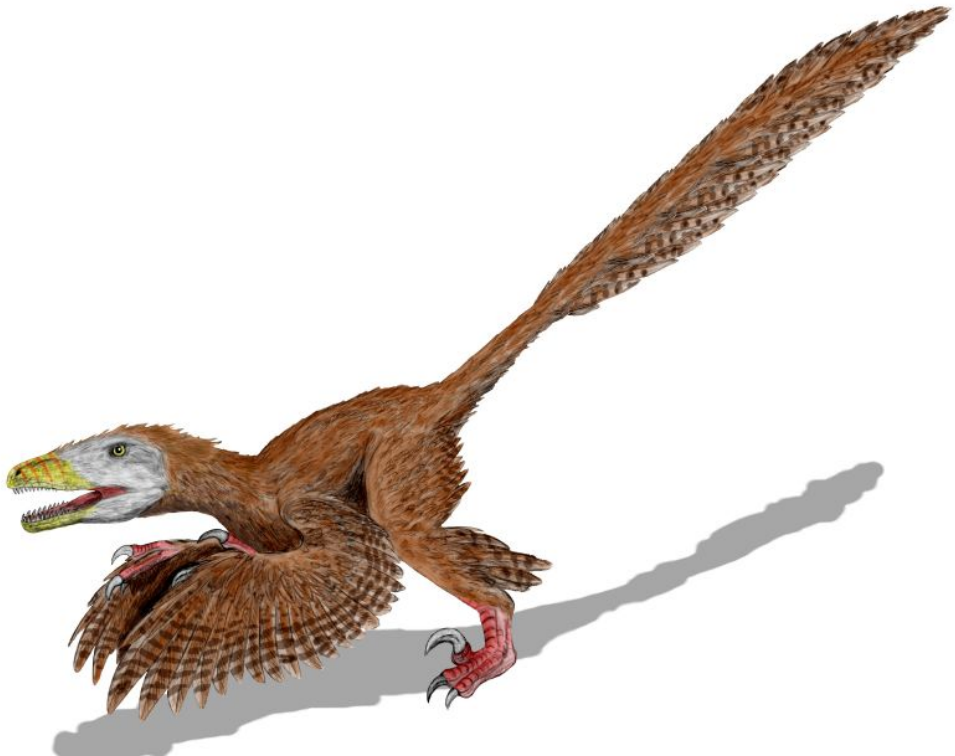


China

- In the 1990s, feathered dinosaurs and birds began to be found in Liaoning Province (Early Cretaceous, 125 Mya)
- Also yielded mammals with hair
- Now dozens of species show that most theropod dinosaurs were feathered

Picturing dinosaurs 5

The new Chinese material has added feathers to most theropods - including *Deinonychus* and *Tyrannosaurus rex*

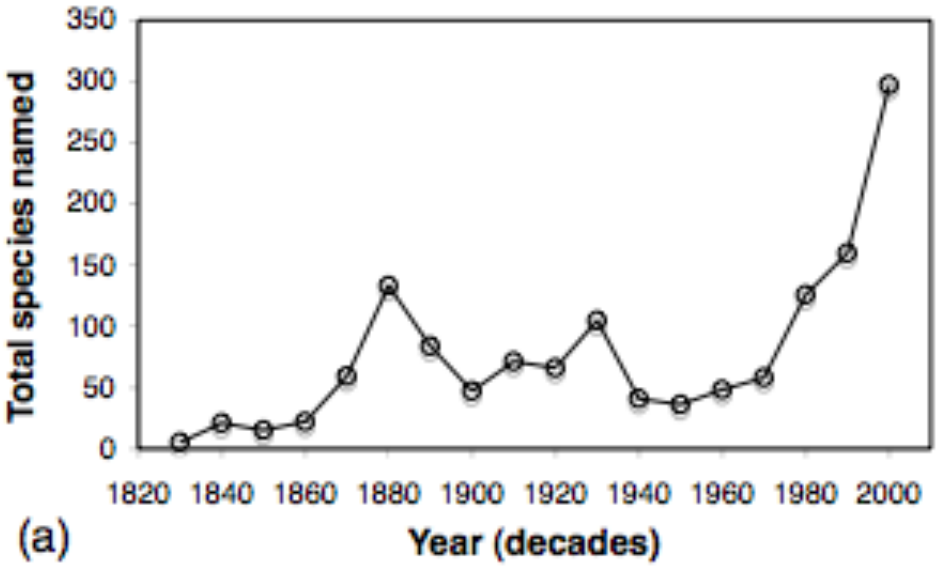


The aims of palaeontology

- Newspaper reports might lead one to believe that palaeobiologists are motivated simply to find new species
- This was clearly the motivation in Victorian times – there were small numbers of scientists, and new species were emerging at a rapid rate…
- …even now, a new dinosaur species is named every week
- However, this is only one aspect of what we do, and frankly isn't intellectually as stimulating as exploring evolution and biology of fossils (also, research councils do not provide funding for us to stack up more fossils in the museums!)
- Let's look briefly at the 'new species' issue, and then at the science of reconstructing past life…

Dinosaur discovery data

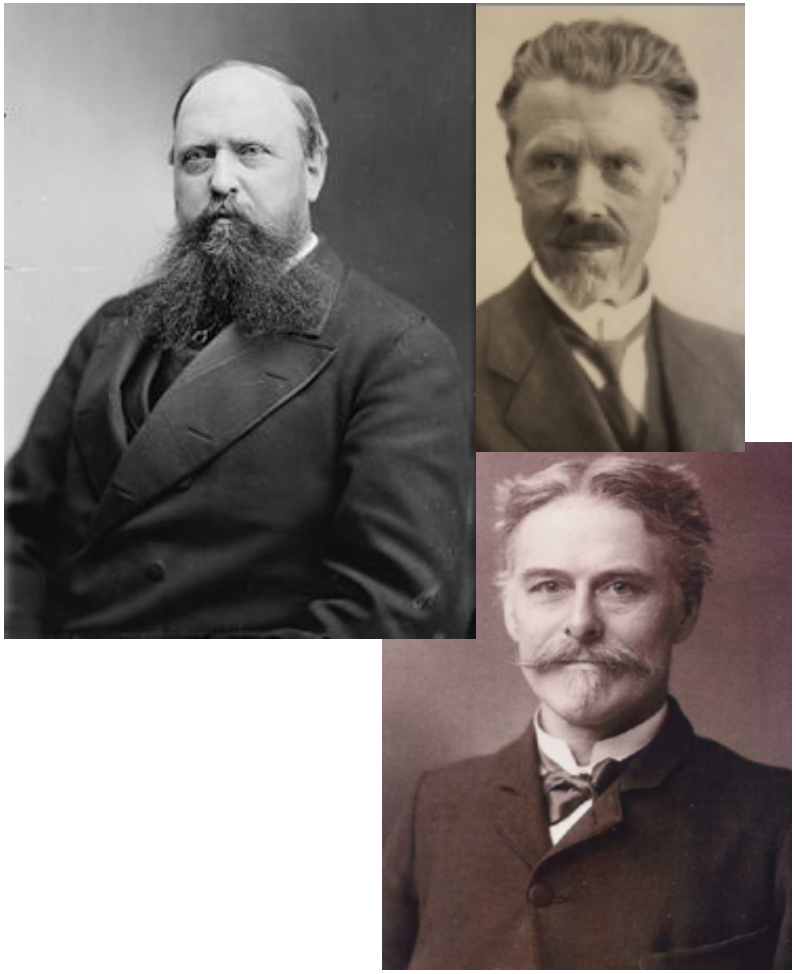
- Slow start in naming new dinosaurs, with only one or two species a year from 1824-1860
- High points in 1876, 1877 (Marsh/ Cope), 1932 (Huene)
- Huge increase recently - a new species every week –but do we believe all these are truly new species?
- 1400 dinosaur species have been named, but only half are valid



Benton, M. J. 2008. How to find a dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology*, 34, 516-533.

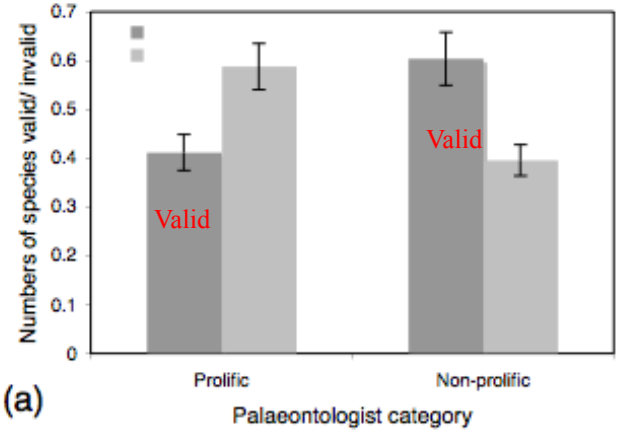
Top dinosaur namers 1

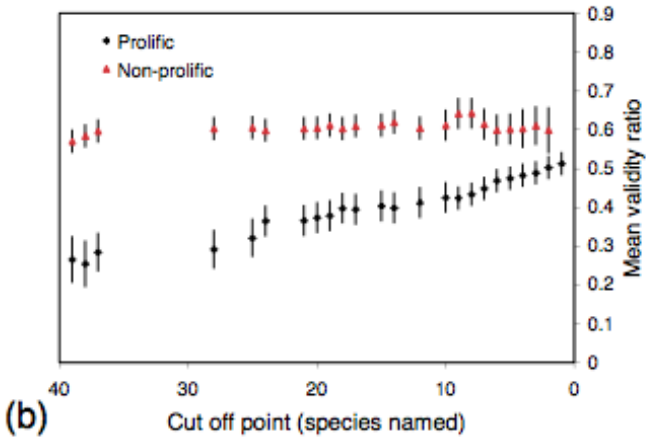
- The three most prolific namers are Marsh, Huene, and Cope
  - Othniel Charles Marsh, naming dinosaurs from 1870-1899, named 80 species (23 still valid; 29% success)
  - Friedrich von Huene, naming dinosaurs from 1902-1956, named 71 species (18 still valid; 25% success)
  - Edward Drinker Cope, naming dinosaurs from 1866-1892, named 64 species (9 still valid; 14% success)
- Lower than overall success rate of 52%



Top dinosaur namers 2

- An expectation is that prolific authors of species names should be better than mere dilettantes
- Among the 321 authors who named one or more of the 1400 dinosaur species names, prolific authors (lifetime total of > 10 species) fare badly (i.e. much higher probability their species will have been rejected by subsequent work)
- In fact, those 147 authors who only ever named one species do markedly better than those who named > 2

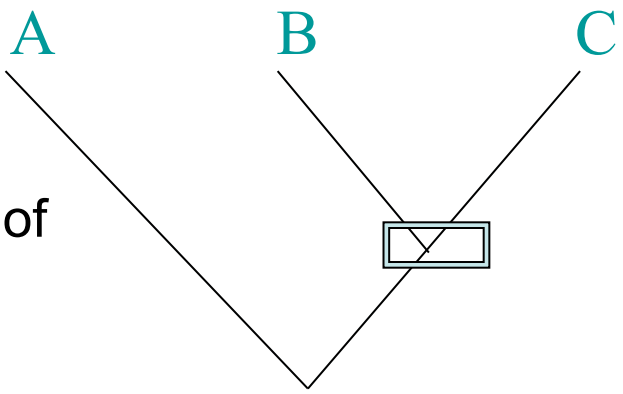




Benton, M. J. 2009. **Naming dinosaur species: the performance of prolific authors**. *PRSB 2010*

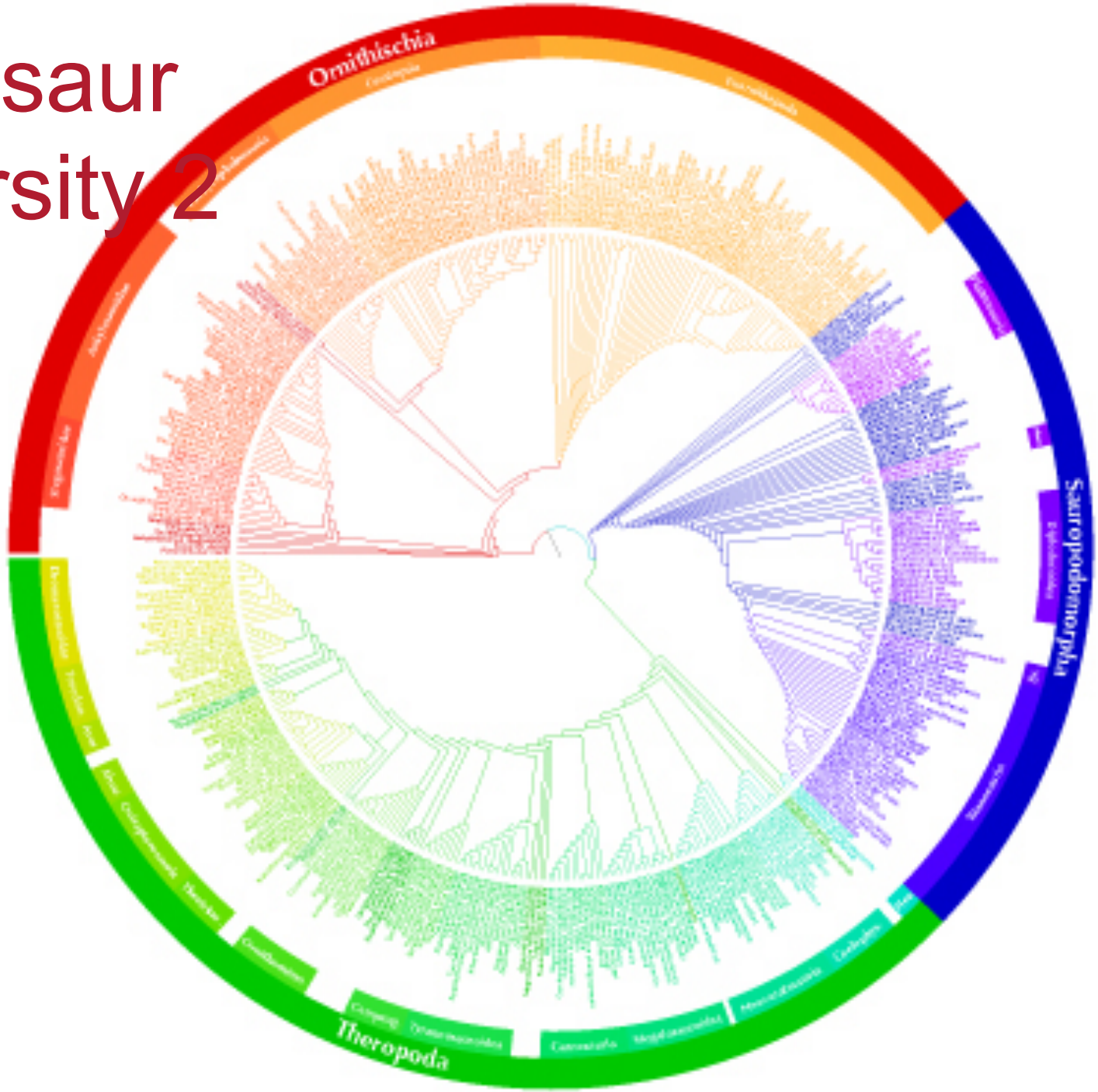
Dinosaur diversity 1

- Since the start of dinosaur studies, palaeontologists have sought to **classify** their finds
- Seeley (1887) noted the fundamental division of Dinosauria into Saurischia and Ornithischia, based on arrangement of hip bones
- Other key groups, such as Theropoda, Sauropoda, Ornithopoda, Stegosauria, Ankylosauria were variously named and used by Cope, Marsh, Huene, etc.
- Since 1980s, we have used principles of cladistics to discover pattern of tree of life
- High-powered computing methods now allow us to deal with massive data matrices of morphological or molecular data

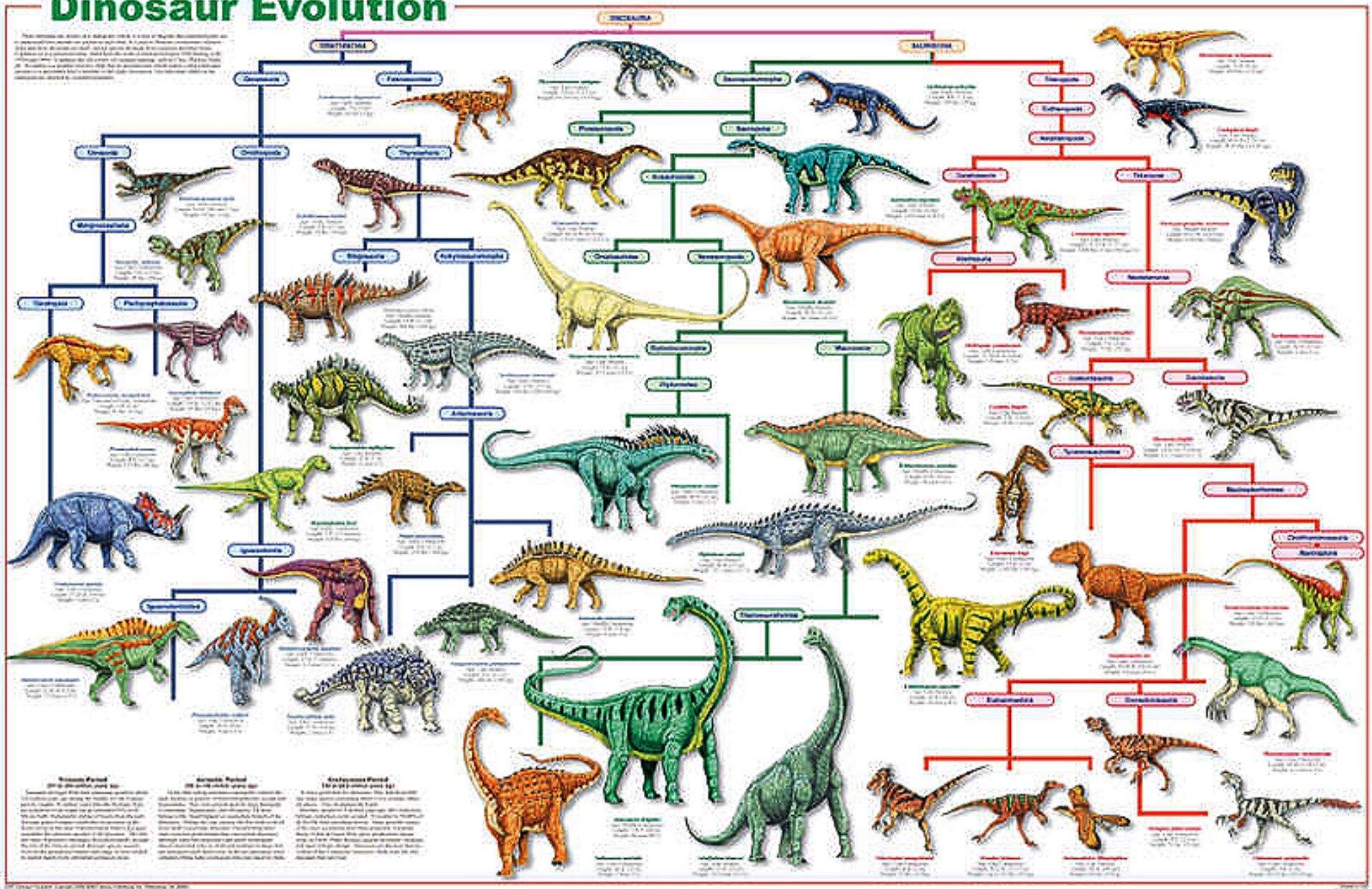


Dinosaur diversity 2

The dinosaur supertree 2008 (Lloyd et al. 2008)



Dinosaur Evolution



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Methods in palaeobiology

1. Empirical evidence
2. Comparison with modern analogues
3. Biomechanical modelling

What is the role of the palaeobiologist/ geologist in reconstructing the past?

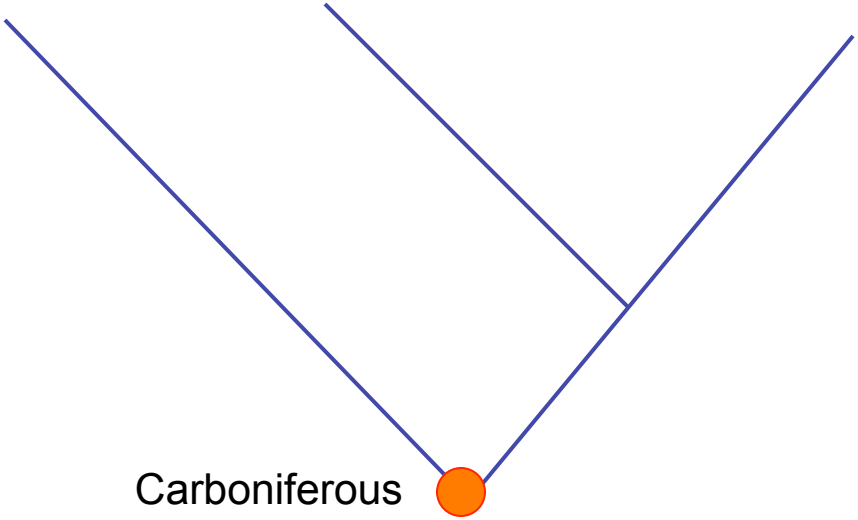
1. Empirical evidence

- The context of the fossil
- Footprints, eggs and nests
- Coprolites and stomach contents
- ‘Caught in the act’
- Plant and animal associations

2. Comparison with modern analogues

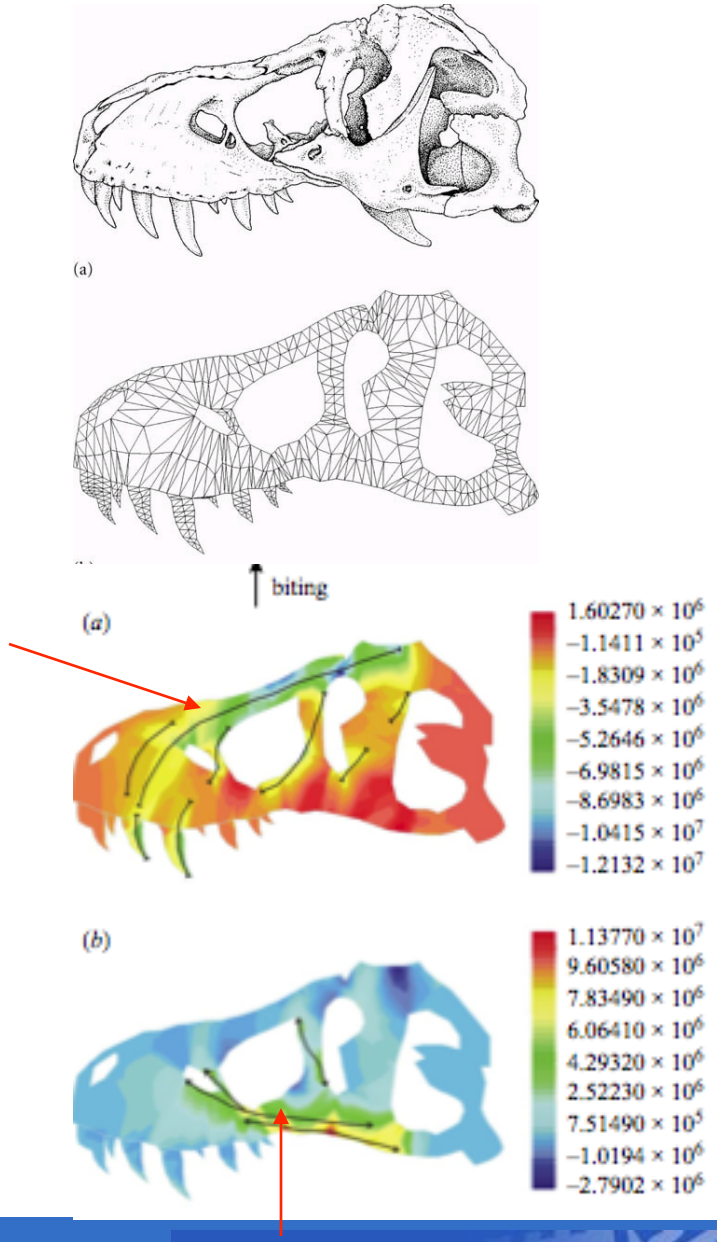
- Phylogeny can indicate much about soft tissues and behaviours – so Carboniferous amniotes laid eggs even though the oldest fossil eggs are Triassic
- The **extant phylogenetic bracket** concept combines phylogenetic bracketing with functional inferences – so dinosaurs had eye sockets, and like their bracketing taxa (birds and crocodiles) also presumably had eyes with certain properties

Mammals Turtles Birds



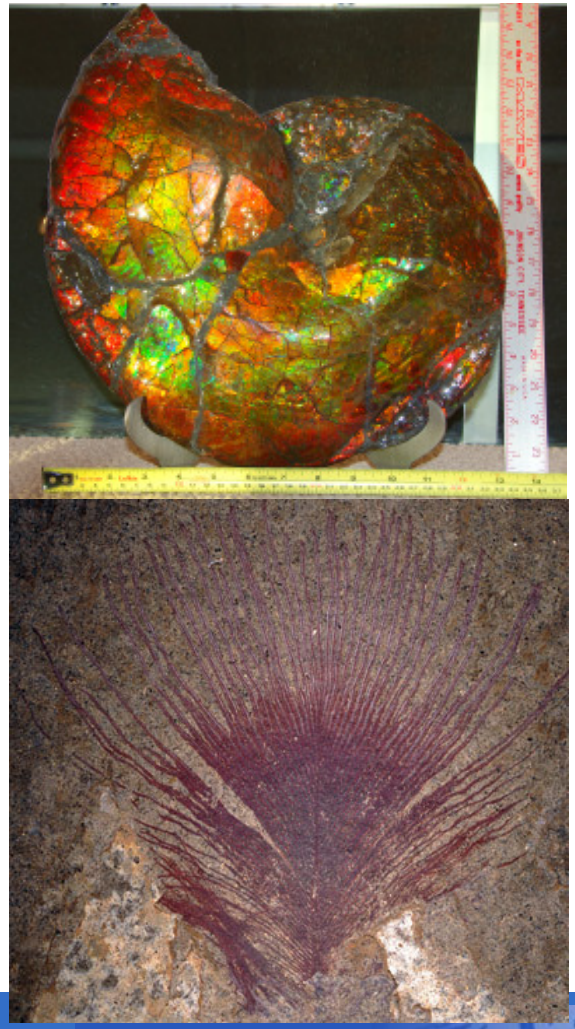
3. Biomechanical modelling

- FEA shows that the cranium is equally adapted to resist biting or tearing forces, so the puncture-pull feeding hypothesis is well supported
- The maxilla-jugal suture provides a tensile shock-absorbing function that reduces localized tension yet weakens the skull overall
- Peak compressive and shear stresses in nasals rather than fronto-parietal region as in *Allosaurus;* a reason why tyrannosaurid nasals are robust [Rayfield 2004]



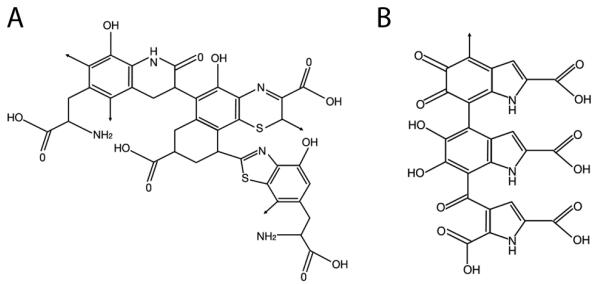
What can we never know?

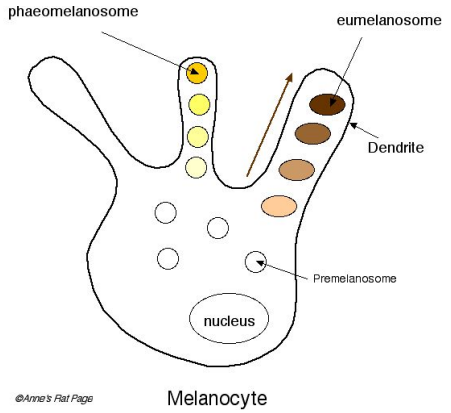
- We can know hard parts, and restore certain soft tissues
- Exceptional fossils may show stomach contents and some soft tissues
- Other analytical studies can say something about feeding, locomotion, breeding
- ‘But we can never know their colours, or the sounds they made’
- Some fossils do show remarkable colours – are these original?



Melanin and melanosomes

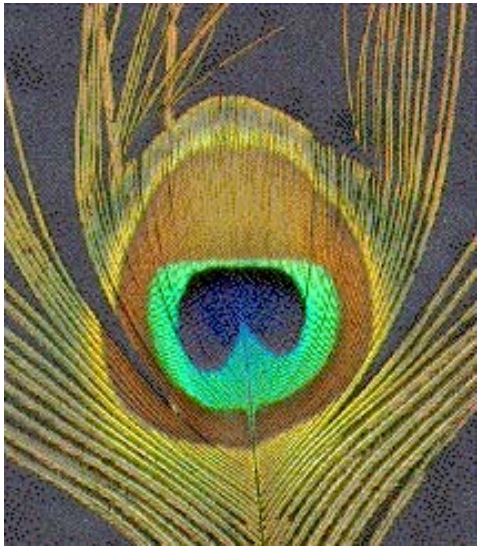
- Melanins are fundamental pigments found in many plants and animals
- Two main kinds in feathers and hairs – black/brown eumelanin (B) and ginger phaeomelanin (A)
- Melanins are produced by **melanocytes** in the skin (cf. sunburn)
- Melanocytes can package the melanin into melanosomes, organelles or capsules, which are transferred into the root of the developing hair/ feather follicle
- Reside within the keratin structure





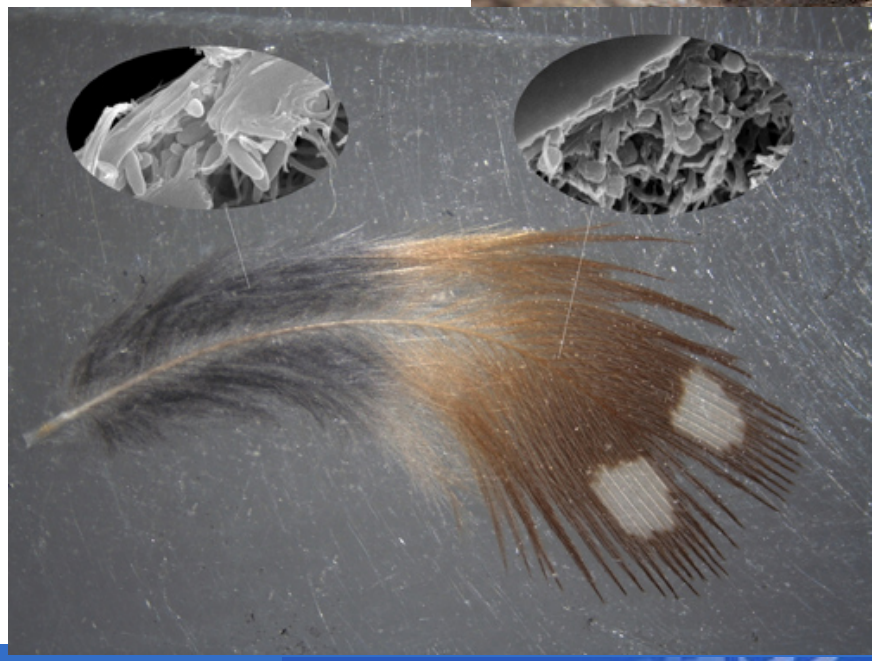
Bird colour

- Bird colour comes from three main sources
  1. Melanins
  2. Carotenes (yellows and reds) and porphyrins (greens and purples)
  3. Nanostructural arrangements of melanosomes (iridescence)
- The first and last are structural features, and so could be determined in fossils



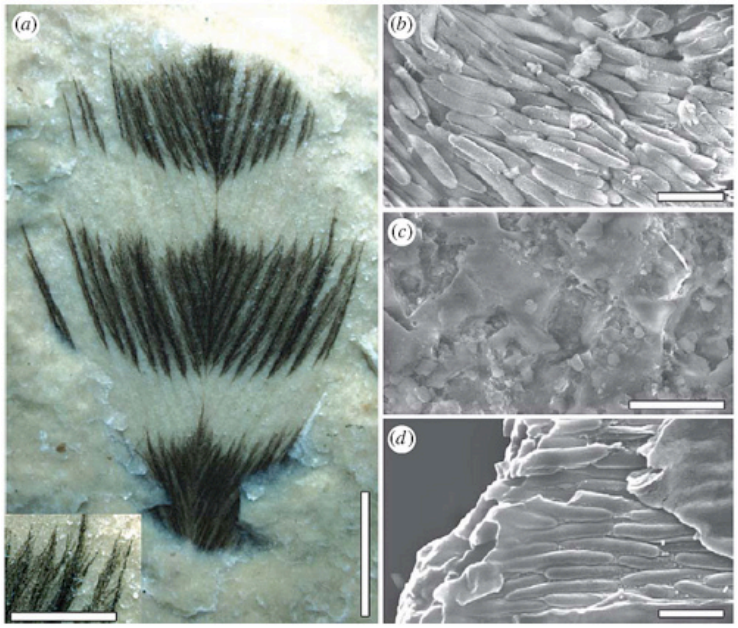
Melanosomes and colour

- We looked at melanosomes in differently coloured feather regions in the zebra finch
- Black and grey colours corresponded to eumelanosomes – sausage-shaped, and up to 1 μm long
- Ginger colours corresponded to phaemelanosomes – spherical and typically 0.5 μm across



First reports of melanosomes in fossils 1

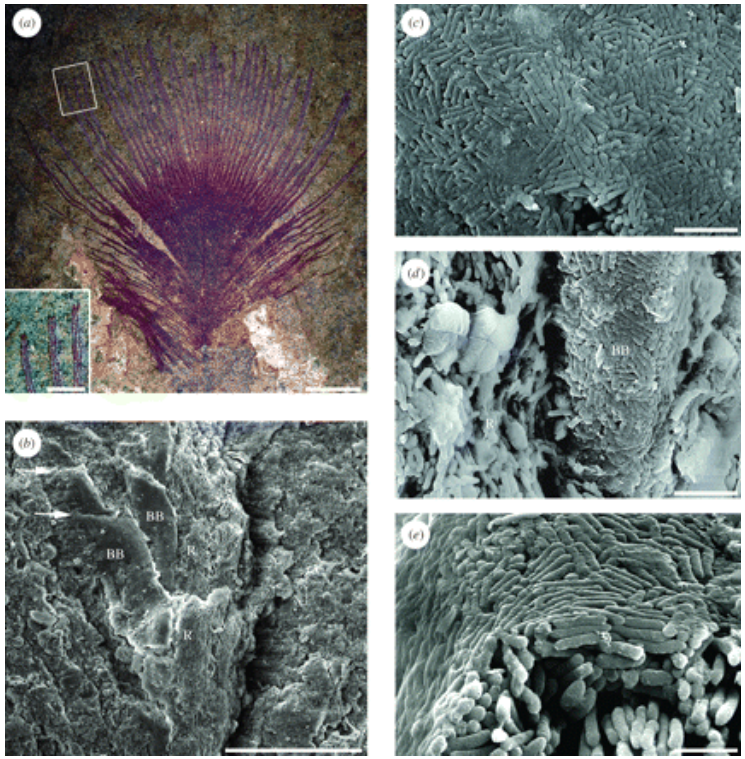
- A team at Yale University announced melanosomes in feathers from Cretaceous and Eocene birds
- Present in dark stripes, absent in light
- A big leap, to realise what they were – they are not bacteria



Vinther et al. (2008, *PRSB*)

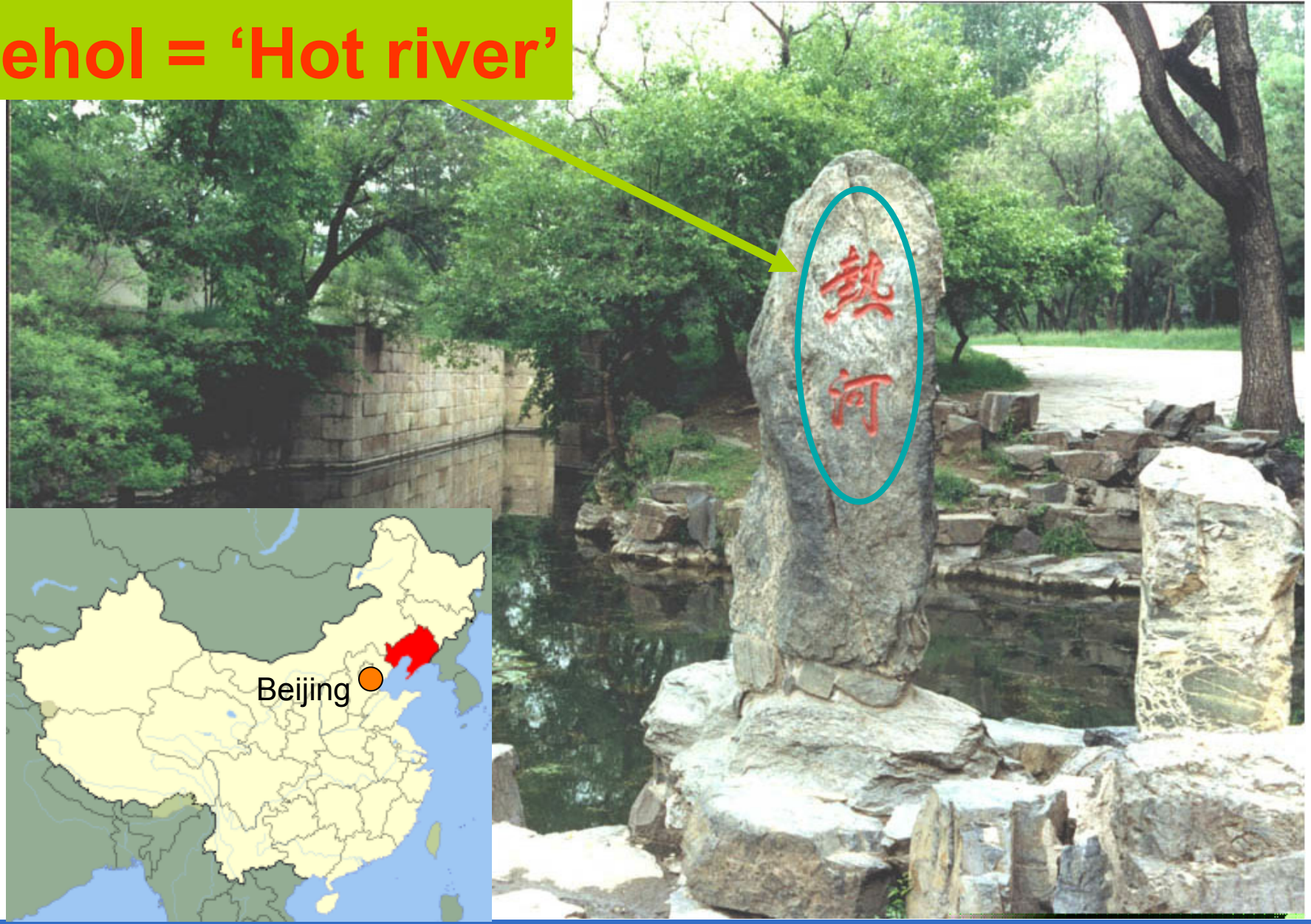
First reports of melanosomes in fossils 2

- In a second paper, they showed evidence of regular packing of eumelanosomes
- Comparison with modern birds show that this kind of nanostructure is responsible for iridescence in bird feathers
- The closely packed organelles reflect light in a uniform manner



Vinther et al. (2010 *PRSB*)

Jehol = ‘Hot river’



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Yixian Formation

- Sihetun locality, Liaoning Province
- 121-125 MYA
- Source of 1000 confuciusornithid specimens
- Public museum on site

Jiufotang Formation

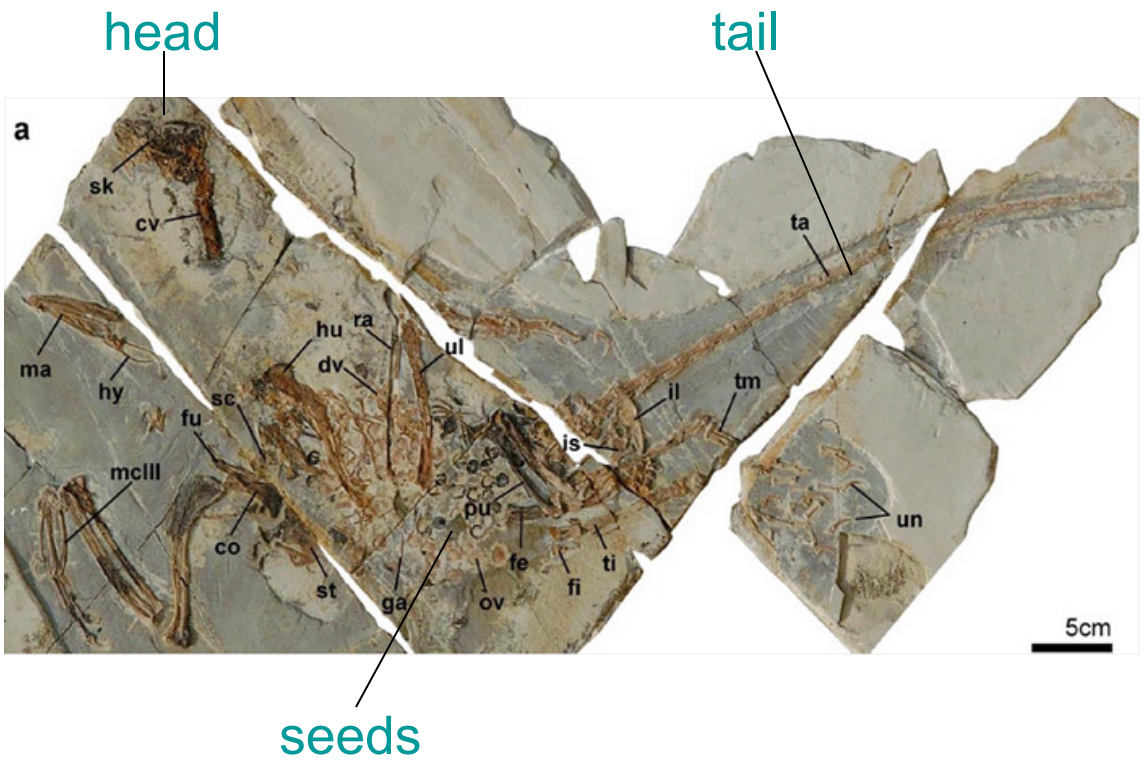
- Chaoyang County, Liaoning Province
- 120 Myr

Memories of the 2007 field trip

- Banquets on all occasions
- Lots of very fresh fish

The Jehol fossils

- Plants
- Aquatic arthropods
- Insects
- Molluscs
- Microfossils
- Fishes
- Amphibians
- Turtles
- Pterosaurs
- Dinosaurs
- Birds
- Mammals



Jeholornis

Dinosaurs 1

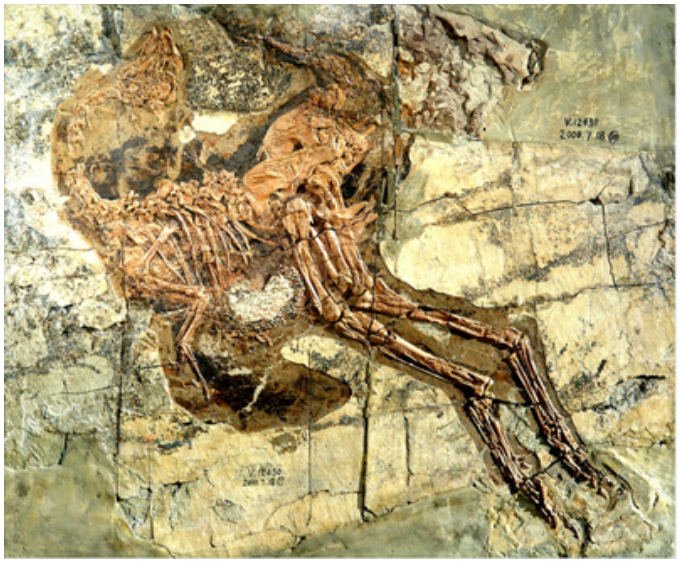
- The first feathered dinosaur reported, *Sinosauropteryx* Ji & Ji, 1996
- Bristles down midline of back from crest on neck to striped tufts down both sides of tail
- Close relative of *Compsognathus* from the Late Jurassic of Germany

Dinosaurs 2

- But what are the ‘feathers’?
- Many argued they were genuine simple modified down feathers
- Others said they are shredded skin…

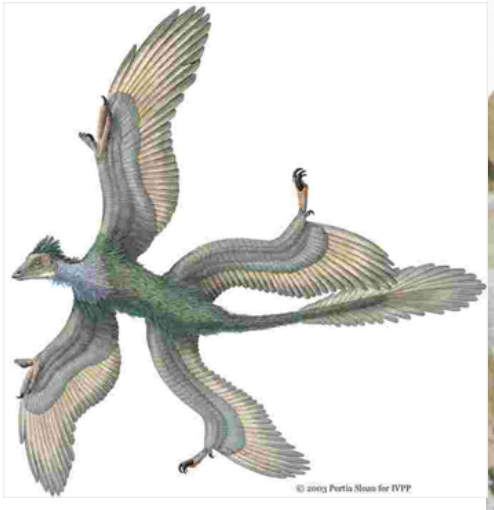
Dinosaurs 3

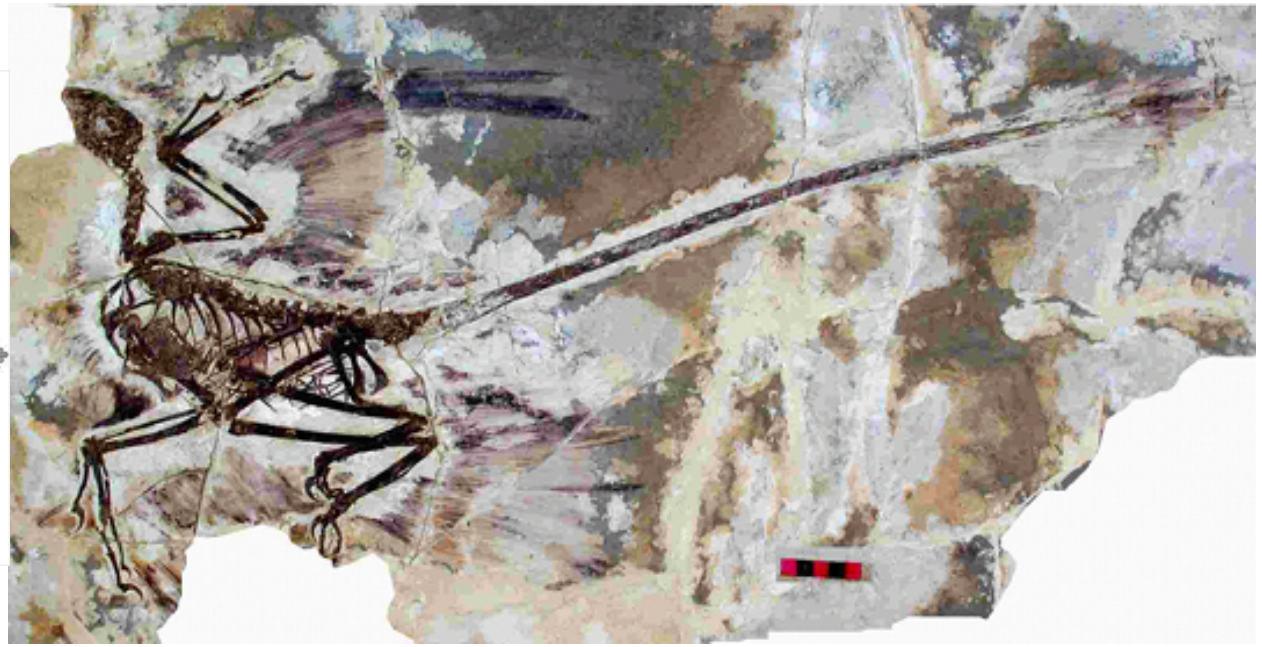
- Most convincing of all was the oviraptorosaur *Caudipteryx* with bird-like pennaceous feathers (feathers with central rachis and lateral pennae) on the hand



Dinosaurs 4

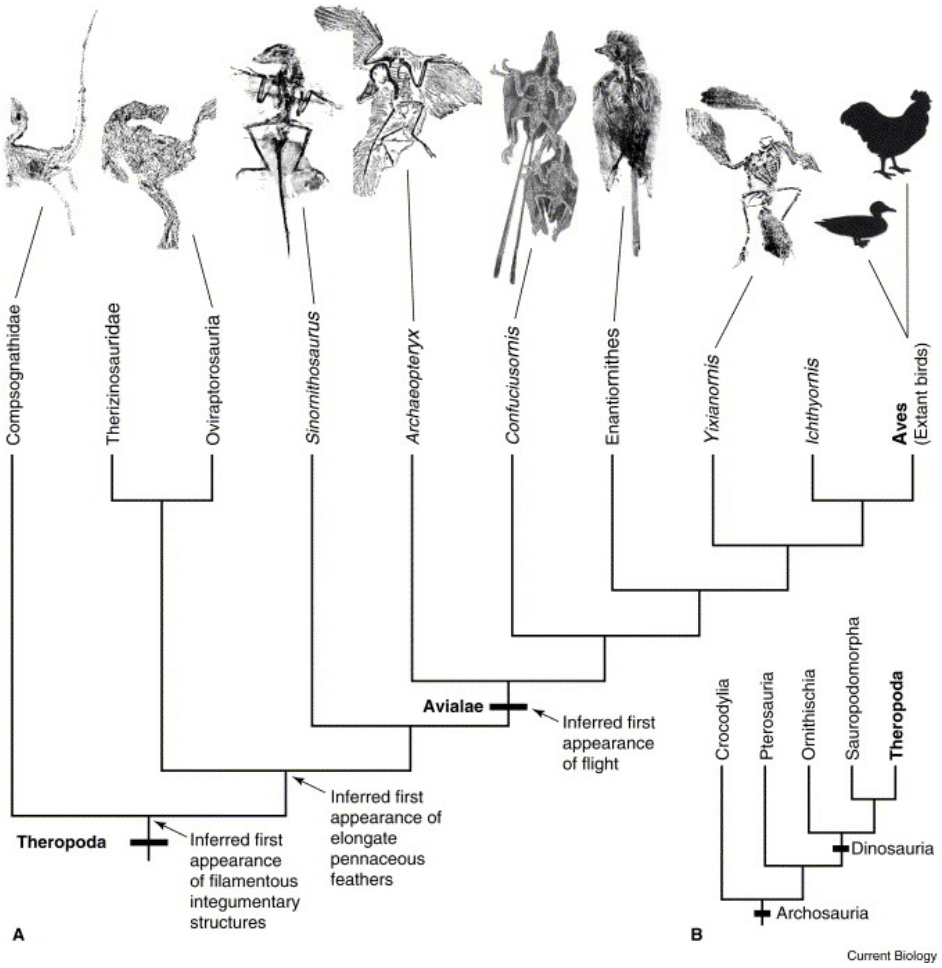
- For the remaining doubters, *Microraptor* Xu *et al*., 2003, was the final clincher
- It has fine flight feathers along **both** fore- and hindlimbs





Dinosaurs 5

- The meaning of feathers and feather-like structures in dinosaurs - proves birds are theropod dinosaurs
- The sequence of bristles -> branched feathers -> pennae -> flight feathers on arms and legs matches theoretical expectations for feather evolution
- Feathers evolved first for insulation or display, and only later adopted an aerodynamic function



Birds 1

- The first bird reported from Liaoning was *Confuciusornis*, named by Hou *et al*. (1995)
- First three specimens were quite scrappy (see below)
- Since then, 3000 specimens have been found, including the famous specimen (right) showing male and female on one slab

Birds 2

- A second major group are the enantiornithines, reported first from South America, as a curiosity, in 1981
- Enantiornithines dominated Cretaceous avifaunas, and well known from China
- *Liaoxiornis* Hou & Chen, 1999 - a juvenile enantiornithine

Birds 3

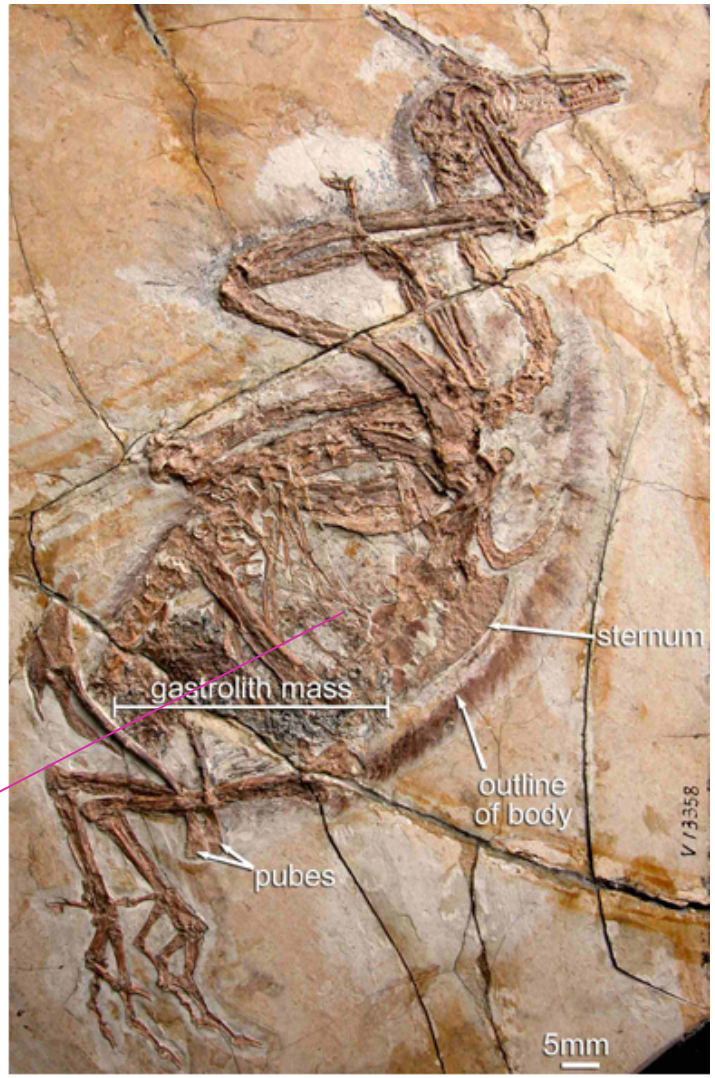
- An enantiornithine embryo in the egg

Zhou Z. & Zhang F. 2004. A precocial avian embryo from the Lower Cretaceous of China. *Science* **306,** 653.

Birds 4

- Ornithurine ('modern') types of birds are also known from Liaoning

Hongshanornis



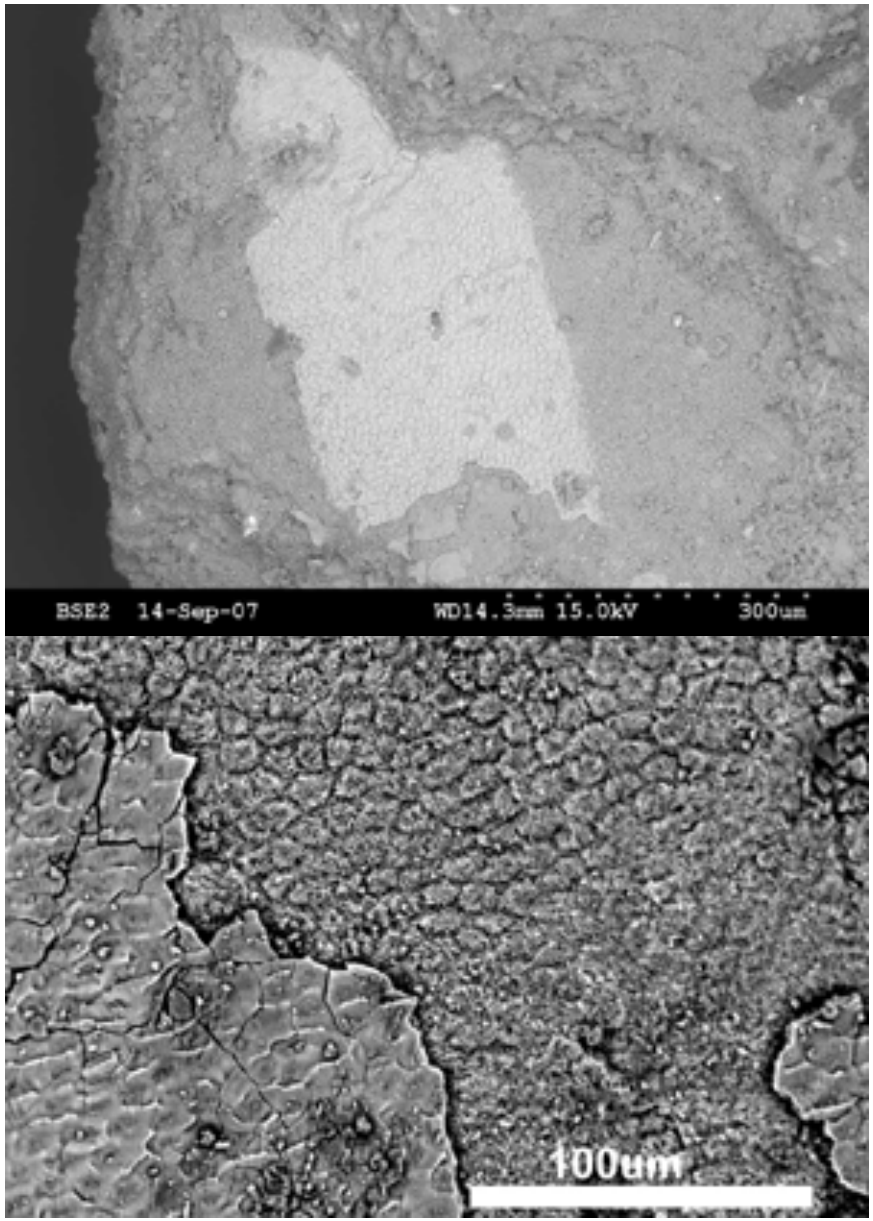
Yanornis

Feathers 1

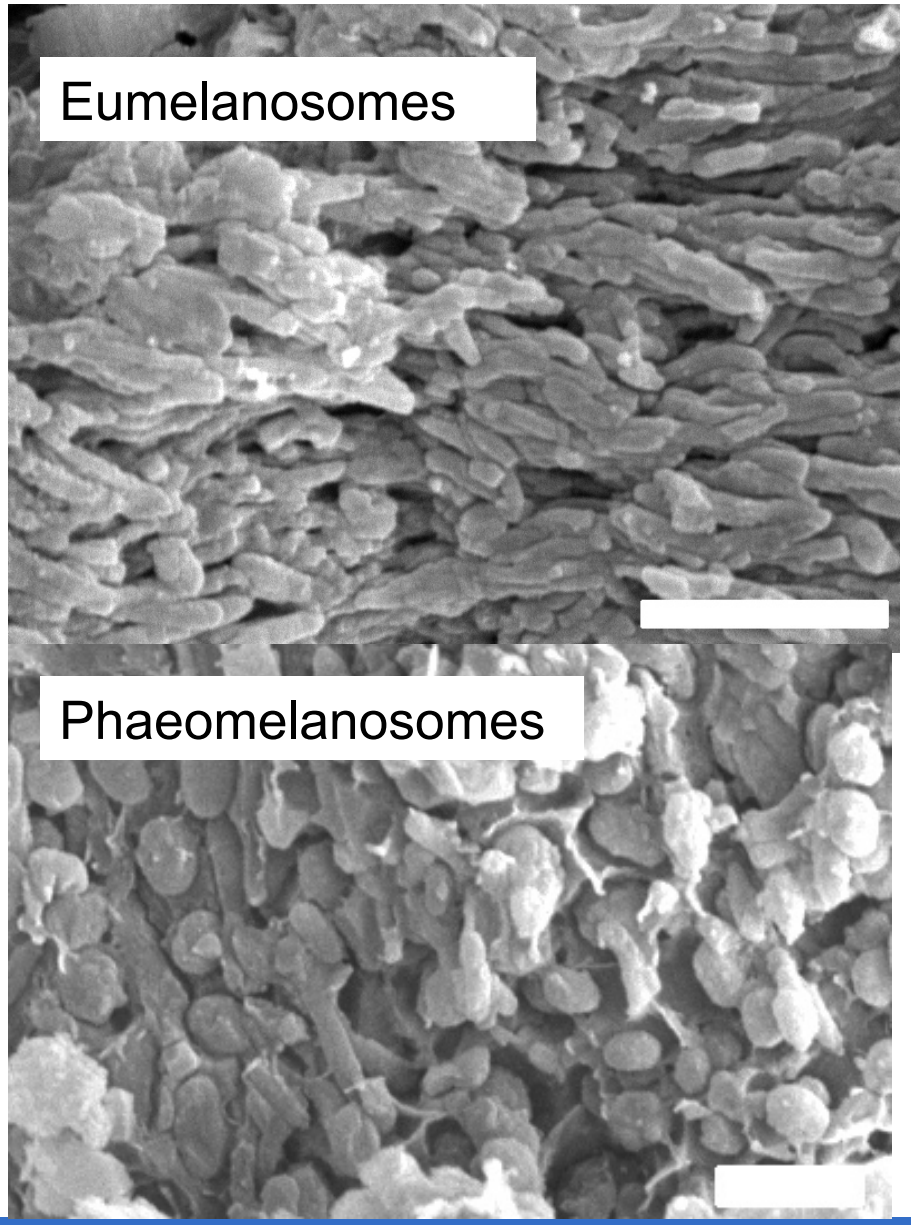
- Thousands of feathers have been found in the Liaoning deposits - floated in the lakes and fell to the bottom
- Preserved as brown, white or black traces, showing full details of vein and barbs

Feathers 2

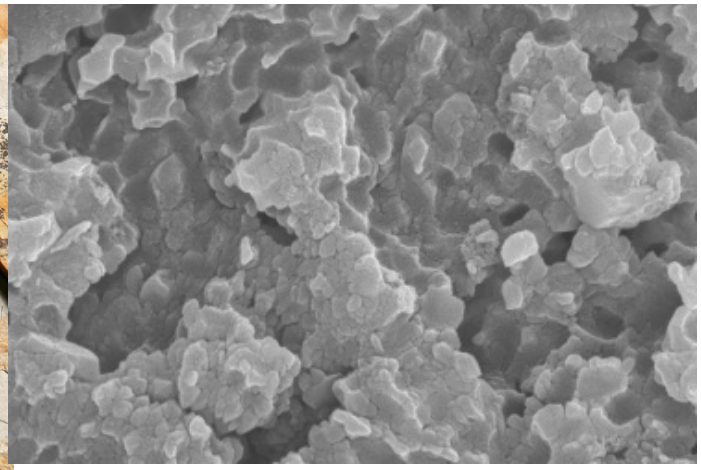
- Under SEM, fine detail can be seen - the ‘patch’ under UV shows squamous dermal cells - the common skin surface cells (= Cretaceous dandruff)
- The white colour suggests the skin is rich in phosphate - probably derived from the skin itself, but also from decaying bones (calcium phosphate/ apatite)
- Some examples show multiple layers within the skin (bottom right)



Confuciusornis



Sinosauropteryx



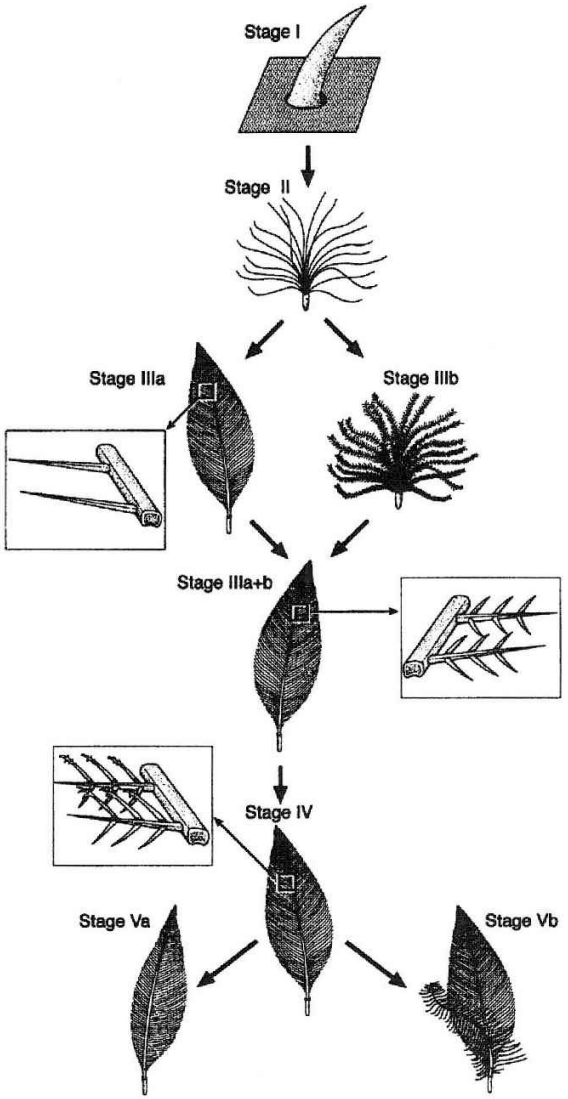
Phaeomelanosomes

- The bristles in *Sinosauropteryx* have been controversial – are they protofeathers or shredded collagen?
- Melanosomes prove they are feathers
- Key in feather evolution – confirms the classic model

Zhang, F., Kearns, S.L, Orr, P.J., Benton, M.J., Zhou, Z., Johnson, D., Xu, X., and Wang, X. 2010. Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature* (doi:nature08740.3d)

Feather evolution

- The classic developmental model for feather evolution (Prum 1999) suggested a sequence from simple bristles, through down feathers, to pennaceous feathers
- *Sinosauropteryx*, the most primitive feathered theropod, has bristles, and theropods higher in the tree have ever-more complex feathers
- Further, in debate about **why** feathers originated, they did not arise for flight, but for insulation, and now we know certainly for display



Anchiornis

- A week after our paper in *Nature* (Zhang et al. 2010), a second paper by the 'Yale group' appeared in *Science* (Li et al. 2010)
- This showed an overall reconstruction of plumage based on 29 spot samples across the feathers in different parts of the fossil
- Shows the possibility of 'whole-body' colour mapping in fossils

Li, Q., Gao, K., Vinther, J., Shawkey, M. D., Clarke, J. A., D'Alba, L., Meng, Q., Briggs, D. E. G., & Prum, R. O. 2010. Plumage color patterns in an extinct dinosaur. *Science* (doi: 10.1126/science.1186290)

Conclusions

- The initial studies on Chinese dinosaurs show the possibilities of using melanosomes to map colours and patterns in fossil birds and dinosaurs
- Studies on modern birds are beginning to show how to interpret colour from ultrastructural organelles, and these methods will be refined
- Palaeobiology need not rely on guesswork, but rather smart inferences
- There are another 20 or so birds and dinosaurs in China with feathers, as well as mammals and pterosaurs with hair… much work yet to do