Thomas Henry Huxley and the reptile to bird transition

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Abstract: The overwhelming evidence that birds evolved from maniraptoran theropod dinosaurs has rekindled an interest in the work of the Victorian anatomist Thomas Henry Huxley. Many popular and technical accounts credit Huxley with being the first to propose that birds evolved from dinosaurs, but this is a misinterpretation of Huxley’s work. During the 1860s Huxley was pre-occupied with identifying the basic ‘groundplans’ that united vertebrate forms. Birds and reptiles were two groups united by a shared body plan, with dinosaurs representing an intermediate form. Huxley did not begin to cast dinosaurs as transitional forms between birds and earlier reptiles until he read Ernst Haeckel’s Generelle Morphologie, at which time Huxley amassed ample anatomical evidence to illustrate how birds could have evolved from something dinosaur-like. Even then, however, Huxley did not say that birds had evolved from dinosaurs. As he explicitly stated in public addresses during the 1870s, small bird-like dinosaurs like Compsognathus only represented the form of what the true ancestors of birds might have looked like. Bird-like dinosaurs chiefly served to show that such a transition was possible. Thus, Huxley’s views on the evolution of birds were much more complex than many modern authors appreciate.

During the 1860s and early 1870s Huxley contributed many papers on the relationship between reptiles and birds, coining the term Sauropsida to unite both groups as early as 1863 (Huxley 1869b, 1871). This arrangement was initially based on similarities between living representatives of both groups, but palaeontological discoveries provided new evidence that bolstered Huxley’s argument.

When Hadrosaurus was first described (Foulke & Leidy 1858), the disparity in fore- and hindlimb length led the authors to suggest that it may have adopted a ‘kangaroo-like’ posture, and Cope came to similar conclusions about the theropod dinosaur ‘Laelaps’ (=Dryptosaurus (Marsh 1877)) (Cope 1867a, 1868). From this Huxley inferred similar bipedal postures for Iguanodon and Megalosaurus, but the description of Compsognathus (Wagner 1861c) and Hyspsilophodon (Huxley 1870a) were more important to Huxley’s hypothesis that birds had evolved from reptiles. While it was difficult to imagine birds arising from something as monstrous as a Megalosaurus, the smaller dinosaurs more closely resembled the hypothetical reptilian ancestor of birds.

Strangely, Archaeopteryx had little significance to Huxley even though he had published on it in 1868 (Huxley 1868b). Huxley’s minimal interest in Archaeopteryx probably stemmed from his view that most evolution had occurred during ancient ‘non-geologic time’, and the consensus that the three-toed tracks from the Triassic of New England (Hitchcock 1836, 1858) were those of birds made the Jurassic Archaeopteryx far too young to be a bird ancestor. Even when Huxley later modified his views on persistence and transitional forms, as reflected in his 1876 lecture tour of America, Archaeopteryx was placed on an evolutionary side branch and he doubted that it resembled a stage in the reptile–bird transition (Huxley 1877). The direct ancestors of birds were also unlikely to be found among the most bird-like of the dinosaurs, and Huxley considered them the ‘modified descendants of Palaeozoic forms through which the transition was actually affected’ (Huxley 1877, p. 67). Marsh’s recently discovered Cretaceous toothed birds Hesperornis and Ichthyornis, however, were marshalled as evidence of the relationship between birds and reptiles, and, although Huxley could not identify a direct line of descent, there were enough intermediates to defend the evolution of birds from reptiles.

Huxley’s work on this problem was never so simple as to assert that birds evolved from dinosaurs, and the evolution of his arguments about the relationship of birds and reptiles marks a transition in his own thinking (Di Gregorio 1982; Lyons 1993) as well as a period of change in the discipline of vertebrate palaeontology.

When Charles Darwin published On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life (Darwin 1859) palaeontology presented major problems for his still-nascent evolutionary hypothesis. Although palaeontology was still a relatively young science, it was generally believed that the geological strata had been sampled adequately enough by 1859 to reveal the diversity of ancient life in each age (Rudwick 1976). If transitional forms had not yet been discovered there was little chance that they existed. What was present in one
Darwin's hypothesis was primarily derived from observations of living organisms (population growth, artificial selection, etc.), but his evolutionary mechanism did make predictions about ancient life. If all of life on Earth shared a common ancestor in the distant past, with evolution branching gradually instead of making 'jumps', then the fossil record should provide graded intermediate forms. Unfortunately, such forms were rare and failed to bridge major gaps between groups of animals. Darwin attempted to explain the negative evidence through the imperfection of the fossil record. That any ancient creature, particularly a soft-bodied animal, should be preserved as a fossil seemed unlikely, and many animals that became fossilized were only known from fragmentary remains.

In order for an evolutionary series to be preserved a group of organisms would have to live in a place with regular sedimentation events over huge expanses of time – a doubtful scenario. The problem was further compounded by the fact that the span of geological time contained gaps, blank spots in the history of life on Earth, and there were too many unpredictable factors required to preserve an evolutionary series (Darwin 1859, pp. 310–311):

For my part, following out Lyell’s metaphor, I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly-changing language, in which the history is supposed to be written, being more or less different in the interrupted succession of chapters, may represent the apparently abruptly changed forms of life, entombed in our consecutive, but widely separated formations. On this view, the difficulties above discussed are greatly diminished, or even disappear.

One of the first major responses by the palaeontological community to Darwin’s work was Life on Earth by geologist John Phillips (1860). Phillips found little evidence of the gradual evolutionary series predicted by Darwin’s hypothesis. Some of the oldest known fossils from the Cambrian and Silurian, for instance, already represented complex forms of life that provided no clues as to their ancestors. Phillips regarded them as new creations consistent across multiple localities generated by some unknown law of nature. As Phillips (1860, p. 214) incredulously asked, ‘How is it conceivable that the second stage should be everywhere preserved, but the first nowhere?’

Many found Darwin’s theory intriguing, a ‘secondary law’ for the creation of species worthy of consideration, but overall it received a mixed reception (Bowler 2007). Of those who were more impressed by Darwin’s work, however, perhaps none is as well known as the British anatomist Thomas Henry Huxley. Today, Huxley is often referred to as ‘Darwin’s Bulldog’, the ‘General’ who fought Darwin’s battles while the elder naturalist remained at his estate, but vertebrate palaeontologists often cite Huxley for a different reason. Since the 1960s an overwhelming flood of evidence has illustrated that birds are living dinosaurs (Zhou 2004; Norell & Xu 2005; Chiappe & Dyke 2007), and Huxley is often credited in both the technical and popular literature as being the first to propose that birds evolved from dinosaurs (e.g. Osborn 1900; Olson & Thomas 1980; Bakker 1986; Paul 1988; Norman 1991; Psихонос & Knoebber 1994; Norell et al. 1995; Weishampel & Young 1996; Chatterjee 1997; Shipman 1998; Feduccia 1999; Larson & Donnan 2002; Zhou 2004; Norell & Xu 2005; Farmer 2006; Chiappe 2007; Codd et al. 2008).

Much like the overblown claim that Huxley trounced Bishop Samuel Wilberforce in a debate at Oxford in 1860 (Gould 1991), however, the idea that Huxley perfectly anticipated the modern confirmation that birds are living dinosaurs is an example of ‘textbook cardboard’ (sensu Gould 1987). This can be defined as a past notion that appears to have predicted recent discoveries but is, in reality, abstracted and ripped from their proper context, a technique often used to lend weight to a particular idea or deconstruct unfavourable notions. In this particular case, authors and researchers have cited Huxley’s work to support the idea that birds were thought to have evolved from dinosaurs as soon as Archaeopteryx was discovered, and that recently discovered evidence confirms what Huxley had hypothesized nearly 150 years ago. A survey of Huxley’s work, however, does not bear out such gross summation.

Owen and Archaeopteryx

Although human interest in fossils has a long history (Mayor 2000), it was not until the late eighteenth century that palaeontology became a systematic study of ancient life (Rudwick 1976). With a scientific framework combining geology and comparative anatomy in place, the bones of dinosaurs began to be recognized as belonging to ancient, non-mythological beasts that had lived and died during some past era. The first fragmentary fossils found were most similar to those of living reptiles, so it
was reasonable that their first describers assumed that the creatures resembled enormous versions of extant lizards and crocodiles (Buckland 1824; Mantell 1825). *Iguanodon*, in particular, was thought to be a gargantuan lizard, nearly identical to the living reptile from which the name of the taxon had been derived. The lizard-like interpretation did not last long. When Richard Owen coined the term ‘Dinosauria’ (Owen 1842) he created a new, mammal-like image for the group. Rather than being gigantic lizards, dinosaurs were more like living ‘pachyderms’, the ‘highest’ of the reptiles. Owen’s revised interpretation of dinosaurs was given physical form in the sculptures created by Benjamin Waterhouse Hawkins, and Owen’s role as scientific advisor to Hawkins allowed him to create lasting monuments of his particular palaeontological vision (Desmond 1982).

It was Owen’s interpretation of dinosaurs that was at the fore when the first skeleton of *Archaeopteryx* was discovered in 1861. At the time the fossil record of birds was thought to stretch back into the Triassic (Hitchcock 1836, 1858) based on fossil tracks, and in 1860 a single feather impression was found from the Jurassic rock of a German limestone quarry. This feather was named *Archaeopteryx lithographica* by palaeontologist Hermann von Meyer (1861a, b, 1862), and in 1861 a fossil skeleton representing the rest of the animal was recovered from a similar quarry. This is the fossil that would become known as the ‘London specimen’ of *Archaeopteryx*, and it was the oldest skeleton of a bird yet discovered. *Archaeopteryx* was no common sparrow or finch, however: it possessed both avian and reptilian characters. As such it was precisely the sort of transitional form that Darwin’s theory predicted. In a letter dated 3 January 1863, palaeontologist Hugh Falconer wrote to Darwin about the fossil (Falconer 1863), beaming:

Had the Solenhofen quarries been commissioned – by August command – to turn out a strange being a` la Archæopteryx – it could not have executed the behest more handsomely – than in the Archæopteryx.

Darwin (1863a) replied that he longed to see the fossil, and in a letter to American palaeontologist J.D. Dana wrote: ‘Oh how I wish a skeleton could be found in your so-called Red Sandstone footstep-beds’, from which the footprints of Triassic ‘birds’ were already known (Darwin 1863b). Not everyone shared Darwin’s enthusiasm, however. One of the earliest descriptions of the fossil, based on the verbal report of a Mr Witte who had seen the fossil while in the possession of its first owner Dr Haberlein, was made by the German palaeontologist Johann Andreas Wagner. Wagner’s publications about the fossil (Wagner 1861a, 1862) warned against evolutionary interpretations and he unequivocally deemed *Archaeopteryx* as a long-tailed pterosaur with feathers. Even if it was a transitional fossil, Wagner argued, it was but one isolated form; where were the other intermediates predicted by Darwin’s theory? (Wagner 1861b).

Wagner died shortly after voicing his concerns in 1861, but the debate over *Archaeopteryx* continued. The fossil was purchased from Haberlein by the British Museum, where it was described by Richard Owen in 1862 (Owen 1863). Owen recognized that the single feather discovered in 1860 which von Meyer used to name *Archaeopteryx* may not have come from the same kind of animal represented by the skeleton, but he retained von Meyer’s appellation and identification. *Archaeopteryx* was a bird, the ‘by-fossil-remains-oldest known feathered Vertebrate’ (Owen 1863, p. 46). Moreover, the caudal vertebrae of *Archaeopteryx* closely resembled those of living birds during embryonic development, and this allowed Owen to make reference to his notion of morphological archetypes because the bird exhibited ‘a retention of a structure embryonal and transitory in the modern representatives of the class, and a closer adhesion to the general vertebrate type’ (Owen 1863, p. 46). Unfortunately, the head of the London *Archaeopteryx* was thought to be missing, and its conspicuous absence caused the bird to be depicted without one in *The World Before the Deluge* (Figuier 1866) (Fig. 1.). This did not bring into question the affinities made clear by the available remains, however, and Owen proposed that when the skull was found it would be much like those of living birds: ‘By the law of correlation we infer that the mouth was devoid of lips, and was a beak-like instrument fitted for preening the plumage of *Archaeopteryx*’ (Owen 1863, p. 47).

**Huxley’s sojourn into palaeontology**

Huxley critiqued Owen’s description of *Archaeopteryx*, motivated at least in part by his grievances with the elder anatomist, but he did not do so until 1868. This delay must be understood in the greater context of Huxley’s sojourn into palaeontology. As a young man Huxley got his scientific start studying cnidarians and other invertebrates collected during his voyage as an assistant surgeon in the Royal Navy aboard the HMS *Rattlesnake* (1846–1850). Influenced by the German school of anatomical science (Di Gregorio 1982), he was most concerned with finding the common denominator of form, an abstract archetype to rival Owen’s Platonic one (Desmond 1997). Palaeontology in and of itself was of little interest, particularly as Huxley viewed it as being tied to notions of ‘Progress’. That Christian theology could co-opt the succession of forms
seen in the fossil record for its own philosophical ends was anathema to Huxley, and the invocation of the Divine in nature become ever more distasteful to him as he moved among the circles of the learned and avant-garde (Desmond 1997).

In 1859 Huxley changed scientific course and described a number of fossil creatures that had been imported from South Africa, and he would soon extend his research to pterosaurs, ‘labyrinthodont’ amphibians, crocodylians and South American fossil mammals. Combined with the influence of On the Origin of Species, this research programme got Huxley thinking about what the fossil record had to say about evolution. Although struck by On the Origin of Species, Huxley’s vision of evolution was starkly different from Darwin’s (Lyons 1993). This is best represented by his paper ‘On the persistent types of animal life’ (Huxley 1859). Taking a cue from Lyell’s uniformitarian philosophy, Huxley recited the consensus view that the Earth had changed little from the Cambrian or Silurian era, and the same geological forces acted then as they did now. Nothing could be said of what occurred during the ages preceding the known strata, however, and the Earth was assuredly older than even the most ancient rocks then known. Huxley applied this programme to palaeontology, and explained that many fossil animals had living representatives with the extant and extinct forms differing little from one another. This showed that many groups had survived for enormous amounts of time and such examples could be called ‘persistent types’.

Citing numerous ‘living fossils’, from crocodylians to conifers, Huxley saw a fossil record that revealed little change. Yet, the concept of persistent types created problems for evolution by natural selection (‘a hypothesis which, though unproven and sadly damaged by some of its supporters, is yet the only one to which physiology lends any countenance’ (Huxley 1859, p. 153)) as it did not answer the question of when certain groups of organisms had evolved. Pre-geological time held the answer, and Huxley supposed that the evolutionary changes that took place before known geological time were far greater than any actually recorded in the known fossil record. Three years later Huxley reiterated these views, using many of the same examples, during an address to the Geological Society on the state of palaeontology (Huxley 1862).

Even though he was still thinking in terms of shared anatomical form, Huxley began to attempt to demonstrate the close relationship between reptiles and birds as early as 1863. Lecturing to students at the Royal College of Surgeons, he applied the
designations of ‘Sauroids’ to both reptiles and birds (later changed to ‘Sauropsida’ (Huxley 1869b), meaning ‘reptile faced’), and explained that birds were ‘so essentially similar to Reptiles in all the most essential features of their organization, that these animals may be said to be merely an extremely modified and aberrant Reptilian type’ (Huxley 1863, 1869b). On the other side of the divide, dinosaurs showed the closest approximation to birds: ‘[t]he pelvis and bones of the hind limb are in many respects very like those of birds’ (Huxley 1865, 1869b). Huxley used much the same reasoning, albeit more explicitly, in his survey of bird classification (1867, p. 415):

The members of the class Aves so nearly approach the Reptilia in all the essential and fundamental points of their structure, that the phrase ‘Birds and greatly modified Reptiles’ would hardly be an exaggerated expression of the closeness of that resemblance.

In perfect strictness, no doubt, it is true that Birds are no more modified Reptiles than Reptiles are modified Birds, the reptilian and the ornithic types being both, in reality, somewhat different superstructures raised upon one and the same ground-plan; but it is also true that some Reptiles deviate so very much less from the groundplan than any Bird does, that they might be taken to represent that which is common to both classes without any serious error.

In Huxley’s view, both birds and reptiles were derived from a common ‘superstructure’ from which birds deviated further than reptiles did. This was not an evolutionary system but an anatomical one. A shared ‘groundplan’ did not necessarily reveal an evolutionary relationship, yet some fossil specimens proved exceptions to Huxley’s morphological delineations. The vertebræ of Archaeopteryx were more reptile-like than bird-like and, as had previously been noted by the German anatomist Carl Gegenbaur (Gegenbaur 1864), the hind limbs of the small dinosaur Compsognathus approximated those of birds.

Although Archaeopteryx gained most of the press, Compsognathus was another exceptional fossil recovered from the Solnhofen quarries in 1861. Wagner was the first to note the very bird-like form of Compsognathus in his description of the fossil (Wagner 1861c), and, although he denied any actual kinship between reptiles and birds, Huxley would use the same similarities to pull the groups into close association. In addition, Huxley used shared characteristics between birds, pterosaurs and dinosaurs to make some striking predictions about the metabolism of dinosaurs, perhaps taking a cue from H.G. Seeley (1864). Although the form of the circulatory systems in birds and bats differed, their shared way of life led them to be physiologically similar. Using this concept, Huxley reasoned that even if dinosaurs had a slightly different circulatory set-up than birds they were similar enough to birds morphologically that they too might have been ‘hot-blooded’ (Huxley 1867, p. 418):

Birds have hot blood, a muscular valve in the right ventricle, a single aortic arch, and remarkably modified respiratory organs; but it is, to say the least, highly probable that the Pterosaurs, if not the Dinosauria, shared some of these characters with them.

**Huxley’s search for ancestors**

The publication of Ernst Haeckel’s *Generelle Morphologie* (1866) marked a major shift in Huxley’s thinking. Although Huxley rejected Owen’s Pla-tonic Archetype, the equivalent of a translated idea from the mind of a Creator, he was more concerned with groundplans than evolutionary branching lineages. Haeckel’s work caused him to change direction and start looking for real ancestors (Di Gregorio 1982; Desmond 1997). In January of 1868, the year that would see Huxley dive head-long into his work on dinosaurs and birds, he wrote to Haeckel stating (quoted in Di Gregorio 1982, p. 415):

In scientific work the main thing just now about which I am engaged is a revision of the Dinosauria – with an eye to the Descendenz Theorie! The road from Reptiles to Birds is by way of Dinosauria to the Rattiae – the Bird ‘Phylum’ was Struthious, and wings grew out of rudimentary fore limbs. You see that among other things I have been reading Ernst Haeckel’s Morphologie.

That same year Huxley published ‘On the animals which are most nearly intermediate between birds and reptiles’ (Huxley 1868a). Although he had treaded carefully over the validity of evolution by natural selection in the past, the opening salvo of the paper reveals Huxley’s zeal; the whole of the universe attested to evolution. Yet, evolution was still plagued by a conspicuous lack of transitional forms. If Darwin’s uniformitarian theory was correct – that evolution acted in the past just as it did today – then transitional fossils linking major groups of organisms should have been discovered. Huxley (1868a, p. 358) likened the state of affairs to a landowner who is not able to come up with any title deeds to his properties:

> If a landed proprietor is asked to produce the title-deeds of his estate, and is obliged to reply that some of them were destroyed in a fire a century ago, that some were carried off by a dishonest attorney, and that the rest are in a safe somewhere, but that he really cannot lay his hands upon them; he cannot, I think, feel pleasantly secure, though all his allegations may be correct and his ownership indisputable. But a doctrine is a
scientific estate, and the holder must always be able to produce his title-deeds, in a way of direct evidence, or take the penalty of that peculiar discomfort to which I have referred.

Huxley had to admit that his petrified ‘title deeds’ were largely missing, but he did have ‘a considerable piece of parchment’ (Huxley 1868a, p. 359) that offered a confirmation of his claims. This tattered piece of evidence had ‘Sauropsida’ written on it, and he stated that while ‘a Stork seems to have little animality in common with the Snake it swallows’ (Huxley 1868a, p. 359) there could be little doubt that birds had evolved from reptiles (Fig. 2). The best evidence among birds was to be found among flightless birds like the kiwi (Apteryx), the moa (Dinornis) and the ostrich (Struthio). Rather than being degenerate birds, these were persistent types that approximated the appearance of the earliest birds. Archaeopteryx, bearing claws and a long tail, brought birds even closer to reptiles. It was not a direct ancestor of modern birds, Huxley explained, but an illustration that birds had evolved from reptiles. Thus, Archaeopteryx marked the limit of the avian side of the divide, and with no earlier reptile-like bird for Huxley to jump to he started to work from the bottom up. For Huxley the closest ‘reptilian’ relatives to birds were to be found on the ground among the Dinosauria.

Richard Owen had envisioned dinosaurs as immense, mammal-like quadrupeds, but his interpretation began to be overturned by new discoveries in North America that sparked the first ‘Dinosaur Renaissance’. The indication that Hadrosaurus was at least facultatively bipedal (Foulke & Leidy 1858; Leidy 1865) was crucial in revising the image of the dinosaur into a form that would fit Huxley’s programme. If the North American Hadrosaurus was bipedal then there was little reason to think Iguanodon differed in the way it walked, especially if the large, bird-like tracks discovered in the Wealden (Beckles 1854) were really those of dinosaurs. The hips of dinosaurs were bird-like, their feet were bird-like and the tracks they left were bird-like; it was the dinosaurs that most ‘wonderfully approached’ birds (Huxley 1868a, p. 365). Most of the dinosaurs then known were far too immense to have given rise to birds, however. Huxley avoided this problem by pointing to the diminutive Compsognathus. Although Huxley was not sure whether to place Compsognathus within the Dinosauria or in a new, closely allied category, the avian characteristics of the fossil brought the reptiles close enough to touch the birds (see Fig. 3). Speculating on the appearance of Compsognathus in life Huxley (1868a, p. 365) wrote:

It is impossible to look at the conformation of this strange reptile and to doubt that it hopped or walked, in an erect or semi-erect position, after the manner of a bird, to which its long neck, slight head, and small anterior limbs must have given it an extraordinary resemblance. Yet, Compsognathus was of the same age as Archaeopteryx, too young to be a real ancestor.

Fig. 2. The skeletons of an eagle and a lizard. As different as they might appear to be, Huxley thought that birds and reptiles shared a common body plan. He placed both within the group ‘Sauropsida’. From Bell (1852).

Fig. 3. A restoration of Compsognathus. Huxley wondered if, had such a creature had been covered in feathers, we would call it a bird. From Huxley (1877).
The presence of ‘bird’ tracks in Connecticut also suggested to Huxley that it would be in Triassic strata that ‘birds so much more reptilian than Archaeopteryx, and reptiles so much more ornithic than Compsognathus, as to obliterate completely the gap which they still leave between reptiles and birds’ (Huxley 1868a, p. 366) would be found. Despite this, Huxley did not think it ‘wild’ or ‘illegitimate’ to propose that ‘the class Aves has its root in the Dinosaurian reptiles’ (Huxley 1868a, p. 366). Thus, *Compsognathus* was a persistent form of an actual creature in the line of descent from reptile to bird, leading up to the flightless ratites from which the carinate birds would then be derived. The hypothetical evolutionary arc approximated by *Compsognathus* → ratites → carinates provided an illustration that confirmed Darwin’s theory.

No scientific programme aimed at studying avian evolution could ignore *Archaeopteryx*; yet, as has been illustrated, it was of little importance to Huxley’s hypothetical evolutionary series. Huxley’s description of the fossil bird, read before the Royal Society on 30 January 1868 (Huxley 1868b), was more of a swipe at Owen than an elucidation of the evolution of birds. Huxley opened by asserting that Owen had confused the ventral side of the London specimen with the dorsal side, and the left leg for the right. If the sides were not properly identified then the anatomy of the animal could not be understood. Huxley further charged that Owen had made mistakes about the hips and shoulder girdles of the animal – the younger anatomist characterized Owen’s interpretation as upside-down and inside-out. As the coup de grâce, Huxley attacked Owen’s hypothesis that the head, when found, would bear a toothless beak, using turtles and the pterosaur *Rhamphorhynchus* to express the variability and diversity found within reptiles. Huxley (1868b, p. 248) quipped:

> If when the head of *Archaeopteryx* is discovered, its jaws contain teeth, it will not the more, to my mind, cease to be a bird, then turtles cease to be reptiles because they have beaks.

Given his previous work, it might be expected that Huxley would devote some section of his description to finding a place for *Archaeopteryx* in his reptile to bird series, but no such explanation was undertaken. The bird was simply too derived to be close to the transition from reptiles, being ‘more remote from the boundary-line between birds and reptiles than some living Ratitae are’ (Huxley 1868b, p. 248). The evidence Huxley was looking for would have to be found elsewhere.

In a paper read before the Geological Society in May of 1869 (Huxley 1869a) Huxley described part of the upper jaw of *Megalosaurus* (see Benson et al. 2008 for a current reassessment of the material refereable to this taxon). The specimen was only part of the skull, and a fracture at the front of the skull that did not appear to run along a defined suture hinted that there was more to the skull than Huxley had to work with. Based on the material available, however, Huxley entertained three options: (1) the premaxilla and maxilla were fused; (2) the premaxilla became detached from the maxilla; or (3) the entire upper jaw was the premaxilla, an option with the potential to further connect dinosaurs and birds. Without more evidence no determination could be made about which of these hypotheses was correct, but the ornithischian dinosaur *Hypsilophodon* would soon provide Huxley with a different piece of his evolutionary puzzle. *Hypsilophodon* was recognized as being closely related to *Iguanodon* (it was initially thought to be a new, miniature species of that genus) and Huxley described it before the Geological Society in November of the same year (Huxley 1870a). Much like his earlier *Archaeopteryx* paper, the description generally lacked evolutionary interpretations, but the small skeleton did reveal at least one important feature; the ischium and pubis were preserved, and both pointed backwards in a fashion similar to that seen in birds.

If Huxley held back his evolutionary considerations in the *Hypsilophodon* description, he opened the floodgates with a paper read at the same meeting entitled ‘Further evidence of the affinity between the dinosaurian reptiles and birds’ (Huxley 1870b). As described in the introduction of the paper, Huxley had coincidentally met up with John Phillips in October of 1867 and Phillips had encouraged Huxley to view the geological collection under his care at Oxford. There Huxley noticed something strange about the *Megalosaurus* bones in the collection: the ‘scapula’ was truly part of the ilium. When he realized this the bird-like traits of the skeleton suddenly became more apparent, and another bone (previously identified as a clavicle) appeared to be part of the ischium. (According to a letter by Phillips included in the paper it seems that the Oxford scientist had already suspected that some of the bones were not correctly identified – Huxley made his visit in the midst of Phillips’ reinvestigation.)

The rearranged bones reflected a creature with small forelimbs and a more bird-like hip, an image of *Megalosaurus* that departed from Owen’s elephantine vision. Huxley resolved to undertake a study of how the anatomy of *Megalosaurus* corresponded to those of other dinosaurs, but what Huxley did not know was that on the other side of the Atlantic the American palaeontologist Edward Drinker Cope was coming to similar conclusions about birds and reptiles (Cope 1866, 1867a, 1868)
based on the bipedal predatory dinosaur *Laelaps* (later changed to *Dryptosaurus* (Marsh 1877)). Cope thought that the ankle joint of the terror of the ancient New Jersey coast resembled that of an embryonic chick, and he also recognized the avian character of the ankle joint in *Compsognathus* as initially pointed out by Gegenbaur (Cope 1867b, 1869). Just as Huxley was doing in his own research, Cope used flightless birds to bring reptiles and birds together, although he favoured penguins as the birds morphologically closest to reptilian ancestors.

Although impressed with Cope’s views, Huxley disagreed on a few points, particularly the shape of the dinosaurian pelvis. Bones identified as the ‘clavicles’ of dinosaurs, for instance, often turned out to be part of the hip — Cope thinking that they were forward-oriented pubes and Huxley insisting that they were rear-pointing ischia. Huxley marshalled the hips of *Hypsilophodon* in support of his view, but it was the whole of the hip, leg and foot morphology that provided the best evidence for a reptile–bird connection (Huxley 1870b, p. 31):

> if the whole hind quarters, from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the Dinosauria.

Not everyone present for the reading of Huxley’s paper was impressed by the similarities, however. Harry Seeley, a young expert on pterosaurs, thought the hindlimb characteristics Huxley used to support a close relationship between dinosaurs and birds were only signs of a shared mode of life. Furthermore, Seeley argued, dinosaurs were so different from birds, mammals and reptiles that they should be separated into a new, distinct group. Huxley disagreed with Seeley, opining that the study of nature revealed a blurring of lineages rather than sharp divisions.

**Huxley reinvents the Dinosauria**

Huxley was now ready to unveil his revised taxonomic groupings of dinosaurs within the Sauropsida (Huxley 1870c). His first step was to permanently tear down the vision of dinosaurs characterized in the works of other authorities like Owen and von Meyer. In so doing Huxley had to rediagnose the entire group, setting out a 12-point list (including two–six sacral vertebrae, thecodont teeth and a bird-like astragalus, among other characters) with which to give the Dinosauria a firm foundation. Under this system he placed the ‘*Megalosauroidae*’, ‘*Scelidosauridae*’ and ‘*Iguanodontidae*’ within the Dinosauria, but *Compsognathus* did not appear to naturally fit into any of these groups even though all were ‘ornithic modification[s] of the Saurian type’ (Huxley 1870c, p. 36). Instead, he placed *Compsognathus* in a separate group, the ‘*Compsognatha*’. Cope had previously created a similar classification, setting *Compsognathus* aside in his ‘Ornithopoda’ while he placed the rest of the Dinosauria in the ‘Goniopoda’, but Huxley disagreed with Cope’s reliance on an ankylosed astragalus as a definitive character and so erected his own groups.

Using terminology to his advantage, Huxley then grouped the Dinosauria and ‘*Compsognatha*’ together in the new group ‘*Ornithoscelida*’, thus recognizing a group of ‘bird-legged reptiles’ within the larger, more inclusive, ‘*Sauropsida*’. Among his reptilian groups, organized by characteristics of the vertebrae, the ‘*Ornithoscelida*’ was grouped with crocodylians, dicynodonts and pterosaurs under the ‘*Suchospondylia*’. Huxley proposed that the dicynodonts and crocodylians were the closest relatives of the dinosaurs, and he predicted that lizard-like ancestral forms for each group might be found during the Permian or some earlier period.

Huxley’s comparison of the ‘*Ornithoscelida*’ with birds, however, was much more important. Huxley ruled out pterosaurs as bird relatives because their similarities arose from common ‘physiological action and not . . . affinity’ (Huxley 1870c, p. 39). In contrast, the similar leg and hip characteristics of the ‘*Ornithoscelida*’ were seen in all birds, both flying and non-flying, but Seeley’s objection about convergence had left a mark on Huxley. Although bipedal dinosaurs were a major part of his new vision for the ‘*Ornithoscelida*’, Huxley deemed the large members of the Dinosauria to be facultative bipeds, doubting that they ‘stood more habitually upon their hind limbs than Kangaroos or Jerboas do’ (Huxley 1870c, p. 39). If all birds always stood on their hind legs but members of the Dinosauria could switch between bipedal and quadrupedal motion then the resemblances in their limb morphology could truly be said to illustrate a ‘genetic connexion’ and not just convergence due to shared habits (Huxley 1870c, p. 39).

With a quick note of how the ‘breast bone’ of dinosaurs resembled the sternum of birds, Huxley dived into a review of Triassic dinosaurs known from Europe, India and North America, but it was again his presentation on the relationship of birds to the ‘*Ornithoscelida*’ that stirred the most commentary. Roderick Murchison, the eminent geologist who established the hotly debated Silurian system, asked of the oldest known strata from which bird-like dinosaurs were known. The reply pointed to the Triassic, if not even older, strata. It was Seeley who, again, challenged Huxley,
however, noting that a common morphological plan for all reptiles had to be identified before a classification could stand. Citing his own work that was shortly to be published (Seeley 1870), Seeley stated that his own classification came out differently. Unfortunately, the transcript of the discussion does not illuminate details, noting only that Huxley ‘was pleased to find that there was such a diversity of opinion between Mr. Seeley and himself, as it was by discussion of opposite views that the truth was to be attained’ (Huxley 1870c, p. 50).

What did Huxley mean by a ‘genetic connexion’ between birds and the Ornithoscelida? Were dinosaurs the progenitors of birds? Although Huxley (1870d, p. 24) called the Dinosaurs ‘the links between reptiles and birds’, in a short review of Triassic dinosaurs in Nature his views on the subject were more explicitly laid out in an address to the Geological Society (Huxley 1870e). Huxley still maintained his notion of persistent types, and his palaeontological work reinforced the concept that he had outlined before the same society years before. If evidence for evolution was to be found, it was amongst the ‘higher’ groups of vertebrates, but Huxley urged caution in teasing out the details. Simply because lineages of intermediates could be constructed connecting one form to another did not automatically mean that evolution occurred in such a sequence. Huxley warned ‘it is always probably that one may not hit upon the exact line of filiation, and, in dealing with fossils, may mistake uncles and nephews for fathers and sons’ (Huxley 1870d, p. xlix). The creatures representing the expected intermediate form, the ‘uncles and nephews’, could be called intercalary types, while those that could be proven to be on the direct line, the ‘fathers and sons’, were dubbed linear types (Huxley 1870d, p. xlix). Despite the amount of effort he put into pulling birds and dinosaurs together, the members of the ‘Ornithoscelida’ could only be considered evolutionary ‘uncles and nephews’ (Huxley 1870d, p. li):

At the present moment we have, in the Ornithoscelida the intercalary type, which proves that transition [‘from the type of the lizard to that of the ostrich’] to be something more than a possibility; but it is very doubtful whether any of the genera of Ornithoscelida with which we are at present acquainted are the actual linear types by which the transition from the lizard to the bird was effected. These, very probably, are still hidden from us in the older formations.

While a known direct line of descent might have been defensible for horses (from Anchitherium to Hipparion to Equus), no such line could be drawn from dinosaurs to birds. The ‘ornithichnites’ from the Triassic sandstone of the Connecticut Valley and the hypothetical existence of dinosaurs during the Permain further complicated matters. If there were Triassic birds and Permian dinosaurs then the creatures from which birds evolved must have been even older still, but their location and age were a mystery. This ran counter to the notion that the geological strata were well sampled and represented a good approximation of the succession of life, and Huxley urged that there was more to discover.

Reptiles into birds: a popular transition

After 1870 Huxley’s research into the relationship between birds and reptiles, and palaeontology in general, slowed. His focus shifted towards bringing nature in from the field to be cut up under the microscope, and he overworked himself to the point that, by the beginning of 1872, his wife Nettie sent him on vacation to Egypt to recuperate (Desmond 1997). When he returned he threw himself back into his work but was more concerned with establishing a sound morphological programme than continuing to pick at gigantic bones. Huxley did not simply drop the subject, however, and the relationship between reptiles and birds ranked as one of his primary illustrations of evolution during his 1876 tour of the United States.

In a lecture delivered in New York on 20 September 1876 (Huxley 1877) Huxley reiterated the presence of persistent types, but with a twist. Darwin’s theory of evolution by natural selection, in which the environment acts upon variation, would cause creatures to evolve if environmental conditions changed. If conditions were stable then the organisms, too, would undergo little change. This made sense of both evolution and persistence, thus negating the problem of lineages that seemed to show little or no evolutionary change. The explanation that the fossil record was an imperfect one further defused objections to Huxley’s arguments; the Triassic red sandstone ‘bird tracks’ were perfect examples of the vagaries of preservation. Although the tracks were seemingly innumerable, no skeletons of the trackmakers had been found.

With living birds and reptiles divided by an anatomical gulf, Huxley set out to connect the two for his audience as he had done in his technical works. The research of O.C. Marsh provided Huxley with extra ammunition: the toothed birds Hesperornis and Ichthyornis (Marsh 1875) were avians with a classic reptilian characteristic, and raised the possibility that the still-headless Archaeopteryx may have had a mouth full of teeth. Still, Marsh’s birds and Archaeopteryx chiefly served to show that taxonomic boundaries erected through the study of extant organisms alone could be broken by evolution, and that fossil creatures featuring a mix of characters from different groups did exist. Archaeopteryx was still, at best, an intercalary
type. Echoing his caveats about ‘uncles and nephews’ from his 1870 Geological Society address Huxley told the audience (Huxley 1877, p. 59):

But it by no means follows, because the Palaeotherium has much in common with the Horse, on the one hand, and with the Rhinoceros on the other, that it is the intermediate form through which Rhinoceroses have passed to become Horses, or vice versa: on the contrary, any such supposition would certainly be erroneous. Nor do I think it likely that the transition from the reptile to the bird has been effected by such a form as Archaeopteryx.

Indeed, it was the ‘Ornithoscelida’ that held the key to the evolutionary puzzle. Using a diagram first printed in his 1871 textbook on vertebrate anatomy (Huxley 1871), Huxley compared the legs and hips of a bird, a generalized dinosaur and a crocodile made to ‘stand up’ (see Fig. 4). The leg of the ‘ornithoscelidan’ more closely resembled that of the bird, but was still intermediate between the bird and crocodile. (This diagram was of sufficient use that it was still being used in Harvard anatomy classes in 1890: Pick & Sloan 2004). The ‘ornithoscelidan’ form, based on Hypsilophodon, seemed to perfectly link the representation of the living bird and reptile, yet it was Compsognathus that Huxley considered to be the most bird-like. The anatomist opined, ‘There is no evidence that Compsognathus possessed feathers; but, if it did, it would be hard indeed to say whether it should be called a reptilian bird or an avian reptile’ (Huxley 1877, p. 66).

Interestingly, compsgnathids with ‘proto-feathers’, like Sinosauropteryx, have since been discovered: Chen et al. 1998).

Huxley also wavered on the notion that the famous Triassic tracks from New England were made by birds. As at least some members of the ‘Ornithoscelida’ were considered to walk bipedally, and dinosaurs had been found in the same strata as immense three-toed tracks from the Wealden, it was possible that the New England tracks were also made by dinosaurs. (This would soon turn out to be the correct interpretation.) Huxley refrained from coming down on one side or the other, but he did think that if the trackmakers could be identified, they would help naturalists to understand the evolution of birds (Huxley 1877, p. 66):

it becomes a very important question whether the tracks in the Trias of Massachusetts, to which I referred some time ago, and which formerly used to be unhesitatingly ascribed to birds, may not all have been made by Ornithoscelidan reptiles; and whether, if we could obtain the skeletons of the animals which made these tracks, we should not find in them the actual steps of the evolutional process by which reptiles gave rise to birds.

Still, even the Triassic creatures might have been too young, and Huxley proposed that birds may have already been present at the beginning of the Mesozoic. The known members of the ‘Ornithoscelida’ may have only been persistent types, descendants of earlier creatures that lived when reptiles evolved into birds (Huxley 1877, p. 67):

Fig. 4. A comparison of the hips and legs of a bird, a generalized ‘ornithoscelidan’ and a crocodile. This figure was meant to illustrate the similarity between the legs and pelves of dinosaurs and birds. From Huxley (1877).
It is, in fact, quite possible that all these more or less avi-form reptiles of the Mesozoic epoch are not terms in the series of progression from birds to reptiles at all, but simply the more or less modified descendants of Palaeozoic forms through which that transition was actually effected.

We are not in a position to say that the known *Ornithoscelida* are intermediate in the order of their appearance on the earth between reptiles and birds. All that can be said is that if independent evidence of the actual occurrence of evolution is producible, then these intercalary forms remove every difficulty in the way of understanding what the actual steps of the process, in the case of birds, may have been.

Huxley would reiterate similar statements in a series of notes on the origins of major vertebrate groups published the same year in *Nature* (Huxley 1876a, b). His reptilian and avian intercalary types were more important for illustrating that evolution by natural selection occurred than solving all the questions about the origin of birds. Huxley again took up this position in an 1880 lecture delivered to the Royal Institution on the state of evolution by natural selection (Huxley 1880) in which he stated that the evolution of birds from reptiles confirmed Darwin’s predictions. Further resolution on the origin of birds proved elusive, however. Huxley had built the avian evolutionary groundwork, but very little had been added to it outside of Marsh’s toothed Cretaceous birds.

**Conclusion**

Huxley (1882) briefly returned to the topic again in one of his last papers, *On the respiratory organs of Apteryx*. After refuting the notion that the respiratory system of this bird closely resembled that of mammals, Huxley noted that pneumatic bones such as those possessed by birds are only seen elsewhere in crocodilians, pterosaurs and dinosaurs. Although the respiratory organs of dinosaurs were entirely missing, and there was no expectation of them being found, Huxley still proposed that the ‘*Ornithoscelida*’ may have had a similar physiology (Huxley 1882, p. 569):

Thus, notwithstanding all the points of difference, there is a fundamental resemblance between the respiratory organs of Birds and those of Crocodiles, pointing to some common form (doubtless exemplified by some of the extinct *Dinosauria*), of which both are modifications.

Such a statement could be easily misconstrued as proposing that dinosaurs were the ancestors of birds (or the intermediate type from which both crocodiles and birds evolved), but the vast amount of literature Huxley produced on this subject does not allow for such a conclusion. Huxley came so tantalizingly close to pinning dinosaurs as the ancestors of birds that later researchers have often posthumously put those words in his mouth, promulgating a ‘textbook cardboard’ version of his views. Even if Huxley privately entertained the idea that birds had evolved from a dinosaur like *Compsognathus*, as implied in his 1868 letter to Haekel, he explicitly urged caution in his published scientific work. Dinosaurs and birds were linked by form, their morphology revealing a common ancestry, but in both his public lectures and scientific papers Huxley was agnostic as to precisely what might have existed at the evolutionary nexus between the groups. Despite such caveats, Huxley did more than any other naturalist of his era to popularize the close relationship between birds and reptiles. Wagner, Gegenbaur, Cope and others recognized the bird-like traits of dinosaurs contemporaneously, but it was Huxley who turned similarities in form into compelling evidence of evolution by natural selection. During a time when the fossil record appeared to be at odds with Darwin’s theory, Huxley endeavoured to find examples of transitional forms and he found just that in the evolution of birds from reptiles.

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