A short history of research on *Archaeopteryx* and its relationship with dinosaurs

PETER WELLNHOFER

Gelbenholzener Strasse 36, D-82256 Fürstenfeldbruck, Germany
(e-mail: p.wellnhofer@t-online.de)

Abstract: *Archaeopteryx*, first discovered in 1861 from the Solnhofen lithographic limestone of Bavaria, is the oldest feathered animal in the fossil record. Since its discovery it has been the focus of discussions about avian ancestry. Its mosaic of saurian and avian skeletal characters made it the classical 'missing link' of the Darwinian Theory of evolution. Even as early as 1868 Huxley advocated a close dinosaurian relationship of birds, a position followed later by such palaeontological luminaries as Marsh, Baur, Nopcsa and Abel, among others. Only in 1926, when Gerhard Heilmann published his seminal work, *The Origin of Birds*, was a 'thecodontian' origin of birds favoured. This book dominated perceptions of avian origins for the next half century, until John H. Ostrom reinvigorated the hypothesis of a dinosaurian ancestry for birds based on more *Archaeopteryx* specimens and new discoveries of theropod dinosaurs. Finally, the advent of cladistic methodology was instrumental in supporting *Archaeopteryx* and Aves within the theropod clade Maniraptora, a view almost ubiquitous today.

Since its initial discovery in 1861 in the Upper Jurassic Solnhofen lithographic limestone of southern Germany, *Archaeopteryx* has been the subject of debate and controversy because of its mix of classically 'reptilian' and 'avian' characters, and because it was the oldest feathered animal in the fossil record. Early discussions about this peculiar animal centred around the question of whether *Archaeopteryx* was optimally classified as a bird or a saurian, or was instead a transitional form between the two categories. Although a 'reptilian' origin of birds was generally accepted, conflicting hypotheses developed about the specific relationships of *Archaeopteryx* to various ancestral groups, predominantly 'thecodonts', crocodylomorphs and theropod dinosaurs.

The *Archaeopteryx* specimens – the fossil evidence

Archaeopteryx discoveries are rare events. The 10 skeletal specimens presently known and an isolated feather derive from the Upper Jurassic Plattenkalk, the Solnhofen lithographic limestone, of Bavaria; no other fossil Lagerstätte has produced one.

The single feather

The *Archaeopteryx* story began in the Solnhofen Community Quarry in the summer of 1861 with the discovery of a single feather, preserved in all its details as an imprint on a plate of limestone. Although seemingly insignificant, this fossil became a scientific sensation, receiving the highest level of attention from palaeontologists. Frankfurt palaeontologist Hermann von Meyer created the scientific name, *Archaeopteryx* ('ancient feather'), in 1861. To record the fossil's origin from the lithographic limestone, he erected the species name, *lithographica.* He referred to the fossil feather as 'the first remnant of a bird from pre-Tertiary times' (Meyer 1861*a*, 1862). It was the first indication of the existence of birds in the Jurassic, and was likewise evidence of the oldest known bird in the fossil record. Both counter slabs of the original fossil are housed today in the museums of Berlin and Munich, respectively.

The London specimen

In the very same year, 1861, in a Langenaltheim quarry near Solnhofen the first skeleton of *Archaeopteryx* was found, showing clear impressions of wing and tail feathers but seemingly lacking the skull (Fig. 1). The specimen was first described by Owen (1863*a*, *b*), who named it *Archaeopteryx macrura.* Designated as the 'London specimen' today, it was bought by the British Museum, London, where it is housed in the Natural History Museum. de Beer (1954) assigned it to *Archaeopteryx lithographica.*

The Berlin specimen

The second skeleton (and still the best *Archaeopteryx* specimen) showing the skull for the first time and displaying the plumage in perfect preservation was found near Eichstätt in 1876. It went to the Mineralogical Museum of Berlin University,

From: Moody, R. T. J., Buffetaut, E., Naish, D. & Martill, D. M. (eds) *Dinosaurs and Other Extinct Saurians: A Historical Perspective*. Geological Society, London, Special Publications, **343**, 237–250.
DOI: 10.1144/SP343.14 0305-8719/10/$15.00

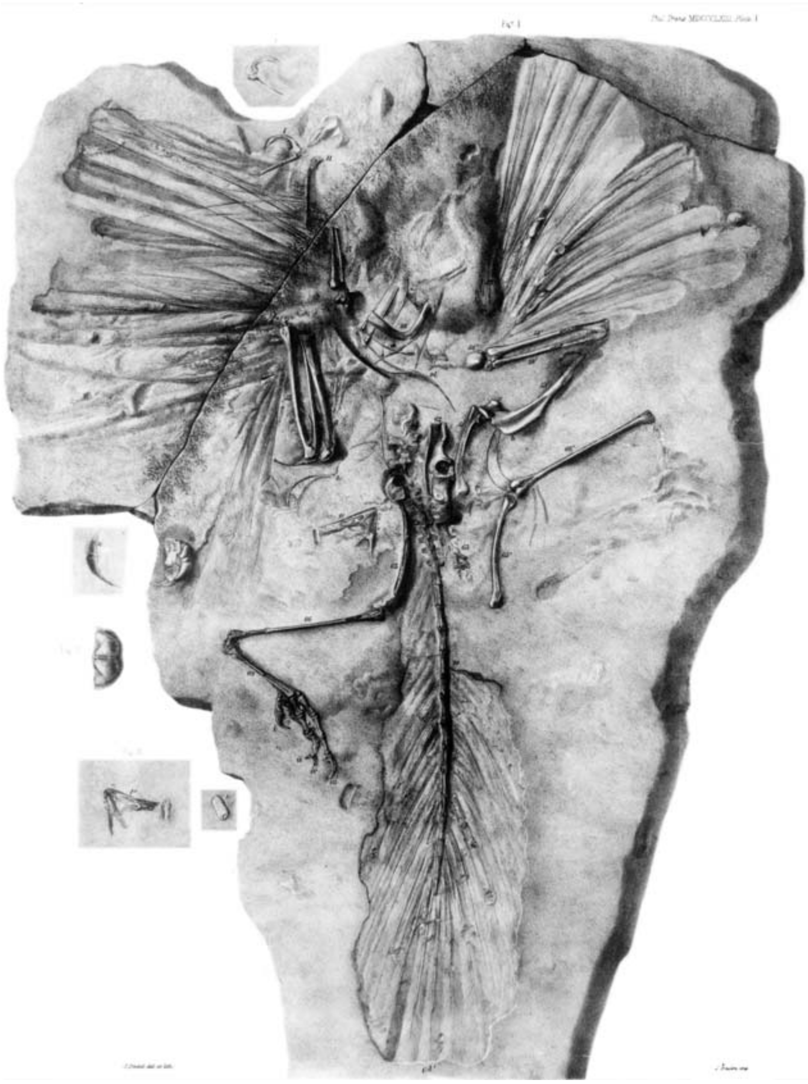

Fig. 1. The London specimen of *Archaeopteryx*, found near Solnhofen in 1861, was figured as a folded lithograph in natural size published by Richard Owen (1863*b*).

later to become the Museum für Naturkunde of Humboldt University, and is known as the 'Berlin specimen'. It was studied first by Dames (1884). Later, in 1897, he named it *Archaeopteryx siemensii*, and Petronievics (1921) gave it a distinct genus, *Archaeornis*, a separation that has not been generally accepted.

The Maxberg specimen

The third specimen, a disarticulated, incomplete skeleton with feather imprints lacking the skull and the tail, was found in 1956, not far from the locality of the London specimen. It had been called the 'Maxberg specimen' because it was on display in the local museum on the Maxberg near Solnhofen. After its owner had withdrawn it from display in 1974, it disappeared and is considered to be lost. The specimen was first described by Heller (1959) as *Archaeopteryx lithographica*.

The Haarlem specimen

Even as early as 1855, a rather fragmentary, partial specimen was found in a Plattenkalk quarry near Riedenburg that was originally identified as a pterodactyl by Meyer (1857, 1859–1860). It was only in 1970 that John Ostrom recognized it in the collections of the Teyler Museum in Haarlem, The Netherlands, as the skeletal remains of an *Archaeopteryx*. He described it in detail and assigned it to *Archaeopteryx lithographica* (Ostrom 1972). It is known as the 'Haarlem specimen' today.

The Eichstätt specimen

The fifth skeletal specimen of *Archaeopteryx* came to light in 1973 when F. X. Mayr announced its existence (Mayr 1973). However, it had actually been found in 1951 in the vicinity of Eichstätt, but not recognized at that time. It is an almost complete skeleton with feather imprints and with a perfectly preserved skull. It is the smallest individual so far known and was taken to be a juvenile of *Archaeopteryx lithographica* by Wellnhofer (1974). However, it was assigned to a new taxon, *Jurapteryx recurva* by Howgate (1985). This 'Eichstätt specimen' is housed in the Jura-Museum in Eichstätt.

The Solnhofen specimen

In 1987 the sixth *Archaeopteryx* specimen, a not quite complete skeleton, became known to the public. It originated from a private collection in Solnhofen and was purchased by the community of Solnhofen for display in the Bürgermeister-Müller-Museum, there. Its original locality and time of discovery have not been disclosed. After the location of its depository, it is called the 'Solnhofen specimen'. The largest individual so far known, it was first described by Wellnhofer (1988) as *Archaeopteryx lithographica*, but was assigned to a new taxon, *Wellnhoferia grandis*, by Elzanowski (2001*a*).

The Munich specimen

Not far from the quarries in which the London and Maxberg specimens had been found, a seventh skeletal specimen of *Archaeopteryx* was discovered in 1992 showing feather impressions and new osteological details. It was secured by the Bavarian State Collection of Palaeontology and Geology in Munich, and is thus called the 'Munich specimen'. It was first described by Wellnhofer (1993) and assigned to a new species, *Archaeopteryx bavarica*.

The eighth specimen

A very fragmentary, badly preserved specimen including skull and a few long bones was obtained from the Mörnsheim Formation overlying the Solnhofen limestone at a quarry near Daiting. It is in private ownership and has recently been deposited in the Munich State Collection. After a preliminary description published by Mäuser (1997) a detailed study has been carried out by Tischlinger (2009). He called it the *Daiting* specimen of *Archaeopteryx*.

The ninth specimen

In 2004 an isolated wing skeleton of an *Archaeopteryx* was found in the oldest Solnhofen quarry. It is in private ownership, but is on public display in the Solnhofen Museum on a permanent loan basis. This 'Ninth specimen' was first described by Wellnhofer & Röper (2005) as *Archaeopteryx lithographica*.

The Thermopolis specimen

Finally, in 2001, a 10th skeletal specimen of *Archaeopteryx* turned up in a private collection in Switzerland, and has been purchased by an anonymous donor for deposition and public display in the Wyoming Dinosaur Center in Thermopolis, Wyoming, USA. Therefore called the 'Thermopolis specimen', it was studied in detail by Mayr *et al.* (2005, 2007) and designated as *Archaeopteryx siemensii*. It is one of the best preserved and most complete *Archaeopteryx* specimens known. Its original locality and horizon were not made public, but it seems to have originated from the Eichstätt quarry district.

Detailed descriptions and the history of all of the *Archaeopteryx* specimens can be found in Wellnhofer (2008, 2009).

Early scientific debates and controversies between 1861 and 1876

Until the discovery of the 'feathered dinosaurs' from China in the 1990s, feathers had been a significant character, diagnostic exclusively for birds. In the traditional Linnaean classification based on extant animals there was a clear separation of the Class Aves from all other vertebrates. The same applied to the Class Reptilia, composed of the extant orders Testudines, Sphenodonta, Squamata and Crocodylia. The boundaries between these discreet categories were rather clear but inflexible, and fossils such as *Archaeopteryx* that exhibit a mosaic of features traditionally identified with different groups posed unique problems. Today, of course, it is widely recognized that evolutionary entities do not naturally occur in discreet groups but instead along a continuous spectrum that is poorly encapsulated by categorization. But even in Linnaean terms, this is especially well exemplified by the continuing debate of whether *Archaeopteryx* was a dinosaur-like bird or a feathered, bird-like dinosaur.

According to modern 'phylogenetic systematics' the traditional class Reptilia is no longer tenable as representing a phylogenetically unified, monophyletic, group. It is considered a paraphyletic association of tetrapods that are not monophyletic, i.e. do not share a common ancestor. However, in this historical context, using the terms 'Reptilia', 'reptiles' and 'reptilian' is justifiable.

Archaeopteryx – bird, saurian or intermediate?

In 1861, even more than the isolated feather, the first *Archaeopteryx* skeleton with feather imprints, the London specimen, aroused emotions. Indeed, it inflamed learned disputation as to whether this animal was a bird with reptilian characteristics, a saurian with bird-like feathers, or some kind of intermediate or transitional form between the reptiles and the birds.

To comprehend the controversies, one must remember the disturbance caused by Charles Darwin, who had recently (November 1859) published his book *The Origin of Species by means of Natural Selection. Or the Preservation of Favoured Races in the Struggle for Life*. Therein Darwin presented his Theory of Evolution, which proposed that all forms of life were related insofar as they ultimately descended from a single organism. With his theory of descent Darwin especially offended believers in biblical creation. One of the first objections to Darwin's theory concerned the so-called missing links. If, indeed, life on Earth had a single origin and all later species have evolved from one another, then there must have been intermediates or transitional forms in the fossil record; and these links seemed to be missing.

Andreas Wagner

Munich palaeontologist Andreas Wagner was one of the first who recognized the meaning of *Archaeopteryx* as a 'missing link' for the Darwinian Theory:

> I must add a few words to ward off Darwinian misinterpretations of our new saurian. At the first glance . . . we might certainly form a notion that we had before us an intermediate creature, engaged in the transition from the saurian to the bird. Darwin and his adherents will probably employ the new discovery as an exceedingly welcome occurrence for the justification of their strange views upon the transformations of animals.
>
> (Wagner 1862b, p. 266)

He concluded that the vertebrate was not a bird but a saurian, which he christened *Griphosaurus* (Greek: *griphos*, enigma). Being an orthodox Protestant, he tried to bring the observations of geology and palaeontology into agreement with the biblical narrative of the Creation. There was no place in Wagner's system of the animal kingdom for an intermediate form. A bird, in his view, could not have existed as early as the Jurassic. Consequently, for Wagner, the feather-like imprints on the *Archaeopteryx* skeleton were no proof that they were produced by the real feathers of a bird. He interpreted them instead as 'peculiar adornments' of the *Griphosaurus* that merely possessed the external appearance of bird feathers. But even at his time Andreas Wagner stood rather alone with such ideas.

Hermann von Meyer

However, the avian nature of *Archaeopteryx* was not generally accepted. Hermann von Meyer, after having identified the single feather as definitely avian, was more cautious in his judgement on the feathered skeleton. When first notified of the creature, he described it as 'a feathered animal which differs from our birds essentially' (Meyer 1861*a*, *b*; Wellnhofer 2001). In a letter to London geologist John Evans, who had discovered isolated cranial fragments including teeth on the London *Archaeopteryx* plate, Hermann von Meyer had something more detailed to say:

> An arming of the jaw with teeth would contradict the view of the *Archaeopteryx* being a bird or an embryonic form of bird. But after all, I do not believe that God formed his creatures after the systems devised by our philosophical wisdom . . . The *Archaeopteryx* is of its kind just as perfect a creature as other creatures, and if we are not able to include this fossil animal in our system, our short-sightedness is alone to blame.
>
> (Meyer in Evans 1865, p. 415)

Ernst Friedrich Witte

Knowledgeable amateur palaeontologist Ernst Friedrich Witte from Hannover considered (Witte 1863) the problem of whether *Archaeopteryx* was a bird or a reptile as a 'fruitless controversy'. In a, perhaps, Solomonic attempt at solution, he pointed out that as the animal had characters of both reptiles and birds then it was actually neither: 'Rather there arises the question which characters predominate, and to which class it has to be assigned to, provisionally' (p. 568). Obviously, Witte expected that tallies would be made of its avian and its reptilian characteristics by the professionals, and whichever tally had more entries should determine how it was classified. Such statements indicate that facets of the debate about whether *Archaeopteryx* was a bird or a reptile were concerned more with the classification of *Archaeopteryx* itself than they had to do with avian evolution.

Richard Owen

The first to study and formally describe the London *Archaeopteryx* specimen was Richard Owen (1863*a*, *b*). From the title of his monograph, it is already obvious that Owen regarded *Archaeopteryx* as a bird, despite the long tail with 20 vertebrae 'resembling in structure and proportions those of a squirrel'. He compared the tail with the embryonic stage of modern birds, and stated that in the young ostrich 18–20 vertebrae could also be counted. Thus, he concluded that in *Archaeopteryx* an embryonic condition was preserved in the adult individual, and that it was closer to the general vertebrate type. This idea was quite in agreement with his concept of archetypes. As an opponent of the evolutionary theory of Charles Darwin, Owen was convinced that all animals within each larger systematic group were only variations of a single theme, the 'ideal archetype', and that the 'divine spirit' who had planned the archetype knew in advance of all its modifications. Of course, such an explanation of the diversity of all life forms, according to a divine plan, was in sharp contrast to the theory of species transformations, a result of natural selection factors in the 'struggle for life' as proposed by Darwin. Thus, he called it a 'long-tailed' bird, albeit a very primitive one, with true feathers, rather than an intermediate form. However, Owen pointed also to structures that are not bird-like, like the long tail and the claws on both preserved fingers. His conclusion was:

> The best-determinable parts of its preserved structure declare it unequivocally to be a bird, with rare peculiarities indicative of a distinct order in that class. By the law of correlation we infer that the mouth was devoid of lips, and was a beak-like instrument fitted for the preening of the plumage of *Archeopteryx*. A broad and keeled breast-bone was doubtless associated in the living bird with the great pectoral ridge of the humerus, with the furculum, and with the other evidences of feathered instruments for flight.
>
> (Owen 1863*b*, p. 46).

However, Owen's speculations on the presence of a beak and a keeled sternum could not be confirmed after the more complete second skeleton that included the skull, the Berlin specimen, became known about 20 years later. But even before, many of Owen's interpretations and conclusions were heavily criticized by Huxley (1868*a*).

Charles Darwin and Thomas Henry Huxley

The London specimen of *Archaeopteryx* was discovered 2 years after the first edition (1859) of Darwin's *Origin of Species*, so it could not be incorporated into Darwin's initial evolutionary formulations. Yet, even in later editions, Darwin definitely showed noticeable restraint with regard to *Archaeopteryx.* In only two places of his 'Origin' did he mention it:

> that strange bird, *Archaeopteryx*, with a long lizard-like tail, bearing a pair of feathers on each joint, and with its wings furnished with two free claws ... Hardly any recent discovery shows more forcibly than this, how little we as yet know of the former inhabitants of the world.
>
> (p. 284).

Then some pages later:

> Even the wide interval between birds and reptiles has been shown ... to be partly bridged over in the most unexpected manner, on the one hand, by the ostrich and extinct *Archaeopteryx*, and on the other hand, by the *Compsognathus*, one of the Dinosaurians – that group which includes the most gigantic of all terrestrial reptiles.
>
> (Darwin 1878, p. 302)

He mentioned *Archaeopteryx* one more time in his book *The Descent of Man* (1871) as: 'that strange bird with a long, lizard-like tail', as an example of an intermediate form.

Darwin apparently accepted the ideas of his friend and advocate of his theory, Thomas Henry Huxley, who, in 1868, had postulated a close relationship between dinosaurs and birds for the first time. But Huxley's conclusions were based not on *Archaeopteryx* but on the small bipedal Solnhofen dinosaur *Compsognathus*, which he regarded as 'still more bird-like than any of the animals ... included in that group', representing a near approximation to the 'missing link' between reptiles and birds (Huxley 1868*b*, p. 73) (Fig. 2). (Incidentally, it is in this discussion that the phrase 'missing link' seems to have been published for the first time.)

It is surprising to read his statement about *Archaeopteryx:* 'In many respects, *Archaeopteryx* is more remote from the boundary-line between birds and reptiles than some living Ratitae are' (Huxley 1868*a*, p. 248). He concluded that the nearest approximation to reptiles was represented among the ostriches and their allies in the flightless Ratitae. Huxley compared the Dinosauria, including *Iguanodon*, *Hadrosaurus*, *Megalosaurus*, *Plateosaurus* and some others known at his time, with the living ratites and concluded that 'the hind quarters of the Dinosauria wonderfully approached those of birds in their general structure, and therefore that these extinct reptiles were more closely allied to birds than any which now live' (Huxley 1868*b*, p. 73).

Nevertheless, Huxley (1868*b*, p. 75) considered both *Compsognathus* and *Archaeopteryx* as

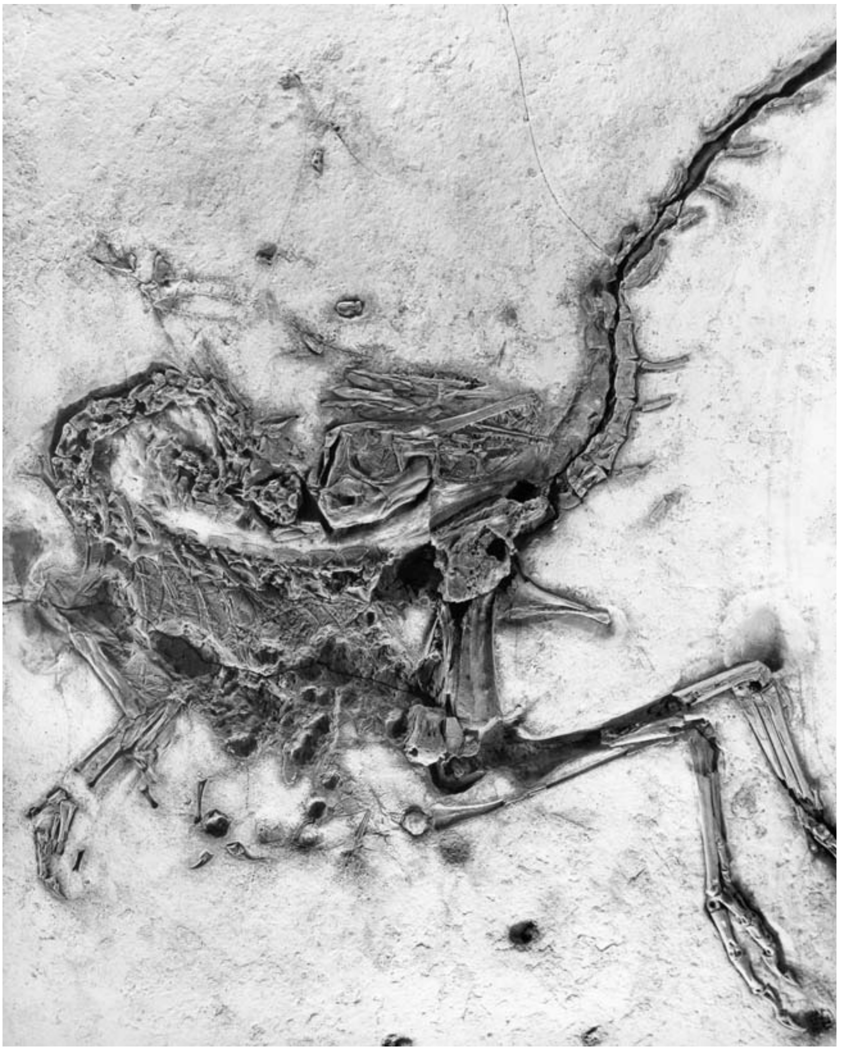

Fig. 2. *Compsognathus longipes* Wagner, from the Upper Jurassic lithographic limestone of Bavaria. This small theropod dinosaur was perceived as the most bird-like reptile by Huxley and was critical to his hypothesis of dinosaur–bird relationships (Bavarian State Collection of Palaeontology and Geology, Munich, BSP AS I 563).

'intermediate forms' and favoured the hypothesis that birds may have been evolved from dinosaurs, although not indicating a particular group. But he was cautious about the position of *Archaeopteryx* because the skull was thought to be missing from the only known (London) specimen at the time, and he was confused by the presence of a furcula in *Archaeopteryx*, which was not then known in any other dinosaur. However, it must be remembered that only a few dinosaur taxa were known, mostly based on fragmentary skeletal material. The concept of the Theropoda for the bipedal, carnivorous saurischians was not established until 1881 by Marsh.

Research after the discovery of the second *Archaeopteryx* specimen: 1876–1926

Wilhelm Dames

A second *Archaeopteryx* skeleton, the 'Berlin specimen' (Fig. 3), included the skull and perfectly preserved feather imprints. Wilhelm Dames, then Curator of the geological–palaeontological collections of the Mineralogical Museum in Berlin, was entrusted with the scientific investigation (Dames 1884). Two years earlier, he had already published a short paper on the skull. He was forced to this premature publication, since Carl Vogt, in 1879,

Fig. 3. The Berlin specimen of *Archaeopteryx*, found near Eichstätt in 1876, was figured as a coloured lithograph in the monograph of Wilhelm Dames (1884).

and O. C. Marsh, in 1881, had already described details of the skull which, after further preparation, turned out to be partly incorrect. Later, Dames (1897) also discussed evolutionary problems and concluded that *Archaeopteryx* was a primitive bird. He also seems to have given up his former caution against the Darwinian evolutionary theory. However, he qualified this by writing that *Archaeopteryx* was no longer a transitional or intermediate link between the classes of reptiles and birds, but was in the series of birds and already far from the point of separation of both branches of the sauropsids (Dames 1897).

Carl Vogt

Carl Vogt, Professor of Geology at the University of Geneva, was a passionate defender of the evolutionary theory and came to the conclusion that *Archaeopteryx* could be interpreted as a flying reptile furnished with bird's feathers and bird-like hind limbs. Actually, he considered it neither a bird nor a reptile, but that it formed a marked intermediate type. He confirmed the idea of Huxley who had combined classes Reptilia and Aves as 'Sauropsida', but did not agree with Huxley's view that the dinosaurs might be ancestral to all birds. Rather, he suggested that the Class Aves was not monophyletic, but rather polyphyletic, originating from different groups, the ratites from dinosaurs and the carinates from *Archaeopteryx*. He speculated that *Archaeopteryx* might have descended from terrestrial, lizard-like saurians covered with rudimentary feathers similar to those of bird embryos (Vogt 1879, 1880).

Harry Govier Seeley

London palaeontologist Harry Govier Seeley refuted most of Vogt's conclusions, since, in his view, he had overestimated the similarity of *Archaeopteryx* to reptiles (Seeley 1881). Seeley considered it a primitive bird, explicitly confirming Owen's interpretation. He argued: 'It would have been reversing of one of the oldest canons of natural history to find well-developed plumage associated with a reptilian skeleton' and 'There would have been no transition here, but an incongruity' (Seeley 1881, p. 305). With such a statement Seeley also criticized Huxley in arguing that obligatory bipedalism in both dinosaurs and birds was the result of convergence rather than indicating a closer relationship. However, he offered no alternative for the ancestry of birds. Comparing the Berlin and London *Archaeopteryx* skeletons, he concluded also that they might be assigned to different species, if not genera; a conclusion followed by Dames (1897) and Petronievics (1921), respectively.

Othniel Charles Marsh

In 1881 Othniel Charles Marsh, had the opportunity to study both the London and Berlin specimens, and reported on his investigations in a lecture at a meeting of the British Association for the Advancement of Science in York, UK. He had found hitherto unknown features of *Archaeopteryx*, such as real teeth, and concluded that *Archaeopteryx* was a bird, but the most reptilian one. He suspected the ancestors of birds to be among more primitive and older dinosaur-like reptiles, still unknown from the fossil record (Marsh 1881).

Fürbringer, Gegenbauer, Williston, Baur, Nopcsa and Abel

In Germany, Fürbringer (1888) argued also that *Archaeopteryx* was a true bird far beyond the reptilian–avian transition, originating from a long series of feathered ancestors without indicating a particular group. He was unable to decide whether it might have been ancestral to modern birds or belonged rather to a line long extinct.

Yet, Huxley's idea of a close dinosaurian relationship of birds (Huxley 1869*a*, *b*) was not dead, but maintained by Gegenbaur (1878), Williston (1879), Baur (1883, 1885*a*, *b*) and others. Baur (1885*b*) supported an ornithopod, rather than theropod, origin of birds based largely on the alleged opisthopubic pelvis of the Berlin specimen of *Archaeopteryx*. (This concept was briefly revived by Galton 1970, although he more broadly examined ornithischian dinosaurs as a whole, rather than just ornithopods. This view was refuted in detail by Charig 1972 on the basis of functional studies of the pelvis and hind limbs of archosaurs.)

Often, research on *Archaeopteryx* and its phylogenetic origin has also included the problem of the origin of flight or, most commonly, was coupled with it. It centred on the problem of whether *Archaeopteryx* could climb tree trunks and was thus an arboreal animal, or was adapted to bipedal running on the ground and was thus a cursorial animal. The idea of modern 'cursorial theory' of the origin of flight from the ground up, goes back to Hungarian Baron Franz Nopcsa who introduced his famous 'running *Proavis*' hypothesis arguing that birds originated from bipedal dinosaur-like running forms in which the anterior extremities, on account of flapping movements, gradually transmuted elongated feathers into wings without thereby affecting terrestrial locomotion (Nopcsa 1907). Viennese palaeobiologist Othenio Abel agreed with Nopcsa insofar as he argued that of all dinosaurs it is the theropods sharing a common ancestor that have the closest similarity to birds. But he disagreed with Nopcsa in suggesting that this ancestor was arboreal (Abel 1911, 1912). However, Abel was not the first who combined the 'arboreal theory' of the origin of flight, from the trees down, with the dinosaurian origin of birds. In 1900 Osborn had already preferred a conjecture about a 'Dinosaur–Avian stem' and urged an arboreal origin of flight (Osborn 1900).

Research on *Archaeopteryx* from Heilmann (1926) to de Beer (1954)

The idea of the dinosaurian ancestry of *Archaeopteryx* and birds was abandoned following Gerhard Heilmann's (1926) landmark monograph *The Origin of Birds*. While Huxley may have created the term 'missing link' when discussing the positions of various reptiles and *Archaeopteryx* with regard to avian origins, Heilmann clearly was able to balance the mosaic of reptilian and avian features, and dismissed the concept, at least for *Archaeopteryx*:

> We may now stop talking about the *missing link* between birds and reptiles. So much so is *Archaeopteryx* this link that we may term it a warm-blooded reptile disguised as a bird.
>
> (Heilmann 1926, p. 36)

He carried out a most comprehensive comparative study of all anatomical details of the skeleton of *Archaeopteryx* (especially the Berlin specimen), as well as of 'thecodonts', 'coelurosaur' dinosaurs (small, gracile theropods, not in the sense of the currently recognized monophyletic Coelurosauria) and extant birds, and concluded:

> From this it would seem a rather obvious conclusion that it is amongst the coelurosaurs that we are to look for the bird-ancestor.

and further:

> The striking points of similarity between coelurosaurs and birds pertained to nearly all the parts of the skeleton.
>
> (Heilmann 1926, p. 182).

Nevertheless, he ultimately decided not to pursue this evidence to its logical conclusion because he felt it was all negated by a single character: the absence in 'coelurosaurs' of ossified clavicles. Clavicles are fused medially to form the furcula in birds, a structure present in *Archaeopteryx* but unknown in theropods at that time. Consequently, he concluded that, according to Dollo's law of evolutionary irreversibility, a bird ancestor simply could not lack clavicles, and as they lacked these bones 'coelurosaurian' dinosaurs could be, at best, distant relatives of birds.

Heilmann perceived that the best possible candidacy for avian ancestry lay somewhere among the Triassic 'thecodonts', probably the 'Pseudosuchia', a theory first explicitly suggested by Broom (1913). They were documented in primitive, generalized forms like *Ornithosuchus* and *Euparkeria*, and Heilmann compared *Archaeopteryx* especially with the Ornithosuchia. Thus, he used the same arguments as Huxley to distance dinosaurs from *Archaeopteryx* because of the presence of a furcula in the latter. However, given his statements concerning the otherwise great similarity between 'coelurosaurs' and birds, had Heilmann known that many theropods indeed possessed ossified clavicles in the form of a median furcula (now known in many taxa, including dromaeosaurids), he would unquestionably have favoured a theropod origin of birds, and the subsequent 'great debate' about bird origins would probably never have transpired (Sereno 2004; Ries 2007). The influence of Heilmann's book, however, was so great that his hypothesis of a 'pseudosuchian' origin was almost universally accepted for almost 50 years.

Relying on the data of Heilmann, the position of *Archaeopteryx* was analysed among others by Lowe (1935, 1944). He interpreted the morphology of the skull as reptilian rather than intermediate between birds and reptiles. He even went so far as to claim that *Archaeopteryx* was not a bird at all, but was an 'arboreal climbing dinosaur with the power to glide'. George Gaylord Simpson, the influential American palaeontologist of the twentieth century, defended Heilmann's position against Lowe's view, which he called 'nothing short of fantastic' (Simpson 1946). In Simpson's view the skull of *Archaeopteryx* was intermediate, 'almost ideally so', between a pseudosuchian reptile-like *Euparkeria* and an advanced bird such as *Columba*. All the resemblances of saurischian dinosaurs to birds were nothing but 'parallelisms and convergences'.

> Birds arose as feathered fliers, even if this development occurred (contrary to probability and without known evidence) in more than one line and if *Archaeopteryx* ... was not in the successful particular line that did give rise to the later Aves as a whole.
>
> (Simpson 1946, p. 95)

In his great monograph on the London *Archaeopteryx* specimen, Gavin de Beer (1954), then Director of the British Museum (Natural History) in London, also discussed in detail its nature and relationships. He argued that *Archaeopteryx* was a bird close to the main line of evolution to modern birds. He accepted Heilmann's view to consider Triassic 'thecodonts', like *Euparkeria* and *Ornithosuchus*, to have been ancestral to birds. He recognized *Archaeopteryx* as an excellent example of a transitionalal form between one group and another. He also applied the principle of the 'mosaic of characters', as proposed by D. M. S. Watson (1919), to *Archaeopteryx*. With regard to the origin of avian flight, de Beer regarded the structures of *Archaeopteryx* of the greatest importance, concluding that 'all the evidence is in favour of the arboreal ... theory' (de Beer 1954, p. 52). With such an authoritative statement the controversial discussions about the meaning of *Archaeopteryx* for the origin and early evolution of birds seemed to be settled once and forever.

The revival of the dinosaurian ancestry of *Archaeopteryx* and birds after 1970

John H. Ostrom

The 'old' idea of a close relationship of birds to dinosaurs underwent a revival beginning 40 years ago with the work of John H. Ostrom. Purely by serendipity, Ostrom 'rediscovered' the fourth *Archaeopteryx* specimen in the Teyler Museum in Haarlem (mislabelled as a specimen of the pterosaur *Pterodactylus*) in 1970, shortly after describing a new theropod dinosaur, *Deinonychus antirrhopus*, from the Lower Cretaceous of Montana. In terms of its skeletal anatomy, *Deinonychus* was a mirror of *Archaeopteryx*, and Ostrom noticed these similarities immediately. These enabled him to hypothesize that the dromaeosaurid *Deinonychus* was one of the closest relatives of *Archaeopteryx* (Ostrom 1969, 1970, 1972, 1973). Ostrom penned a short letter on this subject to *Nature* that was published on 9 of March 1973, entitled 'The ancestry of birds', and ignited an intense reaction from the scientific community. Ostrom, however, laid out his evidence: a series of characters that he considered strong evidence of a coelurosaurian (theropod) ancestry of birds. He was convinced that, were it not for the feather imprints, today the *Archaeopteryx* specimens 'would be identified

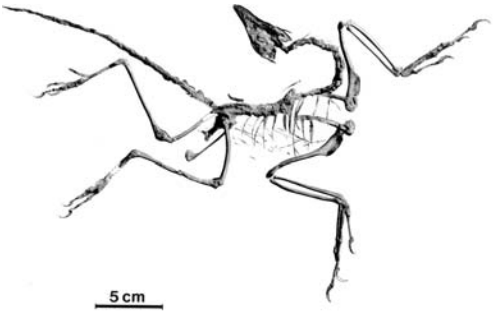

Fig. 4. The Berlin specimen of *Archaeopteryx*, with the plumage removed. Were it not for the feathers, the early authors would probably have identified the skeleton alone as that of a small theropod dinosaur. (Photograph prepared by Frank Haase.)

unquestionably as coelurosaurian theropods' (Ostrom 1976, p. 109) (Fig. 4).

Ostrom's new-found data inspired some adherents, such as Bakker & Galton (1974), who developed rather revolutionary ideas about the classification of the Aves, including *Archaeopteryx*, in general. The argument that birds evolved from small theropod dinosaurs prompted inferences that these possible bird ancestors may also have had an advanced physiology as opposed to that of other reptiles. The idea was entertained especially by Bakker (1975). It was stated that the successful radiation of birds was enabled by their use of aerial space, and that this was, in turn, enabled by a fundamentally theropod physiology and structure. Consequently, 'Dinosauria' was established as a new class of vertebrates and Aves was demoted to a subclass rank within it. Thulborn (1975) took this idea to a different extreme, suggesting that avian ancestors, that is, the entire Suborder Theropoda, should be transferred to the Class Aves, to which Alan Charig (1976, p. 65), in his typically humorous manner, commented 'just as the layman will refuse to accept Bakker and Galton's suggestion that a sparrow is a dinosaur, so will he balk at Thulborn's idea of *Tyrannosaurus rex* as a bird'. Ostrom (1985, p. 163) pragmatically suggested that these 'proposed re-alignments of birds and various archosaurs fail to meet the requirements of a utilitarian and stable systematic framework. I recommend that the class Aves be left where it is and include *Archaeopteryx* as its most archaic member'.

The hypothesis of a theropod origin of birds as advocated by Ostrom was opposed by certain camps of thought, those who argued for a crocodilian – avian relationship, first proposed by Walker (1972) and adopted by Martin *et al.* (1980), and those who argued for a 'pseudosuchian' origin of birds, advocated by Tarsitano & Hecht (1980 and subsequent papers) and others. These two different hypotheses, each using characters of *Archaeopteryx*, were critically discussed in detail by Ostrom (1985) and defeated by Gauthier & Padian (1985). The arguments are lengthy and need not be repeated in the context of this paper.

Classification of *Archaeopteryx* in the light of modern cladistics after 1982

Many of these issues were and are purely semantic, dependent wholly on the lack of rigorous definition and solidity inherent in the Linnaean classification system and its ranks: evidence for a close dinosaur–bird relationship was gaining adherents from the Heilmannian viewpoint, and ensuing quibbles were not about the validity of this relationship but about how to classify the grouping. It required the overhaul of the process for analysing phylogenies and classifying organisms based more solidly on evolutionary relationships to end this debate. On the basis of cladistic character analyses, Padian (1982) and Gauthier (1986) suggested that, in a purely evolutionary sense, birds were nested deeply within the Theropoda – birds, in short, were indeed coelurosaurian dinosaurs, just as they were theropods, saurischians, dinosaurs and archosaurs. Specifically, in this system Aves is a clade within the more inclusive theropod clade Maniraptora. This systematic arrangement, based on ever-increasing amounts of evidence, is nearly universally accepted today (e.g. Padian & Chiappe 1998; Witmer 2002; Chiappe 2007). However, nomenclatural debates have by no means ceased, and *Archaeopteryx* retains a central role in these debates. Pursuing such questions would by far exceed the limits set for this historical approach. Aves, traditionally a class in the Linnaean system, was restricted by Gauthier (1986) to the 'crown group', meaning only extant birds and all descendants of the most recent common ancestor of all extant birds (Fig. 5). To encompass the group including both extant birds and *Archaeopteryx*, he introduced the name Avialae with the intent that the term 'bird' would be a colloquialism not for Aves but for Avialae – *Archaeopteryx* was thus a bird, but not an avian. The Avialae, in turn, is the sister group of the Deinonychosauria, the clade that includes *Deinonychus* and all theropods closer to it than to the Avialae. However, there are other concepts differing in details from the one just mentioned, such as proposed by Clark *et al.* (2002), Sereno (2004) and others.

Some palaeornithologists, however, remain opposed to the idea of birds as derived theropods (e.g. Feduccia 2002) and interpret some of the

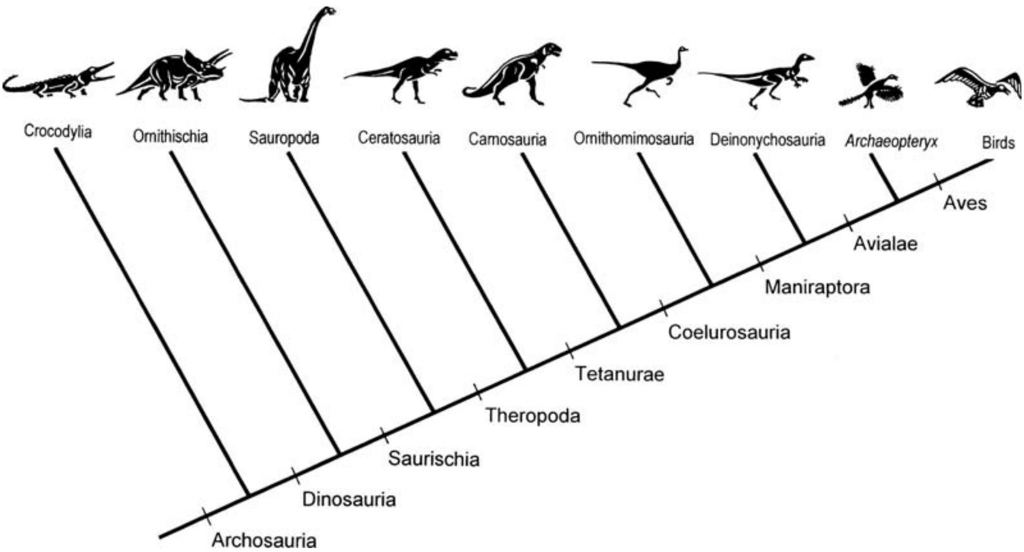

Fig. 5. Phylogenetic relationships of *Archaeopteryx* in a simplified cladogram of the Archosauria after Gauthier (1986) and others, showing its relationship within the Dinosauria.

'feathered dinosaurs' from the Lower Cretaceous of China (Chang 2003) as flightless birds that bear osteological similarities to theropod dinosaurs only due to convergent evolution for functional, but not phylogenetic, reasons, an idea harkening back to that voiced by Seeley (1881). Paul (2002), although not refuting the proposition that birds were dinosaurs, also considered many of these Cretaceous taxa 'neo-flightless birds', apostrophized by some as 'Mesozoic kiwis'.

The problem of a clear-cut distinction between birds and dinosaurs is often circumvented using the informal designations 'non-avian theropods' versus 'avian theropods', that is, in a rank-less nomenclatural system based on phylogenetic systematics. If we then ask 'what is a bird?' we are in danger of mixing up Linnaean and cladistic principles. It seems to be rather a problem of human perception, which has always been influenced by subjective opinions and traditions. Nevertheless, *Archaeopteryx*, now documented by 10 skeletons and a single feather from the Solnhofen limestone of Bavaria, will remain a key taxon in these debates. Possibly, it might best be characterized as 'a theropod dinosaur disguised as a bird', in modification of Heilmann's statement of 1926.

Discussion and conclusion

For almost 150 years, beginning in 1861 up to the present, the significance of *Archaeopteryx* has generated an overwhelming number of scientific publications that could not all be considered within the context of this paper. A short summary up to the 1970s was given by Ostrom (1976). In historical retrospect, research on *Archaeopteryx* has concentrated on three principal points of emphasis: (1) its taxonomic position; (2) its phylogenetic position; and (3) its meaning for the origin of avian flight.

The initial discussions centred on the question of whether *Archaeopteryx* was a saurian, a bird or an intermediate form in between them. Ironically, its meaning as a potential transitional form was recognized first by prominent anti-Darwinist Andreas Wagner (1862*a*, *b*), but not by Darwin's 'bulldog', Thomas Henry Huxley, and following him by Darwin himself. Huxley had introduced the popular term of the 'missing link', in 1868, for the small, bipedal dinosaur *Compsognathus* rather than for *Archaeopteryx*. It seems as if only Gerhard Heilmann (1926) has elevated *Archaeopteryx* to the rank of a 'missing link' par excellence, a label that has been attached to *Archaeopteryx* as the classical textbook example, until today.

With regard to the phylogenetic position of *Archaeopteryx*, different contradictory hypotheses have been developed. Although Huxley recognized a close dinosaurian–bird relationship, the predominant view until the 1970s was Heilmann's conclusion of a 'thecodontian' relationship and the suggestion that the Aves, including *Archaeopteryx* as the oldest member of that class, have descended from Triassic pseudosuchians. Despite the simultaneously developed hypotheses of a crocodylomorph and pseudosuchian (or basal archosaurian) origin, from the early 1980s onwards the theropodan ancestry of *Archaeopteryx* and the birds has been confirmed using cladistic methodology, a hypothesis that is almost universally accepted today.

First ideas about the origin of avian flight were published by Nopcsa (1907, 1923), whose 'running *Proavis*' model initiated the recently prevailing cursorial theory – the beginning of flight 'from the ground up.' This was also in agreement with the theropod-like skeletal morphology of *Archaeopteryx*, indicating its principally bipedal terrestrial locomotion. The opposite view was put forward by the authors who favoured a scenario for the beginning of flight 'from the trees down', called the arboreal theory. Again, *Archaeopteryx* had to support this idea on the basis of other features, as the shape and size of the finger claws, suggesting climbing abilities and arboreal lifestyle. This, in turn, was used as evidence that *Archaeopteryx*, and the birds, could not have descended from bipedally running theropods (Feduccia 1996, 2nd edn in 1999).

These controversies have shown how close these conclusions are to the danger of circular reasoning, according to the pattern: *Archaeopteryx* could climb tree trunks. Thus, it could not have descended from bipedal terrestrial, but from climbing arboreal ancestors; therefore, flight originated from the trees down. Leaving aside that there are no possible candidates for such arboreal ancestors in the fossil record, the entire reasoning can also be read in reverse. The proponents of the cursorial theory have the same problem, of course. But they have the decisive advantage of being able to present possible candidates for avian ancestors that are well documented in the fossil record. These are the dromaeosaurid theropod dinosaurs whose skeletal characters have survived in the skeletons of *Archaeopteryx*.

A fourth problem of avian evolution discussed in the past has been the origin of feathers. It was not stressed here, because *Archaeopteryx* already had well-developed feathers and an advanced, 'modern' plumage. Thus, it cannot contribute to the recent debate that has been initiated by the discoveries of the 'feathered dinosaurs' in China in the mid-1990s.

Many other aspects of research on *Archaeopteryx* have been carried out, such as its flying ability, its physiology, its lifestyle and habitat. These and many other interesting subjects have been treated in several comprehensive publications, such as Feduccia (1996, 1999), Elzanowski (2001*b*, 2002*a*, *b*), Chatterjee (1997), Chiappe (2007) and, last, by the present author (Wellnhofer 2008, 2009).

I would like to thank the organizers of the meeting 'Dinosaurs (and Other Extinct Saurians) – A Historical Perspective' held in London on 6–7 May 2008 – R. Moody, E. Buffetaut, D. Martill and D. Naish. They have made possible the presentation of quite different aspects of this wide field of research during a very interesting, well-organized meeting, and a field excursion to the Isle of Wight. This paper is an extended version of my oral presentation at this meeting, and has been considerably improved by many helpful suggestions from S. Hartmann and an anonymous reviewer. My thanks are extended to F. Haase, who reviewed the final version of the manuscript and corrected my English text.

References

Abel, O. 1911. Die Vorfahren der Vögel und ihre Lebensweise. *Verhandlungen der k. k. zoologisch-botanischen Gesellschaft in Wien*, **61**, 144–191.

Abel, O. 1912. Über den Erwerb des Flugvermögens. *Schriften des Vereins zur Verbreitung naturwissenschaftlicher Kenntnisse*, Wien, **52**, 1–22.

Bakker, R. T. 1975. Dinosaur renaissance. *Scientific American*, **232**, 58–78.

Bakker, R. T. & Galton, P. M. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature*, **248**, 168–172.

Baur, J. G. 1883. Der Tarsus der Vögel und Dinosaurier. *Morphologisches Jahrbuch*, **8**, 417–456.

Baur, J. G. 1885*a*. Dinosaurier und Vögel. Eine Erwiderung an Herrn Prof. W. Dames in Berlin. *Morphologisches Jahrbuch*, **10**, 446–454.

Baur, J. G. 1885*b*. Bemerkungen über das Becken der Vögel und Dinosaurier. *Morphologisches Jahrbuch*, **10**, 613–616.

Broom, R. 1913. On the South African pseudosuchian *Euparkeria* and allied genera. *Proceedings of the Zoological Society, London*, **1913**, 916–933.

Chang, M.-M. (ed.) 2003. *The Jehol Biota. The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*. Shanghai Scientific & Technical Publishers, Shanghai.

Charig, A. J. 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. *In*: Joysey, K. A. & Kemp, T. S. (eds) *Studies in Vertebrate Evolution.* Oliver & Boyd, Edinburgh, 121–155.

Charig, A. J. 1976. 'Dinosaur monophyly and a new class of vertebrates': a critical review. *In*: Bellairs, A. d'A. & Cox, C. B. (eds) *Morphology and Biology of Reptiles*. Academic Press, New York, 65–104.

Chatterjee, S. 1997. *The Rise of Birds*. Johns Hopkins University Press, Baltimore, MD.

Chiappe, L. M. 2007. *Glorified Dinosaurs. The Origin and early Evolution of Birds*. John Wiley, London.

Clark, J. M., Norell, M. A. & Makovicky, P. J. 2002. Cladistic approaches to the relationships of birds to other theropod dinosaurs. *In*: Chiappe, L. M. & Witmer, L. M. (eds) *Mesozoic Birds. Above the Heads of Dinosaurs*. University of California Press, Berkeley, CA, 31–61.

Dames, W. 1884. Über *Archaeopteryx*. *Palaeontologische Abhandlungen*, **2**, 119–196.

Dames, W. 1897. Über Brustbein, Schulter- und Beckengürtel der *Archaeopteryx*. *Sitzungsberichte der königlich-preussischen Akademie der Wissenschaften zu Berlin*, **38**, 818–834.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection: or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London (2nd edn published in January 1860; 3rd edn published in April 1861; 4th edn published in June 1866; 5th edn published in July 1869; 6th edn published in January 1872, revised in 1878).

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London (2nd edition revised, 1885).

de Beer, G. 1954. *Archaeopteryx lithographica*. A study based upon the British Museum specimen. Trustees of the British Museum (Natural History), London, 68 pp.

Elzanowski, A. 2001*a*. A new genus and species for the largest specimen of *Archaeopteryx*. *Acta Palaeontologica Polonica*, **46**, 519–532.

Elzanowski, A. 2001*b*. The life style of *Archaeopteryx* (Aves). *Publicación Especial de la Asociación Paleontológica Argentina*, **7**, 91–99.

Elzanowski, A. 2002*a*. Biology of basal birds and the origin of avian flight. *In*: Zhou, Z. & Zhang, F. (eds) *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing*, 1–4 June 2000. Science Press, Marrickville, NSW, 211–226.

Elzanowski, A. 2002*b*. Archaeopterygidae (Upper Jurassic of Germany). *In*: Chiappe, L. M. & Witmer, L. M. (eds) *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, CA, 129–159.

Evans, J. 1865. On portions of a cranium and of a jaw, in the slab containing the fossil remains of *Archaeopteryx*. *Natural History Review*, **5**, 415–421.

Feduccia, A. 1996. *On the Origin and Evolution of Birds*. Yale University Press, New Haven, CT (2nd edn published in 1999).

Feduccia, A. 2002. Birds are dinosaurs: simple answer to a complex problem. *Auk*, **119**, 187–201.

Fürbringer, M. 1888. *Untersuchungen zur Morphologie und Systematik der Vögel*. Holkema, Amsterdam.

Galton, P. M. 1970. Ornithischian dinosaurs and the origin of birds. *Evolution*, **24**, 448–462.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *In*: Padian, K. (ed.) *The Origin of Birds and the Evolution of Flight*. Memoirs of the Californian Academy of Sciences, **8**, 1–55.

Gauthier, J. & Padian, K. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. *In*: Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P. (eds) *The Beginnings of Birds*. Freunde des Jura-Museums Eichstätt, 185–197.

Gegenbaur, C. 1878. *Grundriss der vergleichenden Anatomie*. Engelmann, Leipzig.

Heilmann, G. 1926. *The Origin of Birds*. F. & G. Witherby, London.

Heller, F. 1959. Ein dritter *Archaeopteryx* – Fund aus den Solnhofener Plattenkalken von Langenaltheim/Mfr. *Erlanger Geologische Abhandlungen*, **31**, 1–25.

Howgate, M. E. 1985. Problems of the osteology of *Archaeopteryx*. Is the Eichstätt specimen a distinct genus? *In*: Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P. (eds) *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt, 105–112.

Huxley, T. H. 1868*a*. Remarks upon *Archaeopteryx lithographica*. *Proceedings of the Royal Society of London*, **16**, 243–248.

Huxley, T. H. 1868*b*. On the animals which are most nearly intermediate between the birds and reptiles. *Annals and Magazine of Natural History*, **4**, 66–75.

Huxley, T. H. 1869*a*. Further evidence of the affinity between the dinosaurian reptiles and birds. *Quarterly Journal of the Geological Society, London*, **26**, 12–31.

Huxley, T. H. 1869*b*. The classification and affinities of the Dinosauria. *Quarterly Journal of the Geological Society, London*, **26**, 32–51.

Lowe, P. R. 1935. On the relationship of the Struthiones to the dinosaurs and to the rest of the avian class, with special reference to the position of *Archaeopteryx*. *Ibis*, **5**, 398–432.

Lowe, P. R. 1944. An analysis of the characters of *Archaeopteryx* and *Archaeornis* . Were they reptiles or birds? *Ibis*, **86**, 517–543.

Marsh, O. C. 1881. Jurassic birds and their allies. *American Journal of Science*, **22** , 337–340.

Martin, L. D., Stewart, J. D. & Whetstone, K. N. 1980. The origin of birds: structure of the tarsus and teeth. *Auk*, **97**, 86–93.

Mäuser, M. 1997. Der achte *Archaeopteryx*. *Fossilien*, **3**, 156–157.

Mayr, F. X. 1973. Ein neuer *Archaeopteryx*-Fund. *Paläontologische Zeitschrift*, **47**, 17–24.

Mayr, G., Pohl, B. & Peters, D. S. 2005. A well-preserved *Archaeopteryx* specimen with theropod features. *Science*, **310**, 1483–1486.

Mayr, G., Pohl, B., Hartman, S. & Peters, D. S. 2007. The tenth skeletal specimen of *Archaeopteryx*. *Zoological Journal of the Linnean Society*, **149**, 97–116.

Meyer, H. von 1857. Beiträge zur näheren Kenntnis fossiler Reptilien. *Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefakten-Kunde*, **1857**, 532–543.

Meyer, H. von 1859–1860. *Zur Fauna der Vorwelt. Vierte Abteilung: Reptilien aus dem lithographischen Schiefer des Jura in Deutschland und Frankreich*, Frankfurt.

Meyer, H. von 1861*a*. Vogel-Feder und *Palpipes priscus* von Solenhofen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, **1861**, 561.

Meyer, H. von 1861*b*. *Archaeopterix lithographica* (Vogel-Feder) und *Pterodactylus* von Solenhofen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, **1861**, 678–679.

Meyer, H. von 1862. *Archaeopteryx lithographica* aus dem lithographischen Schiefer von Solnhofen. *Palaeontographica*, **10**, 53–56.

Nopcsa, F. 1907. Ideas on the origin of flight. *Proceedings of the Zoological Society, London*, **1907**, 223–236.

Nopcsa, F. 1923. On the origin of flight in birds. *Proceedings of the Zoological Society, London*, **1923**, 463–477.

Osborn, H. F. 1900. Reconsideration of the evidence for a common dinosaur–avian stem in the Permian. *American Naturalist*, **34**, 777–799.

Ostrom, J. H. 1969. *Osteology of Deinonychus antirrhopus, an* Unusual Theropod from the Lower Cretaceous of Montana. Peabody Museum Bulletin, Yale University, New Haven, CT, **30**, 1–165.

Ostrom, J. H. 1970. *Archaeopteryx*: notice of a 'new' specimen. *Science*, **170**, 537–538.

Ostrom, J. H. 1972. Description of the *Archaeopteryx* specimen in the Teyler Museum, Haarlem. *Proceedings Koninklijk Nederlandse Akademie van Wetenschappen, B*, **75**, 289–305.

Ostrom, J. H. 1973. The ancestry of birds. *Nature*, **242**, 136.

Ostrom, J. H. 1976. *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society, London*, **8**, 91–182.

Ostrom, J. H. 1985. The meaning of *Archaeopteryx*. *In*: Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P. (eds) *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt, 161–176.

Owen, R. 1863*a*. On the fossil remains of a long-tailed bird (*Archeopteryx macrurus* Ow.) from the lithographic slate of Solenhofen (Abstract). *Proceedings of the Royal Society of London*, **12**, 272–273.

Owen, R. 1863*b*. On the *Archeopteryx* of von Meyer with a description of the fossil remains of a long-tailed species, from the lithographic stone of Solenhofen. *Philosophical Transactions of the Royal Society of London*, **153**, 33–47.

Padian, K. 1982. Macroevolution and the origin of major adaptations: vertebrate flight as a paradigm for the analysis of patterns. *American Paleontological Convention, Proceedings*, **2**, 387–392.

Padian, K. & Chiappe, L. M. 1998. The origin and early evolution of birds. *Biological Review*, **73**, 1–42.

Paul, G. S. 2002. *Dinosaurs of the Air. The Evolution and Loss of Flight in Dinosaurs and Birds*. Johns Hopkins University Press, Baltimore, MD.

Petronievics, B. 1921. Über das Becken, den Schultergürtel und einige andere Teile der Londoner *Archaeopteryx*. Georg and Co., Genf.

Ries, C. J. 2007. Creating the proavis: bird origins in the art and science of Gerhard Heilmann 1913–1926. *Archives of Natural History*, **34**, 1–19.

Seeley, H. G. 1881. Prof. Carl Vogt on the *Archaeopteryx*. *Geological Magazine*, Series 2, **8**, 300–309.

Sereno, P. K. 2004. Birds as dinosaurs. *Acta Zoologica Sinica*, **50**, 991–1001.

Simpson, G. G. 1946. Fossil Penguins. *Bulletin of the American Museum of Natural History*, **87**, 1–99.

Tarsitano, S. & Hecht, M. K. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zoological Journal of the Linnean Society*, **69**, 149–182.

Thulborn, R. A. 1975. Dinosaur polyphyly and the classification of dinosaurs and birds. *Australian Journal of Zoology*, **23**, 249–270.

Tischlinger, H. 2009. Der achte *Archaeopteryx* – das Daitinger Exemplar. *Archaeopteryx*, **27**, 1–20.

Vogt, C. 1879. *Archaeopteryx macrura*, an intermediate form between birds and reptiles. *Annals and Magazine of Natural History*, Series 5, **5**, 185–188.

Vogt, C. 1880. *Archaeopteryx macroura*, an intermediate form between birds and reptiles. *Ibis*, **4**, 434–456.

Wagner, J. A. 1862*a*. Über ein neues, angeblich mit Vogelfedern versehenes Reptil aus den Solenhofener lithographischen Schiefern. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, mathematisch-physikalische Classe*, Sitzung vom 9. November, München, **1861**, 146–154.

Wagner, J. A. 1862*b*. On a new Fossil Reptile supposed to be furnished with Feathers. *Annals and Magazine of Natural History*, Series 3, **9**, 261–267. (Translation of Wagner 1862*a* by W. S. Dallas).

Walker, A. D. 1972. New light on the origin of birds and crocodiles. *Nature*, **237**, 257–263.

Watson, D. M. S. 1919. On *Seymouria* the most primitive known reptile. *Proceedings of the Zoological Society London*, **1919**, 267–301.

Wellnhofer, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. The fifth skeletal specimen of *Archaeopteryx*. *Palaeontographica, A*, **147**, 169–216.

Wellnhofer, P. 1988. Ein neues Exemplar von *Archaeopteryx*. *Archaeopteryx*, **6**, 1–30.

Wellnhofer, P. 1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. *Archaeopteryx*, **11**, 1–48.

Wellnhofer, P. 2001. Hermann von Meyer und der Solnhofener Urvogel *Archaeopteryx lithographica*. *In*: Keller, T. & Storch, G. (eds), *Hermann von Meyer – Frankfurter Bürger und Begründer der Wirbeltierpaläontologie in Deutschland. Kleine Senckenberg-Reihe*, **40**, 11–18.

Wellnhofer, P. 2008. *Archaeopteryx. Der Urvogel von Solnhofen*. Dr. F. Pfeil-Verlag, München.

Wellnhofer, P. 2009. *Archaeopteryx. The Icon of Evolution*. Dr. F. Pfeil-Verlag, München.

Wellnhofer, P. & Röper, M. 2005. Das neunte *Archaeopteryx* – Exemplar von Solnhofen. *Archaeopteryx*, **23**, 3–21.

Williston, S. W. 1879. Are birds derived from dinosaurs? *Kansas City Revue of Sciences*, **3**, 457–460.

Witmer, L. M. 2002. The debate on avian ancestry. Phylogeny, function, and fossils. *In*: Chiappe, L. M. & Witmer, L. M. (eds) *Mesozoic Birds. Above the Heads of Dinosaurs*. University of California Press, Berkeley, CA, 3–30.

Witte, F. E. 1863. Die *Archaeopteryx lithographica* (Briefliche Mitteilung an Prof. H. B. Geinitz). *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie*, **1863**, 567–568.