The Feathers of the Jurassic Urvogel *Archaeopteryx*

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Abstract
The Jurassic stem bird *Archaeopteryx* is an iconic transitional fossil, with an intermediate morphology combining features of non-avian dinosaurs and crown Aves. Importantly, fossils of *Archaeopteryx* preserve not only the bones, but details of the plumage, and therefore help shed light on the evolution of feathers, wings, and avian flight. Plumage is preserved in multiple individuals, allowing a detailed documentation of the feathers of the wings, tail, hindlimbs, and body. In some features *Archaeopteryx*' plumage is remarkably modern, yet in others, it is strikingly primitive. As in extant birds, remiges and coverts are enlarged and overlap to form airfoils. Remiges and rectrices exhibit asymmetrical, pennaceous vanes, with interlocking barbules. In contrast to crown birds, remiges have relatively slender rectrices, and differ in the development of coverts. Hindlimbs bear large, vaned feathers as in *Microraptor* and *Anchiornis*. Rectrices are numerous and extend the full length of the tail to the hips. The plumage of crown Aves was assembled in a stepwise fashion from *Anchiornis* through *Archaeopteryx*, culminating in a modern arrangement in ornithothoracines. Subsequent stasis in feather and wing morphology likely reflects aerodynamic and developmental constraints. Feather morphology and arrangement in *Archaeopteryx* are consistent with lift-generating function, and the wing loading and aspect ratio are comparable to modern birds, consistent with gliding and perhaps flapping flight. The plumage of *Archaeopteryx* is intermediate between *Anchiornis* and more derived Pygostylia, suggesting a degree of flight ability intermediate between the two.

1. INTRODUCTION
1.1 *Archaeopteryx* as a transitional fossil
How does evolution produce novel forms and novel functions? Studying the variation of birds under domestication, Darwin (1859) hypothesized that the environment selects upon variants in a population and, over generations, slowly transform one species to another. He hypothesized that this mechanism, natural selection, not only produced the variety of mockingbirds and finches on the Galápagos islands, but ultimately produced birds themselves, and all other species on the planet.

Darwin's hypothesis for a shared ancestry uniting all vertebrates predicted that intermediate forms must have existed in deep time linking one group of organisms, such as birds, to another, such as reptiles. However, no such intermediates were known, either living or fossil. Yet in 1861, just two years after the publication of 'On the Origin of Species', Darwin's prediction was borne out by the discovery of the Jurassic *Archaeopteryx* (Owen, 1863; Fig. 1, 2). In subsequent editions of the Origin, Darwin would cite *Archaeopteryx* as a transitional fossil, and it has literally been a textbook example of evolution ever since.

Archaeopteryx was precisely the kind of creature predicted by Darwin's theory. It combined uniquely avian features such as feathers, wing, and furculum, with primitive features including teeth, clawed fingers, and a long bony tail. Since the first specimen, a total of 12 skeletal specimens have been referred to the genus *Archaeopteryx* (Wellnhofer, 2009; Foth et al., 2014; Rauhut et al. 2018). These fossils have helped to bridge the divide between birds and their reptilian ancestors, and they have continue to shed light on, and spur debate about, the origins of birds and their flight.

In all these discussions, the plumage has played a central role, helping to understand the affinities of *Archaeopteryx*, its biology, and the evolution of avian flight.

1.2 *Archaeopteryx* and the dinosaurian ancestry of birds

While the primitive morphology of Archaeopteryx was critical to recognizing the dinosaurian ancestry of birds, it was the feathers that were critical to establishing the avian affinities of *Archaeopteryx* in the first place. The feathered wings of birds are not just unique to birds but so complex that they are unlikely to have evolved more than once. Because of this, there has never been any serious debate about the avian affinities of *Archaeopteryx*, despite its primitive skeletal morphology. But without the wings, it is unlikely that the transitional nature of *Archaeopteryx* would have been appreciated; as John Ostrom remarked, if not for the feathers, it is probable that *Archaeopteryx* would have been classified as a dinosaur'- as indeed happened for the Eichstätt specimen (Wellnhofer, 2009), where the feathers are only faintly preserved. It was this combination of avian-like feathers and a primitive skeletal morphology, resembling that of basal coelurosaurs such as Compsognathus, that first led Huxley to propose a link between dinosaurs and birds (Huxley, 1868, 1870). This idea was later revived and extended by the work of Ostrom (1973, 1976) and the phylogenetic analyses of Gauthier (1986).

Historically, the rarity of early birds meant that the problem of the origins of birds was synonymous with the origins of *Archaeopteryx*. However, recent discoveries have broken up the long branch that once separated crown birds from non-avian theropods such as *Compsognathus* and *Tyrannosaurus*. Such discoveries include feathered coelurosaurs (Ji et al., 1998; Currie and Chen, 2001), winged maniraptorans such as *Anchiornis* (Hu et al., 2009) and *Microraptor* (Xu et al., 2003), and basal avialans including *Jeholornis* (Zhou and Zhang, 2003a), *Sapeornis* (Zhou and Zhang, 2003b), and Confuciusornithidae (Chiappe et al., 1999). Along with the wealth of osteological evidence for a dinosaurian origin of birds, such fossils have provided new and unexpected evidence for the dinosaurian ancestry of birds. These include not only the presence of proto-feathers in non-avialan theropods (Currie and Chen, 2001; Xu et al., 2012), but derived, avian-like features of physiology and behaviour in non-avialan dinosaurs, including rapid growth rates (Erickson et al., 2001, 2004), endothermy (Eagle et al., 2011), avian-like sleeping posture (Xu and Norell, 2004), and brooding of eggs (Norell et al., 1995).

As a result of these discoveries, *Archaeopteryx* is no longer quite so central to the problem of the origins and early evolution of birds. Nevertheless, *Archaeopteryx* is still among the oldest representative of Avialae, and its anatomy is well-understood due to the exceptional preservation of both the skeleton and feathers. It therefore continues to be important to our understanding of the evolution of birds and the relationships between non-avian coelurosaurs and stem birds (Longrich et al., 2012; Foth et al., 2014), and in particular to the origin of flight.

1.3 The flight ability of *Archaeopteryx*, and the origin of flight

If the origins of birds have been largely resolved, the origin of avian flight remains controversial. Hypotheses continue to be divided into two general classes, arboreal and cursorial. In the arboreal hypothesis (Norberg, 1985a, 1990; Feduccia, 1996; Chatterjee and Templin, 2003; Longrich, 2006), airfoils initially evolve to slow descents, extend leaps, and provide stability and control as animals leap and fall through the forest canopy. Incremental increases in both the surface area and aspect ratio of airfoils improve performance. These include increased lift for slower descents, improved lift:drag ratios with glide angles below 45°, and improved stability, control, and maneuverability. Finally, flapping evolves, not to generate lift, but to generate thrust to compensate for drag, allowing for flatter descents and ultimately, level flight. In these scenarios, control and lift evolve first, followed by thrust.

Cursorial hypotheses (Ostrom, 1979) and its variants, such as wing-assisted incline running (Dial, 2003) envision the wings evolving in the context of running, either along the ground, or up inclines. These scenarios tend to emphasize initial use of the wings to produce thrust, followed by the evolution of lift sufficient to support the body in flight. These scenarios are not necessarily

mutually exclusive in that an arboreal bird ancestor may have exploited terrestrial environments to some degree and vice versa.

To some degree, biomechanical modelling and modern analogues (or lack thereof) can be used to test the feasibility of these hypotheses. However, they must ultimately be tested against the fossil record. Here, *Archaeopteryx* is critical because it represents one of the earliest and most primitive dinosaurs to use the feathers in an aerodynamic context. It is unlikely to represent a direct ancestor of modern birds, but *Archaeopteryx* exhibits few if any specializations that would rule it out as being an ancestor. It most likely lies at the tip of a short side-branch, and can therefore be used as a model for the ancestor, providing insight into how it did or did not fly. For example, if flight evolved in a ground-up context then *Archaeopteryx* should retain adaptations for ground-up takeoff at relatively low speeds. Conversely, a trees-down scenario would predict that *Archaeopteryx* would be well adapted for launching from heights and maneuvering within vegetation. The morphology of *Archaeopteryx* is therefore important to testing hypotheses about the origins and evolution of bird flight.

The purpose of this chapter is not to review all that has been written about the feathers of *Archaeopteryx*, which has already been done (Wellnhofer, 2009). Rather, this chapter is meant to sum up our current knowledge: what we know, and do not know about feather taphonomy, morphology, arrangement, and last their functional and evolutionary implications. Furthermore, the fact that *Archaeopteryx* is no longer lies alone at the base of the avian tree, rather than diminishing its importance, allows a deeper understanding of its morphology and biology. Comparisons with other basal forms, particularly *Anchiornis* and *Microraptor*, allow for reciprocal illumination (e.g. (Longrich et al., 2012). Hypotheses about feather structure, arrangement and function in Archaeopteryx can be tested against other taxa, and vice versa.

Archaeopteryx is an animal that is of exceptional interest to paleontology and the source of no small degree of controversy. And so while the current work is unlikely to answer all questions or agree with all opinions, it provides an updated summary of our understanding and a starting point for future discussions.

2. PRESERVATION, TAPHONOMY AND INTERPRETATION OF THE FEATHERS

All *Archaeopteryx* skeletons are preserved with at least some trace of plumage, except for the 12th (Schamhaupten) specimen. However, the feathers are poorly preserved in most specimens and do not allow for a detailed study of the plumage or feather structure. The exceptions are the Berlin (Wellnhofer, 2009; Longrich et al., 2012; Fig. 3) and Altmühl (11th) specimens (Foth et al., 2014) which show both the most extensive and best preserved feathering, while the London (Wellnhofer, 2009), Munich (Wellnhofer, 2009), and Thermopolis (Mayr et al., 2005; Mayr et al., 2007) specimens preserve remiges and rectrices. The Maxberg specimen, unfortunately lost since 1991, preserves wing and leg feathers (Wellnhofer, 2009) but existing casts and photos do not allow a detailed study of its plumage.

Although the feathers of *Archaeopteryx* are often described as impressions, it is more accurate to refer to them as collapsed molds (Rietschel, 1985; Longrich et al., 2012). In the case of the isolated feather, it is preserved as organic residues of feather melanins and keratins (Bergmann et al., 2010; Carney et al., 2012).

2.1. Preservational environment and burial

All known specimens of Archaeopteryx come from the Jurassic lithographic limestones of Bavaria (Wellnhofer, 2009) which are lower Tithonian in age (Viohl, 1985). Feather preservation is the result of the unusual environmental conditions of the ancient Solnhofen Archipelago. The lagoons of the plattenkalk basins lay along the northern edge of the Tethys Sea, located between sponge-microbial mounds and coral patch reefs, which protected them from the open ocean (Viohl, 1985; Wellnhofer, 2009). The climate was warm and semiarid (Viohl, 1985; Wellnhofer, 2009), resulting in high evaporation rates, which in turn led to a hypersaline, anoxic bottom layer (Wellnhofer, 2009). These conditions were hostile to animal life, as shown by the absence of bioturbation or

epibionts, and would have protected the soft tissues from scavenging or disturbance before and after burial (Wellnhofer, 2009; Arratia et al., 2015). Under these conditions, animals sinking to the seafloor could remain undisturbed and were slowly buried under a rain of fine limestone particles, which then molded the soft tissues.

In some specimens, such as the London, Maxberg, Munich, Thermopolis, and Altmühl specimens, the skeletons exhibit a degree of disarticulation (Wellnhofer, 2009) suggesting scavenging and/or decomposition of soft tissues. In such cases, the position of feathers may have been shifted prior to burial and taphonomic processes must be taken into consideration in interpreting these fossils. However, in some extraordinarily specimens, including the Berlin and Eichstätt specimen, the skeletons are preserved in articulation and with feathers in life position (Wellnhofer, 2009). Here, burial probably occurred very soon after death, within days or even hours, with minimal scavenging or decomposition. These specimens are significant because they preserve not only feathers, but the position of the feathers in life, or at least, at the moment of death.

2.2 Preservation of feathers

After sinking to the bottom, the body and feathers were buried by fine particles of calcium carbonate that rained down from the water column (Rietschel, 1985; Wellnhofer, 2009). Rietschel (1985) proposed a taphonomic model, followed here, where the feathers were encased in and molded by fine sediment particles. Following burial, the soft tissues broke down and the natural molds collapsed under the sediment's weight. A similar model has been proposed for fossils such as ammonites (de Buisonjé, 1985; Viohl, 1985). In this model, the molds collapse vertically under the sediment load, but do not expand laterally because the surrounding sediments are also under pressure. If so, then features such as diameters of the feather shafts should be preserved accurately. Finally, when discovered, the fossils are split along the bedding plane, which may result in the molds being split open, revealing the morphology of the feathers (Fig. 4).

A key implication of this model, in which feathers preserve as molds, rather than impressions, is that although we can only see a cross-section through the wing, the feathers are actually preserved in three dimensions in the matrix, albeit compressed in the vertical dimension. In places, the feathers may be split away to reveal different layers of the wings (Rietschel, 1985; Longrich et al., 2012). In the Berlin specimen (Fig. 3), for example, the main slab is exposes the wing in dorsal view, as the dorsal surface of the skeletal elements is visible. However, although from above, it is actually the ventral surface of the wing that is seen (Rietschel, 1985). The situation is analogous to an archaeological site in which the upper stories of a building have been removed and we are looking down at the foundations of the building.

Another implication of this model is that 'shaft shadows', grooves that pass through the remiges (Heilmann, 1926), represent not a taphonomic artefact ('double struck' impressions) but are traces of feathers concealed beneath other feathers (Rietschel, 1985; Longrich et al., 2012, Fig. 4). This means that unlike the feathered dinosaurs of the Jehol (Ji et al., 1998; Xu et al., 2003; Norell and Xu, 2005) and Daohugou (Hu et al., 2009; Sullivan et al., 2014; Xu et al., 2016) assemblages, where the plumage is preserved as a thin, essentially two-dimensional organic layer (Zhang et al., 2006; Foth, 2012), the preservation of the feathers in *Archaeopteryx* makes it possible to examine three dimensional patterns of overlap and layering of the plumage.

Another implication is that in some cases, poorly preserved traces of feathers may not be the molds themselves, but rather the 'printing' of the collapsed molds into overlying or underlying layers of sediment. Following Rietschel's (1985) model, collapse of the rachis causes displacement of the overlying and underlying sediment layers. If so, the poorly preserved feathers seen in some specimens, notably the Maxberg, the 9th ('Chicken wing'), and for the most part the Munich specimen, may not correspond to the feathers themselves, but represent artefacts or a palimpsest of the feathers. Similarly, some specimens in which feathers are not visible, including the Solnhofen and Daiting specimens, could preserve feathers deeper in the limestone.

2.3 Organic Preservation

Soft tissues also preserve as organic traces in at least some *Archaeopteryx* specimens. In contrast to the skeletal specimens, the single feather is preserved as a thin organic layer. Although previously interpreted as remains of precipitated manganese dioxide (MnO_2) (Griffiths, 1996; Wellnhofer, 2004) when analysed using backscattered SEM and synchrotron rapid scanning X-ray fluorescence mapping, the traces show no evidence for MnO_2. Instead they show high concentrations of organic copper, organic sulphur (Carney et al., 2012), sulphate and nickel (Manning et al., 2013). The sulphur most likely comes from the original feather keratin (Wogelius et al., 2011) while the copper is potentially a biomarker for eumelanin pigmentation (Wogelius et al., 2011). Remains of eumelanins are detectable across the feather. Although the preservation of melanosomes has been disputed (Manning et al., 2013; Moyer et al., 2014), the identification of melanosomes is consistent with the regular arrangement of the preserved bodies, their orientation in line with the barbules, and the fact that color patterns are preserved (Tischlinger and Unwin, 2004), with feather tip being darker than the proximal vane (Carney et al., 2012). Similarly, X-ray fluorescence mapping shows that copper, nickel and sulphur are not uniformly distributed, and instead the distal tip and outer vane of the feather were darker than inner vane (Manning et al., 2013). Examination of the fossils using synchrotron imaging also reveals the presence of elevated levels of phosphorus in association with the rachis (Bergmann et al., 2010). These traces suggest that organic residues may be more common in *Archaeopteryx* than previously thought.

2.4 Feather non-preservation

Given the exceptional preservation of soft tissues seen in some specimens, particularly the Berlin, London, and Altmühl specimens, it is tempting to conclude that we have a highly complete picture of the plumage. However, this is almost certainly not the case. As seen by comparing specimens (Table 1), feather preservation is variable. In the Berlin and Altmühl the specimen, remiges, coverts, rectrices, leg feathers, and body contour feathers are preserved in detail. In many specimens, including the London, Munich, Thermopolis and Eichstätt specimen, only remiges and rectrices preserve. In others, including the Haarlem (see Foth and Rauhut, 2017 for alternative taxonomic classification), Solnhofen and 'Chicken wing' specimen, only poorly preserved traces of the remiges are visible, and in the Schamhaupten (12th) specimen, feathers are absent (Rauhut et al. 2018). In the Daiting specimen no feathers are visible under normal light, but neck feathers are visible under ultraviolet (Tischlinger, 2009).

This emphasizes that even in the Solnhofen, where exceptional soft tissue preservation is relatively common (Arratia et al., 2015), non-preservation is the rule. It is therefore unlikely that a small sample of 12 specimens has revealed all important aspects of the plumage. We currently lack clear evidence for feathers (or their absence) on the snout, head, alular digit, feet, or toes, for example. However, given that there is no trace of scales in these regions, and because closely related forms from the Jehol and Daohugou bear feathers on these parts of the body, it would be premature to conclude that feathers are absent. Soft tissues need to be reconstructed based on positive evidence, and absence of evidence for soft tissues should not be taken as strong evidence for their absence.

3. FEATHER MORPHOLOGY
3.1 Feather structure

The morphology of the individual feathers of *Archaeopteryx* is remarkably similar to modern birds (Lucas and Stettenheim, 1972; Fig. 1). However, they differ in significant details. In traditional terms, the feathers have a modern 'bauplan'. In modern terms, the similarities in morphology suggest that the developmental genes and processes determining feather morphology were similar to those of crown birds (see Chapter 2: Lin et al.). All the observed feathers are variations on this basic bauplan; for purposes of description we start with the isolated feather.

Proximally, the shaft of the feather is developed as a hollow calamus, which distally gives rise to a central rachis. As preserved the calamus is rather short, but originally von Meyer (1862) figures and describes faint traces of a longer calamus. The rachis is slightly curved posteriorly,

while the vanes show a slight asymmetry (Elzanowski, 2002; Wellnhofer, 2009). A series of large barbs branch off either side of the rachis. Proximally, the barbs are separated, but distally they interlock to form closed vanes. In his initial description, von Meyer (Meyer, 1862) identified barbules, which has been confirmed by modern imaging techniques (Carney et al., 2012). Barbule morphology is not readily visible, but the barbs lock together to form vanes, as in the contour and flight feathers of modern birds. Most likely the hooklets of distal barbules grasped the pennulum of proximal barbules to hold the barbs together as in crown birds (Lucas and Stettenheim, 1972).

Studies of the microstructure of the feather likewise suggest that it was structurally similar to modern feathers. Melanosomes, microscopic bodies containing melanin, are visible aligned parallel to the barbs, as in modern birds (Carney et al., 2012). Melanins serve multiple purposes, including camouflage and display, but also protect the feathers against decay (Goldstein et al., 2004; Gunderson et al., 2008), and provide resistance to wear, and damage from ultraviolet (Bergman, 1982). *Archaeopteryx* would undoubtedly have been subject to all of these selective forces, needing to court mates, conceal itself from prey and predators, and protect its feathers against damage. Based on the morphology, the single feather likely represents a dorsal covert from the primary region, indicated by its asymmetry (Carney et al., 2012).

3.2 Ptilosis

In contrast to the scales of dinosaurs and other diapsids, the feathers of *Archaeopteryx* were regularly arranged. The primitive condition in diapsids is for the body scales to be arranged into an irregular or semi-regular mosaic over most of the body, but often with larger scales or scutes regularly arranged along the back (Chang et al., 2009). Such a pattern is seen in many non-avian dinosaurs including hadrosaurids (Bell, 2014), ceratopsians (Vinther et al., 2016), thyreophorans (Christiansen and Tschopp, 2010; Arbour et al., 2014), and sauropods (Chiappe et al., 1998) and more distant relatives of birds including crocodylians (Grigg and Kirshner, 2015), turtles, and many lepidosaurs (Pianka and Vitt, 2003), as well as on the feet of birds (Lucas and Stettenheim, 1972).

By contrast, the arrangement of the feathers of the wings and body in *Archaeopteryx* and crown birds (Lucas and Stettenheim, 1972) is far more regular, with feathers regularly spaced. Feathers of birds and eumaniraptorans are spaced in a diagonal grid across the body, which is critical to the function of the feathers. The base of each feather embedded in skin and fatty tissue, and linked to other feathers by an elaborate network of erector and depressor muscles (Lucas and Stettenheim, 1972; Homberger and de Silva, 2000). These muscles allow feather tracts to be raised and lowered, which is used for thermoregulation, controlling aerodynamic forces, and display (Lucas and Stettenheim, 1972; Homberger and de Silva, 2000).

Although the arrangement between individual pennaceous feathers of the body cannot be identified in *Archaeopteryx*, the remiges and coverts are arranged in alternating tiers, a feature shared with *Anchiornis* (Longrich et al., 2012; Pei, 2017) and crown birds (Lucas and Stettenheim, 1972). The alternating rows of feathers seem to simply be an elaboration of the diagonal grid. Most likely, the regular spacing of the feathers across the body evolved first (Christiansen and Bonde, 2004) to allow insulator feathers to be raised and lowered synchronously, with this pattern retained and modified to produce the regular arrangement of feathers on the wing and tail.

3.3 Body contour feathers

Body feathers are preserved in the Berlin and Altmühl specimens. In the Berlin specimen, contour feathers are preserved above the back and anterior to the pectoral girdle (Christiansen and Bonde, 2004). In the Altmühl specimen, body feathers run along the neck and surround the thorax (Foth et al., 2014; Fig. 5).

Some of the hackle (neck) feathers of the Altmühl specimen are dissociated from the cervical region along with the skull, and are instead preserved between the tail and the skull (Fig. 5B). They show that the hackle feathers are about half the length of the body feathers, and covered the neck at least up to the head. The Berlin specimen shows that body feathers possess a rachis as in the contour feathers of crown birds, but due to poor preservation, it is unclear whether they had

closed or open vanes (Christiansen and Bonde, 2004). Two isolated feathers exposed in the belly region of the Altmühl specimen clearly show a pennaceous morphology (Fig. 5C). They also show a long rachis that curves posteriorly as in crown birds (Lucas and Stettenheim, 1972). The vanes are symmetrical, but narrower than in modern birds (Lucas and Stettenheim, 1972). In this respect, the body feathers resemble the remiges and rectrices. This is consistent with the idea that differentiation of the various feather types was more poorly developed in early Paraves (see Chapter 5: Xu).

In contrast to nonvolant coelurosaurs such as *Sinosauropteryx* (Currie and Chen, 2001) and the tyrannosaur *Yutyrannus* (Xu et al., 2012), body feathers are extremely elongate, with the feathers of the belly region being longer than their associated ribs. Similarly elongate body feathers occur in *Anchiornis* (Hu et al., 2009), *Microraptor* (Xu et al., 2003), and ornithothoracine birds (see Chapter 9: O'Connor; Lucas and Stettenheim, 1972). In modern birds, the length of the feathers means that the body can be covered and effectively insulated by a combination of feathered tracts (pterylae) and unfeathered tracts of the skin (apteria) (Lucas and Stettenheim, 1972). Given the existence of elongate body feathers in *Archaeopteryx, Anchiornis,* and other Paraves, the may would not have needed to be fully feathered to adequately insulate and streamline the body. It is possible that basal paraves possessed pterylae and apteria as hypothesized by Christiansen and Bonde (2004) for *Archaeopteryx*. Although this interpretation is plausible, it is difficult to test on the basis of the available fossils.

3.4 Remiges and Coverts

All specimens except for the Daiting and Schamhaupten specimens preserve wing feathers. Details of the wing plumage, including rachi and barbs, are well-preserved in the Berlin, London, Munich, Thermopolis, and Altmühl specimens (Table 1), with the feathers best seen in the Berlin (Fig. 6, 7), London (Fig. 2), and Altmühl specimens (Fig. 8).

The wing skeleton of these specimens is seen in dorsal view. However, it is not the dorsal but the ventral surface of the wing that appears to be preserved in the Berlin, Munich and Thermopolis specimens (Heinroth, 1923; Helms, 1982; Mayr et al., 2007; Wellnhofer, 2009; Longrich et al., 2012) as indicated by the exposure of the ventral coverts; i.e. we are looking down at the lower layers of the wing (Rietschel, 1985) and the upper layers of the wing have been pulled away. The London specimen appears to preserve the ventral surface of the left wing, and the dorsal surface of the right (Longrich et al., 2012).

The situation is less clear for the Altmühl specimen (Fig. 8): Because the leading edge vane of the more proximal primaries overlaps and obscures the trailing edge vane of the nearby distal feathers, Foth et al. (2014) hypothesized that the dorsal wing surface is seen (interpretation followed by CF). However, as the preserved primary coverts extend obliquely and having their tips angled inward relative to the primaries, the arrangement corresponds more to the situation of the ventral surface in modern bird wings (interpretation followed by NRL). Therefore, a detailed taphonomic study of the wing preservation is necessary for this specimen.

The remiges resemble those of modern birds in many features, but also exhibit primitive features not seen in crown birds. The feather shafts are curved posteriorly in the distal primaries and secondaries. However, at least the distal half of the proximal primaries in the Berlin and Altmühl specimen show the opposite curvature, with the tips curving forward (Norberg, 1985b; Longrich et al., 2012; Foth et al., 2014). Modern birds do not exhibit this anterior curvature of the primaries. Vanes are asymmetrical with the trailing edge vanes being about twice as wide as the leading edge vanes (Feduccia and Tordoff, 1979; Norberg, 1995). This asymmetry is primarily due to asymmetry in barb length rather than asymmetry in barb angle, with trailing edge barbs being much longer than leading edge barbs (Feo et al., 2015). Although Speakman and Thomsen (1994) argued that the primaries of *Archaeopteryx* are symmetrical as in flightless birds (based on the London and Berlin specimen), this is an artefact caused by vanes of neighbouring feathers obscuring the trailing edge; where fully exposed the trailing edges are wide and the feathers are clearly asymmetrical (ratio > 3 for outer primaries in the Altmühl specimen) as in volant birds (Norberg, 1995; Longrich et al., 2012). This suggests adaptation for aerodynamic function, although it should be noted that some

secondary flightless birds retain asymmetric remiges, the ratio of which overlaps with that of volant birds (Speakman and Thomsen, 1994; Wang et al., 2017a). Angulation of the barbs in the primary remiges is also asymmetrical, with leading edge barbs being more strongly angled than trailing edge barbs (Foth et al., 2014; Feo et al., 2015). However this asymmetry is more weakly developed in crown birds (Feo et al., 2015), and in this respect *Archaeopteryx* resembles *Anchiornis*. Asymmetry is more weakly developed in the secondaries. In addition, barb curvature is also asymmetrical. Leading edge barbs are straight or weakly curved posteriorly, trailing edge barbs are strongly curved posteriorly along most of their length, with a inflection at the distal end of the barbs, where the barbs curve towards the tip of the feather. Again, this resembles the condition in modern birds. This asymmetry in curvature is more weakly developed in *Anchiornis* (Longrich et al., 2012).

The rachi are broad proximally, but become thinner in their distal 25%. Rachi are robust compared to thosea of body contour feathers, but relatively slender compared to the remiges of crown birds. Although Nudds and Dyke (2010) apparently used incorrect values for both feather diameter and body mass of *Archaeopteryx* in calculating the robusticity of the remiges (Longrich et al., 2012), using more appropriate estimates confirms that the proximal feather shafts are slender compared to volant crown group birds, but similar to those of *Anchiornis* (Longrich et al., 2012). In its distal quarter, however, the relative rachis diameter of the remiges is comparable to modern birds (Foth et al., 2014).

Remiges vary in morphology from distal to proximal, as in modern birds. Distal primary feathers, particularly the four comprising the wing's leading edge, are highly asymmetrical. They have rachi that are strongly curved posteriorly, strongly asymmetrical vanes, and strong asymmetry in both barb angulation and curvature. The tips of the distal primaries feather are also narrow and acutely pointed. Proximally, the rachi of the primaries become straighter and then begin to curve distally (Longrich et al., 2012; Foth et al., 2014). Vanes of proximal remiges are more symmetrical, with broader leading edge vanes, and barb angulation becomes more symmetrical as well. The tips of the proximal primary feathers are much broader and have a blunter end. Secondaries resemble the inner primaries in having relatively broad tips, weakly asymmetrical vanes, and a weak asymmetry in barb angulation.

The wings themselves are relatively short and broad compared to modern birds, with a pointed tip. The leading edge of the wing is formed by four feathers that become successively longer towards the tip of the wing. This design is in contrast to modern birds, where the outermost primary is typically elongate and forms most of the leading edge. From the wingtip, the feathers slowly become shorter again.

The precise number of primaries and secondaries is unclear. Depending on the specimen and interpretation the number of primaries has been estimated as being anywhere from eight (Longrich et al., 2012) to eleven (Rietschel, 1985; Mayr et al., 2007) or twelve (Heilmann, 1926; Norberg, 1985b; Stephan, 1985; Wellnhofer, 2009; Foth et al., 2014). The number of secondaries is at least ten (Longrich et al., 2012) but others identify 12 (Steiner, 1962) to 15 (Stephan, 1987).

The Berlin specimen preserves the tips of at least eight primaries (Longrich et al., 2012), indicating a minimum of eight primaries, however the transition between primaries and secondaries is unclear. The Altmühl specimen has been described as preserving 12 primaries (Foth et al., 2014). There is a distinct gap between the inner and outer remiges in the Altmühl specimen, which is also associated with a shift in feather morphology, however. If this gap represents the transition between primaries and secondaries, there are 10 primaries; however Foth et al. (2014) interpret this gap originally as an artificial disruption of the wing when the forelimb was disarticulated from the axial skeleton and drifted under the left hindlimb before burial (Fig. 8).

The ambiguity in the number of primaries is due not just to the difficulty in identifying the primary-secondary transition. In the Berlin *Archaeopteryx*, four to six additional pairs of wing feathers are preserved, concealed beneath the primaries (Rietschel, 1985; Longrich et al., 2012). These feathers are visible as shallow grooves or 'shaft shadows' which corresponding to rachi underlying the visible primaries. In places, the primaries have been split away and reveal the rachi

and barbs of these feathers, showing that they do in fact correspond to feathers (Rietschel, 1985; Longrich et al., 2012).

Although these concealed are typically interpreted as displaced primaries (Rietschel, 1985; Foth et al., 2014), several lines of evidence argue against this hypothesis. First, these feathers are not exposed distally on either the right or left wing, and the 'shadows' of the shafts disappear before the edge of the wing suggesting that they are shorter than the primaries (Longrich et al., 2012). Second, the shadow shafts are slightly angled relative to the primary series, rather than lying in parallel with them (Longrich et al., 2012). Third, the feathers alternate with the primaries on both the left and right wings. This regularity of this arrangement is difficult to explain as a taphonomic artefact (Longrich et al., 2012). Fourth, the rest of the wing plumage is in place down to individual feathers and barbs. Given that the feather preservation in the Berlin specimen is superior to most other specimens, and the arrangement most likely represents the state of the plumage in life (Longrich et al., 2012). If some primaries had been displaced, one would expect to see other feathers and barbs displaced from their life position. Thus, these concealed feathers were interpreted as dorsal coverts (Longrich, 2006; Longrich et al., 2012). A similar arrangement can be seen in the London *Archaeopteryx* (Longrich et al., 2012) with feathers that are shorter than the primaries overlying them (Longrich et al., 2012). A similar arrangement to the one proposed for *Archaeopteryx*, with the wing being composed of multiple layers of feathers instead of just the primaries, was subsequently identified in *Anchiornis* (Longrich et al., 2012). The hypothesis of elongate dorsal coverts has not been universally accepted. Foth et al. (2014) have argued that the Altmühl specimen exhibits 12 primaries (see above) and that the concealed feathers in the Berlin specimen represent the "missing" primaries, as suggested by Rietschel (1985) (Fig. 9).

Dorsal secondary coverts appear to be visible on the right wing of the London specimen, where several feathers overlie the secondaries but fail to extend the full chord of the wing. They overly the primaries and pass obliquely over them, with their tips angled distally. These appear to represent dorsal coverts and extend almost the full width of the wing. They lack the broad, pennaceous vanes of the ventral coverts seen in the Berlin specimen, and instead appear to have narrower, closed vanes. The elongation of the dorsal coverts again matches the condition in *Anchiornis*.

Ventral primary coverts are identifiable in the Berlin specimen. They are short distally but become longer proximally. The ventral coverts extend obliquely across the primaries and have their tips angled inward relative to the primaries, as in the primary feathers of crown birds. Ventral secondary coverts are well-preserved in the Berlin specimen on the left and right wing (Longrich et al., 2012). As with the ventral primary coverts, they lie with their tips angled inward relative to the associated secondaries. Ventral secondary coverts extend almost the entire chord of the wing, such that only the tips of the secondaries are exposed (Longrich et al. 2012). The ventral coverts have an open pennaceous structure, the barbs interlock at their bases but distally they are separated, which in the Berlin specimen gives the underside of the wing a shaggy appearance.

The wing of *Archaeopteryx* is usually reconstructed without alular feathers on the first digit (Wellnhofer 2009), which in extant birds increase lift generation at low speeds (Nachtigall and Kempf, 1971). Instead it has been hypothesized that the first digit of the manus might have had an analogous function (Meseger et al. 2012). However, the Berlin specimen has a possible feather impression distal to the ungual of digit I on the right wing, which may represent an alula or a homologue of the alula. In the Altmühl specimen the same region is covered by tibial feathers, so that this observation cannot be verified. Although the evidence is weak for *Archaeopteryx*, alular feathers are preserved in other Eumaniraptora, including *Anchiornis* (Longrich et al., 2012), *Microraptor* (Xu et al., 2003) and stem birds such as Enantiornithes (Sanz et al., 1996; Xing et al., 2016). It is therefore likely that *Archaeopteryx* had alular feathers, but if so, new fossils are needed to verify their presence.

The leading edge of the wing may also have been extended by short feathers projecting anterodistally. Traces of these feathers appear to be present in the Berlin *Archaeopteryx* (Longrich et al., 2012) and in the Altmühl specimen. Again these feathers are seen in *Anchiornis* (Longrich et al.,

2012) and **Microraptor** (Czerkas et al., 2002). This sharp leading edge is absent in modern birds, where instead the leading edge is covered by small contour feathers that give the leading edge a rounded cross section.

The presence of a propatagium forming the anterior edge between humerus and radius is indicated by a spray of feathers anterior to the deltopectoral crest and the shaft of the humerus of the Berlin specimen. These feathers are similar in position and arrangement to the subhumeral tract of the humerus (Lucas and Stettenheim, 1972) and suggest that *Archaeopteryx* had a well-developed propatagium (Martin and Lim, 2005). A similar structure can be also found in *Caudipteryx* (Feduccia and Czerkas, 2015), *Anchiornis* (Longrich et al., 2012; Wang et al., 2017b) and Microraptor (Xu et al., 2003; Feduccia and Czerkas, 2015), where an extensive pigmented region anterior to the elbow appears to represent the densely feathered skin of the propatagium.

3.2 Hindlimb feathers

The hindlimb feathers are preserved in the Berlin, Maxberg, and Altmühl specimen, and perhaps in the Eichstätt specimens. They are best seen in the Berlin and Altmühl specimen (Fig. 10, 11). Unfortunately, the feathers on the main slab of the Berlin specimen were partly destroyed during preparation (Tischlinger and Unwin, 2004; Tischlinger, 2005). Fortunately, they are still preserved on the counterslab (Fig. 10), and casts, photos and illustrations of the main slab before preparation exist (see Dames 1884; Longrich 2006; Wellnhofer 2009; Fig. 3B).

The Berlin specimen has elongate feathers posterior to the femur, and tibial feathers that project at an angle from the anterior and posterior margins of the tibia (Longrich, 2006). The number of hindlimb feathers is difficult to determine. In the Altmühl specimen at least 18 to 20 vaned feathers are preserved anterior to the tibia, with their long axes oriented roughly perpendicular to the bone. Proximally the tibial feathers measure 51-58% of the tibia length, and distally they decrease to around 37% (Fig. 11A). In both specimens the hindlimb feathers are preserved in the sagittal plane, and overlap each other to form a large, fan-shaped structure.

The tibial feathers have a slender rachis that curves posteriorly, as in remiges and rectrices. Vanes are long and slender, again resembling remiges and rectrices (Fig. 11B). Longrich (2006) suggested that the vanes were asymmetrical based on the counterslab of the Berlin specimen, but preservation here is poor. The more complete feathers of the Altmühl specimen suggest that the hindlimb feathers are more or less symmetrical (Foth et al., 2014). Barb angulation likewise appears to be relatively symmetrical. However, barb curvature is highly asymmetrical, with both leading and trailing edge barbs curving posteriorly, as in remiges and rectrices, rather than contour feathers.

No feathers are visible on the foot of the Berlin specimen, but a few short feathers project dorsally from the proximal end of the right metatarsus in the Altmühl specimen. In contrast to the long, broad feathers on the tibia, metatarsal feathers appear to have been short and narrow. Proximally they extend at an angle of approximately 60º relative to the foot; more distally they project at an angle of around 45º. Elongate, vaned feathers are preserved posterior to the right metatarsus, however they parallel it rather than projecting away from it. This suggests that they are not in fact part of the foot feathers, and may instead be part of the wing.

The feather arrangement seen in *Archaeopteryx* is similar to that of *Anchiornis* (Hu et al., 2009) and, to a lesser degree, microraptorines including *Microraptor* (Norell et al., 2002; Xu et al., 2003; Pei et al., 2014; Xu and Li, 2016) and Changyuraptor (Han et al., 2014). In both *Anchiornis* and Microraptorinae, feathers project both from the anterior margin of the tibia, and from the posterior margin. The foot bears a short fringe of feathers on its anterior margin, and longer, vaned feathers on its posterior margin, which are elaborated in *Microraptor*. The femur appears to bear feathers in *Microraptor* (Norell et al., 2002) and perhaps *Anchiornis* as well (Hu et al., 2009). However the hindlimb feathers of *Archaeopteryx* are much shorter than either *Anchiornis* or *Microraptor*. *Archaeopteryx* also appears to lack long foot feathers. It is possible that short feathers attached to posterior of the metatarsus and are simply not preserved, but it is unlikely that the elongated feathers seen in *Anchiornis* and *Microraptor* would have escaped preservation. However, given the presence of feathers at the base of the foot, and the fact that the metatarsus is feathered,

not scaled, in *Anchiornis* and *Microraptor,* the metatarsus and probably the tops of the toes were probably feathered, rather than scaly.

3.3 Rectrices

Archaeopteryx bears a series of rectrices extending along either side of the tail (Fig. 12). The number of rectrices is unclear; there are at least 35 pairs of rectrices extending distally from the tip of the bony tail proximally towards the proximal caudals and then to the hips. Rectrices are relatively long at the hips, become shorter at the base of the tail, and then become progressively longer again towards the tip of the tail. Distally, rectrices are longer and more symmetrical (Foth et al., 2014). The distal tail is not preserved except for the Altmühl specimen (Foth et al., 2014). It shows a distinct gap between the last pair of rectrices (Fig. 11C). It is unclear if this gap is real, the result of a molt (Foth et al., 2014), or an artefact of taphonomy. The feathers overlap as in modern birds, with distal feathers overlying more proximal feathers. As with the wings (Norberg, 1985b), this pattern of overlap causes the asymmetrical feathers to twist up against the succeeding feather to form a continuous airfoil surface in flight.

It is unclear whether coverts were present. In crown birds, the tail fan is composed of a single layer of rectrices, with little contribution from coverts. This contrasts with the wings, where coverts overlap the base of the remiges, bracing them and creating a thicker airfoil cross section. Whether coverts have been present in the tail of *Archaeopteryx* is unclear. Several tail feathers in the Altmühl specimen are shorter than the remaining tail feathers, and cross them obliquely. It is possible that these represent covert feathers, but it is also possible that they represent molting feathers.

The morphology of the rectrices is similar to that of the remiges. Rectrices have a broad calamus and an elongate rachis that curves posteriorly in the plane of the feather. Vanes are long, narrow, and in the proximal feathers strongly asymmetrical, with the trailing edge vane being at least 200% the width of the leading edge vane. This is similar to the situation of the flightless troodontid *Jianianhualong* from the Early Cretaceous Jehol group (Xu et al., 2017). The tips of the rectrices form an obtuse angle in proximal feathers, and are ovate in the distal rectrices. Barb angulation is symmetrical, but barb curvature is asymmetrical with leading and trailing edge barbs curved towards the trailing edge.

4. DISCUSSION
4.1 Feather Evolution

In many respects, the feather morphology and arrangement of *Archaeopteryx* is strikingly modern, or seen from another perspective, modern birds are remarkably primitive. Together with *Anchiornis,* *Archaeopteryx* shows that many aspects of feather morphology and arrangement found in modern birds originated in the Jurassic and are retained, within minimal modification, in modern birds (Wellnhofer, 2009; Longrich et al., 2012). Conserved features include the basic structure of the pennate feather, including the rachis, barbs, and interlocking barbules, and also the developmental patterns that underly their growth and molting. Other conserved features are adaptations for flight, such as curved rachi, vane asymmetry, asymmetry of barb angle and barb curvature, and the overlap of feather vanes to create an airfoil. Last, the basic arrangement of feathers into feather tracts and the associated soft tissues also appear to be ancient. It would not be fair to say that the feathers and their arrangement have not changed, clearly major changes did occur between *Anchiornis* and *Archaeopteryx* and crown birds in feather structure (Feo et al., 2015) and arrangement (Gatesy and Dial, 1996; Longrich et al., 2012). However, these adaptations notwithstanding, the feathers of birds represent a remarkable example of stasis. Birds are typically considered highly advanced organisms and yet in terms of feather morphology, they are every bit as much a "living fossil" as a crocodile or a coelacanth.

Why the feathers have changed so little is uncertain. It may be that given basic constraints on the mechanical properties of feather proteins and aerodynamics, further refinement simply became impossible. Given the materials available to work with and the basic principles of fluid

mechanics, Jurassic feathers were already an optimal or near-optimal solution to creating a wing from elaborated scales. In this respect avian evolution parallels the evolution of aircraft, where the basic layout of the jet airliner has not changed in half a century, because it represents a mature design that is a near-optimal solution giving existing mechanical and aerodynamic constraints (Longrich et al., 2012). This hypothesis is supported by two observations. First, when birds become secondarily flightless, their feathers often evolve radically different morphologies that differ from those of flying birds (Lüdicke, 1974; McGowan, 1989; Livezey, 2003). Second, feathers that are selected for display, rather than for flight, exhibit a similar departure from the limited range of morphologies seen among flight and contour feathers (Brinckmann, 1958; Bleiweiss, 1987; Stavenga et al., 2011). Both observations suggest that radical evolution in feather structure is possible, once the selective pressures of flight are removed or at least no longer dominant. However, existing developmental patterns may also constrain feather morphology. Although the feathers of flightless birds and display feathers do depart from the overall morphology of flight and contour feathers, they are derived from the same basic morphology of a central rachis that branches to create barbs and barbules (see chapter 2: Lin et al.). Once evolved, the developmental processes that underly feather formation can be modified to produce a diverse but ultimately constrained range of forms. Together, these two forces- stabilizing selection towards an optimal solution, and developmental processes that constrain feather variation- probably explain why flight feathers have remained relatively unchanged in the 145 million years since *Archaeopteryx*.

But while the feathering is in many ways similar to those of crown birds, *Archaeopteryx* also shows archaic features that are not seen in living birds. Primitive features of the feathers themselves include relatively slender rachi, and the relatively symmetrical barbs. Despite the overall modern appearance of the plumage, *Archaeopteryx* was not a modern bird and so it is unsurprising that in certain details it is more primitive. Instead its morphology appears to have been transitional between the older and more primitive *Anchiornis*, and more derived pygostylians such as *Confuciusornis*. Primitive features of feather arrangement include the long feathers on the hindlimbs, the development of rectrices along the length of the tail and onto the hips, and the poor differentiation of remiges and coverts. In many of these features *Archaeopteryx* resembles *Anchiornis* and *Microraptor*, suggesting that these features represent the ancestral condition, rather than specializations.

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One of the more striking differences between *Archaeopteryx* and modern birds is the limited differentiation between feather tracts, within feather tracts, and within feathers themselves. Elongated, curved feathers with closed, pennaceous vanes are developed on the hindlimbs and forelimbs, and tail in *Archaeopteryx*, whereas in most crown group birds, hindlimb feathers resemble the morphology of body contour feathers (see Lucas and Stettenheim, 1972). Similarly the supposed elongation of the coverts relative to the primaries and secondaries shows limited differential within the wing feathers. Even within the individual primary feathers, differentiation of barbs is weakly developed, with angulation of anterior and posterior barbs being relatively symmetrical. A similar pattern is seen in Anchiornis, except more extreme, with symmetrical feathers that show very little differentiation between primaries and secondaries, remiges and coverts, or forelimbs and hindlimbs (Hu et al., 2009). This suggests that in the early stages of avian evolution, stem birds had yet to fully develop the ability to fully specify feather morphology either within or between feathers. A higher degree of differentiation is seen in Pygostylia. Here, we see highly asymmetrical flight feathers, differentiation of primaries, secondaries, and coverts, reduction of hindlimb feathers, and differentiated rectrices (see chapter 9: O'Connor). The feather differentiation seen here approaches that of crown Aves, suggesting more refined control of

feathering and feather morphogenesis resulting from improvements in regulation of the genes that specify feather morphology.

4.2 Feather Function and Behavior

The structure of the feathers and wings of *Archaeopteryx* suggests that they functioned as efficient airfoils, which served to maintain lift, stability, control, and perhaps to generate thrust. The body feathers probably functioned to insulate and streamline the animal. None of the feathers appear specialized for display, but courtship in birds is heavily dependent on visual cues, and so even if display was not a primary function, the feathers would almost certainly have served a secondary role as display structures. Last, the carefully arranged feathers and barbs strongly indicate that *Archaeopteryx* had evolved grooming behaviors to maintain its plumage.

The flight ability of *Archaeopteryx* has been and remains highly controversial. Although some have proposed that *Archaeopteryx* was incapable of flight (Ostrom, 1979), the asymmetry of the feathers as well as their arrangement indicates that the wings and the tail were adapted to function as airfoils (Feduccia and Tordoff, 1979; Norberg, 1985b). Asymmetry of the distal primaries is seen in all volant birds, but tends to be poorly developed or absent in flightless birds (Feduccia and Tordoff, 1979; Speakman and Thompson 1994). Although Speakman and Thompson (1994) argued that the feathers were symmetrical, Norberg (1995) pointed out that the apparent symmetry is a taphonomic artefact, and that feather asymmetry in *Archaeopteryx* is comparable to asymmetry in flying birds.

The asymmetry of the feather is an adaptation to the asymmetrical loads experienced in flight. The center of pressure for an individual feather lies near its leading edge, requiring the main support to be located towards the leading edge (Norberg, 1985b). The asymmetry is also important to stabilizing the feather in flight; by shifting the main support anterior to the center of pressure, the feather develops a nose-down pitching moment that causes the trailing edge to twist up against trailing feathers, causing the feathers to automatically assemble into an airfoil (Norberg, 1985b).

Vane asymmetry, however, is only one of several features that differentiate flight feathers from ordinary down, display, and body contour feathers. Flight feathers are characterized by a suite of adaptations for lift generation, which are variably developed depending on their position in the wing. Distal primaries and remiges are oriented at a strong angle relative to the airflow and therefore tend to be under highly asymmetric loads, and exhibit corresponding adaptations. The proximal primaries and secondaries are oriented parallel to the airstream and tend to exhibit these features to a lesser degree. Such features (Table 2) include long and robust calami and rachises, posterior curvature of the rachis within the vane, elongate vanes, vane asymmetry, asymmetrical barb angulation and barb curvature, tightly interlocking barbs, and reduction of the downy part of the vane (Lucas and Stettenheim, 1972; Norberg, 1985b; Longrich, 2006; Feo et al., 2015). This suite of features can be considered as functional correlates of an aerodynamic, lift-generating function in feathers.

However, as some secondary flightless birds still possess asymmetric vane ratios falling into the lower range of volant birds, and other features cited above as potential adaptations for aerodynamic function, these parameters should be still considered with caution in interpreting the flight capacity of extinct stem birds (see Wang et al., 2017a). Asymmetry is consistent with adaptation for aerodynamic function, but adaptation for a function does not necessarily mean use for that particular function: the asymmetric tail feathers of the Early Cretaceous troodontid *Jianianhualong* show adaptation to flight, but do not function for flight (Xu et al. 2017). It is therefore important to consider other features, such as wing loading or skeletal correlates of gliding or flapping flight, in inferring flight ability.

In addition to the shape, the arrangement of the feathers is critical to forming an airfoil. The asymmetry and posterior curvature of the feathers is important in creating a nose-up pitching moment. When arranged in series, they cause distal feathers to twist up against the proximal feather, automatically assembling into an airfoil and stabilizing the wing surface in flight (Norberg, 1985b). This arrangement, with proximal feathers overlapping trailing feathers, is seen in the wings and tail

of *Archaeopteryx*, and perhaps also the legs. All of these features are found, to varying degrees, in the remiges and rectrices of *Archaeopteryx*, arguing for a lift-generating function.

In addition to the structure and arrangement of individual feathers, the shape of the wings and tail in *Archaeopteryx* suggests that they were effective and efficient lift generating airfoils capable of supporting and steering the bird in flight. To fly, a bird requires relatively low mass relative to wing area, a parameter known as wing loading. Estimates of wing loading in *Archaeopteryx* vary, but they consistently show that it was comparable to modern birds and would have been adequate to support the animal during either gliding or flapping flight (Norberg, 1990). Furthermore, to generate lift efficiently, wings must have a relatively long span compared to the chord, a parameter known as aspect ratio, and tapered tips, which help create an elliptical distribution of lift. This shape helps to minimize the wingtip vortices that generate lift-induced drag. Again, *Archaeopteryx* is comparable to modern birds here (Norberg, 1990), suggesting well-developed gliding or flapping flight. The tail and perhaps hindlimbs would have also been able to contribute to lift generation (Longrich, 2006).

The existence of control structures is also critical, in that flight is of little use if not lethal when it cannot be controlled. The tail of *Archaeopteryx* would have been effective as a delta wing (Gatesy and Dial, 1996), which could have functioned as a horizontal stabilizer and elevator to stabilize and control the bird in pitch. In addition, the hindlimb feathers may also have been able to contribute to stability and control (Longrich, 2006; Foth et al. 2014) (see below).

There is little doubt that *Archaeopteryx* was capable of aerial locomotion (Fig. 13), but whether it was capable of powered flight or not remains open to debate. Nothing in the morphology of the wings and feathers would appear to have prevented flapping flight, and the shape and size of the wings are consistent with a bird capable of powered flight (Voeten et al. 2018). However, there are no adaptations to the wings that are specific to powered flight: asymmetric, curved feathers are found both in the wings and the tail. The high aspect ratio that is required for powered flight is also effective in improving glide performance. A number of features of the skeleton do suggest adaptation for powered flight, however. The robust furcula and coracoids may have supported the muscles to make a down stroke possible (Olson and Feduccia, 1979), while the sharp angle between the coracoids and the scapula would have allowed the pectoralis to both depress and retract the humerus against the lift and thrust produced by flapping flight. The elongate coracoids would also have increased the length of the pectoralis muscles and therefore the distance over which they could contract, increasing the potential amplitude of a wingbeat. These features may represent adaptations for powered flight, but are also seen in Dromaeosauridae (Paul, 2002). Either they do not in fact represent flight adaptations (but were exaptated for flight later on), or flight may have evolved earlier than generally believed.

However, the primitive morphology of the glenoid, the small and unossified sternum, the short coracoids and the lack of a supracoracoideus pulley (acrocoracoid process) (Wellnhofer, 2009) suggest that flapping flight, if it was possible, was rudimentary. Flap-gliding of the sort practiced by petrels and gulls, with glides interspersed with low-amplitude flapping flight using a continuous-vortex gait, was likely possible. Sustained level flight at high speeds, again using low-amplitude flapping and continuous vortex gait, may have been possible, given that flight is less expensive and flight kinematics are simpler (Rayner, 2001). Low speed flight, requiring more elaborate wing kinematics and high power output, seems less likely.

The function of the hindlimb feathers remains unclear. The morphology, shape and arrangement of the feathers suggests that they may not simply be simply body feathers as traditionally thought. Instead they appear to be homologous with the elongate feathers seen on the hindlimbs of *Anchiornis* (Hu et al., 2009), *Microraptor* (Xu et al., 2003), and at least some basal pygostylians, including enantiornithes (Zhang and Zhou, 2004; Zheng et al., 2013). The arrangement of the feathers in *Archaeopteryx* also indicates that current reconstructions of *Anchiornis* and microraptorines are incorrect in having feathers extending only from the trailing edge of the leg; instead as in *Archaeopteryx*, feathers of *Anchiornis* (Hu et al., 2009) and

microraptorines (Czerkas et al., 2002; Xu and Li, 2016) both show that a large fan of feathers extends from the anterior edge of the tibia and the posterior.

As discussed above, flight feathers exhibit a suite of features that are absent in body contour feathers (Lucas and Stettenheim, 1972; Longrich, 2006), and which can be considered functional correlates for flight. The hindlimb feathers of *Archaeopteryx* exhibit some, but not all of these features (Table 2). Features shared with remiges and rectrices feathers include long and narrow vanes, sharp vane edges, posterior curvature of the rachis, and the asymmetry of barb curvature. Yet the hindlimb feathers lack asymmetry in barb angulation and the vanes appear to be symmetrical or very weakly asymmetrical. These features vary depending on position in the airfoil, however Outer primaries and lateral rectrices invariably show all of these functional correlates. More proximal remiges and inner rectrices, however, tend to be more symmetrical in terms of vane width, barb angulation, and barb curvature. The weakly developed asymmetry of the vanes of the hindlimb feather therefore does not preclude aerodynamic function, any more than it precludes aerodynamic function for inner secondaries and rectrices.

It is also possible that the hindlimb feathers, although exhibiting features associated with flight, did not actually function for flight, and were simply vestiges of the earlier four-winged designs seen in Anchiornis and dromaeosaurids. If so, *Archaeopteryx* might be transitional between the earlier 'four-winged' forms and the later, two-winged forms (Prum, 2003; Longrich, 2006). In contrast, Foth et al. (2014) hypothesized that the homoplastic variation in terms of size, shape and regional distribution of the hindlimb feathers within Eumaniraptora may indicate an initial display function, which is supported by the presence of complex and gleaming color patterns within Pennaraptora (e.g., Li et al., 2010, 2012).

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TABLES

Table 1. Preservation of feathers in the 12 currently known specimens of Archaeopteryx (numbering of specimens in parenthesis).

Specimen	Remiges	Dorsal Coverts	Ventral Coverts	Leg Feathers	Rectrices	Body contour Feathers
Feather (0)	-	X	-	-	-	-
London (1)	X	X	-	-	X	-
Berlin (2)	X	X	X	X	X	X
Maxberg (3)	X	-	-	X	-	-
Haarlem (4)	X	-	-	-	-	-
Eichstätt (5)	X	-	-	?	X	-
Solnhofen (6)	X	-	-	-	-	-
Munich (7)	X	-	-	-	X	-
Daiting (8)	-	-	-	-	-	X
"Chicken wing" (9)	X	-	-	-	-	-
Thermopolis (10)	X	-	-	-	-	-
Altmühl specimen (11)	X	X	X	X	X	-
Schamhaupten (12)	-	-	-	-	-	-

Table 2. Aeordynamic features of pennaceous feathers (after Longrich, 2006) of Archaeopteryx from different body regions.

	Remiges	Rectrices	Hindlimb
Calamus and rachis slender (0) or robust (1)	**1**	**1**	**0**
Rachis straight (0) or curved in plane of feather (1)	**1**	**1**	**1**
Vanes broad (0) or feathers long and slender (1)	**1**	**1**	**1**
Vanes symmetrical (0) or asymmetrical (1)	**1**	**1**	**0**
Barb angulation symmetrical (0) or asymmetrical (1)	**1**	**1**	**0**
Barb curvature symmetrical (0) or asymmetrical (1)	**1**	**1**	**1**
Barbs loosely interlocked, vane edge ragged (0) or tightly interlocked along their length, vane edge sharp (1)	**1**	**1**	**1**

Figures
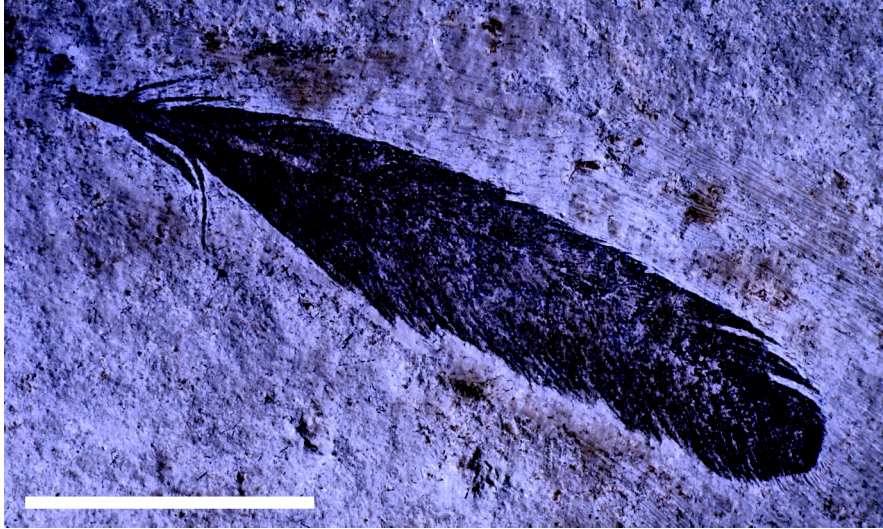
Figure 1. The isolated feather. Discovered in 1861, it was the first specimen to be discovered and the original holotype of *Archaeopteryx lithographica*. Despite dating to the Late Jurassic, it is remarkably similar to the wing feathers of extant birds. It is likely to represent a covert. Total length = 58 mm.
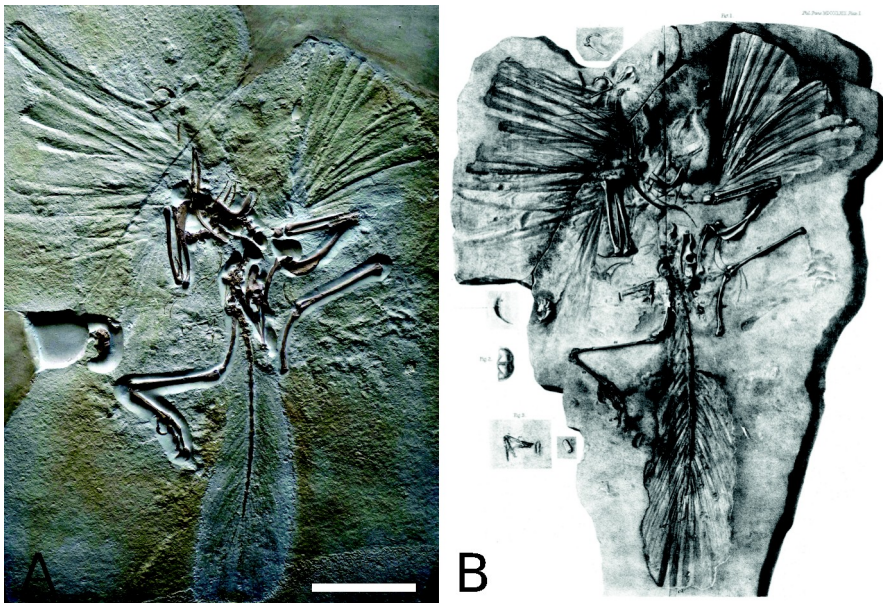
Figure 2. (A) The neotype of *Archaeopteryx lithographica* (London specimen). Discovered in 1861, it demonstrated the association of advanced, avian-like plumage with a primitive skeletal structure similar to that of dinosaurs such as *Compsognathus longipes*. (B) Owen's illustration of the London *Archaeopteryx*. Femur length = 61 mm.
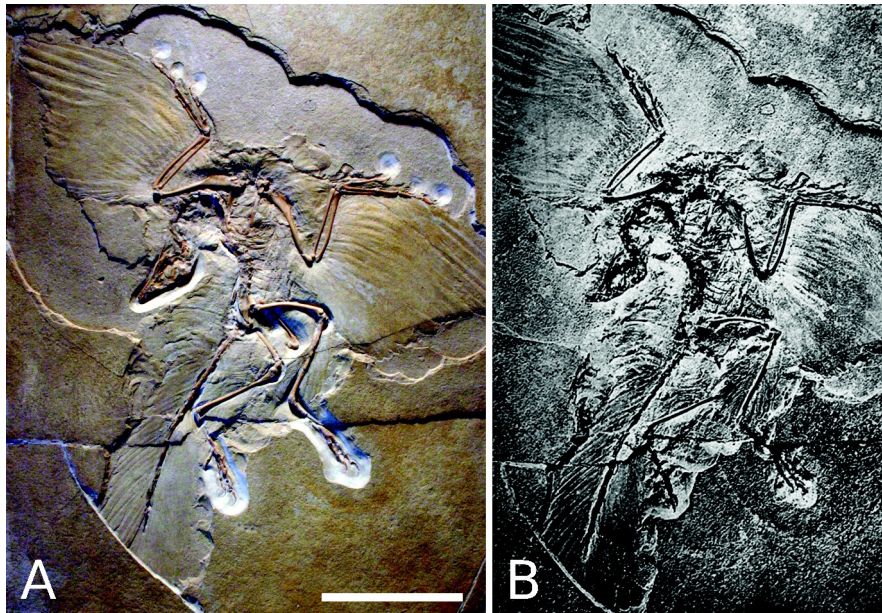
Figure 3. (A) Main slab of Berlin specimen of *Archaeopteryx*, which has the most completely preserved plumage of any specimen. (B) First photograph of the Berlin specimen (published in 1879) prior to preparation, showing long feathers around the hindlimbs and neck that have since been prepared away. Femur length = 52 mm.
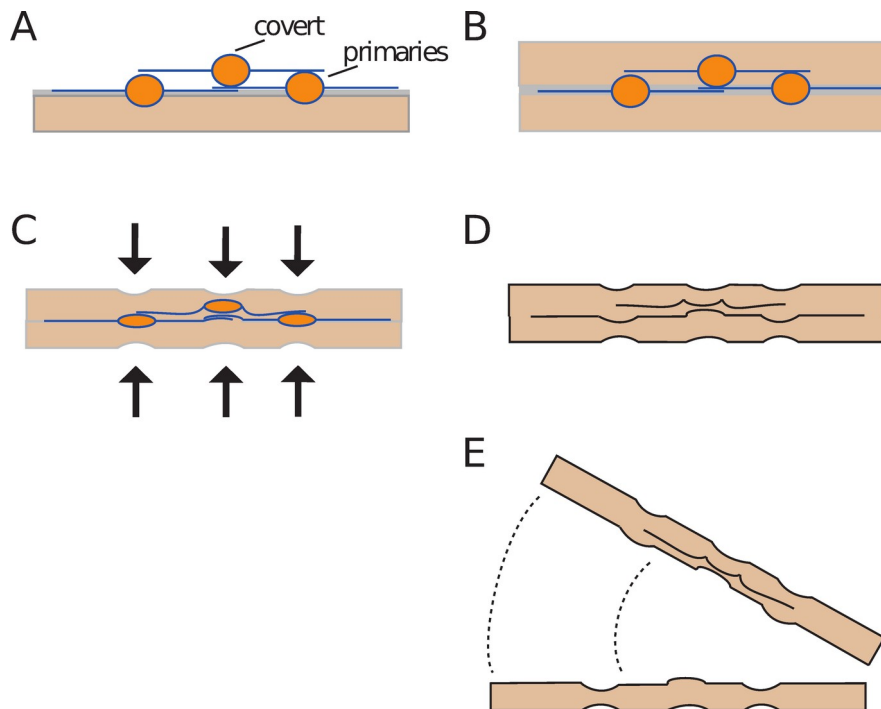
Figure 4. Taphonomic model for the preservation of *Archaeopteryx* feathers, from Longrich et al. (2012) and modified from Rietschel 1985. Primaries and coverts are pressed into the sediment (A) and then buried (B). Compaction of the feathers (C) leads to displacement of sediment above and below the rachi (D). When the slab is split apart, a single layer of feathers is revealed, along with "shaft shadows" resulting from compaction of the sediment.
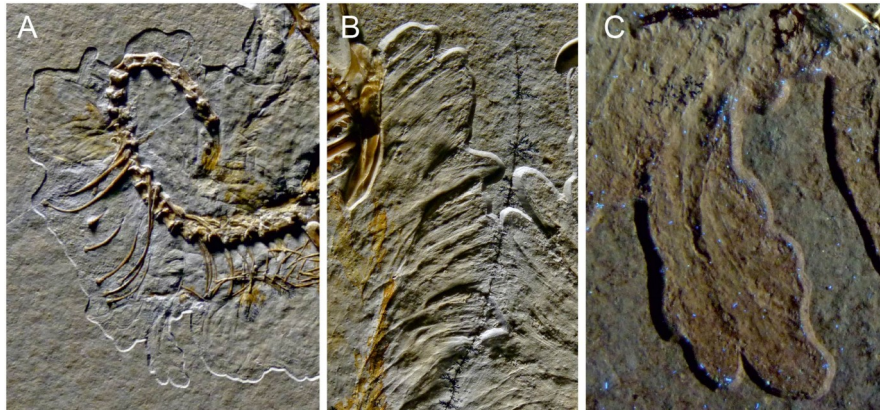
Figure 5. Body feathers of the Altmühl *Archaeopteryx*. (A) Feathers of the neck and body; (B) close-up of hackle feathers in the neck region; (C) close-up of a pair of body features from (A).
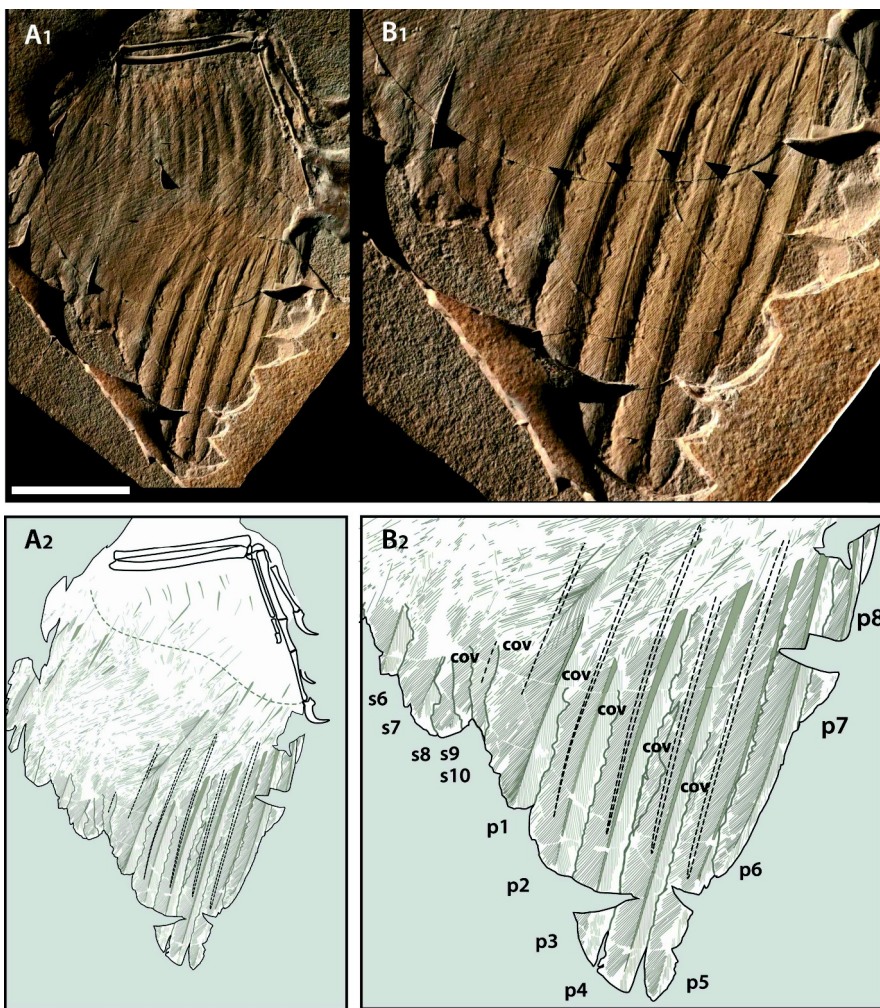
Figure 6. Left wing of the Berlin Archaeopteryx, counterslab showing primaries, secondaries, coverts, and impressions of concealed feathers as interpreted by Longrich et al. (2012). Abbreviations: p8-p1, primaries 1-8; s6-10, secondaries 6-10, cov, coverts. Ulna length = 56 mm.
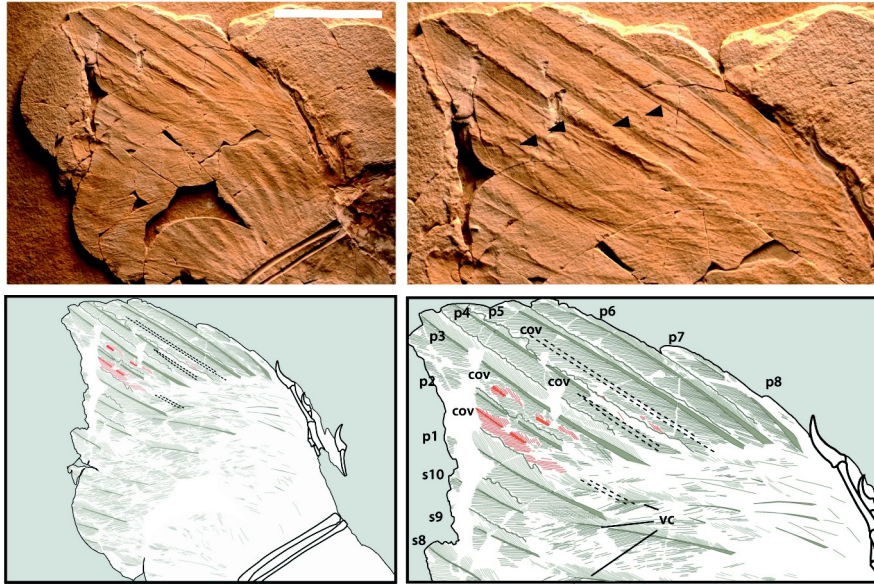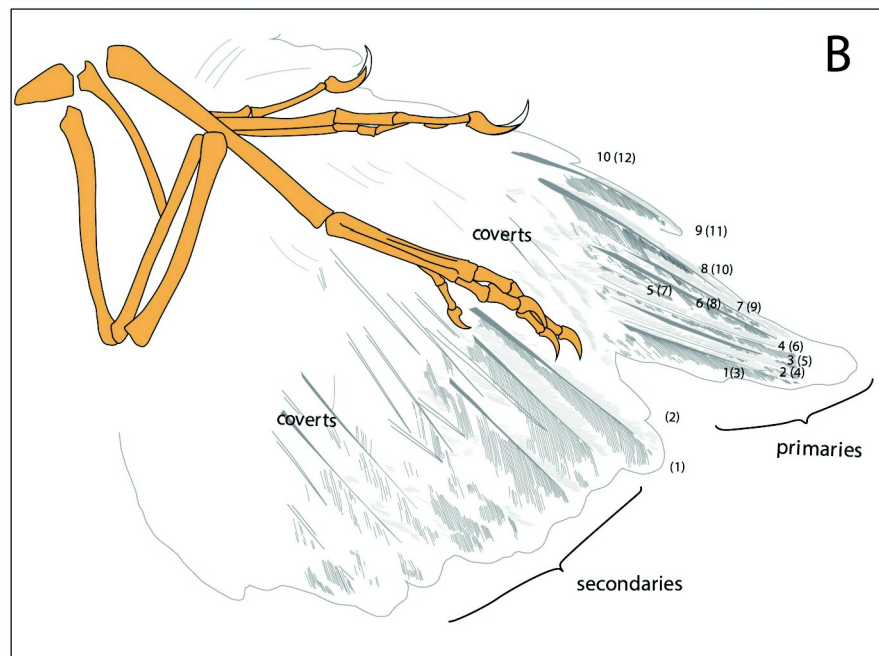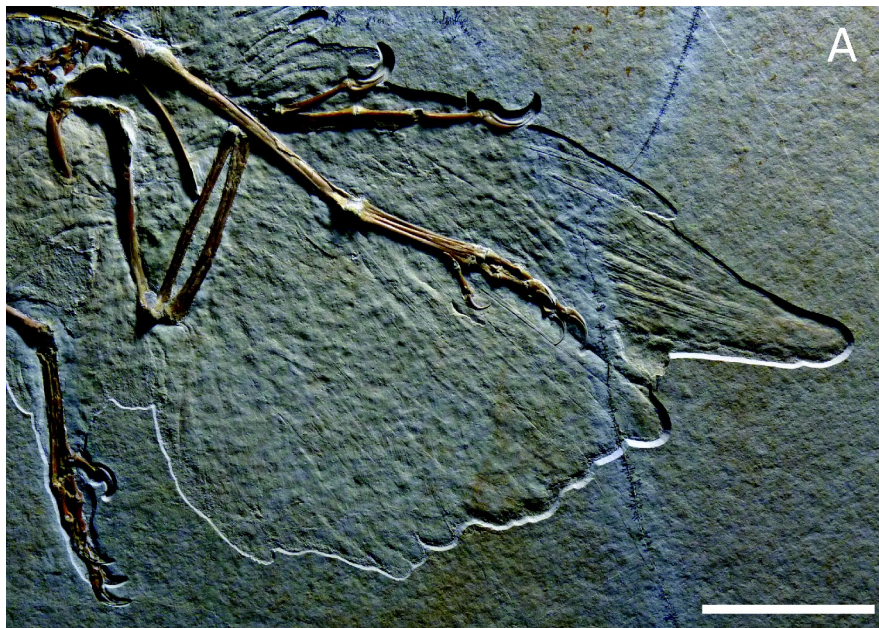
Figure 7. Right wing of the Berlin *Archaeopteryx,* counterslab showing primaries, secondaries coverts and impressions of concealed feathers as interpreted by Longrich et al. (2012).
Abbreviations: p8-p1, primaries 1-8; s8-10, secondaries 8-10, cov, coverts.

Figure 8. Right wing of the Altmühl specimen of *Archaeopteryx*, showing primaries, secondaries and unidentified coverts. There are at least 10 primaries visible (labeled 1-10 in black), and Foth et al. (2014) identify 12 (labelled 1-12 in gray). Humerus length = 66 mm.
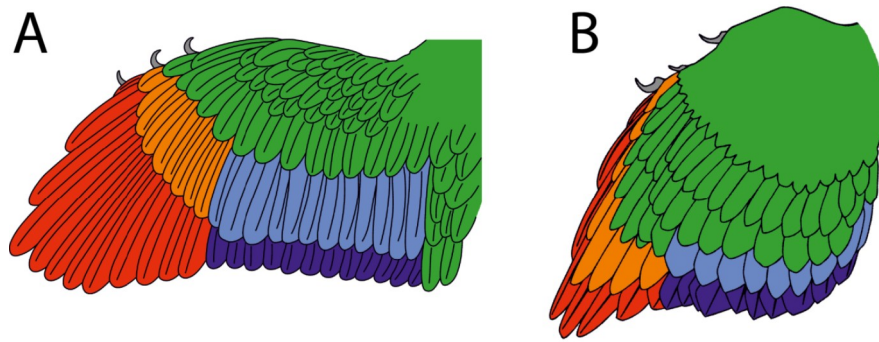
Figure 9. Different reconstructions of the wing of *Archaeopteryx*. (A) Original reconstruction, with numerous primaries and short dorsal primary coverts, (B) as interpreted by Longrich et al. (2012) with elongate coverts. Red = Primaries; orange = major dorsal coverts, dark blue = secondaries; light blue = major secondary coverts.
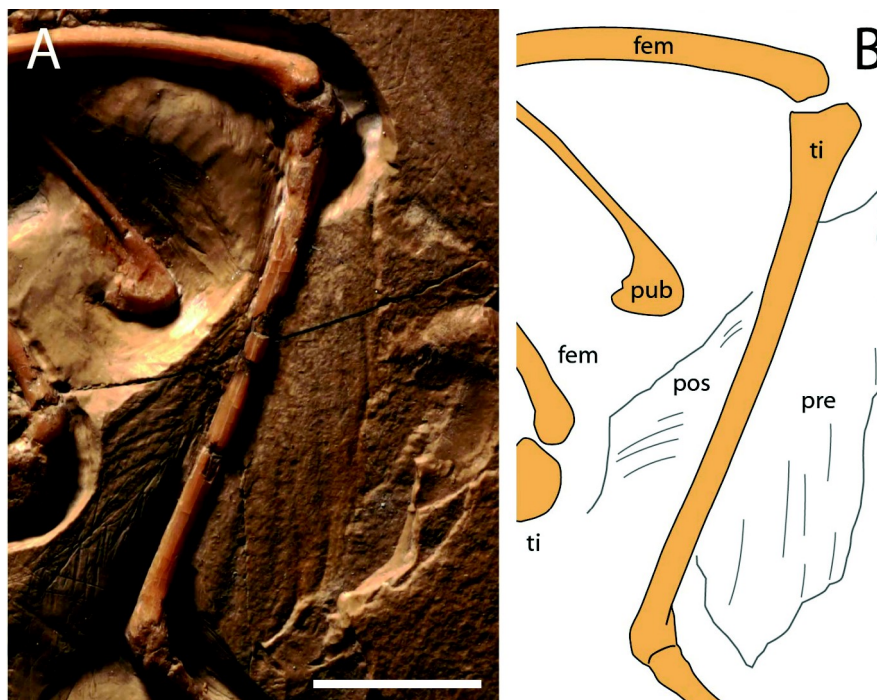

Figure 10. Tibial feathers of the Berlin *Archaeopteryx*. (A) Main slab; (B) interpretive drawing. Abbreviations: fem, femur, ti, tibia, pos, posttibial feathers, pre, pretibial feathers. Tibiatarsus length = 71 mm.
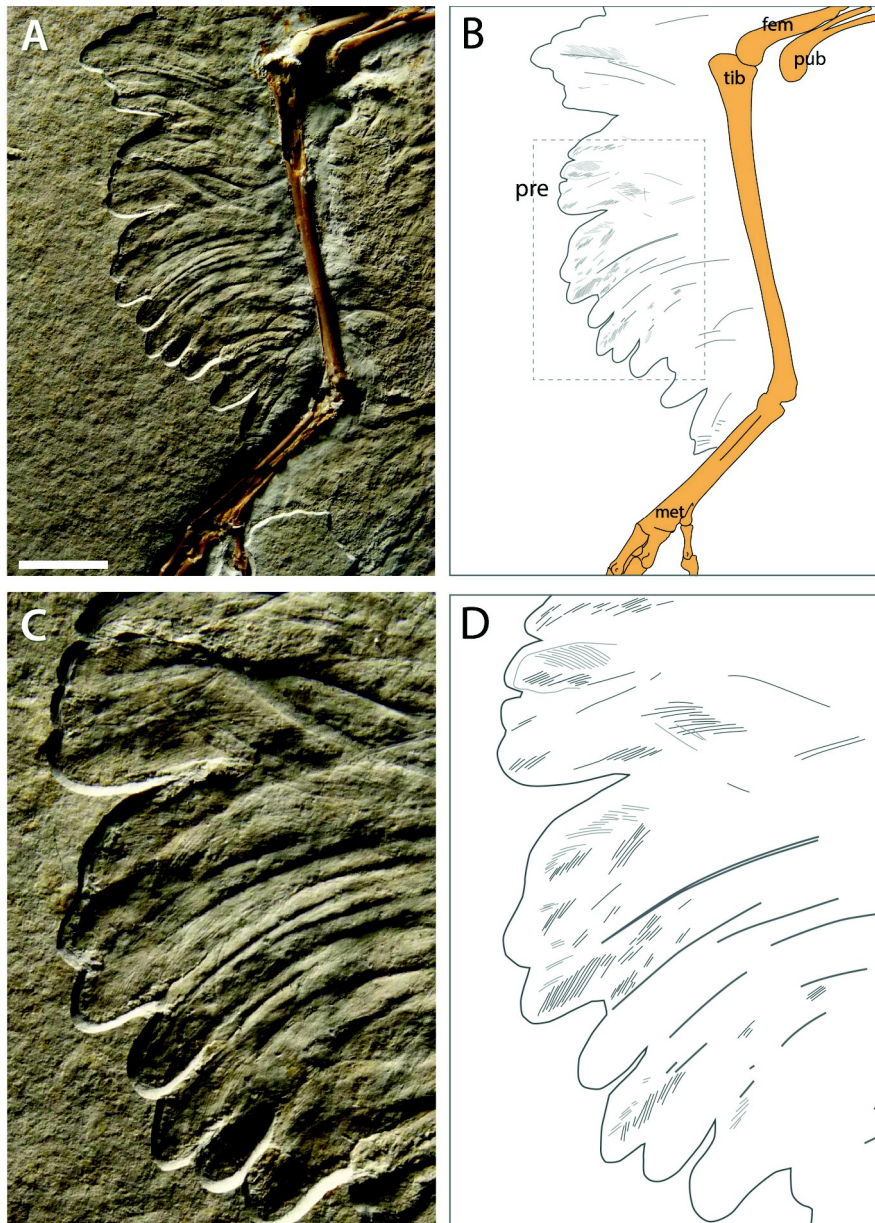
Figure 11. Tibial feathers of the Altmühl *Archaeopteryx*. (A) Hindlimb and feathers; (B) interpretive drawing; (C) closeup of boxed region in (B); (D) interpretive drawing. Abbreviations: fem, femur, ti, tibia, met, metatarsus, pre, pretibial feathers. Tibiatarsus length = 78 mm.
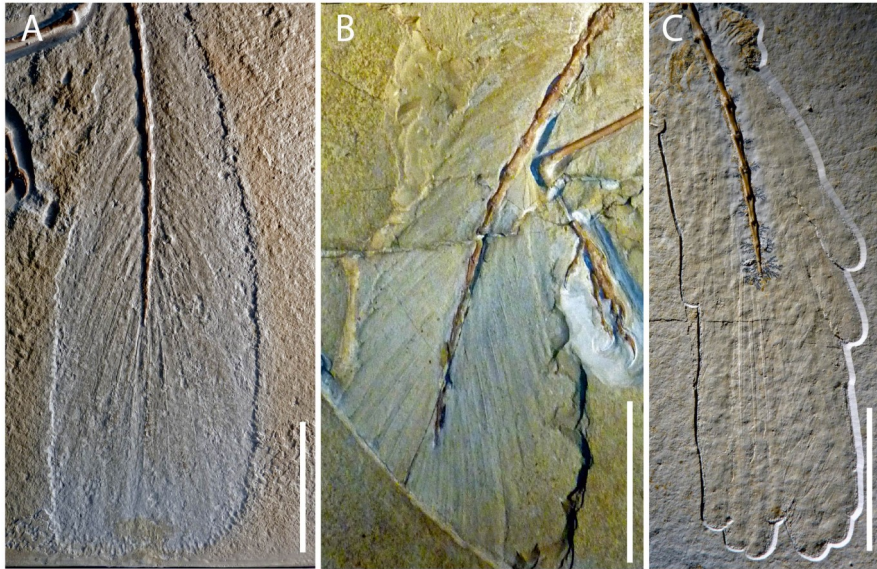
Figure 12. Tail feathers of *Archaeopteryx*. (A) London specimen; (B) Berlin specimen; (C) Altmühl specimen. Scale = 50 mm.

Figure 13. Reconstruction of a pair of *Archaeopteryx* lithographica in flight by Carl Buell.