The Feathers of the Jurassic Urvogel *Archaeopteryx*

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8.1 Introduction

8.1.1 *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 transforms 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 2 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; Figs. 8.1 and 8.2). 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 11 skeletal specimens have been referred to the genus *Archaeopteryx* with certainty (Wellnhofer 2009; Foth et al. 2014; Rauhut et al. 2018), while the Haarlem and the newly discovered Mühlheim (13th) specimen are considered representing different genera (see Foth and Rauhut 2017; Rauhut et al. 2019). These fossils have helped to bridge the divide between birds and their reptilian ancestors, and they have continued 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.

8.1.2 *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

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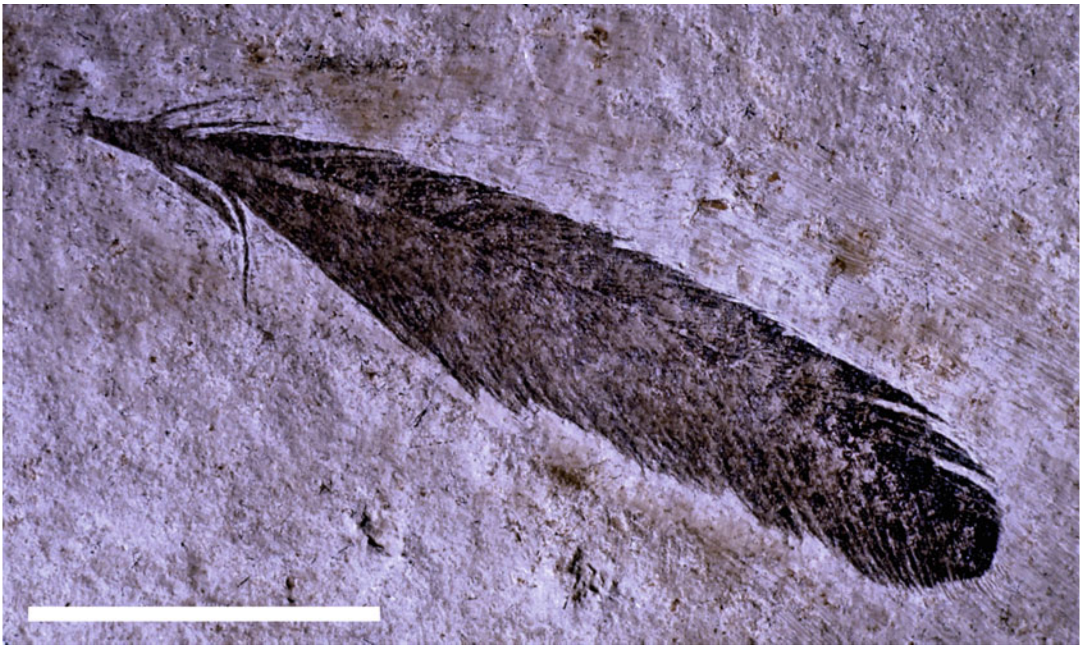

Fig. 8.1 The isolated feather. Discovered in 1861, it was the first specimen to be discovered and the original holotype of *Archaeopteryx lithographica*. Despite dating to the Late Jurassic, it is remarkably similar to the wing feathers of extant birds. It is likely to represent a covert. Scale = 25 mm

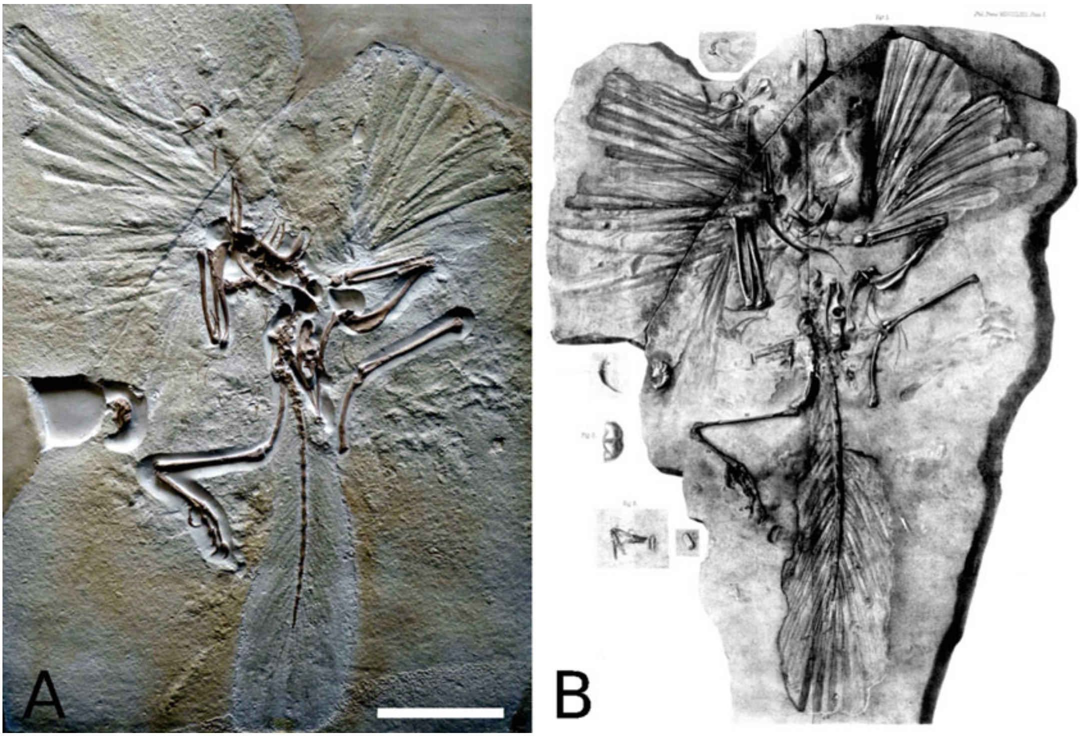

Fig. 8.2 (**a**) The neotype of *Archaeopteryx lithographica* (London specimen). Discovered in 1861, it demonstrated the association of advanced, avian-like plumage with a primitive skeletal structure similar to that of dinosaurs such as *Compsognathus longipes*. (**b**) Owen's illustration of the London *Archaeopteryx*. Scale = 100 mm

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*, which 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 also 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. Therefore, it continues to be important to our understanding of the evolution of birds and the relationships between non-avialan coelurosaurs and stem birds (Longrich et al. 2012; Foth et al. 2014) and, in particular, to the origin of flight.

8.1.3 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 manoeuvrability. 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 manoeuvring within vegetation. The morphology of *Archaeopteryx* is therefore important to test 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* 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. Furthermore, 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.

8.2 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. 8.3) 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, 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 them as collapsed moulds (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).

8.2.1 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

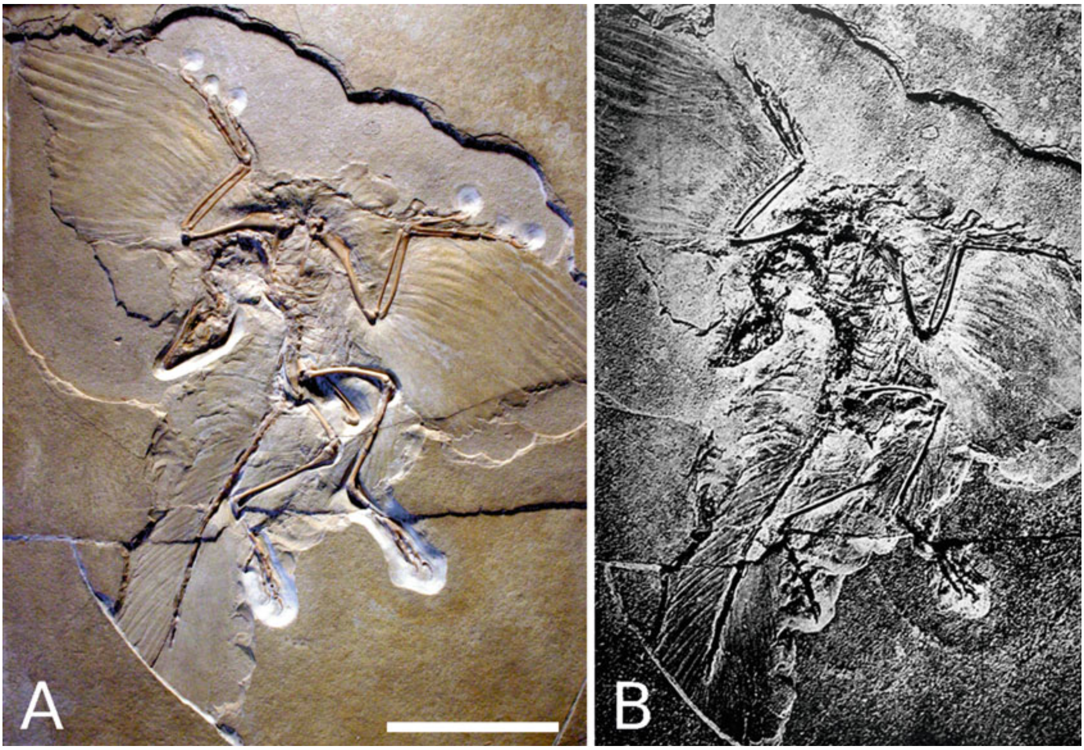

Fig. 8.3 (**a**) Main slab of Berlin specimen of *Archaeopteryx*, which has the most completely preserved plumage of any specimen. (**b**) First photograph of the Berlin specimen (published in 1879) prior to preparation, showing long feathers around the hindlimbs and neck that have since been prepared away. Scale = 100 mm

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 moulded 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 also the position of the feathers in life, or at least, at the moment of death.

8.2.2 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

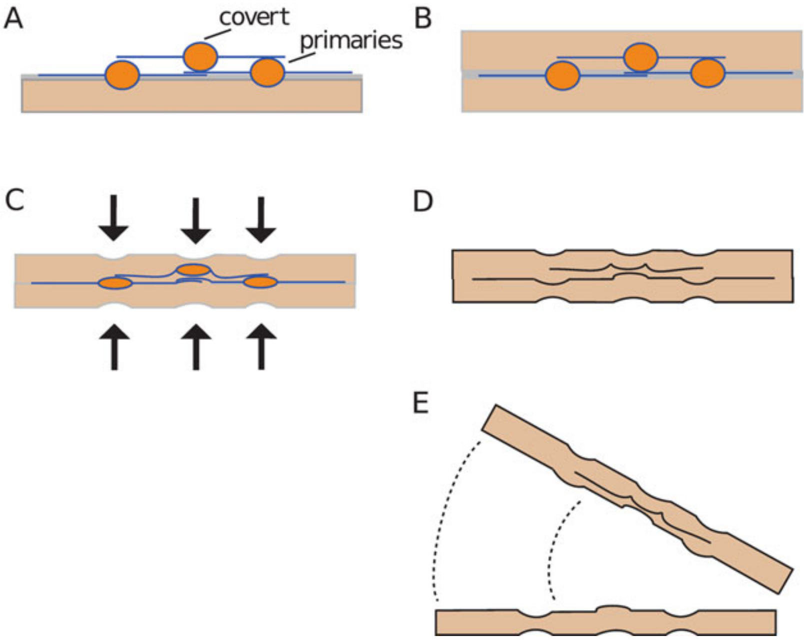

Fig. 8.4 Taphonomic model for the preservation of *Archaeopteryx* feathers, from Longrich et al. (2012) and modified from Rietschel (1985). Primaries and coverts are pressed into the sediment (**a**) and then buried (**b**). Compaction of the feathers (**c**) leads to displacement of sediment above and below the rachis (**d**). When the slab is split apart, a single layer of feathers is revealed, along with 'shaft shadows' resulting from compaction of the sediment (**e**)

here, where the feathers were encased in and moulded by fine sediment particles. Following burial, the soft tissues broke down and the natural moulds 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 moulds 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 moulds being split open, revealing the morphology of the feathers (Fig. 8.4).

A key implication of this model, in which feathers are preserved as moulds 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. 8.3), for example, the main slab 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), do not represent a taphonomic artefact ('double struck' impressions) but are traces of feathers concealed beneath other feathers (Rietschel 1985; Longrich et al. 2012; Fig. 8.4).

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 moulds themselves but rather the ‘printing’ of the collapsed moulds 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 (Ottmann and Steil specimen, ‘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.

8.2.3 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 possess high concentrations of organic copper, organic sulphur (Carney et al. 2012), sulphate and nickel (Manning et al. 2013). Sulphur most likely comes from the original feather keratin (Wogelius et al. 2011), while 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 colour 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.

8.2.4 Feather Nonpreservation

Given the exceptional preservation of soft tissues seen in some Urvogel 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 8.1), feather preservation is variable. In the Berlin and Altmühl 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 were preserved. In others, including the Haarlem (see Foth and Rauhut 2017 for alternative taxonomic classification), Solnhofen, and Ottmann and Steil (‘chicken wing’) specimen, only poorly preserved traces of the remiges are visible, and in the Schamhaupten (12th) and Mühlheim (13th) specimen, feathers are absent (Rauhut et al. 2018, 2019). 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), nonpreservation is the rule. Therefore, it is unlikely that a small sample of 11 *Archaeopteryx* 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

Table 8.1 Preservation of feathers in the currently known specimens of *Archaeopteryx*, *Ostromia*∗ and *Alcomonavis*∗∗ (numbering of Urvogel 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
Ottmann and Steil (9)	X	–	–	–	–	–
Thermopolis (10)	X	–	–	–	–	–
Altmühl (11)	X	X	X	X	X	–
Schamhaupten (12)	–	–	–	–	–	–
Mühlheim∗∗ (13)	–	–	–	–	–	–

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 the absence of evidence for soft tissues should not be taken as strong evidence for their absence.

8.3 Feather Morphology

8.3.1 Feather Structure

The morphology of the individual feathers of *Archaeopteryx* is remarkably similar to modern birds (Lucas and Stettenheim 1972; Fig. 8.1). 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 Chap. 2). 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 on either side of the rachis. Proximally, the barbs are separated, but distally they interlock to form closed vanes. In his initial description, von 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 visibly 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 light

(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).

8.3.2 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 semiregular 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 is 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 et al. 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.

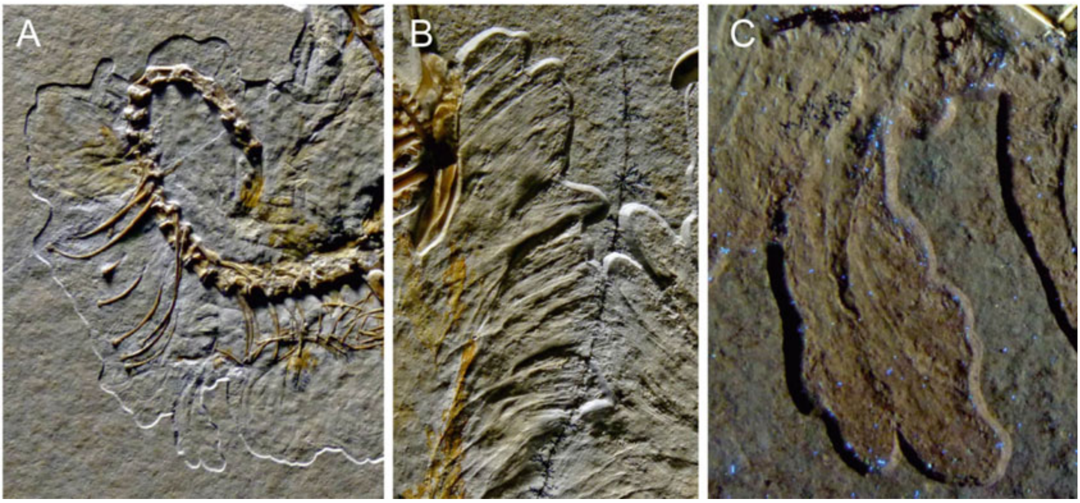

Fig. 8.5 Body feathers of the Altmühl *Archaeopteryx*. (**a**) Feathers of the neck and body; (**b**) close-up of hackle feathers in the neck region; (**c**) close-up of a pair of body features from (**a**)

8.3.3 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. 8.5).

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. 8.5b). 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. 8.5c). 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 Chap. 5).

In contrast to nonvolant coelurosaurs such as the compsognathid *Sinosauropteryx* (Currie and Chen 2001) and the tyrannosauroid *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 Chap. 9; 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, they may would not have needed to be fully feathered to adequately insulate and streamline the body. It is possible that basal Paraves already 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.

8.3.4 Remiges and Coverts

All specimens except for the Daiting and Schamhaupten specimens preserve wing feathers. Details of the wing plumage, including rachis and barbs, are well preserved in the Berlin, London, Munich, Thermopolis, and Altmühl specimens (Table 8.1), with the feathers best seen in the Berlin (Figs. 8.6 and 8.7), London (Fig. 8.2), and Altmühl specimens (Fig. 8.8).

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. 8.8). 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 have their tips angled inward relative to the primaries, the

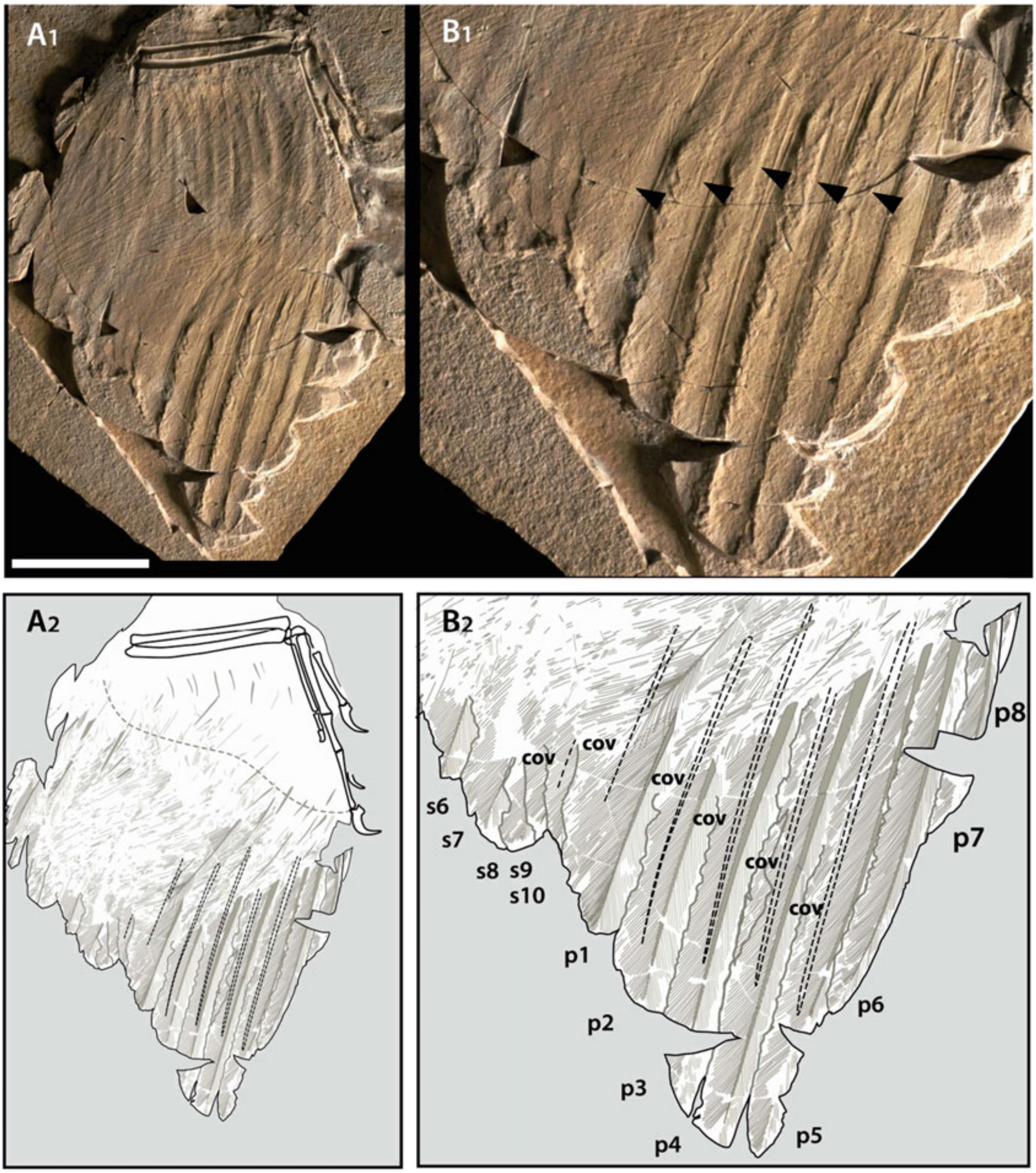

Fig. 8.6 Left wing of the Berlin *Archaeopteryx*, counterslab showing primaries, secondaries, coverts, and impressions of concealed feathers as interpreted by Longrich et al. (2012). Abbreviations: *p8-p1* primaries 1–8; *s6-10* secondaries 6–10, *cov* coverts. Scale = 50 mm

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).

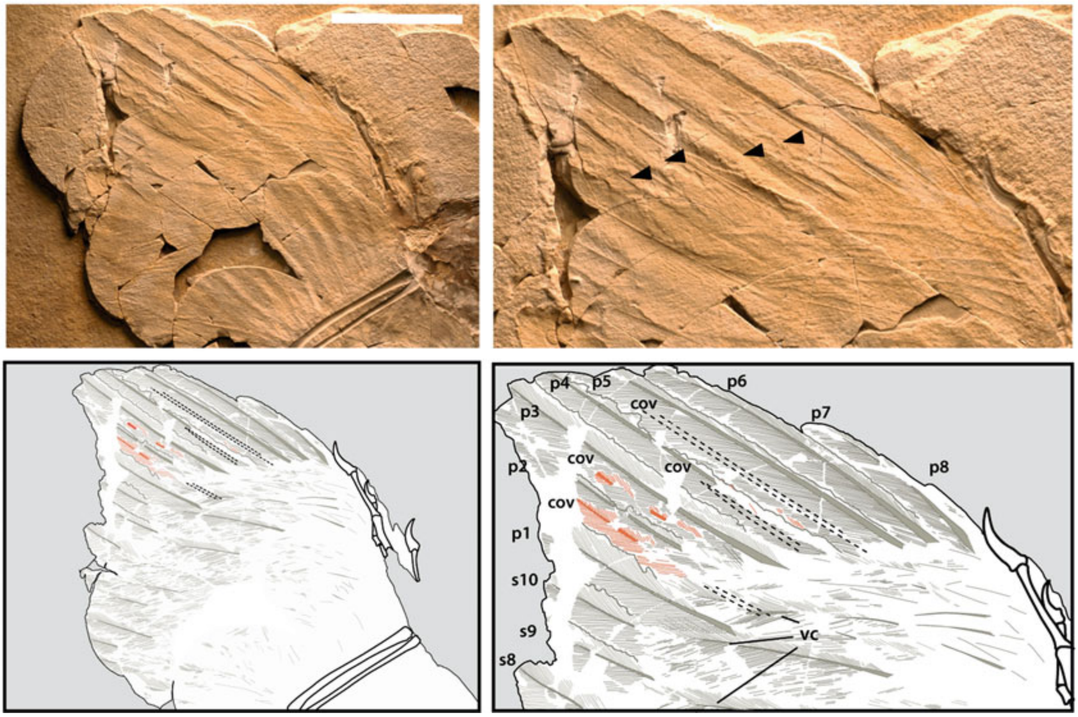

Fig. 8.7 Right wing of the Berlin *Archaeopteryx*, counterslab showing primaries, secondaries coverts and impressions of concealed feathers as interpreted by Longrich et al. (2012). Abbreviations: *p8-p1* primaries 1–8; *s8-10* secondaries 8–10, *cov* coverts. Scale = 50 mm

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 Thompson (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 the fully exposed 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, having a ratio that partly overlaps with that of volant birds (Speakman and Thompson 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, while trailing edge barbs are strongly curved posteriorly along most of their length, with an 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 rachis is broad proximally, but becomes thinner in their distal 25%. Rachis is robust

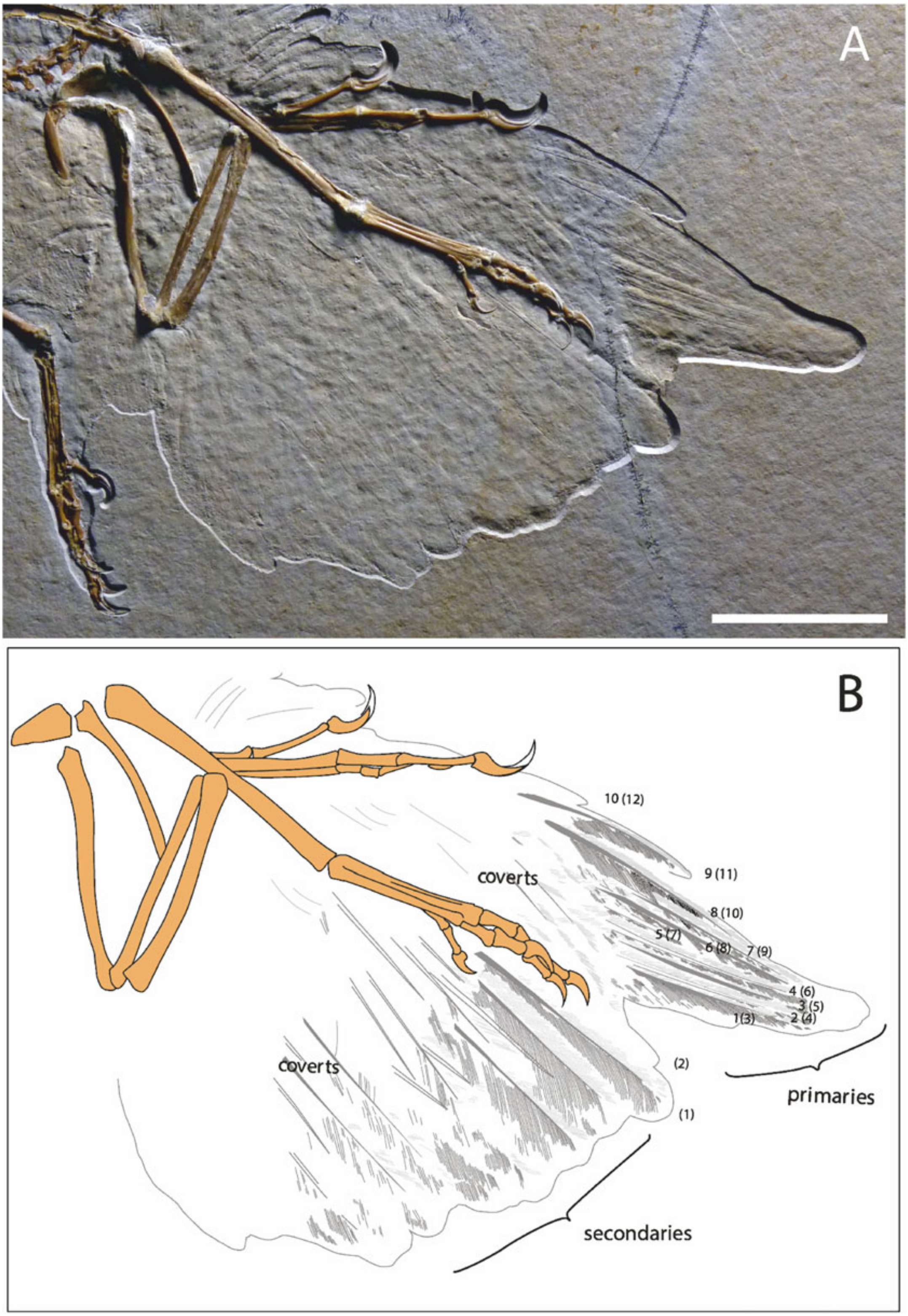

Fig. 8.8 Right wing of the Altmühl specimen of *Archaeopteryx*, showing primaries, secondaries and unidentified coverts. There are at least 10 primaries visible (labelled 1–10 in black), and Foth et al. (2014) identify 12 (labelled 1–12 in grey). Scale = 50 mm

compared to those 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 rachis that is strongly curved posteriorly and has strong asymmetrical vanes and strong asymmetry in both barb angulation and curvature. The tips of the distal primary feather are also narrow and acutely pointed. Proximally, the rachis of the primaries becomes straighter and then begins 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 8 (Longrich et al. 2012) to 11 (Rietschel 1985; Mayr et al. 2007) or 12 (Heilmann 1926; Norberg 1985b; Stephan 1985; Wellnhofer 2009; Foth et al. 2014). The number of secondaries is at least 10 (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. 8.8).

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 correspond to rachis underlying the visible primaries. In places, the primaries have been split away and reveal the rachis 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. The regularity of this arrangement is difficult to explain as a

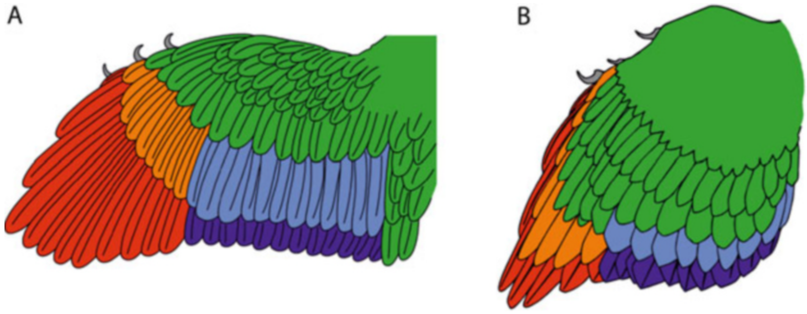

Fig. 8.9 Different reconstructions of the wing of *Archaeopteryx*. (**a**) Original reconstruction, with numerous primaries and short dorsal primary coverts, (**b**) as interpreted by Longrich et al. (2012) with elongate coverts. Red = Primaries; orange = major dorsal coverts, dark blue = secondaries; light blue = major secondary coverts

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, 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. 8.9).

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 overlie 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 (Meseguer 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.

8.3.5 Hindlimb Feathers

The hindlimb feathers are preserved in the Berlin, Maxberg, and Altmühl specimens and perhaps in the Eichstätt specimen. They are best seen in the Berlin and Altmühl specimen (Figs. 8.10 and 8.11). 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. 8.10) and cast photos and illustrations of the main slab before

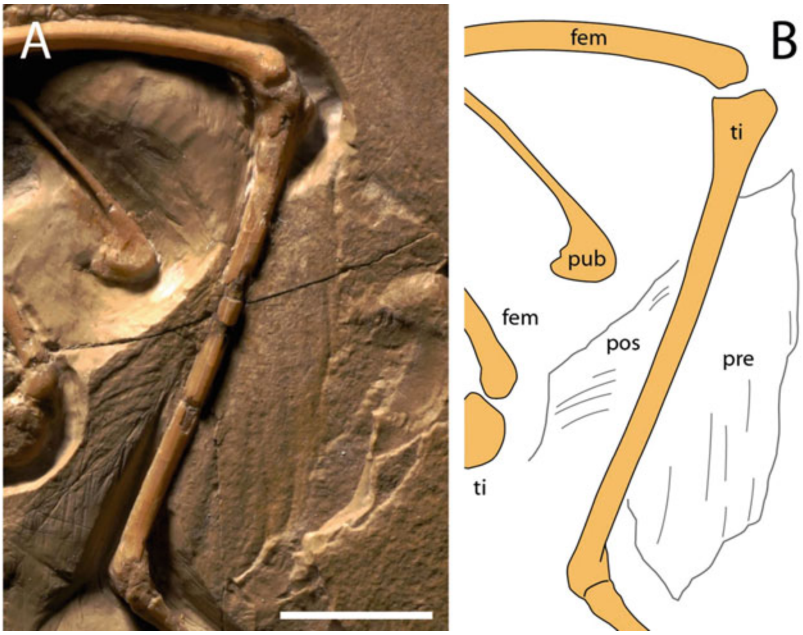

Fig. 8.10 Tibial feathers of the Berlin *Archaeopteryx*. (**a**) Main slab; (**b**) interpretive drawing. Abbreviations: *fem* femur, *ti* tibia, *pos* posttibial feathers, *pre* pretibial feathers. Scale = 25 mm

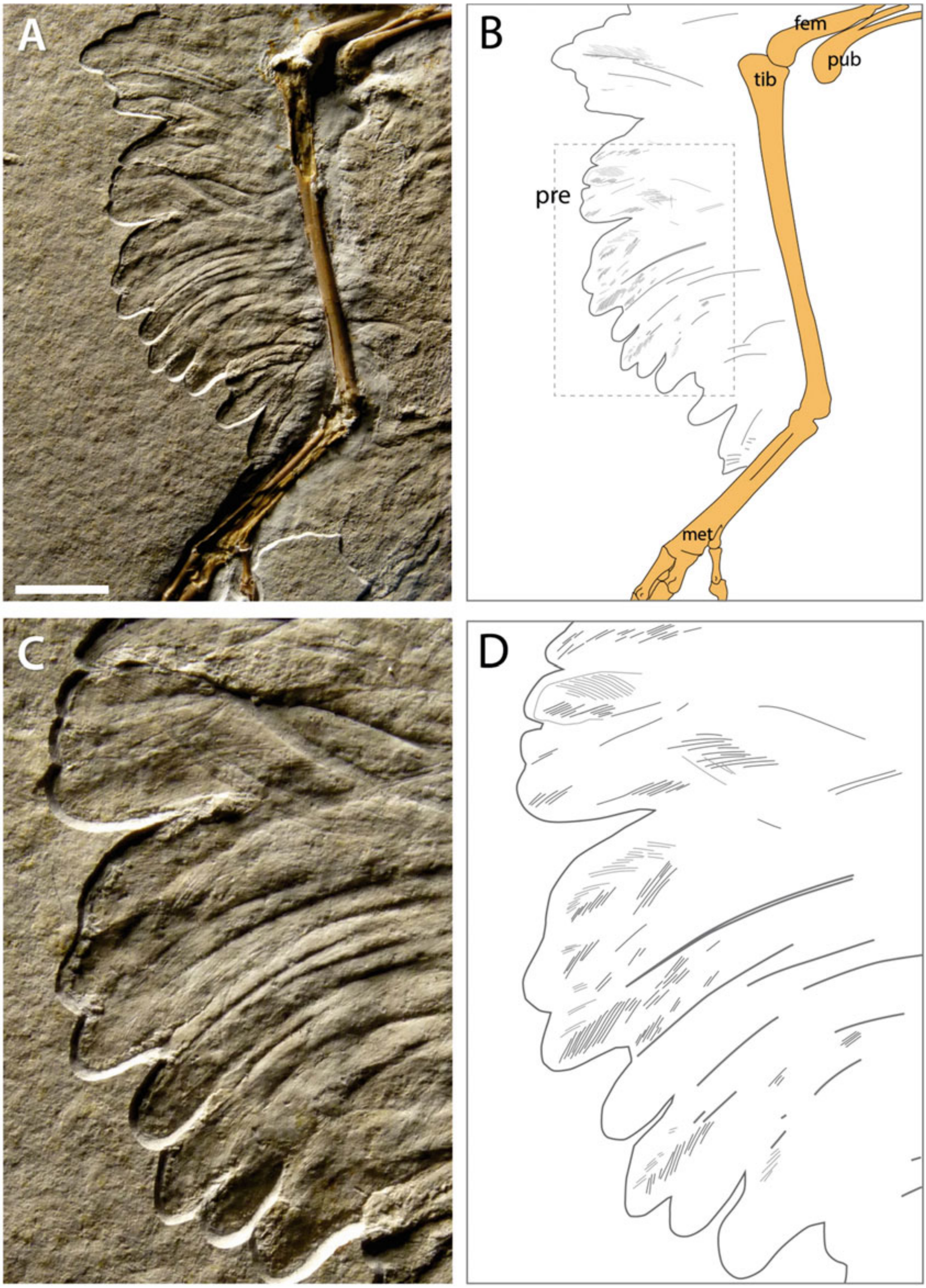

Fig. 8.11 Tibial feathers of the Altmühl *Archaeopteryx*. (**a**) Hindlimb and feathers; (**b**) interpretive drawing; (**c**) close-up of boxed region in (**b**); (**d**) interpretive drawing. Abbreviations: *fem* femur, *ti* tibia, *met* metatarsus, *pre* pretibial feathers. Scale = 25 mm

preparation exist (see Dames 1884; Longrich 2006; Wellnhofer 2009; Fig. 8.3b).

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 18–20 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. 8.11a). 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. 8.11b). 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 60° relative to the foot; more distally, they project at an angle of around 45°. Elongate, vaned feathers are preserved posterior to the right metatarsus; however, they are 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 are attached posterior to 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.

8.3.6 Rectrices

Archaeopteryx bears a series of rectrices extending along either side of the tail (Fig. 8.12). 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. 8.11c). It is unclear if this gap is real, the result of a moult (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

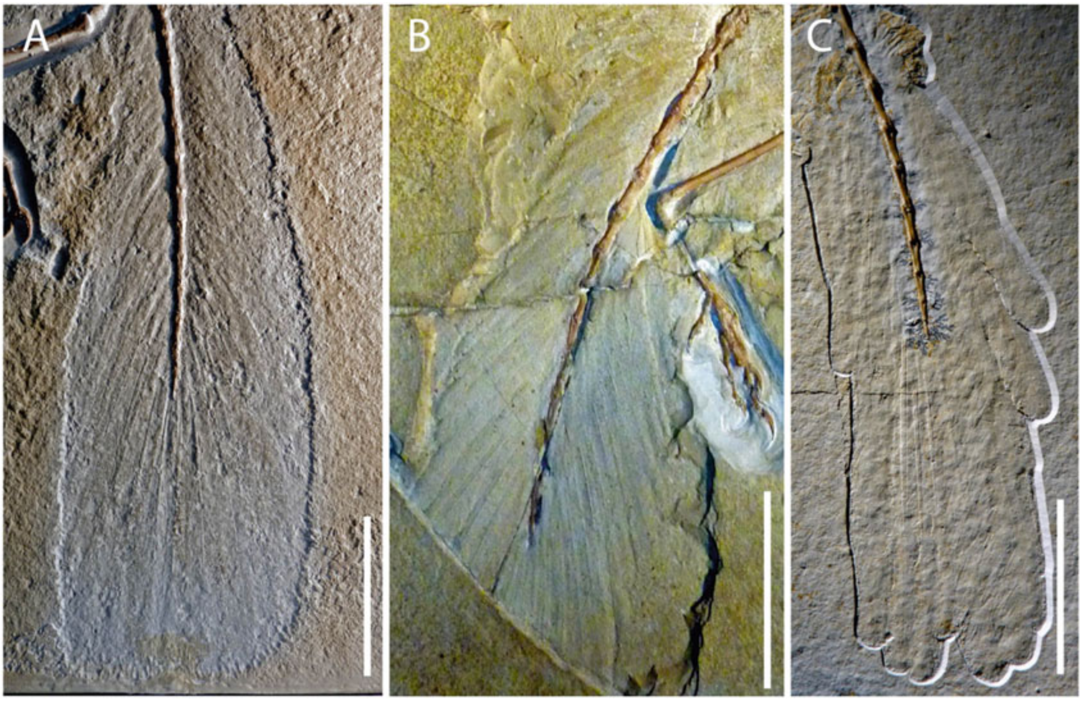

Fig. 8.12 Tail feathers of *Archaeopteryx*. (**a**) London specimen; (**b**) Berlin specimen; (**c**) Altmühl specimen. Scale = 50 mm

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 moulting 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.

8.4 Discussion

8.4.1 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 underlie their growth and moulting. Other conserved features are adaptations for flight, such as curved rachis, 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 Chap. 2). Once evolved, the developmental processes that underlie 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 rachis 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.

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 remiges 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 Chap. 9). 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.

8.4.2 Feather Function and Behaviour

The structure of the feathers and wings of *Archaeopteryx* suggests that they functioned as efficient airfoils, which served to maintain lift, stability, and 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 behaviours 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, 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 centre 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 stabilize the feather in flight; by shifting the main support anterior to the centre 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).

However, vane asymmetry 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 8.2) 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;

Table 8.2 Aerodynamic 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

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, all features cited above as potential adaptations for aerodynamic function, 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 the use of 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). Therefore, it is 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 are 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).

Fig. 8.13 Reconstruction of a pair of *Archaeopteryx lithographica* in flight by Carl Buell

There is little doubt that *Archaeopteryx* was capable of aerial locomotion (Fig. 8.13), 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 the bird's capability 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 large 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 unossified sternum, and the lack of a supracoracoideus pulley (acrocoracoid process) (Wellnhofer 2009) suggest that flapping flight, if it was possible, was rudimentary. In constrast, 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 suggest that they may not simply be 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), which can be considered functional correlates for flight. The hindlimb feathers of *Archaeopteryx* exhibit some, but not all, of these features (Table 8.2). 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; the outer primaries and lateral rectrices invariably show all of these functional correlates, while more proximal remiges and inner rectrices 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 some 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 colour patterns within Pennaraptora (e.g. Li et al. 2010, 2012).

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