Available online at www.sciencedirect.com
SCIENCE DIRECT®
C. R. Palevol 3 (2004) 99–118
COMPTES RENDUS PALEVOL

Concise Review Paper

Body plumage in *Archaeopteryx*: a review, and new evidence from the Berlin specimen

Per Christiansen [a,*], Niels Bonde [b]

[a] *Department of Vertebrates, Zoological Museum, Universitetsparken 15, 2100 København Ø, Denmark*
[b] *Division of Palaeontology, Geological Institute, Øster Voldgade 10, 1350 København K, Denmark*

Received 6 August 2003; accepted 15 December 2003

Written on invitation of the Editorial Board

Abstract

The feathers of *Archaeopteryx* have been known for over 140 years, are the most important reason for its fame and avian status. Previous analyses have almost unanimously focused on the remiges and rectrices. Faint remains of what appears to be body contour feathers are, however, present in the Berlin specimen along the back, around the legs, and possibly anterior to the basal part of the neck. Although noted by numerous previous authors every reference to these feathers was anecdotal. Recent claims that body feathers were once present but were mechanically removed appear unsubstantiated. Rather, the Berlin *Archaeopteryx* has to this day the same regions more or less intact as depicted on early drawings. The present study reveals that the impressions are very different from preparation scratches, and are consistent with body feathers. The counterslab corroborates this, and in several cases both raches and barbs can be made out. The preserved body feathers of the back and the legs evidently were considerably smaller than the flight feathers, and clearly pennaceous in nature. The state of preservation does not, however, permit secure inferences that these body feathers necessarily resembled body contour feathers on most extant volant birds, nor that such feathers were distributed all over the body, although this is one possible scenario. Alternatively, the feathers on the back and legs could have resembled more simple contour feathers with open vanes, present in, for instance, ratites. Faint impressions at the base of the neck may even represent 'hair-like proto-feathers', and if so have been generated from some sort of 'proto-apteria', whereas the longer feathers with vanes on back and legs grew from 'proto-pterylae', corresponding to those areas with the longest neoptiles (embryonic downs), the first feathers to appear in embryos of several modern birds. ***To cite this article: P. Christiansen, N. Bonde, C. R. Palevol 3 (2004).***

Résumé

Plumage sur le corps de l'*Archæopteryx* : une revue et nouvelles indications fournies par le spécimen de Berlin. Les plumes d'*Archaeopteryx* sont connues depuis 140 ans, la raison la plus importante en étant le renom et le statut d'oiseau de cet animal. Les analyses préalables se sont presque toujours unanimement concentrées sur les rémiges et les rectrices. Des restes flous de ce qui apparaît comme étant des plumes dessinant le contour du corps sont néanmoins présentes, dans l'échantillon de Berlin, le long du dos, autour des pattes et probablement antérieurement à la partie basale du cou. Bien qu'étant notée par de nombreux auteurs précurseurs, toute référence à ces plumes était anecdotique. De récentes hypothèses selon lesquelles les

* Corresponding author.
E-mail address: p2christiansen@zmuc.ku.dk (P. Christiansen).

doi:10.1016/j.crpv.2003.12.001

plumes du corps avaient été autrefois présentes mais enlevées mécaniquement apparaissent dénuées de fondement. L'*Archaeopteryx* de Berlin a, à ce jour, ces mêmes zones plus au moins intactes, comme le représentent les premiers dessins. La présente étude révèle que les impressions sont très différentes des rayures dues à la préparation et sont compatibles avec des plumes de corps. La contre-plaque corrobore ceci et, dans certains cas, des barbes et des axes de plume peuvent être distingués. Les plumes de corps préservées sur le dos et les pattes sont à l'évidence considérablement plus petites que les plumes de vol et nettement pennées. L'état de préservation ne permet cependant, ni d'avoir l'assurance que ces plumes de corps ressemblent nécessairement aux plumes des contours du corps sur la plupart des oiseaux volants actuels, ni que de telles plumes soient réparties sur tout le corps, bien que ce soit un scénario possible. Alternativement, les plumes sur le dos et les pattes peuvent avoir ressemblé à des plumes plus simples du contour du corps avec des barbes ouvertes, comme on en observe, par exemple, chez les ratites. Des impressions floues à la base du cou peuvent même représenter des proto-plumes de type poil et, si c'est le cas, être issues d'une sorte de « proto-aptères », tandis que les plus longues plumes avec barbes, sur le dos et les pattes, se développent à partir de « proto-ptérylre » correspondant à ces zones à longues néoptiles (duvet embryonnaire), les premières plumes qui apparaissent chez les embryons de certains oiseaux modernes. ***To cite this article: P. Christiansen, N. Bonde, C. R. Palevol 3 (2004).***

1. Introduction

Since its discovery in 1860 ([74] disregarding von Schlotheim's [108] reference to feathered fossils from the Jurassic Limestone of Pappenheim and Solnhofen), the Late Jurassic Urvogel *Archaeopteryx* (Figs. 1 and 2) has been the pivotal point in all subsequent debates on avian origins and the origins of feathers and flight. Over 100 years after its discovery it stood nearly alone as a very archaic avialan (*sensu* [43]) since the other known Mesozoic birds were clearly much more advanced and thus of little relevance to the above questions, despite the retention of several plesiomorphic traits, such as toothed jaws (e.g., [46,67,68,70]).

Recently, this has changed dramatically and in the 1990s the number of known archaic avialans has virtually exploded [e.g. 16–19,56,57,92,152]. Initial claims that the Chinese *Confuciusornis* was as ancient as *Archaeopteryx* [58] have subsequently been refuted, and the age of the Chinese Liaoning beds is now considered Early Cretaceous [112,121] (see also [113]). This is corroborated by the somewhat more advanced anatomy of *Confuciusornis* and *Chanchengornis*, notably the presence of a pygostyle and absence of teeth in these birds [148]. To this day *Archaeopteryx* has remained the earliest and most primitive avialan, but see [54,55].

A total of seven skeletal specimens of *Archaeopteryx* are known (a fragmentary and, as yet, unofficial eighth specimen appears to have been discovered recently [71,133], but the third, the privately owned Maxberg specimen [51], has been missing since the death of its owner Eduard Opitsch in 1991. Over the decades many studies have been made of the plumage of *Archaeopteryx*, mainly the Berlin specimen. These have nearly all focused on the well preserved remiges and rectrices in order to establish to which degree these

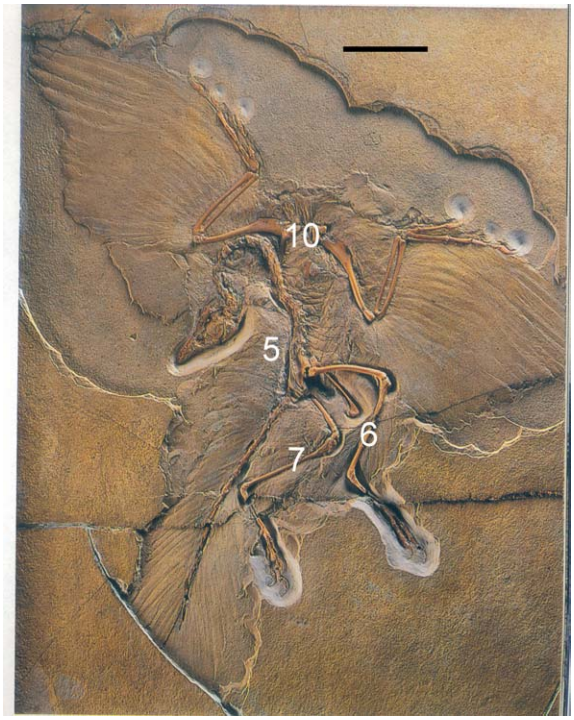

Fig. 1. The Berlin *Archaeopteryx*, main slab ('Museum für Naturkunde', Berlin). Numbers refer to the regions shown in detail in Figs. 5–7 and 10. Scale bar equals 5 cm.
Fig. 1 L'*Archaeopteryx* de Berlin, dalle principale (Museum für Naturkunde, Berlin). Les numéros renvoient aux zones étudiées en détail sur les Figs. 5–7 et 10. Barre d'échelle = 5 cm.

Fig. 2. The counterslab of the Berlin specimen of *Archaeopteryx* (Museum für Naturkunde, Berlin). Number refers to the region shown in detail in Fig. 8. Scale bar equals 5 cm.
Fig. 2 Contre-plaque du spécimen d'*Archaeopteryx* de Berlin (Museum für Naturkunde, Berlin). Le chiffre se rapporte à la zone représentée en détail sur la Fig. 8. Barre d'échelle = 5 cm.

Fig. 3. The very first drawing ever made of the Berlin specimen of *Archaeopteryx*, made in 1878–1879. Note how the unknown illustrator was evidently unambiguous in considering the faint impressions along the back, the throat area and around the legs to be feathers, albeit more hair-like than is probably the case. The rectrices are, however, also made much more hair-like than they really are. From Ostrom [89].
Fig. 3. Le tout premier dessin du spécimen de Berlin, réalisé en 1878–1879. Noter combien le dessinateur non averti a été sans équivoque, en considérant que les impressions floues le long du dos, de la région de la gorge et autour des pattes étaient des plumes, quoique plus semblables à des poils que ce n'était probablement le cas. Les rectrices sont néanmoins aussi plus proches de poils qu'elles ne l'étaient réellement. D'après Ostrom [89].

resemble flight feathers in extant birds and their bearing on the aerial capabilities of *Archaeopteryx*, the evolution of the avian tail, the number of primaries, secondaries and coverts, the nature of flight feather preservation or the origins of feathers *per se* [5,6,13,30,35,37,41,42,47,50,52,65,76,77,88,89,94,98,104,106,111,114–119,144]. Some have even had to refute naïve and obviously absurd claims of forgery [14].

Much less attention has been given to what appears to be faint impressions of body contour feathers around the legs, back and neck in the Berlin specimen (Figs. 1 and 3). Impressions of remiges and rectrices are prominent in the London, Berlin and Maxberg specimens but are present on all seven skeletal specimens, although considerably less distinct in the Teyler [85], the sixth from Solnhofen, *Wellnhoferia grandis* [31,128,129], the seventh skeleton, *A. bavarica* ([130,133] and pers. obs.), and the Eichstätt ([127] and pers. obs.) specimens. Historically, although there has been some doubt about the nature of these body feather impressions, they appear not to have caused much controversy; some have simply assumed that they were feathers and others that they were not. With the exception of [26] and in part [30,51], most authors have not detailed their reasons for noting and thus accepting, or ignoring (and dismissing?) the feathery origin of these impressions. Even [143], who assessed the mass of the body feathers (Table 1, p. 183), did not discuss their possible morphology or why he accepted their presence, seemingly at face value.

Scholars studying the feathers in *Archaeopteryx* have possibly failed to recognize the impressions along the legs as body feathers, because the modern looking

flight feathers would suggest that the former would also be modern in appearance, or have simply ignored them. In part this is, however, clearly due to their much poorer state of preservation than the remiges and rectrices, despite the latter being attached to a distinctly non-avian tail (but see [116 (pl. 1)]). The remiges and rectrices are described as nearly identical to modern flight feathers (e.g. [37,106]); [114], however, criticised the latter analysis and [97] in turn criticised their analysis, while [65] assumed that the *Archaeopteryx* remiges are distinctly different from those of extant birds). It would appear only natural that body contour feathers should also be fairly modern in appearance, and statements such as 'the whole plumage has a very modern aspect' [34 (p. 311), 69 (p. 179)] are common in the literature [12,47,64,94,102,111,122,131,145].

The poor state of preservation combined with the possibly not so modern morphology of some of these purported body feathers could make it reasonable to dismiss the impressions as either diagenetic or even artificial. A diagenetic origin can probably be ruled out, since the extensive dendrites present on the Eichstätt specimen are extremely different from the presumed remains of body plumage in the Berlin specimen. Significantly, however, some authors consider the current state of the Berlin *Archaeopteryx* impoverished, so that body contour feathers used to be present but have subsequently been mechanically removed [36 (pp. 29, 31, 113, also 1999 edition)]. Thus, the 'body feathers' currently visible should merely be preparation marks.

2. Earlier discussions of the body feathers

Previously, several authors have noted the presence of body feathers in *Archaeopteryx* (London specimen [90]; Berlin specimen [4,26,30,33,49,102]; *Archaeopteryx* in general [1 (p. 495), 119, 143 (e.g., p. 183)]) – although [1] and [143] undoubtedly referred to the Berlin specimen) –; Maxberg specimen [51,107]). What appears in early drawings to represent faint impressions of feathers along the lower part of the back has usually been only casually discussed, for instance by [26 (p. 157), 30 (pp. 37–38)]: "the tail coverts form a continuous series with the body feathers on the back" [30 (pp. 37–38)]. It is unclear if the remark by Ostrom [86 (p. 118)] referred to the presumed body plumage or the flight feathers. The inference of body feathers in the London specimen is incorrect ([30] and pers. obs.), and the Maxberg specimen is missing. The plumages of the other specimens are much more poorly preserved, leaving only the Berlin specimen relevant for study.

In the original description of the Berlin *Archaeopteryx*, Dames [26 (pp. 39–42)] provided the most detailed account of its possible body feathers. He described the feathers around the base of the neck and of the tibia, the latter of which he thought were somewhat ellipsoid in outline and more simple and soft than the rectrices. Heller [51] discussed the feathers on the legs in comparison with corresponding ones in the Maxberg specimen, which are symmetrical, but more oval than those of the Berlin specimen. Feduccia [36 (p. 113)] stated that the latter were "typical contour feathers". Gauthier and de Queiroz [44 (p. 13)] even thought that the legs feathers in the Berlin *Archaeopteryx* had open vanes, i.e. lacking hamuli, although they offered no evidence for this claim. It does, however, appear to be correct, as noted below. Elzanowski [32] also accepted the feathers on the lower leg as "contour feathers", but did not describe them.

There is also indirect information in the innumerable illustrations made of *Archaeopteryx* over the years, since they presumable reflect the current opinion of the distribution and morphology of its plumage. Many early authors illustrated *Archaeopteryx* with feathered epipodials (e.g., Fig. 3, [44 (frontispiece and Figs. 2, 50, 64: pp. 92–93), 91 (Figs. 3, 102, 105]. This is similar to some more modern reconstructions (e.g., Hayward in [30], Freund in [94], Sibbick in [82], Sovak in [23 (pp. 99, 111)], [39], Nichols' in [132], Desselberger in [32], Rey in [21 (front cover)], and in [45]. However, the majority of reconstructions depict *Archaeopteryx* with short feathers on the legs (e.g., Charles Knight in his classical 'murals', see e.g. [96], Sibbick in [75,83,132], Bakker [2,3], Thulborn and Hamley [123], Paul in [95,97]. Feduccia [36] illustrated *Archaeopteryx* with a sort of narrow "feather trousers"(but also with a 'tuft' on its head, for which there is no evidence) A detailed and critical review of earlier attempts to reconstruct *Archaeopteryx* is given by Stephan [119], but ends (Fig. 107) with an illustration lacking any indication of longer feathers on the lower legs, and throughout his otherwise very detailed book, these feathers are not described, only mentioned once (p. 68).

Short leg feathers are frequently attributed to the hypothetical reconstructions of a 'proavian' stage, (e.g., [87,122]), whereas Heilmann [48, 49 (Figs. 139, 142)] endowed his 'Proavis' with a sort of short "feather trousers", a single line of slightly longer feathers posterior to the femora, and more narrow feathers on both sides of the tibiae, the former equivalent to the so-called "pelvic or femoral wing" (pp. 195–196) inspired by the *Tetrapteryx* idea of Beebe [4]. Heilmann's feather frills along the neck and body appear unsubstantiated both in fossils and in embryology, but seem inspired by the lateral 'skin-folds' of the gliding gecko (Fig. 141). His "*Proavis*" resemble that of [115].

Pycraft's [103] *Proavis* had short arms, emerging remiges, and scaly legs, and he depicted *Archaeopteryx* with longer "feather trousers" on the lower legs. Steiner's [115] lizard-like *Proavis* (nearly identical picture in Feduccia [36 (p. 92)], with small leg-scales is similar to Heilmann's, but the distally narrow, tapering tail-fan, also seen in Pycraft [103], is contrary to current fossil evidence of fan-like rectrices in avialean outgroups, as noted below. The rectrices appear to evolve from the broader distal to the proximally narrower part of the tail, as predicted in Tarsitano's [122] parachuting to gliding proavian stages. All of these glider models are, however, erroneous in having rather long tertiaries, which is unsubstantiated both from fossils [40,118], and nearly all recent and embryonic birds. This also applies to Bakker's [2], Thulborn & Hamley's [123] and Paul's [97 (Fig. 9.1)] *Archaeopteryx* models. A more convincing '*Proavis*' was reconstructed by Paul [97] as a stem-Paraves (*sensu* [110]), Based on current fossil evidence, it would appear that a stem-avialean '*Proavis*' would have had much longer feathers on the hind legs, possibly even 'wing-like' (cf. [123,142]).

3. Taxonomy

Although the Berlin specimen, some years after its description, was named *Archaeopteryx siemensis* [27], and [98] referred it to *Archaeornis*, we here, despite the slight (10–15 %) size differences, consider it conspecific with the London specimen, *Archaeopteryx lithographica* von Meyer 1861 ([74]; assuming that this is the proper name for the London skeleton – Opinion 1070 [84]; contra [32], the species under consideration here). The history behind von Meyer's name can be found in [30,134].

From a taxonomic viewpoint it is worth noting that the taxon *Archaeopteryx*, as normally perceived, is probably not a monophyletic group, but rather encompasses several species, perhaps even genera, whose exact interrelationships are presently unknown [9]. Apart from *Archaeopteryx lithographica*, the most significant taxa suggested for other specimens are *Jurapteryx recurva* (Eichstätt specimen, [59]), *Archaeopteryx bavarica* (the 7th specimen, [130]), and the hitherto largest known specimen, the 6th or Solnhofen specimen [129] has recently been selected as type specimen of a new genus and species, *Wellnhoferia grandis* [31,32]. Both the interrelationships of these taxa, and the relationship to later avialeans are unclear, but it is clear that the taxon *Archaeopteryx sensu lato* (for all the specimens from the Lithographic limestone) is a so-called 'mixotaxon', not necessarily monophyletic [9] (despite [32]).

Thus, it follows that these specimens need not have been uniform in ecology and soft tissue anatomy. This has implications for inferences of plumage, because what is present in the Berlin specimen needs not have been similar in all species.

4. The phylogenetic bracket of body plumage

Witmer [137], in his phylogenetic bracket methodology, has argued in detail how to infer the presence of soft tissue structures in fossils in a cladistic framework by reference to the living sistergroup and their combined living outgroup. The broader, general conditions and arguments for estimating such unknown features (or as the case were, the palaeoecology) on a well-known phylogenetic background were earlier outlined by Bonde [8]. This requires that soft tissue inferences pass both the test of morphological similarity and phylogenetic congruence.

For every species of *Archaeopteryx*** (see [9] and Elzanowski's 'Archaeopterygidae' [32]) the recent sistergroup is Aves and the outgroup Crocodylia, making it impossible to infer whether the fossils had feathers or not, as these do not usually leave distinct osteological signs, with the exception of quill nodes or a pygostyle. However, in the present case fossil preservation allows prediction with certainty that at least some and prob-

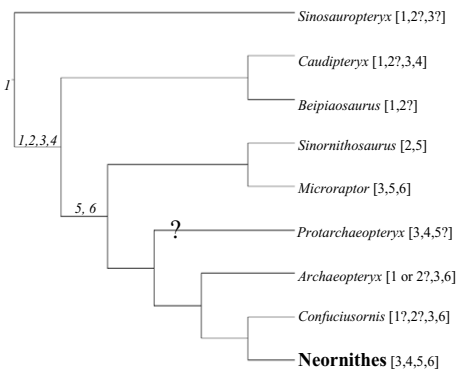

Fig. 4. Diagram of relationships of the hitherto published non-avian theropods from Liaoning, northeastern China, along with basal avialans *Archaeopteryx* and *Confuciusornis*. The numbers succeeding the taxon names refer to various stages of plumage evolution, and the italic numbers at the nodes indicate the most parsimonious condition. Diagram after Holtz [54] and Ji et al. [61]: **1**, simple, superficially hair-like body feathers; **2**, more complex, although still superficially hair-like body feathers (see Xu et al. [141]); **3**, pennaceous feathers on arms and/or tail; **4**, plumulaceous feathers; **5**, pennaceous body contour feathers; **6**, flight feathers with asymmetrical, closed vexillae (i.e. hamuli).

Fig. 4. Diagramme montrant la relation entre les Théropodes non aviens publiés jusqu'à présent, en provenance de Liaoning, Nord-Est de la Chine, avec *Archaeopteryx* et *Confuciusornis*. Les chiffres suivant les taxons correspondent à différentes étapes de l'évolution du plumage et les nombres en italiques, aux nœuds, indiquent la condition la plus parcimonieuse. Diagramme selon Holtz [54] et Ji et al. [61] : **1**, plumes de corps simples, superficiellement semblables à des poils; **2**, plumes plus complexes, bien qu'encore semblables superficiellement à des poils (voir Xu et al. [141]) ; **3**, plumes pennées sur les pattes avant et/ou la queue ; **4**, plumes à plumules ; **5**, plumes pennées au contour du corps ; **6**, plumes de vol asymétriques, à vexilles fermées (i.e. hamuli).

ably all specimens had feathers in the form of remiges and rectrices. This, however, implies neither the unquestionable presence of body plumage (see, e.g., Bakker [2 (p. 69)]), nor the resemblance of these, if present, to those of modern birds. Only fossil discoveries in an outgroup position to birds plus *Archaeopteryx* (= Avialae) with preserved body feathers would make such inferences possible.

Phylogenetic analyses have demonstrated with overwhelming certainty (Fig. 4) that Avialae is the sistergroup of advanced theropod dinosaurs, most often dromaeosaurs (the two groups combined in Paraves, *sensu* Sereno [110]). Since the mid 1990s, theropods have emerged from Early Cretaceous beds of Liaoning, northeastern China, with primitive, superficially hair-like feathers preserved on their bodies [15,62,138,139], and some with down-like structures ([93] and NB's pers. obs.) and even with large remiges and rectrices [16,61,62,78,81,150,151], despite being non-Avialan theropods [21,24,54,55,61,79,80,110,120].

The hair-like body feathers are clearly different from mammalian hair [15,25,62] and probably correspond to early evolutionary stages of 'proto-feathers' [10,141] (see also Prum [100]). Thus, they would be equivalent to 'cryptoptiles' [10], a term used by neornithologists (e.g., [22,124]) for a hypothetical early stage of feather evolution. Curiously, feathered theropod dinosaurs were not only foretold, but also outright advocated by Lowe [65], who also considered *Archaeopteryx* simply a feathered, arboreal dinosaur unrelated to birds!

A very small dromaeosaurid has structures preserved behind the hind legs that resemble elongate contour feathers [141], and more recently described dromaeosaurids have very large, distinctly pennaceous feathers along the forelimbs, hind limbs and tail [45, 101, 81 (*Cryptovolans*), 142 (*Microraptor*)]. Feather morphology, especially the asymmetrical remiges, in these forms suggest gliding or even flying abilities, although more analyses are required to firmly establish this [91]. *Microraptor* [142] also appears to possess not only *Archaeopteryx*-like wings, but apparently distinct 'hind limb wings', providing some credibility to Beebe's [4] *Tetrapteryx* hypothesis [10,142].

To make a more definite statement about possible hind limb wings in stem-avialeans, i.e. the direct forerunners of birds, we need information from well-preserved feathered hind limbs of fossils in sistergroup position to Paraves, as it cannot be ruled out that 'four wings' might be an apomorphy of primitive dromaeosaurs [101]. To date fossils in the desired position are oviraptorosaurs, and among these *Caudipteryx* seem to have short feathers on the lower legs and nothing on the feet ([61,149,150] and NB's pers. obs.]. The inference for the stem-bird would be absence of 'hind limb wings', unless *Archaeopteryx* does, in fact, show something else (below). Studying other early birds with plumage (partly) preserved (like *Confuciusornis* [20]) is another possibility to establish a 'phylogenetic bracket' of extinct animals around the origin of avialans. But the fact that these early birds from China [57] seem to exhibit no feathers on the feet and only

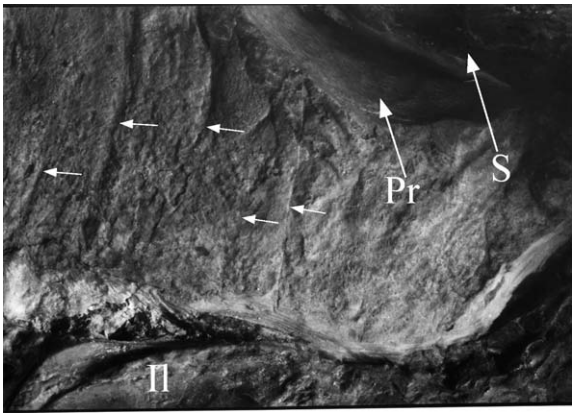

Fig. 5. Feathers on the back (preparation at the skull roof seen above them). Main slab. Abbreviations: **Il**, ilium; **Pr**, preparation ; **S**, skull. Arrows denote feather rachides. Beebe [4], among others, originally referred to these feathers as the 'femoral wing', which supposedly had drifted away from the femur, and settled along the back.
Fig. 5. Plumes sur le dos (préparation à la voûte crânienne, vue de dessus). Dalle principale. Abréviations : **Il**, illium ; **Pr**, préparation ; **S**, crâne. Les flèches indiquent les axes des plumes. Beebe [4], parmi d'autres, se réfère, à l'origine, à ces plumes en tant qu'« aile fémorale », qui est supposée s'être éloignée du fémur et déposée le long du dos.

rather short ones on the lower legs (e.g., [20,146]), i.e. 'modern' features like most living Aves, does tend to support the deduction above: no *Tetrapteryx* stage in the direct lineage towards modern birds (contra [142], see also [91]).

Many confuciusornithid birds from these Chinese deposits have the plumage partly preserved, often showing very long and narrow, asymmetrical primaries, but the rest of the plumage is often poorly preserved, mainly as a dark 'halo' round the neck, body and wings ([20,60,147] and pers. obs. on a dozen specimens). Even secondaries are difficult to distinguish, and there is no evidence of tertiaries, as shown in [97 (Fig. 6.2)]. The body feathers appear superficially rather similar to the 'hair-like feathers present on many of the non-avialan theropods, or at least more simple than modern pennaceous body contour feathers, and this appears also to be the case with early enantiornithine birds, such as like *Longipteryx* [146], although the early ornithurine *Archaeovolans* is said to have contour feathers on the neck [16,57].

Thus, the body feathers of *Archaeopteryx* may not have been quite as modern as the remiges and rectrices could suggest, and as illustrated in most reconstructions, including [48,49]. They could have been simpler than in most modern birds, except perhaps flightless ratites such as *Apteryx* and *Casuarius*, with less developed and simpler vexillae (probably a secondary reversal). Because detailed studies of the variably preserved plumages of the Chinese feathered birds are still wanting (but see [16,93,145,147]), it does not follow that neither their body feathers nor those of *Archaeopteryx* were very different from modern contour feathers, especially as dromaeosaurs had some with a superficially rather modern appearance [81,141]. But it cannot be ruled out that the early birds had body plumage more like the simple body covering of most non-avialan theropods, that is unbranched 'hair-like protofeathers' [15,93,138,139], albeit sometimes with a little branching [16,25] and then called 'down-like' – and definite down-like structures were described in e.g. *Protarchaeopteryx* [93] and *Scansoriopteryx* [16] and are in *Caudipteryx* (NB's pers. obs.).

5. The history of preparation of the Berlin specimen

The history of the preparation of the Berlin specimen can roughly be followed from figures in [26 (Pl. 15, drawing), 30 (photo), 49 (Fig. 2, drawing), 87 (photo), 97 (recent photos from the late 1990s), 119 (Figs. 12–13)], and the photos presented in this study, taken in 2002. What probably represents the first drawing of the Berlin *Archaeopteryx* from 1879 (Fig. 3) clearly illustrates the specimen with feathers around the legs, back and neck. Feduccia [36 (1999 edition, pp. 29 and 113)] argues that this early drawing shows true body feathers, which were subsequently removed during the ongoing preparation of the specimen, and the 'feathers' present on the slab today are thus merely preparation marks. These 'feathers' appear more slender and morphologically simpler than the remiges and rectrices. This is in contrast to the remains of the purported 'feather trousers' of the Maxberg specimen, which Heller [51 (pls. 5 and 15), 107 (Fig. 1b)] illustrates as near-typical contour feathers, i.e. pennaceous, presumably sempiplume feathers.

Dames' [26] plate shows that in his day almost nothing was exposed of the pelvis, and little of the left femur, knee and proximal metatarsus. Ribs and gastralia were visible immediately in front of the right femur, but no feathers are seen in that area, apart from remiges

from the elbow just anterior to the right knee. Posterior to the knee is an irregular lump of matrix, and the striations (described below) behind the right tibia reach the left knee region. Posterior to the left femur is a large patch of faint, slightly curved and near parallel striations, extending away from the femoral shaft at a near perpendicular angle. This is less evident in [49], but rather evident in all the photos by [88,97,119] and the new photos presented here. Purported feathers along the posterior part of the back are evident in [26], but very faint in Heilmann's [49] drawing. As noted below, they are clearly body feathers.

The left femur and knee, as well as ischium and pubis, had been disclosed, and the area behind the right knee had been evened out by preparation before Heilmann [49] made his drawing (about 1924). His illustration shows an area with very thin, sub-parallel, and very tightly set striations (probably preparation marks), nearly perpendicular to the distal femur. These striae seem to have vanished after a preparation done prior to the 1950s, as seen in de Beer [30] (note the illumination from opposite direction). Before the 1980s, only slight additional preparation around the distal pubis and between the knees was done, removing a little more of the feathers behind the right tibia (Figs. 1 and 6). Additional preparation around the skull has removed a little of the tips of the anterior feathers on the back (Fig. 5). Since the 1980s, only a little detailed preparation around the finger claws has been done, and a bit along the neck has made the slab paper thin, actually piercing several small holes through it (pers. obs., 1996, 2001).

The above is interesting since the current appearance of the Berlin *Archaeopteryx*, compared to the early drawing (Fig. 3, although erroneous in some respects; compare to Dames [26 (pl. 1)] and Heilmann [49 (Fig. 2)] who also show these imprints) clearly demonstrates that systematic removal of major portions of the purported feathers, as suggested by Feduccia [36], has not taken place. Either the faint striae at the base of the neck and the legs are feathers and still present, or they were never present at all.

6. Body feathers in the Berlin specimen

In May 2001, we studied the slab and counterslab (Figs. 1 and 2) of the Berlin specimen of *Archaeopteryx*, using traditional light microscopy and camera lucida for illustrations. On the ventral side of the cervical vertebral column are faint, superficially 'hair-like' impressions, which may or may not be remains of feathers. The individual striations are faint and the matrix appears a little too coarse to identify these structures as evidence of feathers with any degree of certainty, although this appears a likely explanation.

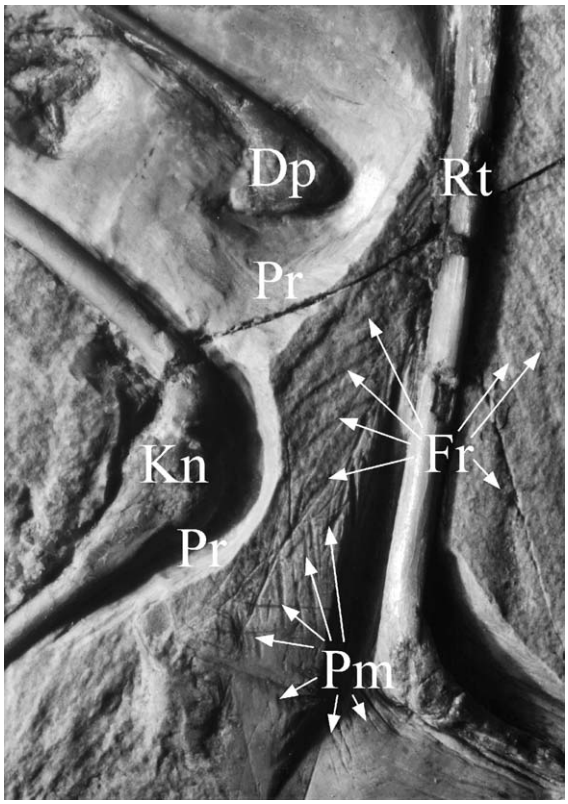

Fig. 6. Feather patches in front of and behind the right tibia. Left knee and distal pubis and the preparation around them. Main slab. Abbreviations: **Dp**, distal pubis; **Fr**, feather rhachis; **Kn**, knee; **Pm**, preparation marks; **Pr**, preparation area; **Rt**, right tibia.
Fig.6. Amas de plumes devant et derrière le tibia droit. Genou gauche, pubis distal et préparation à l'entour. Plaque principale. Abréviations : **Dp**, pubis distal ; **Fr**, axe de plume ; **Kn** : genou ; **Pm**, marques de préparation ; **Pr**, zone de préparation ; **Rt** ; tibia droit.

Dames [26 (p. 39)] thought that the weak striations in front of the chest at the base of the neck (see also Fig. 10) had been made by wet and collapsed pennaceous body feathers, but his experiments with soaked chicks and doves could not reproduce the pattern seen in *Archaeopteryx*. In fact, he thought that these feathers might have formed a 'collar' like in some vultures because of the way they were bent (his pl. I). Other

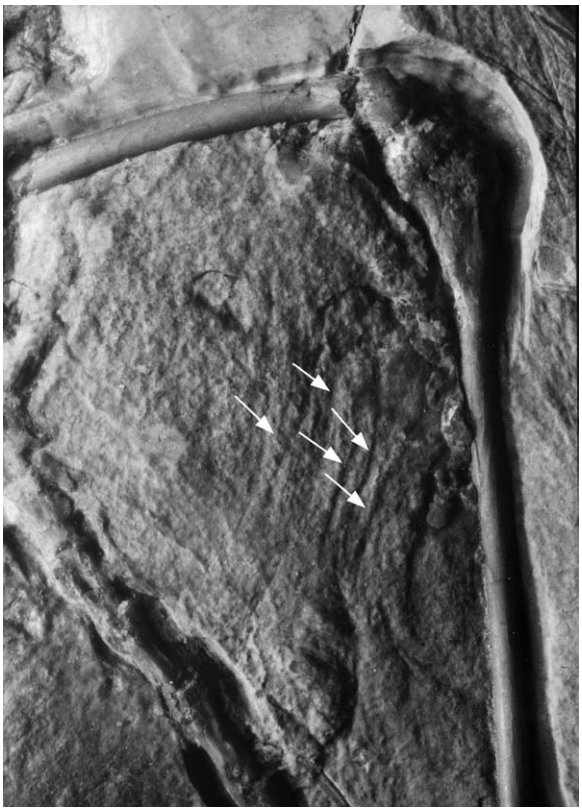

Fig. 7. Left femur and tibia and part of the tail and in between them feather imprints (arrows), probably from both thigh and shin. The convex limestone area in front of tibia may hide feather imprints from the shin. Main slab.

Fig. 7. Fémur gauche, tibia et partie de la queue, avec empreintes de plumes entre ces pièces (flèches), provenant probablement à la fois de la cuisse et du jarret. La zone calcaire convexe devant le tibia peut cacher des empreintes de plumes de la cuisse. Plaque principale.

scholars accepted their presence [30,50], seemingly at face value. These earlier authors did not doubt their feathery nature, while most others simply ignored them, but their simple, 'hair-like' morphology could be indicative of their having been rather simple or a preservation artefact (see further below).

Much more informative are structures on the slab around the dorsal vertebral column and left and right tibiae. The impressions above the dorsal vertebral column are clearly feathers. Historically there seems not to have been much dispute about this, although they are not usually included in discussions of the *Archaeopteryx* plumage. The impressions could not have come from the tail region as they extend considerably past the ilia. The remiges and rectrices are preserved in what appear to be approximately their natural positions, and none appears to have come away and settled elsewhere, which would have had to be the case if the feathers along the back were indeed rectrices. Furthermore, the impressions radiate away at near right angles from the dorsal vertebral column, and are not jumbled, but arranged in what appears to be one row along the vertebral column, again strongly suggesting that their occurrence along the back was not a result of post-mortem displacement.

The dorsal feathers extend from slightly posterior to the ilia to the middle of the dorsal column, after which they seem to fade out (Fig. 5). There are about eight of them with nearly parallel raches. The distal tips of the anterior ones were removed by the preparation of the skull roof. But the anterior feathers were probably slightly shorter than the posterior ones, which when bent backwards could well have covered the proximal, muscular part of the tail. Anteriorly, where the feathers fade out, are some irregularities in the matrix (and a bone?), and of course the skull. It is impossible to verify if there was originally only a single row near the dorsal midline, and one (or a few) could well be hidden below the thin laminae of limestone. The reconstruction in [30] shows rather large contour feathers in about two rows in this region.

Their feathery nature seems unequivocal, as they bear resemblance to undisputed rectrices, but they appear to have been smaller and less rigid. Easily discernible are central raches, faint and sometimes incomplete and(or) overlapping outlines of the apparently symmetrical vexillae, and in several places even clear impressions of barbs. Barbules cannot be made out, but the ordered appearance of the vexillae would suggest the presence in life even of modified barbicles (hamuli). Toward the apices, the vexillae lose their ordered structure and appear more 'plumulaceous', suggesting that hamuli were absent in this region. This further corroborates the notion that they are not rectrices, because rectricial vexillae appear to preserve their three-dimensional integrity all the way to the apices. Thus, the dorsal feathers alone would suffice in assigning evidence of body contour feathers to *Archaeopteryx*, and clearly pennaceous ones at that.

Faint impressions are also evident posteriorly and perpendicular to the left femur (Fig. 7), but contrary to popular opinion this does not represent the 'hind wing' of Beebe [4], who believed that the feathers along the

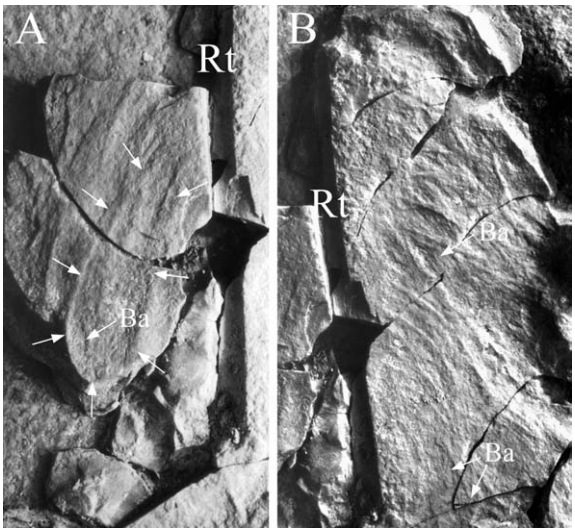

Fig. 8. Imprint of the right tibia with possible feathers and barbules. Counterslab. Arrows denote the possible outline of a vexillum. **A**, Left hand side of tibia; **B**, right hand side. Abbreviations: **Ba**, barbules; **Rt**, right tibia.

Fig. 8 Empreinte de tibia droit, avec de possibles plumes et barbules. Contre-plaque. Les flèches soulignent le contour possible d'un vexillum. **A**, côté gauche du tibia ; **B**, côté droit. Abréviations : **Ba**, barbules ; **Rt**, tibia droit.

back represented the pelvic alar wing (pp. 49–50) that had drifted away from its original position (see also Fig. 5). The femoral impressions are similar to the impressions around the tibiae, but bend slightly away from the left tibia. The impressions around the left tibia could stem from the tail feathers, since the left leg lies adjacent to the tail, but the orientation of the striations in the impression, bending towards the tibia, is different and the microstructure also differs from that of undisputed rectrices, notably in the weak shaft impressions and lack of clearly discernible vanes and barbs (see further below). However, the patch around the posterior part of the left tibia appears very similar to those posterior and anterior to the right tibia. Thus, the latter were the primary subjects of this study. There are a substantial number of reasons as to why these impressions are not man-made preparation marks, as has been suggested [36], but are truly feathery in origin. Some of the striations proximally behind the left femur may, in fact, be imprints of feathers that hafted to the thigh. This is likely partly to have prompted both [4] and [33] to suggest 'wings' on the hind limbs (see de Beer's [30] remarks, and further on *Tetrapteryx* below).

A comparison with preparation marks from around the slab reveals a number of substantial differences between the presumed leg feathers and undisputed preparation marks. The patch anterior to the right tibia (Fig 6; henceforth termed the integumentary patch) is subdivided into a number of near-parallel fine and very faint striations, which, although often fragmentary and with sections missing or very indistinct, clearly extend all the way through the patch in nearly straight lines. The striations are set at roughly 40° to the long axis of the tibia. They are clearly not the result of smaller individual lines adjacent or in succession to each other. The striations are up to 3.5 cm long, but the actual length is tentative because they are very faint and often not preserved in their entity. The striations do not reach the tibial bone but terminate a few millimetres anterior to it, just like the integumentary structures preserved with the Chinese non-avian and avian theropods. This is probably because these structures were imbedded in the skin, which has long since rotted away.

There are several reasons why these are not preparation marks. First, the striations in the integumentary patches are uniformly fainter than preparation marks (e.g., along the long axes of the bones, feet, hands, claws, vertebral column, adjacent to remiges, etc.). Second, they are much longer, forming lines up to 3.5 cm in length. This is up to 10 times the length of typical preparation marks around the feet. Third, preparation lines are not only shorter, but also much more clear in outline. Each preparation mark is a short, sharp longitudinal excavation with well-defined edges that are offset clearly from the surrounding matrix. In a typical preparation area are many such small, sharp lines lying right next to and in succession to each other. The striations in the integumentary patch are not broken up like this.

Fourth, when examining a larger area that has been prepared (e.g., along a long bone or around the feet), it is evident that preparation marks that run parallel to each other are found in localized patches within the preparation area. This is due to the preparator's work from different angles in order to remove matrix most efficiently and with less danger of damage to the fossil (compare, e.g., descriptions of preparation given by [38,126,135,136]). This creates a pattern of many individual, small, sharp, clearly offset lines lying parallel and in succession to each other, and right next to this localized patch is another with the exact same mor-

phology within the patch (i.e. all individual lines are parallel and/or in succession). The angles of the individual lines in this patch are, however, different from those of the previous patch, since the preparator has now moved the slab slightly. This differs markedly from the long, fine striations inside the integumentary patch.

Fifth, preparation marks are not only sharper and more clearly offset from the surrounding matrix, but are clearly also deeper. Sixth, the striations in the integumentary patch are up to 3.5 cm long. Had the patch indeed been the result of preparation, it seems hard to explain why 3.5 cm of matrix should have been taken away, since this is much more than has been taken away anywhere else on the fossil. This seems particularly unlikely, since matrix has clearly not been removed at all in this area! This is easily recognized since the matrix lies nearly halfway up the mediolateral extent of the tibia.

Comparison of the Berlin specimen with older drawings reveals that preparation has taken place around the pelvic area, mainly to free the pubes, thus slightly damaging the integumentary patch behind the right tibia, whereas the integumentary patch in front of the right tibia is today as it was in 1877. In other places where the matrix has been prepared away from the bones, these are nearly completely exposed, and preparation has been done only on the main slab. Additionally, as noted above, the fine striations do not start until a few millimetres away from the bone. Why should a preparator prepare an area that does not include the bone itself?

The above differences are most clearly demonstrated on the small integumentary patch that lies behind the right tibia (with longitudinal striations running at a roughly 60° to the long axis of the bone), where the fine striations have been damaged by preparation marks toward the distal part of the patch (Fig. 6). Under the microscope, the difference between the fine striations and undisputed preparation marks is striking. Some of this posterior patch has in fact been removed because of preparation around the knee and to free the pubes, and by preparation down the distal part of the tibia. Interestingly, towards the apex of the posterior integumentary patch, very fine, short lines can be made out that extend from the longitudinal striations. These small lines are set at roughly 80–85° to the long axis of the striations, exactly as would be expected if the long

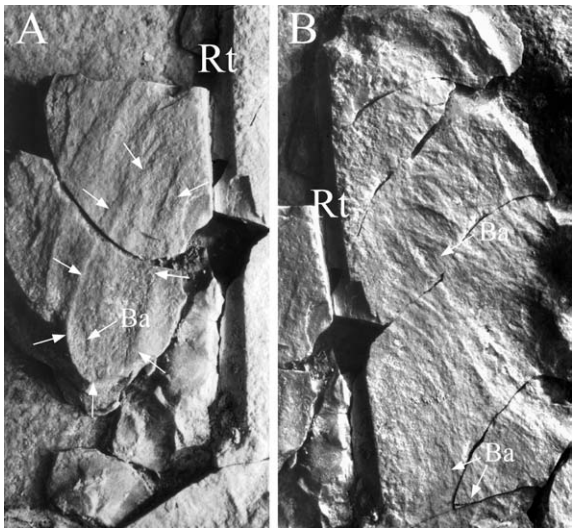

Fig. 9. Drawing of the feather patches surrounding the right tibia on the counterslab. Tiny areas showing barbs indicated. Camera lucida by NB, schematic. Stippled, grey lines are shaft impressions.
Fig. 9. Dessin d'amas de plumes entourant le tibia droit sur la contre-plaque. Petites zones montrant des barbules. Les lignes grises pointillées sont des impressions dues à l'extraction.

striations represented soft raches and the smaller, finer lines represented barbs. A vexillum cannot, however, be traced, because the outline of each feather is quite blurred.

Seventh, even slight preparation clearly changes the colour and microstructure of the slab. This is easily recognized by comparing the surface structure of the integumentary patch to any preparation patch on the slab. The colour and surface structure of the integumentary patch does differ from parts on the slab where nothing is preserved (see, e.g., [14,52,107] for explanations of local differences in sediment structure on the *Archaeopteryx* fossils), but these differences are clearly of a different nature to the changes brought about by preparation. Rather, the colour and surface texture of the integumentary patch is very similar to those patches with undisputed feather impressions, such as wings or tail.

Finally, examination of the counterslab (Figs. 2 and 8) reveals structures of the integumentary patches that are less discernible on the slab. The main slab contains nearly all the bone material, and the counterslab contains clear impressions of forelimbs, including the hands, legs, feet and vertebral column, including the tail. The central part of the fossil is, however, missing on the counterslab. Bone is present only as rib frag-

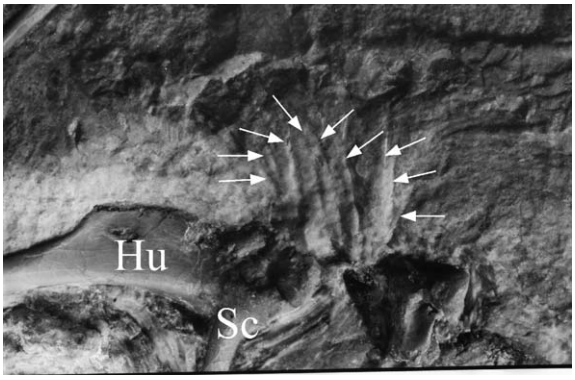

Fig. 10. Anterior chest region, with left humerus and scapula and numerous striations, possibly representing body feathers (arrows). Main slab. Abbreviations: **Hu**, humerus; **Sc**, scapula.
Fig. 10. Région antérieure de la poitrine avec humérus gauche, scapula et nombreuses striations pouvant représenter des plumes de corps (flèches). Plaque principale. Abréviations : **Hu**, humérus ; **Sc**, scapula.

ments and fragments of the caudals near the articulating facets of several vertebrae. Impressions of the remiges and rectrices are, however, excellent, and for many feathers a central rachis, both vexillae and their barbs can be made out with the naked eye.

Microscopy failed to identify with certainty any evidence of barbules, because the otherwise very fine sediment simply appears too coarse for the preservation of such delicate structures, although the ordered structure of the vexillae strongly suggests the presence of barbicles modified into hamuli, as noted above. In all specimens of *Archaeopteryx*, we have studied (four skeletons and the isolated feather) possible barbules that can only be made out in a few regions of the distal part of the slab of the isolated feather. The isolated feather was clearly preserved under different circumstances from the skeletal specimens [47].

The integumentary patch of the right tibia on the counterslab (Fig. 8) bears the same fine striations as are preserved in the patches around the anterior and posterior face of the tibiae on the slab, especially the right tibia. On the counterslab it is, however, evident that the fine, nearly 3-cm-long striations in several places have short structures preserved that extend away from the primary striations at a roughly 70° (Fig. 9). These resemble the barbs of the remiges and rectrices (provided that the shallow longitudinal striations are indeed imprints of rachides), though they appear to be much shorter. Since no preparation has been done at all on this part of the counterslab, none of the above structures can be preparation marks.

Overall, the patches around the legs (presumable also the femur) are so different from preparation marks that this explanation must be discarded. The most likely explanation is that they represent the remains of body contour feathers, as observed originally by both Evans [33] and Dames [30], and where barbs cannot be seen, they are still covered by a very thin limestone crust, blurring the outline of the structures.

The integumentary patches on the slab failed to show evidence of a distinct vexillum or tertiary structures (barbules). On the counterslab, secondary structures (barbs), although clearly present, are not preserved in very many places and not very distinct (Fig. 9). However, faint vexillae may be reconstructed from several of the long striations (evidently the raches) by following the small, short striations until their termination (Fig. 8). Our illustrations of the Berlin specimen bear some resemblance to those of Heller [51 (pls. 5 and 15)] for the Maxberg specimen, albeit with proportionally more narrow vanes with more squarish tips and more simple construction of the vanes, and not so fully modern in appearance (cf. Figs. 8 and 9).

7. Tetrapteryx?

Some early authors (e.g., [26,125]) inferred that the tibia feathers in the Berlin specimen formed ‘feather trousers’, whereas Evans [33] suggested that they were more confined to the periphery of the bone, forming some sort of vane, and being directly involved in flight. The most important conclusion from the above observations is that some of the striations (the proximal ones behind left femur) may represent long hind-limb feathers, and this seems to be what prompted Beebe [4] to accept from a photo of the Berlin specimen “a diminutive wing” in the pelvic region (*contra* [99]), as discussed by Heilmann [49 (pp. 194–196)], who thought that *Archaeornis*’ “thigh feathers are [...] too weak” for a wing. Heilmann does not discuss these ‘feathers’ of the fossil any further, but he does reconstruct his *Proavis* with a border of short feathers behind the thigh (Figs. 139 and 142). He does not show the thigh in the reconstructions of *‘Archaeornis’*, but Beebe’s rather schematic figure clearly shows them (but not much on the lower leg).

The presumed tibial and femoral feathers of the Berlin *Archaeopteryx* appear to have assumed an important role, first in Evans' [33] introductory remarks about flight with both fore- and hind limbs, and later in Beebe's [4] *Tetrapteryx* hypothesis, which was discussed in detail by Heilmann [49 (194 ff.)] with some part of Beebe's idea about this intermediate stage being accepted (see further above). De Beer [30] and Heller [51] accepted these feathers around the legs (though not as 'wings', but rather as 'breeches' – note that de Beer seems to confuse femoral feathers and breeches on the lower legs).

Recent finds of some small and primitive dromaeosaurs show long feathers behind the legs [81,141], and *Microraptor* possibly even had a 'wing' of very elongate contour feathers behind the whole length of the leg, including the metatarsals carrying the longest and asymmetrical 'flight feathers' [142] (but see [91]). This has revived the '*Tetrapteryx*-theory', and prompted Xu et al. [142] to implicate such 'hind wings' in their common ancestor with birds (that is, in the stem-Paraves in the sense of Sereno 1999 [110]), but later lost in the bird-lineage. Prum [99], however, warns that perhaps the 'hind wings' were apomorphic to dromaeosaurids, implying that the direct lineage towards birds never had such hind wings, and urged that *Archaeopteryx* be closely inspected to illuminate this problem, as we have done here.

We conclude that *Archaeopteryx* had rather long contour feathers along the legs, apparently both upper and lower, and that they may have formed 'edges' rather than 'trousers'. Thus, they might be considered remnants of former 'hind wings' in the bird-lineage, but only finds of feathered representatives of outgroups close to Paraves may solve this puzzle [10,22], e.g., better preserved specimens of *Protarchaeopteryx* (cf. [61]).

8. A comparison with other fossils

The body contour feathers on the back and legs of *Archaeopteryx* appear to have been fairly modern in appearance, although perhaps not as similar to feathers on most extant, volant birds as are the remiges. However, this is tentative because their state of preservation is not good enough to draw firm conclusions about their detailed morphology (contra [26]). Both the feathers that extend from the back and legs (Figs. 5, 6, 8 and 9) appear to have been elongate, with rather narrow vanes (i.e. not as wide, ovoid and plate-like as a 'typical' semiplume body contour feathers) and were clearly more pliable than the flight feathers. Furthermore, they appear not to have had vanes as closed as the flight feathers, as evidenced by the morphology of the feathers along the back (Fig. 6).

Evidently, they were not, however, nearly as simple and hair-like as the feathers recovered with the primitive coelurosaurian *Sinosauropteryx* [15,25]. More advanced theropods, such as *Sinornithosaurus* [139,141] and *Microraptor* [142] had more complex, albeit still superficially 'hair-like' body contour feathers and down-like structures, corresponding approximately to stage 2 of Prum's [99] model for feather evolution. *Protarchaeopteryx* is said to have 'down' and apparently had pennaceous contour feathers [61 (Fig. 3a), 93]. However, these were recovered separately on the slab, not associated with any particular part of the body. Accordingly, their identification as body contour feathers should be regarded as tentative, and they may represent coverts instead. *Caudipteryx* also has remiges and rectrices and even downs (pers. obs. and [93]); as noted above (Fig. 4), they might correspond to Prum's [99] stage 2.

In *Cryptovolans* [81] and *Microraptor*, there appears to have been body contour feathers of a superficially modern appearance, those of *Microraptor* being called 'plumulaceous' [142]. Whether these correspond to Prum's [99] stages 3a (rachis + unbranched barbs) or the more complex stage 3a+b (rachis, barbs and barbules), is still not clear, and will require more analyses of vane morphology. The body contour feathers in *Archaeopteryx* also appear to correspond to Prum's [99] stage 3, but the stage of preservation is such that even careful analyses failed to distinguish between stages 3a or 3a+b. At an approximate length of 3.5 cm along the epipodials this may seem a lot for a bird of *Archaeopteryx*' size [144] and could represent the remains of 'hind-limb wings', as are present in *Microraptor gui* [142] (but see [91]) and possibly *M. zhaoianus* [140]. In *Archaeopteryx* the 'hind-wings' were apparently much less prominent than in *M. gui*, and probably absent from the metapodials, thus perhaps representing a more modern way of flight with the forelimbs only. Thus, if *Archaeopteryx* really did possess a vestigial 'hind-limb wing', this might be regarded as an avialean plesiomorphy.

The plumages of the many specimens of confuciusornithid birds recovered from northeastern China are usually in a much poorer state of preservation, and are likewise preserved mainly as carbonised residue, not as imprints [20], rendering analyses of their detailed morphology difficult. At a glance the body contour feathers appear hair-like, not unlike the simple filaments recovered with several of the non-avian theropods. However, the phylogenetic position of the Confuciusornithidae (Fig. 4) and the probable morphology of the body feathers, at least around the legs and back, of *Archaeopteryx* (and feathers in some dromaeosaurs), suggest that future analyses of the detailed morphology of body feathers in well-preserved confuciusornithids will reveal pennaceous, not simple and 'hair-like' body feathers.

9. Points on preservation

The Berlin *Archaeopteryx* exhibits well-preserved rectrices and remiges with coverts [106] as sharp imprints, but rather weak imprints of the feathers on the back and hind limbs, and questionable structures below the throat and on the chest. Thus, two models for the type of preservation must be taken into account.

The pattern observed today approximates a realistic image of the plumage in the living animals, although a few layers of feathers may be hidden under thin crusts of limestone (see [106,107]). The near-absence of larger feathers on the body (apart from the back) is primary, indicating that, at most, rather simple 'down-like' feathers or 'hair-like' cryptoptiles (e.g. not unlike those of *Sinosauropteryx* [25]) covered the body. These were lost during fossilization. The faint striations below the neck and at the chest could be the only remains of such feathers. Rietschel [106] discussed the preservation of the wing and tail feathers as imprints of only the ventral surface, but the body feathers are not even mentioned, nor were they discussed by Stephan [119].

Alternatively the observed pattern is only the trivial result of taphonomic processes (cf. [28,29]; criticised by [63]) leaving only reasonably well-preserved feathers as a 'halo' at the circumference of the carcass (already suggested by [90,109]), indicating that the body itself may well have been covered by contour feathers at least as well developed as the ones along the back. The preserved pattern is exclusively secondary, and, thus, of limited significance. Such an explanation has been offered for the preservation of feathers in *Confuciusornis* [20] and in the Middle Eocene deposit of Messel [53,72]. Model (2) is the less interesting alternative and is close to an *ad hoc* assumption. There is little reason to believe that *Archaeopteryx* did not have some feather covering all over the body, apart from perhaps the feet and parts of the face. Both models can be tested by new and better-preserved fossil finds.

How may the feathers have been arranged? As [119] noted, there is universal agreement that the rectrices, symmetrically preserved in the London and Berlin specimens, were arranged in one row along the lateral sides of the tail, although in the former specimen the caudals are viewed from above and in the latter from the side. To our knowledge, it has never been argued that they were arranged vertically, or that rectrices were present all the way round the caudals (as appears to be the case with the strange fibres recovered with a *Psittacosaurus* specimen [73]), and the cryptoptiles in *Sinosauropteryx* [15,25]. Accordingly, an *ad hoc* explanation of missing rectrices owing to a decomposing carcass has not been advanced in this respect.

With the feathers preserved rather symmetrical along the lower legs (also a slender structure with little flesh for decomposition) the situation is, however, different. Most often these have been regarded as forming 'feather trousers' or at least having had a circumferential distribution, analogous, or most probably homologous, to extant neornithines. It cannot, however, be ruled out that they too were primarily arranged as feather borders, at most a few rows in thickness. The extremely large hind limb feathers in *Microraptor* are interpreted in just this fashion [99,142], and not as the leftover remains of a preservation artefact. Additionally, it would be a rather peculiar incidence if just one (or a few at most) of the feather rows got preserved, lying with near-parallel raches in apparently just one level, without any trace of neighbouring rows, if indeed they were present. Yet such seems to be the case in *Archaeopteryx* (and *Microraptor*). We could only determine one incident of a crossing of two supposed raches.

Accordingly, an interpretation of *Archaeopteryx* as endowed with a sort of *'Tetrapteryx* - hind limb wing', albeit reduced compared to both Evans' [33] and

Beebe's [4] hypothetical *Proavis*-stages (and certain members of the plesiomorphic sister taxon Dromaeosauridae). Minimally the preservation pattern appears to support "feather fringes" along the legs of *Archaeopteryx* instead of 'feather trousers'.

10. Proto-pterylosis?

If model (1) for the preservation of the plumage of the Berlin *Archaeopteryx* is correct, this implies that some parts of the body (back and legs) bore, at most, a few rows of larger feathers, while other areas (main part of the corpus, perhaps most of the neck) had, at most, smaller proto-feathers or 'proto-down'. This implies that some areas had large pennaceous feathers while others lacked them and only had 'simpler' structures, and perhaps even were unfeathered. Thus, something similar to pterylae could have been present on the legs and at the midline of the back, i.e. 'proto-pterylae' and 'proto-apteria'. Obviously, this idea can be tested by new discoveries of fossil of either *Archaeopteryx* or close relatives, with more well-preserved plumage.

In the development of pterylae in extant birds (even comprising the down plumage of more simplified structures [11,66]), it becomes evident that the middle of the back and legs (both upper and lower) nearly always carry pterylae with pennaceous feathers. There are many other areas with pterylae and apteria in general in neognaths, save penguins that have a rather uniform feather covering. Such uniformity is also found in ratites but not in tinamous, implying an uncertainty of the polarity of this character in the last common ancestor of crown-clade Aves (= Neornithes). Did this common ancestor have apteria or a uniform feather covering?

The pattern of pterylae ('pterylosis' according to [66 (p. 73)]) is generally also mirrored in the pattern of papillae for the embryonic down (neoptiles – see [11]). The stripes on the back are often paired, but set close to the midline (op. cit., Fig. 50), or unpaired in the anterior region of the back, and these tracts are composed of only a few rows of feathers. As mentioned above, in the Berlin specimen, we cannot be sure whether there was only a single row of feathers as observed, or one or a few rows hidden below the laminae. From a functional point of view, this one (or a few) row(s) along the back hardly stood upright in life, as in the fossil. It seems more likely that the feathers were lying down to cover the muscular part of the proximal tail. The row as preserved apparently ends around the middle of the back, at least it fades out in the matrix. Whether this was the case in the living animal is unknown, but smaller and simpler feathers may well have covered the anterior part of the back and neck. There is no obvious, taphonomic reason why larger feathers should have disappeared from these areas when being preserved posteriorly.

It is perhaps of interest that in some birds the ontogenetically earliest feathers (neoptiles) to develop are often of considerable length, and are situated at the midline above the pelvis and the posterior back and on the thighs [11], e.g., in crows, and in others species, e.g., herons, these long feathers are also present on the thighs, and are arranged in double rows close to the entire midline of the back (op. cit., Fig. 26). Could such a pattern be yet another case of recapitulation or is it just fortuitous? We prefer the former, which supports Haeckel's theories (see also [7]). Thus, it is possible that the early development of these long neoptiles in extant birds, to be replaced by pennaceous feathers in the pterylae, could represent the pattern observed in archaic avialeans, as exemplified by *Archaeopteryx*.

Such 'proto-pterylosis' may in fact be even older, characterising the ancestral maniraptoran, as indicated by the plumage in *Caudipteryx* and dromaeosaurs. Thus, the polarity within primitive Neornithes may be solved. They had pterylosis, not a uniform feather covering. On the other hand, we believe that the 'patterning' of the integumental covering in *Sinosauropteryx* as shown by the ringed appearance of the tail [15,25] is a preservation artefact conditioned by the vertebral arches (pers. obs.). *Sinosauropteryx* probably had a more uniform covering of cryptoptiles [25]. Accordingly, early coelurosaurs may not yet have been 'pterylized'.

11. Summary

The Berlin specimen of *Archaeopteryx* is the only one to preserve remnants of body plumage (apart from the now missing Maxberg specimen), which is here described in detail. The London specimen shows no indications of body feathers. Most of the body feathers that were originally present are still present today and

preparation has only damaged a few. They have been largely overlooked in 130 years of debate on *Archaeopteryx*, feathers.

3–4-cm long feathers are present around the legs, and although not well preserved, shafts and in some places parallel, closely set barbs can be observed. Barbules are not visible, but may be inferred. The vanes can be vaguely outlined, and the feathers may have formed 'trousers', or, alternatively, narrow 'edges' on the fore and aft sides of the limbs. Less well preserved feathers of roughly the same type are present behind the femora, albeit only as weak impressions of parallel raches. Undisputed feathers with raches and faint vexillae are present nearly perpendicular to the vertebral column, from the ilium to halfway up the back. Their slightly bent shafts appear quite similar to the feathers on the lower legs. The dorsal row of feathers (one row apparently, although more may be hidden below thin limestone crust) probably covered the back and the proximal tail in life. These feathers are clearly body contour feathers.

Faint imprints in front of the breast may be shafts of more simple and 'hair-like' feathers, or collapsed pennaceous contour feathers. No other feathers can be observed on the body, and if this represents the original distribution, then the pattern of feathers along the back and legs and either none or only small, simple and less easily preservable feathers on the rest of the body could indicate the presence of pteria and apteria and some sort of pterylosis (here termed 'protopterylosis').

Comparison with feathered theropod dinosaurs and primitive birds lead to the following conclusions: (1) feathers, even pennate remiges and rectrices, originated long before flight, no later than in stem-Maniraptora, which also had down; (2) simple hair-like proto-feathers with little branching (resembling the hypothetical 'cryptoptiles' of ornithological literature) are even older, a synapomorphy of at least Coelurosauria; they might have been retained on part of the body up to the level of confuciusornithids or even early ornithurines and enantiornithines; (3) 'protopterylosis' is characteristic of Maniraptora, as some regions have remiges and rectrices, others have pennate body contour feathers, and others have down or 'cryptoptiles', the latter two types most likely covering 'proto-apteria'; (4) the feather rows on the back and the thigh of *Archaeopteryx* may correspond to the rows of very long neoptiles present in the pteria very early in the ontogeny of several living birds. If so, they perhaps illustrate a case of Haeckel's 'biogenetic law'; (5) comparison of the 'feather trousers' of *Archaeopteryx* to the so-called 'hind wings' of primitive dromaeosaurs indicates that their common ancestor minimally had long feathers on the legs, not necessarily 'wings', so whether birds went through a *'Tetrapteryx* stage' remains uncertain.

Acknowledgements

We are indebted to Dr. Angela Milner and Mrs. Sandra Chapman at the Natural History Museum in London, Dr. Günther Viohl and Mr. Pino Völkl at the Jura Museum in Eichstätt, Drs. Helmut Mayr and Peter Wellnhofer at the Bayerische Staatssammlung in Munich, and Professor Dieter Stefan Peters and Drs. Gerald Mayr and Michael Gudo at Forschungsinstitut Senckenberg in Frankfurt for hospitability during our visits. We are particularly indebted to Professor Hans Peter Schultze and Drs. Wolf Dieter Heinrich, David Unwin and Oliver Hampe at the Museum für Naturkunde in Berlin for their never failing kindness and hospitability whenever we come to Berlin and for kindly providing us with high resolution photographs of *Archaeopteryx*, skilfully taken by Mrs. Carola Radke. Thanks to Dr. Jane Richter, School of Conservation, Copenhagen, for criticism of our manuscript, to Christian Hagen, Geological Institute, for finishing the drawing. We are particularly indebted to Dr. Wolf-Dieter Heinrich for kindly providing us with his own personal illustration of the slab (Fig. 2) and to Professor Kevin Padian and Dr. Peter Wellnhofer who provided much insightful criticism for improvement of the manuscript. This study was supported by a grant from the Danish National Science Research Council to PC and a travel grant from the Geological Institute to NB.

References

[1] O. Abel, Lebensbilder aus der Tierwelt der Vorzeit, G. Fischer Verlag, Jena, 1922.
[2] R.T. Bakker, Dinosaur renaissance, Sci. Am. 232 (4) (1975) 58–78.
[3] R.T. Bakker, The Dinosaur Heresies, William Morrow Co., New York, 1986.
[4] C.W. Beebe, A *Tetrapteryx* stage in the ancestry of birds, Zoologica 2 (1915) 39–52.

[5] W.J. Bock, The arboreal theory for the origin of birds, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 199–207.

[6] B. Bohlin, The wing in the Archaeornithes, Zool.Bidrag från Uppsala 25 (1947) 328–334.

[7] N. Bonde, Primitive features and ontogeny in phylogenetic reconstructions, Videnskab. Medd. Dansk Naturhist. Foren. 145 (1984) 219–236.

[8] N. Bonde, Indledning - især om palæoøkologisk rekonstruktion, Dansk Geol. Foren. (1985) 117–122 Årsskr.for 1984 (in Danish: Intro on palaeoecology; English captions & abstract).

[9] N. Bonde, The systematic and classificatory status of *Archaeopteryx***, Mus. Northern Arizona Bull. 60 (1996) 193–199.

[10] N. Bonde, P. Christiansen, The problem of becoming feathered (Abstr. 2002, Int. Ornithol. Congr., Beijing; extended abstr. 2002: The evolution of plumage from dinosaur to early bird, 12 p. in Bonde N. (Ed.): Bird Evolution Syump., Geol. Inst., Copenhagen).

[11] I. Broman, Über die Entstehung und Bedeutung der Embryonaldunen, Morphol. Jahrb. 86 (1941) 141–217.

[12] A. Brush, Evolving a protofeather and feather diversity, Am. Zool. 40 (2000) 631–639.

[13] P. Burgers, L.M. Chiappe, The wing of *Archaeopteryx* as a primary thrust generator, Nature 399 (1999) 60–62.

[14] A.J. Charig, F. Greenaway, A.C. Milner, C. A. Walker, P.J. Whybrow, *Archaeopteryx* is not a forgery, Science 232 (4750) (1986) 622–626.

[15] P.-J. Chen, Z.-M. Dong, P.J. Currie, An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China, Nature 391 (6663) (1998) 147–152.

[16] S.J. Czerkas (Ed.), Feathered Dinosaurs and the Origin of Flight, 1, The Dinosaur Museum, J.Blanding, Utah, 2002.

[17] L.M. Chiappe, The first 85 million years of avian evolution, Nature 378 (6555) (1995) 349–355.

[18] L.M. Chiappe, Aves, in: P.J. Currie, K. Padian (Eds.), Encyclopedia of Dinosaurs, Academic Press, San Diego, 1997, pp. 32–38.

[19] L.M. Chiappe, Phylogenetic relationships among basal birds, in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale University, New Haven, Connecticut, pp. 125–139.

[20] L.M. Chiappe, S.A. Ji, Q. Ji, M.A. Norell, Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China, Bull. Am. Mus. Nat. Hist. 242 (1999) 1–89.

[21] P. Christiansen, N. Bonde, Axial and appendicular pneumaticity in *Archaeopteryx*, Proc. Zool. Soc. Lond. (ser. B) 267 (2000) 2501–2505.

[22] P. Christiansen, N. Bonde, Limb proportions and avian terrestrial locomotion, J. Ornithol. 143 (3) (2002) 356–371.

[23] P.J. Currie, The Flying Dinosaurs, Red Deer Coll. Press, Red Deer, Alberta, 1991.

[24] P.J. Currie, Feathered dinosaurs, in: G.S. Paul (Ed.), The Scientific American Book of Dinosaurs, St. Martin's Press, New York, 2000, pp. 183–189.

[25] P.J. Currie, P.-J. Chen, Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China, Can. J. Earth Sci. 38 (2001) 1705–1727.

[26] W. Dames, Über *Archaeopteryx*, Paläontol. Abh. 2 (1884) 119–198.

[27] W. Dames, Über Brustbein, Schulter- und Beckengürtel der *Archaeopteryx*, 1897, Sitzungsber. K. Preuss. Akad. Wiss, Berlin, 1897, pp. 818–834.

[28] P.G. Davis, The taphonomy of *Archaeopteryx*, Bull. Nat. Sci. Mus., Tokyo, C 22 (1996) 91–106.

[29] P.G. Davis, D.E.G. Briggs, Fossilization of feathers, Geology 23 (1995) 783–786.

[30] G. de Beer, *Archaeopteryx lithographica*, A study based upon the British Museum specimen, Trustees Brit. Mus. (Nat. Hist.), London, Publ. 224 (1954) 1–68.

[31] A. Elzanowski, A new genus and species for the largest specimen of *Archaeopteryx*, Acta Paleontol. Pol. 46 (4) (2001) 519–532.

[32] A. Elzanowski, Archaeopterygidae (Upper Jurassic of Germany), in: L.M. Chiappe, L.M. Witmer (Eds.), Mesozoic Birds, University of California Press, Berkeley, 2002, pp. 129–159.

[33] J. Evans, Reprint by Virtue & Co, London, with new intro of Evans (1865): On portions of a cranium and of a jaw, in the slab containing the fossil remains of *Archaeopteryx*, Nat. Hist. Evol. 5 (1881) 415–425.

[34] D.E. Fastovsky, D.B. Weishampel, The Evolution and Extinction of the Dinosaurs, Cambridge University Press, Cambridge, UK, 1996.

[35] A. Feduccia, On why the dinosaur lacked feathers, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 75–80.

[36] A. Feduccia, The Origin and Evolution of Birds, Yale University Press, New Haven, 1996 (2nd ed., 1999).

[37] A. Feduccia, H.B. Tordoff, Feathers of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function, Science 203 (1979) 1021–1022.

[38] K. Fischer, H.H. Krueger, Neue Präparationen am Berliner Exemplar des Urvogels *Archaeopteryx lithographica* H. V. Meyer, 1861, Z. Geol. Wiss. 7 (1979) 575–579.

[39] K.A. Frickhinger, Die Fossilien von Solnhofen, Goldschneck Verlag, Korb, 1994.

[40] P. Garner, G. Taylor, A.L.R. Thomas, On the origin of birds, Proc. R. Soc. Lond., Ser. B 266 (1999) 1259–1266.

[41] S.M. Gatesy, The evolutionary history of the theropod caudal locomotor module, in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale Univ., New Haven, Connecticut, pp. 333–347.

[42] S.M. Gatesy, K.P. Dial, From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds, Evolution 50 (1996) 2037–2048.

[43] J. Gauthier, Saurischian monophyly and the origin of birds, in: K. Padian (Ed.), The Origin of Birds and the Evolution of Flight, Mem. Calif. Acad. Sci. 8 (1986) 1–55.

[44] J. Gauthier, K. de Queiroz, Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name 'Aves', in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale Univ., New Haven, Connecticut, pp. 7–41.

[45] H. Gee, L.V. Rey, A Field Guide to Dinosaurs, Quarto Publ, 2002.

[46] P.D. Gingerich, Skull of *Hesperornis* and early evolution of birds, Nature 243 (1973) 70–73.

[47] P.J. Griffiths, The isolated *Archaeopteryx* feather, Archaeopteryx 14 (1996) 1–26.

[48] G. Heilmann, Vor nuværende Viden om Fuglenes Afstamning. I-V, Da. Ornitol. Foren. Tidsskr. 8–10 (1913–16) 255 (in Danish: Our Present Knowledge of the Ancestry of Birds).

[49] G. Heilmann, The Origin of Birds, H.F. & G. Witherby, London, 1926.

[50] O. Heinroth, Die Flügel von *Archaeopteryx*, J. Ornithol. 71 (1923) 277–283.

[51] F. Heller, Ein dritter *Archaeopteryx*-Fund aus den Solnhofener Plattenkalken von Langenaltheim/Mfr, Erlanger Geol. Abh. 31 (1959) 1–25.

[52] J. Helms, Zur Fossilization der Federn des Urvogels (Berliner Exemplar), Wiss. Z. Humboldt-Univ. zu Berlin (Math.-Nat. Reihe) 31 (3) (1982) 185–199.

[53] H.J. Hoffmann, Messel – window on an ancient world, Nat. Geogr. 197 (2) (2000) 34–51.

[54] T.R. Holtz Jr, A new phylogeny of the carnivorous dinosaurs, in: B.P. Pérez-Moreno, T.R. Holtz Jr, J.L. Sanz, J.J. Moratalla (Eds.), Aspects of Theropod Paleobiology, Gaia 15 (1998) 5–61.

[55] T.R. Holtz Jr. Arctometatarsalia revisited: the problem of homoplasy in reconstructing theropod phylogeny, in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale Univ., New Haven, Connecticut, USA, pp. 99–122.

[56] L.-H. Hou, Morphological comparisons between *Confuciusornis* and *Archaeopteryx*, in: A. Sun, Y. Wang (Eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, short papers, China Ocean Press, Beijing, 1995, pp. 193–201.

[57] L.-H. Hou, Mesozoic Birds of China, Taiwan Provincial Feng Huang Ku Bird Park, Nan Tou, Taiwan, 1997.

[58] L.-H. Hou, Z.-H. Zhou, L.D. Martin, A. Feduccia, A beaked bird from the Jurassic of China, Nature 377 (6550) (1995) 616–618.

[59] M.E. Howgate, Problems of the osteology of *Archaeopteryx* – Is the Eichstätt specimen a distinct genus? in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 104–112.

[60] Q. Ji, L.M. Chiappe, S.-A. Ji, A new Late Mesozoic confuciusornithid bird from China, J. Vert. Paleontol. 19 (1) (1999) 1–7.

[61] Q. Ji, P.J. Currie, M.A. Norell, S.-A. Ji, Two feathered dinosaurs from northeastern China, Nature 393 (6687) (1998) 753–761.

[62] Q. Ji, M.A. Norell, K.-Q. Gao, S.-A. Ji, D. Ren, The distribution of integumentary structures in a feathered dinosaur, Nature 410 (6862) (2001) 1084–1088.

[63] R.A. Kemp, D. Unwin, Skeletal taphonomy of *Archaeopteryx*: a quantitative approach, Lethaia 30 (1997) 229–238.

[64] K. Lambrecht, Handbuch der Palaeornithologie, Verlag Gebrüder Borntraeger, Berlin, 1933.

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

[66] A.M. Lucas, P.R. Stettenheim, Avian Anatomy, Integument, Agricultura Handbook 362, Washington DC, 1972 Part I, 340 p.

[67] O.C. Marsh, Characters of the Odontornithes, with notice of a new allied genus, Am. J. Sci. (Ser. 3) 14 (1877) 85–87.

[68] O.C. Marsh, Odontornithes, a monograph of the extinct toothed birds of North America, Rep. US Geol. Expl. Fortieth Parallel 7 (1880) 1–201.

[69] L.D. Martin, The relationship of *Archaeopteryx* to other birds, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 177–183.

[70] L.D. Martin, J.D. Stewart, Teeth in *Ichthyornis* (Class: Aves), Science 195 (4284) (1977) 1331–1332.

[71] M. Mäuser, Der achte *Archaeopteryx*, Fossilien 3 (1997) 156–157.

[72] G. Mayr, C. Moureer-Chauvire, Rollers from the Middle Eocene of Messel (Germany) and the Upper Eocene of the Quercy (France), J. Vert. Paleontol. 20 (2000) 533–546.

[73] G. Mayr, G.D.S. Peters, G. Plodowski, O. Vogel, Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*, Naturwissenschaften 89 (2002) 361–365.

[74] H. von Meyer, *Archaeopteryx lithographica* (Vogel-Feder) und *Pterodactylus* von Solnhofen, N. Jahrb. Mineral. Geol. Palaeontol. (1861) 678–679.

[75] A. Milner, Dino-birds Nat, History Mus., London, 2002, 64 p.

[76] F. Nopsca, Ideas on the origin of flight, Proc. Zool. Soc. Lond. 1907 (1907) 223–236.

[77] R.Å. Norberg, Function of vane asymmetry and shaft curvature in bird flight feathers: inferences on flight ability of Archaeopteryx, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 177–183.

[78] M.A. Norell, The proof is in the plumage, Nat. Hist. 110 (6) (2001) 58–63.

[79] M.A. Norell, J.M. Clark, P.J. Makovicky, Phylogenetic relationships among coelurosaurian theropods, in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale Univ., New Haven, Connecticut, pp. 47–67.

[80] M.A. Norell, J.A. Clarke, Fossil that fills a critical gap in avian evolution, Nature 409 (6817) (2001) 181–184.

[81] M.A. Norell, Q. Ji, K. Gao, C. Yan, Y. Zhao, L. Wang, 'Modern' feathers on a non-avian dinosaur, Nature 416 (6876) (2002) 36–37.

[82] D. Norman, The Illustrated Encyclopedia of Dinosaurs, Salamander Books, London, 1985.

[83] D. Norman, Prehistoric Life, Macmillan, New York, 1994.

[84] Opinion 1070: International Commission on Zoological Nomenclature. Opinion 1070. Conservation of *Archaeopteryx lithographica* von Meyer 1861 (Aves), Bull. Zool. Nomencl. 33 (1977) 165–166.

[85] J.H. Ostrom, Description of the *Archaeopteryx* specimen in the Teyler Museum, Haarlem Proc. Kon. Ned. Akad. Wetensch, Ser. B 75 (1972) 289–305.

[86] J.H. Ostrom, *Archaeopteryx* and the origin of birds, Biol. J. Linn. Soc. 8 (1976) 91–182.

[87] J.H. Ostrom, Bird flight: How did it begin? Am. Sci. 67 (1979) 46–66.

[88] J.H. Ostrom, The meaning of *Archaeopteryx*, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 161–176.

[89] J.H. Ostrom, The Yale *Archaeopteryx*: the one that flew the coop, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, Germany, 1985, pp. 359–367.

[90] R. Owen, On the *Archaeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species, from the Lithographic Stone of Solenhofen, Phil. Trans. R. Soc. Lond. 153 (1862) 33–47.

[91] K. Padian, Four-winged dinosaurs, bird precursors, or neither?, BioSci. 53 (5) (2003) 450–452.

[92] K. Padian, L.M. Chiappe, The origin and early evolution of birds, Biol. Rev. 73 (1) (1998) 1–42.

[93] K. Padian, Q. Ji, S.-A. Ji, Feathered dinosaurs and the origin of flight, in: D.H. Tanke, K. Carpenter (Eds.), Mesozoic Vertebrate Life, Indiana University Press, Bloomington, 2001, pp. 117–135.

[94] K.C. Parkes, Speculations on the origin of feathers, The Living Bird 5 (1966) 77–86.

[95] G.S. Paul, Predatory Dinosaurs of the World, Simon & Schuster, New York, 1988.

[96] G.S. Paul, The art of Charles R. Knight, Sci. Am. 274 (6) (1996) 74–81.

[97] G.S. Paul, Dinosaurs of the Air, J. Hopkins, London, 2002.

[98] B. Petronievics, A.S. Woodward, On the pectoral and pelvic arches of the British Museum specimen of *Archaeopteryx*, Proc. Zool. Soc. Lond. 1 (1917) 1–6.

[99] R.O. Prum, Development and evolutionary origin of feathers, J. Exp. Zool. (Mol. Dev. Evol.) 285 (1999) 291–306.

[100] R.O. Prum, Dinosaurs take to the air, Nature 421 (2003) 323–324.

[101] R.O. Prum, A.H. Brush, Which came first, the feather or the bird?, Sci. Am. 288 (3) (2003) 60–69.

[102] W.P. Pycraft, The wing of *Archaeopteryx*, Nat. Sci. Lond. 8 (5) (1896) 261–266.

[103] W.P. Pycraft, A History of Birds, London, 1910.

[104] P.J. Regal, The evolutionary origin of feathers, Q. Rev. Biol. 50 (1975) 35–65.

[105] M. Reichel, L'*Archaeopteryx* : un ancêtre des oiseaux, Nos Oiseaux 16 (1941) 93–107.

[106] S. Rietschel, Feathers and wings of *Archaeopteryx*, and the question of her flight ability, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 251–260.

[107] S. Rietschel, False forgery, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 371–376.

[108] E.F. von Schlotheim, Die Petrefactenkunde, Becker'schen Buchhandlung, Gotha, 1820.

[109] H.G. Seeley, Professor Carl Vogt on the *Archaeopteryx*, Geol. Mag. 1881 (1881) 300–302.

[110] P.C. Sereno, The evolution of dinosaurs, Science 284 (5423) (1999) 2137–2147.

[111] P. Shipman, Taking Wing: *Archaeopteryx* and the Evolution of Bird Flight, Simon & Schuster, New York, 1998.

[112] J.B. Smith, Y. Hailu, P. Dodson, The age of the *Sinosauropteryx* quarry, northeastern China, J. Vert. Paleontol. 18 (Suppl. 3) (1998) 78A.

[113] J.B. Smith, H.D. Harris, G.I. Omar, P. Dodson, Biostrategraphy and avian origins in northeastern China, in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale Univ., New Haven, Connecticut, pp. 549–589.

[114] J.R. Speakman, S.C. Thomson, Flight capabilities of *Archaeopteryx*, Nature 370 (1994) 514.

[115] H. Steiner, Das Problem der Diasttaxie des Vogelflügels, Jenaische Zeitschr. Naturwiss 55 (1917) 221–496.

[116] H. Steiner, Der *Archaeopteryx*-Schwanz der Vogelembryonen, Vierteljschr. Naturforsch. Ges. Zürich 83 (30) (1938) 279–300.

[117] B. Stephan, Zeigt das Berliner Exemplar des Urvogels die Ventral-oder die Dorsalseite von Schwantz und Flügeln?, Orn. Jahresber. Mus. Hein. 1 (1976) 71–77.

[118] B. Stephan, Remarks on the reconstruction of *Archaeopteryx* wing, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, Germany, 1985, pp. 261–265.

[119] B. Stephan, Urvogel. Archaeopterygiformes, Neue Brehm. Buch., 465 (3rd ed.), Wittenberg Lutherstadt, 1987, pp. 216.

[120] S.S. Sumida, C.A. Brochu, Phylogenetic context for the origin of feathers, Am. Zool. 40 (2000) 486–503.

[121] C.C. Swisher III, Y.-Q. Wang, X.-L. Wang, X. Xu, Y. Wang, Cretaceous age for the feathered dinosaurs of Liaoning, China, Nature 400 (6739) (1999) 58–61.

[122] S.F. Tarsitano, The morphological and aerodynamic constraints on the origin of avian flight, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, 1985, pp. 319–332.

[123] R.A. Thulborn, T.C. Hamley, The reptilian relationships of *Archaeopteryx*, Aust. J. Zool. 30 (1982) 611–634.

[124] J. van Tyne, A.J. Berger, Fundamentals of Ornithology, John Wiley & Sons, New York, 1961.

[125] C. Vogt, *L'Archaeopteryx macroura*. Un intermediaire entre les oiseaux et les reptiles, Rev. Sci. France 2 (9) (1879) 241–248.

[126] A.D. Walker, The pelvis of *Archaeopteryx*, Geol. Mag. 117 (1980) 595–600.
[127] P. Wellnhofer, Das fünfte Skelettexsemplar von *Archaeopteryx*, Palaeontographica A147 (1974) 169–216.
[128] P. Wellnhofer, A new specimen of *Archaeopteryx*, Science 240 (4860) (1988) 1790–1792.
[129] P. Wellnhofer, A new specimen of *Archaeopteryx* from the Solnhofen Limestone, in: K.E. Campbell Jr (Ed.), Papers in Avian Biology honoring Pierce Brodkorb, Nat. Hist. Mus. Los Angeles County Sci. Ser. 36 (1992) 3–23.
[130] P. Wellnhofer, Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten, Archaeopteryx 11 (1993) 1–47.
[131] P. Wellnhofer, Zur Lebensweise der Solnhofener Urvögel, Fossilien 5 (1995) 296–307.
[132] P. Wellnhofer, *Archaeopteryx* – Der Urvogel aus Bayern, Messekatalog Mineralientage München (1995) 114–135.
[133] P. Wellnhofer, Der bayerische Urvogel, *Archaeopteryx bavarica*, AVH Mitt. 75 (2000) 3–10.
[134] P. Wellnhofer, Hermann von Meyer und der Solnhofener Urvogel, *Archaeopteryx lithographica*, in: T. Keller, G. Storsch (Eds.), Hermann von Meyer. Frankfurter Buerger und Begruender der Wirbeltierpalaeontologie in Deutschland, Kleine Senckenb.-Reihe, 40, Schweizerbart'scher Verlag, Stuttgart, 2001, pp. 11–18.
[135] K.N. Whetstone, Braincase of Mesozoic birds: I. New preparation of the 'London' *Archaeopteryx*, J. Vert. Paleontol. 2 (4) (1983) 439–452.
[136] P.J. Whybrow, Preparation of the cranium of the holotype of *Archaeopteryx lithographica* from the collections of the British Museum (Natural History), Neues Jahrb. Geol. Paläontol. Mh. 3 (1982) 184–192.
[137] L.M. Witmer, The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils, in: J.J. Thomason (Ed.), Functional Morphology in Vertebrate Paleontology, Cambridge University Press, Cambridge, UK, 1995, pp. 19–33.
[138] X. Xu, Z.-L. Tang, X.-L. Wang, A therizinosaurid dinosaur with integumentary structures from China, Nature 399 (6734) (1999) 350–354.
[139] X. Xu, X.-L. Wang, X.-C. Wu, A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China, Nature 401 (6750) (1999) 262–266.
[140] X. Xu, Z.-H. Zhou, X.-L. Wang, The smallest known non-avian theropod dinosaur, Nature 408 (6813) (2000) 705–708.
[141] X. Xu, Z.-H. Zhou, R.O. Prum, Branched integumental structures in *Sinornithosaurus* and the origin of feathers, Nature 410 (6825) (2001) 200–204.
[142] X. Xu, Z.-H. Zhou, X.-L. Wang, X. Kuang, F. Zhang, X. Du, Four-winged dinosaurs from China, Nature 421 (2003) 335–340.
[143] D.W. Yalden, What size was *Archaeopteryx*?, Zool. J. Linn. Soc. 82 (1–2) (1984) 177–188.
[144] D.W. Yalden, Forelimb function in *Archaeopteryx*, in: M.K. Hecht, J.H. Ostrom, G. Viohl, P. Wellnhofer (Eds.), The Beginnings of Birds, Freunde des Jura Museums Eichstätt, Willibaldsburg, Germany, 1985, pp. 91–97.
[145] F. Zhang, Z.-H. Zhou, A primitive enantiornithine bird and the origin of feathers, Science 290 (5498) (2000) 1955–1959.
[146] F. Zhang, Z. Zhou, L. Hou, G. Gu, Early diversification of birds: evidence from a new opposite bird, Chin. Sci. Bull. 46 (11) (2001) 945–949.
[147] Z.-H. Zhou, Origin of feathers: perspectives from fossil evidence in China, Int. Ornithol. Congr., Beijing, 2002, pp. 25–26 (Abstract).
[148] Z.-H. Zhou, J.O. Farlow, Flight capability and habits of *Confuciusornis*, in: J. Gauthier, L.F. Gall (Eds.), New Perspectives on the Origin and Early Evolution of Birds, Spec. Publ. Peabody Mus. Nat. Hist., Yale University, New Haven, Connecticut, 2001, pp. 237–254.
[149] Z.-H. Zhou, L.-H. Hou, *Confuciusornis* and the early evolution of birds, Vertebrata PalAsiatica 26 (2) (1998) 137–146.
[150] Z.-H. Zhou, X.-L. Wang, A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeastern China, Vertebrata PalAsiatica 38 (2) (2000) 111–127.
[151] Z.-H. Zhou, X.-L. Wang, F. Zhang, X. Xu, Important features of *Caudipteryx* – Evidence from two nearly complete new specimens, Vert. Pal-Asiatica 38 (2001) 241–254.
[152] Z.-H. Zhou, F. Zhang, A long-tailed seed-eating bird from the Early Cretaceous of China, Nature 418 (6896) (2002) 405–409.