Evidence corroborates identity of isolated fossil feather as a wing covert of Archaeopteryx

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The historic fossil feather from the Jurassic Solnhofen has played a pivotal but controversial role in our evolutionary understanding of dinosaurs and birds. Recently, a study confirmed the diagnostic morphology of the feather’s original calamus, but nonetheless challenged the proposed identity as an Archaeopteryx covert. However, there are errors in the results and interpretations presented. Here we show that the feather is most likely an upper major primary covert, based on its long calamus (23.3% total length) and eight other anatomical attributes. Critically, this hypothesis is independently supported by evidence of similar primary coverts in multiple specimens of Archaeopteryx—including from the same fossil site and horizon as the isolated feather. We also provide additional insights, such as an updated colour reconstruction of the entire feather as matte black, with 90% probability. Given the isolated nature of the fossil feather, we can never know the anatomical and taxonomic provenance with 100% certainty. However, based on all available evidence, the most empirical and parsimonious conclusion is that this feather represents a primary covert from the ancient wing of Archaeopteryx.

Renowned as the first fossil feather ever known1–3, the isolated feather specimen has played an important scientific role since its discovery in 18614,5 (Fig. 1a, Supplementary Figs. S1, S2; MB.Av.100, BSP 1869 VIII 1). Seemingly misplaced in time—a modern-looking feather plucked from the Jurassic limestone—this prehistoric plume rewrote our understanding of the evolutionary history of birds and their dinosaur ancestors. This “Urfeder” (first feather) was the holotype of Archaeopteryx lithographica2, the archetypal Urvogel (first bird), until the feather was replaced by the more diagnostic London specimen6 (neotype, NHMUK PV OR 37001). Indeed, given its dissociation from any skeletal context, the isolated feather has always been in dispute4,5: where on the body did it come from, and is it from the same animal as the Archaeopteryx skeletons? Soon after the feather was unearthed, Owen7 cautioned against confusing anatomical variation with taxonomic affiliation, as this could lead to the erroneous conclusion that “the impression of a second feather differing greatly in its shape and proportions […] would represent a distinct species in Palaeontology”. In a recent study, Kaye et al.8 conflate such issues of anatomy and taxonomy, and challenge the proposed identity of the isolated feather as an upper major primary covert (UMPC) of Archaeopteryx9. They go even further in their press release, claiming with certainty that the “First discovered fossil feather did not belong to iconic bird Archaeopteryx”10. The three key arguments in Kaye et al. 20198 are identified (boldface) and refuted as follows:

“This ‘S-shaped’ centerline described here for the first time, appears to be a defining characteristic of primary coverts across a very broad range of modern species…” - The form and function of this S-shaped centerline had already been described elsewhere, however11–14. Specifically, a sigmoid curvature can cause the rachis of a primary covert to diverge anteriad and overlay at least one additional primary feather, for greater support during downstroke (Supplementary Figs. S3–S5). Critically, these previous studies also noted that the presence and degree of this S-curve is highly variable across species, and especially along the UMPC tract. The latter is not adequately considered in Kaye et al. 20199, which only includes strongly S-shaped centerlines that are not representative of the overall morphological diversity, and thus do not provide for a valid comparison. For example, their “Crane” trace (Fig. 1c, below) appears to have been based on the most extreme S-curve (feather VII) in the photograph of UMPCs from the Common Crane (Grus grus)15 (Supplementary Fig. S6). Conversely, the Common Crane feathers X’ and XI’ exhibit no S-curve at all, and instead curve posteriad

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towards the trailing edge (Fig. 1d: dotted blue centerlines). Plotting the full morphological range from the feather tract of this specimen alone more than doubles the area covered by modern feathers (Fig. 1d: yellow zone). Nearly half (46%, 11/24) of the species measured by Kaye et al. had one or more UMPCs with no S-shaped centerline (e.g., Supplementary Figs. S6–S8). Not only are not all UMPC feathers S-shaped, but not all S-shaped feathers are UMPCs: such centerlines can also be present in primaries, secondaries, upper major secondary coverts, underwing coverts, and alular feathers.

“...the isolated feathers [sic] centerline is a large departure from modern primary coverts”. However, their “Archaeopteryx” centerline is incorrect and cannot be reproduced from the paper’s results (Fig. 1c,d). In Fig. 1d, we overlay their original figure with a corrected centerline (solid blue) reconstructed from their laser-stimulated fluorescence image (LSF; Fig. 1b) and von Meyer’s 1862 mirror trace (Fig. 1a; see also below). This new centerline is substantially different from that originally presented. Correcting for this error—and that of omission, above—completely eliminates the purported large departure of the fossil feather centerline, which now falls within the range of the selected modern species.

Compared to secondary feathers in the Berlin specimen, “significant foreshortening of the isolated feather does not support its association with Archaeopteryx”. This argument is problematic for three reasons. First, the comparison is not appropriate given that secondaries had already been ruled out based on the aspect ratio of the isolated feather. Second, this interpretation conflates the anatomical and taxonomic identities in an overly restrictive manner: just because the isolated feather is inconsistent with the secondaries of Archaeopteryx does not mean that the feather does not belong to Archaeopteryx—it could simply be a different type of feather. Indeed, while Kaye et al. state that “the isolated feather is not conformal to known Archaeopteryx specimens as a primary, secondary or tail feather”, they overlook impressions of other relevant feather tracts present in multiple specimens of Archaeopteryx. Third, the study’s alternative taxonomic hypothesis is a hypothetical undescribed dinosaur, a position that circumvents the burden of proof and cannot be falsified.

To best elucidate the nature of this feather, we must rely on an inferential “consilience of inductions” convergence among the independent classes of available evidence. Here we propose the following heuristic framework:

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**Figure 1.** Centerlines of the isolated fossil feather and modern upper major primary coverts (UMPCs) from Kaye et al. 2019. (a) Modified from von Meyer 1862: Plate VIII, Fig. 3. (b) Laser-stimulated fluorescence image of MB.Av.100, modified from Kaye et al. 2019: Fig. 1. In (a) and (b), the centerline comprises the calamus (red) and rachis (blue), and the feather is oriented so that calamus endpoints are vertically aligned. Images are reversed to match (c). Scalebar: 1 cm. (c) Reproduced from Kaye et al. 2019: Fig. 3. The modern UMPCs presented here exhibit a strong anterior bend (leftward, towards the leading edge) near the calamus-rachis junction, creating an inflection point (S-curve) in the centerline. Note the yellow zone, representing the purported range of modern centerlines. (d) Modified figure from (c), including a more representative range of modern centerline morphologies (Common Crane X and XI' from Supplementary Fig. S6, oriented so that calamus endpoints are vertically aligned). The correct Archaeopteryx centerline from (a,b) is overlaid as a solid blue line. This centerline was also overlaid onto the incorrect centerline to replicate the proximal end (red), revealing an alignment error. Note the substantial discrepancy between the correct and incorrect Archaeopteryx centerlines, the former of which now falls within the range of these modern primary coverts (yellow zone).
I. What anatomical identity is most supported?
   We evaluate the isolated feather across nine attributes, particularly the relative calamus length.

II. What taxonomic identity is most supported?
   We discuss the provenance, classification, and biological contexts relevant to the isolated feather.

III. Are feathers of the anatomical identity preserved in fossils of the taxonomic identity?
   We test these two hypotheses against all known skeletal specimens of Archaeopteryx.

Results and Discussion
Anatomical identity. Relative calamus length. Penaceous feathers have a centerline (central shaft) that consists of a rachis distally and a calamus (quill) proximally (Fig. 1a). The rachis anchors the barbs that comprise the leading and trailing vane, whereas the calamus is embedded within the skin. In both modern and Mesozoic birds, the calamus inserts into a follicle and is attached to connective tissue and muscle that stabilize and control the feather21,22 (Supplementary Figs. S9, S10). Unlike the essentially solid and occasionally pigmented rachis, the calamus is a thin-walled and somewhat transparent hollow tube that is almost never pigmented21. These traits explain the relatively faint preservation of the fossil calamus as initially observed and illustrated by von Meyer1, and which has since become unobservable under visible and UV light23 (Supplementary Information: 11. Calamus preservation).

Using LSF, Kaye et al.8 confirmed the morphology of the missing elongate calamus as matching that of von Meyer’s original description3 (Fig. 1a,b). This finding corroborates, rather than challenges, the proposed identity of the isolated feather as an upper major primary covert (UMPC)9—which was based on that same original description. Von Meyer3 measured the straight-line lengths of the entire feather as 69 mm and the vaned portion as 54 mm, and the 15 mm difference was subsequently used for an estimate of relative calamus length (22%, 15/69 mm)9. Here, more accurate and precise measurements are obtained directly from a high-resolution digital scan of von Meyer’s 1862 feather (Fig. 1a), originally traced at actual size using a drawing mirror24. Measuring from the lowermost barbs (which demarcate the calamus and rachis21), this yields a relative calamus length of 23.3% (16.4/70.3 mm). These measurements are congruent with those of the LSF image8 (Fig. 1b). See also Supplementary Information: 12. Calamus measurements and Supplementary Fig. S11.

When this relative calamus length is compared with those of modern feathers (n = 66; chicken, Gallus gallus domesticus)25, the closest matches are the UMPCs—particularly the distal members such as feather IX (25.7%, 18/70 mm; Fig. 2a, Supplementary Fig. S12). This similarity is reflected in Table 1, attribute #1. Among these modern feathers, the relative calamus lengths of the UMPC tract (n = 10) are found to be significantly longer than those of the five other tracts (P-values < 0.0001 for combined and all pairwise comparisons with the UMPC tract; Supplementary Fig. S12b). The extraordinarily long calami of UMPCs function to support the primaries during downstroke13,25.

Anatomical attributes. Including the diagnostic relative calamus length, all nine anatomical attributes of the isolated feather are most consistent with an identity as a UMPC, to the exclusion of all other candidate feather tracts. These attributes include feather length, width, and aspect ratio, along with five attributes related to aerodynamics: lateral curvature, barb angle, vane asymmetry, vane closure, and angled distal tip (Fig. 2b). Table 1 summarizes general designations for each tract and attribute based on modern feathers15,16,21 (Supplementary Information: 15. Anatomical attributes). Furthermore, attributes of the isolated feather that support it being a distal member of the UMPC tract include the relative calamus length being more similar (as mentioned above), vanes that are relatively asymmetric, and the angled distal tip: lack of an S-shaped centerline is also more consistent with distal UMPCs in some modern birds (e.g., compare these traits in distal vs. proximal members in Supplementary Fig. S69,11,15,16,21).

If we consider all anatomical attributes aside from the relative calamus length, the next most-supported identity of the isolated feather would still be a primary covert, albeit from a ventral tract—specifically, an under major primary covert (uMPC). The isolated feather would remain inconsistent with all other tracts. Kaye et al.8 hypothesized that the fossil could represent a contour feather, which is the predominant type of tract that covers the body. However, contours can be eliminated as a possibility given that almost every anatomical attribute is inconsistent with that of the isolated feather (Table 1). In particular, contours characteristically have a short calamus length, as well as symmetric barb angles and vane21,26.

Taxonomic identity. Kaye et al.8 state of the feather, "The possibility remains that it stems from a different feathered dinosaur that lived in the Solnhofen Archipelago". Philosophically, we agree—that possibility will always remain, as we can never identify the isolated feather with absolute, 100% certainty. However, the existence of two possibilities does not necessitate that they are equally probable. We must consider the full scope of available evidence, in order to provide the critical context with which to ground our assumptions. Ultimately, is it more probable that the isolated feather belongs to Archaeopteryx, or to a different taxon?

Provenance. The most important evidence to consider is the overlooked fact that the isolated feather was actually found at the same fossil site as four specimens of Archaeopteryx (Fig. 3). These include the London (type), Maxberg, Munich, and Ottmann & Steil (9th) specimens4,5, all within ~750–2,200 meters of the isolated feather. These five fossils are also coeval, within the same Ammonite Zone (Upper Jurassic ammonite horizons). Therefore, on the basis of this spatiotemporal proximity alone, the feather most likely originated from an Archaeopteryx.
Classification. The aforementioned four skeletons represent approximately one third of the 13 described *Archaeopteryx* specimens, and along with the Altmühl and Berlin specimens examined below, are all unequivocally classified as *Archaeopteryx*. Overall, the taxonomy of the Urvogel specimens has been a complicated and contested topic—since their discovery, virtually every one of the skeletons has been referred to as a unique species and/or genus. Recently, this includes controversial proposed assignments to a new species, a new genus, and even a different family. It should be acknowledged, however, that these particular fossils represent three of the most fragmentary and poorly preserved specimens, and contain no clear feather impressions.

Biological context. What about the alternative taxonomic hypothesis? It may be tempting and convenient to invoke some hypothetical undescribed dinosaur as the source of this isolated feather. However, it is important to
keep in mind that the biodiversity within this small group of islands was finite, and represented but a brief snapshot in geologic time. While we are certainly not arguing against there being future discoveries, a great deal of this famous Lagerstätte’s biodiversity is already known—extraordinarily well-documented by ~600 species unearthed throughout hundreds of years of intense commercial quarrying and scientific efforts4,5. Among this voluminous and well-preserved fossil record, the other species of feathered dinosaurs—Juravenator starki41 and Sciurumimus albersdoerferi42—exhibit only the most ancestral class of feathers: unbranching monofilaments known as “proto-feathers” (Stage I of Prum 199943, Morphotype 1 and 2 of Xu et al. 201044). Only Archaeopteryx specimens contain the most derived class of feathers to which the isolated feather belongs, with vanes that are pennaceous, closed, and asymmetric (Stage Va43, Morphotype 944).

Even if such derived flight feathers were discovered in a new dinosaur species from these deposits—or if there were a permanent supraspecific reclassification of one of the 13 described Urvogels—the much higher abundance of Archaeopteryx specimens would still represent a much more likely affiliation for the isolated feather. And regardless, given that four of these unequivocal Archaeopteryx specimens were found at the same geologic time and place as the isolated feather, it is most probable that the isolated feather came from an Archaeopteryx.

Fossil evidence. So far, we have demonstrated that the isolated feather is most likely a primary covert (anatomical identity), and most likely affiliated with Archaeopteryx (taxonomic identity). We now test these two hypotheses by examining all skeletal specimens of Archaeopteryx for evidence of primary coverts (consilience). See also Supplementary Information: Fossil evidence.

Altmühl specimen. In 2014, Foth et al.45 described a new, 11th specimen of Archaeopteryx, referred to as the “Altmühl specimen”33. Notably, this is the first and only known Archaeopteryx fossil to reveal a well-preserved dorsal surface of the wing—as evidenced by the overlapping pattern of primaries46, convex vanes with positive casts of barbs, absence of ventral furrows on rachises, and absence of elongate under covert barbs overlying the secondaries (cf. Berlin specimen, below). This right wing exhibits impressions of at least four UMPCs, approximately half the length of their respective primaries (Fig. 4; Foth et al. 2014: Extended Data Fig. 5b45).

Strikingly, the two best-preserved UMPCs are identical to the isolated feather in every observable attribute of size and shape, including barb angle (Fig. 4; Table 2). Barb angles on the distal half of one leading vane measure a mean of 25.2° (n = 5); the corresponding barb angles on the isolated feather measure a mean of 24.4° (n = 5) (Supplementary Fig. S15). The vanes are closed (#8) and asymmetric (#7), albeit each trailing edge is overlapped by the adjacent UMPC, inhibiting exact measurements of feather width. However, inferring from the leading vane widths and spacing of the UMPCs, as well as the widths and spacing of the primaries, the UMPC width (#3) and consequent aspect ratio (#4) are considered consistent with those of the isolated feather. The presence of an angled distal tip cannot be ascertained in the UMPCs (#9), nor can relative calamus length (#1) due to overlying median and minor covert tracts.

This congruence corroborates the isolated feather’s approximate location as a distal member of the UMPC tract, as hypothesized by Carney et al. 20122 (Fig. 4b inset). The fact that the feathers are equivalent in size also suggests that the isolated feather may have originated from an individual approximately the same size as the Altmühl specimen, depending on the exact feather number. (Relative specimen sizes4,5,45: Berlin < Altmühl < London).
While the entire UMPC centerlines are not directly observable, we can infer that they were not S-shaped, based on three observations. First, the UMPCs are angled too posteriorly (diagonally) from the manus. Such oblique orientation also causes the UMPCs to diverge from the primaries—and especially the penultimate primary, which is S-shaped (Fig. 4; see also45,46). Second, this posterior divergence is dissimilar to the anterior divergence of modern UMPCs from the primaries47 (e.g., Supplementary Fig. S3). Therefore, any dissimilarity with respect to modern S-shaped centerlines would be unsurprising. Third, this posterior divergence is similar to that of under primary coverts in both wings of the Berlin specimen, and those feathers clearly lack S-shaped centerlines (Fig. 5b). Elzanowski48 noted that those coverts "preserved, strongly diagonal position with respect to the primaries has yet to be explained". Here we offer the explanation that the posterior divergence in both specimens

| Feather tract (specimen) | 1. Relative calamus length | 2. Length | 3. Width | 4. Aspect ratio | 5. Lateral curvature | 6. Barb angle | 7. Vane asymmetry | 8. Vane closure | 9. Angled distal tip |
|--------------------------|---------------------------|-----------|----------|-----------------|---------------------|--------------|------------------|-----------------|------------------|
| UMPC (Altmühl)           | ?                         | yes       | yes      | yes             | yes                 | yes          | yes              | yes             | ?                |
| uMPC (Berlin)            | ?                         | yes       | yes      | yes             | yes                 | yes          | yes              | no              | no               |
| uMPC (London)            | ?                         | yes       | ?        | ?               | yes                 | yes          | yes              | ?               | ?                |

Table 2. Comparison of anatomical attributes shared by the isolated fossil feather and major primary coverts of *Archaeopteryx* specimens. Rows ranked by level of support. Consistency between the isolated feather and a given feather tract is designated "yes", "no", or "?" (not observable) (see Supplementary Information: 15. Anatomical attributes). See Supplementary Table S1 for other tracts. Abbreviations: UMPC, upper (dorsal) major primary covert; uMPC, under (ventral) major primary covert.
may have strengthened the wing for flapping flight. Namely, such primary coverts—angled via calamus attachment and/or rachis curvature—would have supported the primaries during downstroke by crossing over them posteriorly, instead of anteriorly as in the case of S-shaped centerlines discussed above.

Berlin specimen. As mentioned above, the second most-supported anatomical identity of the isolated feather is a uMPC. Such uMPC centerlines in the Berlin specimen (MB.Av.101) were first illustrated in Dames 1884 and Steiner 1918, and subsequently illustrated, photographed, and described in Heinroth 1923, Heilmann 1926, de Beer 1954, Helms 1982, and Rietschel 1985. Multiple tracts of primary coverts are visible on the main slab, and especially the counterslab, where they are less worn and preserved as positive casts (Fig. 5b). It is difficult to attribute some centerlines to distinct coverts. Both slabs represent the ventral surface, as evidenced by the ventral furrows of rachises, pattern of feather overlap, and corresponding positive and negative casts of the barbs. As noted by previous authors, elongate “floating” barbs are apparent in coverts of the secondary and proximal primary feathers.

In the uMPCs, relative calamus lengths are not observable (#1), but attributes #2–7 are consistent with those of the isolated feather (Table 2). A total of at least seven uMPCs from both wings exhibit a rounded distal tip (#9) and/or open pennaceous vanes (#8; Fig. 5b: white arrowheads). Both an angled distal tip and vane closure are aerodynamic features that may not be present in modern uMPCs, or that may appear in wing coverts later in ontogeny.

**Figure 5.** Under primary coverts in the Berlin and London specimens of *Archaeopteryx*. White arrows indicate proximal orientation of centerlines. (a) Berlin specimen (MB.Av.101), main slab. (b) Right wing region from white box in (a), from the counterslab under oblique lighting. Reconstruction of the isolated feather is overlaid at scale. White arrowheads denote the non-interlocking “split” barbs of open pennaceous vanes. Red arrow and arrowhead denote centerline of a uMPC, which exhibits a ventral furrow on the proximal end. Yellow arrow denotes S-shaped centerline in the penultimate primary. Note the orientation of the coverts, and their posterior divergence from the primaries. (c) London specimen, main slab (NHMUK PV OR 37001); reproduced by permission from Wellnhofer 2009, 2008. (d) Reconstruction of the isolated feather. Yellow lines indicate barb angle measured in the London specimen in (e); angle of the corresponding barb in the isolated feather measures 25.8°. (e) Left wing region from white box in (c), from a cast of the counterslab (image is reversed). Centerline is preserved as a positive cast. Yellow lines indicate a representative barb angle, which measures 24.6°. Shown at same scale as (d). (f) Left wing region from white box in (c), from the original main slab under oblique lighting. Centerline is preserved as a negative impression. Negative impression of digit II phalanx 2 is denoted by “p”. Note the very close match in size, curvature, and barb angles between the isolated feather and primary coverts from both specimens. Scale bars: 1 cm.
Both wings have a well-preserved uMPC\textsuperscript{22,55} originating from the same approximate midpoint of the manus, with a ventral furrow in the rachis similar to that of the primaries (Fig. 5b: red arrow). Such furrows increase dorsoventral stiffness\textsuperscript{26}, indicating a supportive function. As discussed above, the primary coverts from multiple tracts have a strongly posterior (diagonal) orientation with respect to the manus and primaries\textsuperscript{48,54} (Fig. 5b: white and red arrows), similar to the UMPCs in the Altmühlen specimen, and which likely strengthened the wing. This posterior divergence is due to the centerlines’ angled attachments, as well as their curvature, which is consistent with that of the isolated feather but not with an S-curve. Conversely, a distinct S-shaped centerline is evident in the penultimate primary of both wings (Fig. 5b: yellow arrow), similar to the penultimate primary of the Altmühlen specimen (above), and the distalmost, diminutive primary of some modern birds as well\textsuperscript{15,18}.

**London specimen.** The London specimen of Archaeopteryx also preserves fine details of the ventral wing surfaces\textsuperscript{4,5,56,53} (Supplementary Fig. S14). In his classic monograph, de Beer\textsuperscript{3} remarked that the isolated feather’s “similarity to one of the shorter remiges is very great...the impressions in the British Museum specimen might well have been made by feathers identical with von Meyer’s feather”. On the left wing, he counted impressions of seven UMPCs, approximately half the length of their respective primaries. On the right wing, Steiner\textsuperscript{60} measured the lengths of two proximal uMPCs as 55 and 60 mm (identified as upper I’ and II, albeit as under II’ and III’ per de Beer\textsuperscript{3}; Supplementary Fig. S14c). All visible primary coverts exhibit a laterally curved or straight centerline, with no evidence of an S-curve. Notably, the most conspicuous centerline is indistinguishable from that of the isolated feather with respect to length (#2) and lateral curvature (#5) (Fig. 5d–f; Table 2). Tentatively, this centerline may represent the distal uMPC X’, based on a presumed attachment at the proximal half of digit II phalanx 2 (Fig. 5f: p; see also Supplementary Fig. S14b; Fig. 6.17a in Wellnhofer 2009\textsuperscript{4}, 2008\textsuperscript{5}). Barbs are visible on the leading vane of this feather in the counterslab, and to a lesser extent in the main slab (Fig. 5e–f). These barb angles are consistent with those of the isolated feather (#6; Fig. 5d) and primary coverts in the Altmühlen and Berlin specimens. Presence of the remaining attributes cannot be determined in the uMPCs.

**Anatomical attributes.** Ultimately, we accept the dual hypotheses that the isolated feather is a UMPC of Archaeopteryx, given that the isolated feather is consistent with UMPCs of the Altmühlen specimen in every observable anatomical attribute (Table 2). Most of the isolated feather’s attributes are also consistent with those of the Berlin and London specimens’ uMPCs—which serve as proxies given that uMPCs generally resemble UMPC counterparts\textsuperscript{21,47}. However, there is less overall support for the isolated feather being a uMPC, given that such feathers visible in the Berlin specimen exhibit open vanes and rounded distal tips. The centerline of the isolated feather is also thicker\textsuperscript{24} than those of the uMPCs observable in the Berlin and London specimens (Fig. 5), but is consistent with the robust centerlines of modern UMPCs\textsuperscript{21,22}. The isolated feather is inconsistent with all of the other tracts in Archaeopteryx (Supplementary Table S1).

**Additional insights.** **Designation.** There has been perpetual disagreement in the literature regarding which half is designated as the main slab (versus the counterslab): the Munich slab\textsuperscript{4,5,57,59,53} (BSP 1869 VIII 1) or the Berlin slab\textsuperscript{21,47} (MB.Av.100). Here, we propose that the Berlin slab be formally designated as the main slab, given 1). von Meyer’s\textsuperscript{3} original terminology (Supplementary Information: 21. **Designation**), as well as the fact that the Berlin slab 2), has always contained much better-preserved traces of the feather\textsuperscript{3,8,23,3,5,24,4}. is thicker and 2.6X larger by area\textsuperscript{3,24,4}, and 4), contains more positive remains of fossil material (i.e., Saccocoma tenella crinoids)\textsuperscript{23}, which typically distinguish main slabs in Solnhofen fossils\textsuperscript{50} (Supplementary Figs. S1, S2). The darker trace on the Berlin slab, coupled with microstructural evidence, also indicates that the feather originated from the left wing of the animal (Supplementary Information: 22. **Feather chirality**, Supplementary Fig. S16).

**Preservation.** The feather was most likely shed during moult, given the otherwise firm attachment of wing feathers, even post-mortem\textsuperscript{4,5,57,59}. This same dissociation that obfuscates the feather’s identity is likely also responsible for the dark preservation, compared with that of the plumage in the skeletal specimens (taphonomy reviewed in Wellnhofer 2009\textsuperscript{4}, 2008\textsuperscript{5}). While Kaye et al.\textsuperscript{8} state that the isolated feather may be preserved as a film of manganese dioxide, Carney et al.\textsuperscript{6} had previously detected no such manganese, and instead interpreted this dark film to be a melanin organosulphur residue. This interpretation was subsequently supported by molecular evidence of melanin associated with such residues in other fossil and extant feathers, even when the melanosome structures themselves have completely degraded\textsuperscript{6,61}. Thousands of melanosomes (not microbes, contra Moyer et al.\textsuperscript{24,54}–see Supplementary Information: 24. **Melanomes**) are observable in varying states of preservation within the isolated feather, and the melanin residue is ubiquitous throughout both vanes\textsuperscript{3}. This pervasive residue darkens towards the distal tip on both slabs\textsuperscript{8} (Supplementary Figs. S1, S2), representing a subtle melanin concentration gradient\textsuperscript{62,63}. Together, these modern results confirm von Meyer’s original 1862 hypothesis, that the darker tip was “caused by the original colouration”\textsuperscript{3}.

**Colouration.** Melanosomes morphology previously predicted the original colour of the isolated feather to be black\textsuperscript{2}, based on statistical comparison with a dataset of melanosomes from extant bird\textsuperscript{4,65}. Using a subsequently expanded dataset that includes iridescent melanosome morphologies\textsuperscript{66}, our current reanalysis of the fossil feather’s melanosome imprints (n = 86) predicts that the black colouration was matte, with 90% probability (0% probability of iridescent; Fig. 6). Adding measurements from the three-dimensionally (3D) preserved melanosomes to the analysis yields a prediction of matte black with 85% probability (n = 108, 15% probability of iridescent), whereas analysis of the 3D melanosomes alone predicts iridescent with 79% probability (n = 22, 21% probability of matte black). This difference in results is due to diagenetic contraction of the 3D melanosomes\textsuperscript{61,67}, a phenomenon which should have negligible effect on the melanosome imprints in the limestone matrix\textsuperscript{4,68}. We therefore...
consider the imprint-only results to be the most reliable. Such matte black colouration is associated with the lower mean aspect ratio of these eumelanosomes ($n = 86, 3.8 \pm 0.1$ SE), compared with the more elongate iridescent morphology.

Thus, we clarify and refine our previous findings, by reconstructing the entire feather as matte black with a darker distal tip (contra the incorrect black and white reconstruction of Manning et al. 201379—see Supplementary Information: 25. Colouration and Supplementary Fig. S17). Such black colouration throughout the entire feather—including the non-visible (obscured) proximal region—is consistent with the observation that modern UMPCs “are most frequently whole-coloured and dark”70. As in modern feathers, this black pigmentation (especially at the distal tip) would have provided various structural9 and aerodynamic71 advantages to the wings of Archaeopteryx.

The similar presence of dark remiges across Paraves (e.g., Microraptor66, Caihong72) suggests an important functional role for melanization in the evolution of dinosaur flight.

Summary
The fossil record serves as life’s time capsule, albeit a vastly imperfect one. By virtue of the fossil feather’s isolated nature, we can never know the exact follicle or species from which the Urfeder originated with complete certainty. Rather, we must rely on a framework of consilience: the convergence among the independent classes of available evidence. What are the most likely anatomical and taxonomic identities, and are both of these hypotheses supported by the fossil data?

Anatomically, lack of an S-shaped centerline does not preclude the isolated feather from being a UMPC. Comparing the corrected fossil feather centerline with a more representative range of extant morphological diversity eliminates all purported disparity. The isolated feather had a proportionately long calamus—an attribute diagnostic of UMPCs, which have the greatest relative calamus length of any feather tract. All eight of the other anatomical attributes corroborate the hypothesis that the isolated feather is a UMPC, to the exclusion of all other feather tracts.

With respect to taxonomic identity, the most critical piece of evidence is that the feather specimen came from the same fossil site and horizon as four Archaeopteryx skeletons, including the type specimen. Furthermore, within the extraordinarily well-documented and spatiotemporally limited Solnhofen Archipelago, only Archaeopteryx specimens exhibit such a highly derived feather morphotype. In the future, even if a new feathered dinosaur species were revealed (or reclassified) from these deposits, the present fossil would still most likely represent a feather from the much more coincident and abundant Archaeopteryx.

Testing these anatomical and taxonomic hypotheses against the fossil data, the isolated feather is conformal to the primary coverts of Archaeopteryx. Specifically, the isolated feather is identical in size, shape, and barb angles to UMPCs in the Altmühl specimen, and to a lesser extent, to uMPCs in the Berlin and London specimens. None of these feathers exhibit any indication of an S-shaped centerline. All other tracts in Archaeopteryx are inconsistent with the isolated feather.

Ultimately, supported by all of the anatomical and taxonomic evidence, independently confirmed by close morphological connections to multiple skeletal specimens, the most empirical and parsimonious conclusion is that the isolated feather represents a primary covert of Archaeopteryx. Additionally, we recommend that the Berlin slab be designated as the main slab, reveal that the feather originated from the left wing, and reconstruct the original feather colour as entirely matte black.
Methods

The von Meyer 1862: Plate VIII, Fig. 3 was digitally scanned along with a mm ruler for validation at 1,200 dpi using an HP OfficeJet 5255 flatbed scanner. Linear, curvilinear, and area measurements of the isolated fossil feather and five tracts were taken in Adobe Illustrator CS6 using the Telescope Inc Patharea filter version 1.2b3 (http://telegraphics.com.au/sw/product/patharea). The isolated feather reconstruction was based on Fig. 4 from Carney et al. 2012—originally recreated in Adobe Illustrator CS4 based on photographs of the von Meyer reconstruction—with modifications made in Adobe Illustrator CS6 based on the high-resolution scan of the von Meyer reconstruction, photographs, and the LSF image of the Berlin slab (MB.Av.100), and ultraviolet light photographs of the Munich slab (BSP 1869 VIII 1; e.g., Supplementary Fig. S11). Barb angles for the skeletal specimens were defined using the Line Segment Tool in Adobe Illustrator CS6 (blindly, without the isolated feather overlay). In the Altmühl specimen, bars are preserved as positive (convex) casts; for better precision the bar angles were defined using the narrower negative impression of the space between adjacent bars. All bar angles were subsequently measured using ImageJ version 1.52k (https://imagej.nih.gov/ij/). Relative calamus lengths of modern feathers (n = 66) were calculated using published measurements from a male Comb White Leghorn Chicken (Gallus gallus domesticus) at least one year old, and analyzed using JMP Pro version 14.0 (SAS Institute Inc.). Pairwise comparisons among the six feather tracts were made using one-way ANOVA with Tukey-Kramer HSD. Each tract was found to be normally distributed using the Shapiro-Wilk test, with the exception of the rectrices (n = 8, P-value = 0.0017), and when the five tracts of non-UMPC feathers were combined (n = 56, P-value = 0.0208). Therefore, values from these five tracts combined were compared with those of the UMPC tract (n = 10) using the one-tailed Wilcoxon exact test (sum of rank scores = 615). All variances were found to be equal. Melanosome measurements from the isolated feather were taken from Carney et al. 2012: Supplementary Table S1. For details on the quadratic discriminant analysis, see Li et al. 2012.

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Author contributions

R.M.C. composed and conducted the research. R.M.C., H.T., and M.D.S. contributed data and discussions. R.M.C. measured the barb angles and analyzed the calamus data. M.D.S. analyzed the melanosome data. R.M.C. wrote the manuscript. H.T. and M.D.S. reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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