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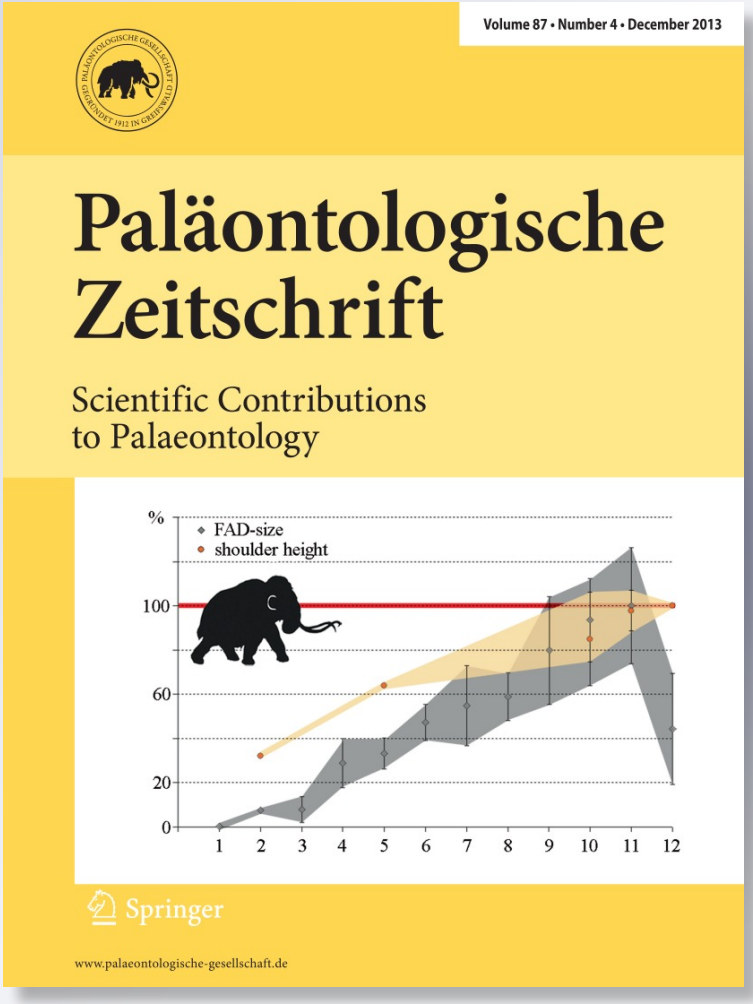

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RESEARCH PAPER

Exceptional three-dimensional preservation and coloration of an originally iridescent fossil feather from the Middle Eocene Messel Oil Shale

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Abstract A feather from the Eocene Messel Formation, Germany, has been demonstrated to have been originally structurally colored by densely packed sheets of melanosomes similar to modern iridescent feathers exhibiting thin-film diffraction. The fossil itself currently exhibits a silvery sheen, but the mechanism for generating this optical effect was not fully understood. Here we use scanning electron microscopy, electron probe microanalysis, and dual-beam focused ion beam scanning electron microscopy to investigate the source of the silvery sheen that occurs in the apical feather barbules. Focused ion beam scanning electron microscopy provides a powerful tool for studying three-dimensionality of nanostructures in fossils. Use of the method reveals that the flattened apical barbules are preserved almost perfectly, including smooth structural melanosome sheets on the obverse surface of the fossil feather that are identical to those that cause iridescence in modern bird feathers. Most of each apical barbule is preserved beneath a thin layer of sediment. The silvery sheen is generated by incoherent light diffraction between this sediment layer and melanosomes and, although related to the original iridescence of the feather, is not a feature of the feather itself. The reddish and greenish hues frequently exhibited by fossil feathers from the Messel Formation appear to be due to precipitates on the surface of individual melanosomes.

Keywords Exceptional preservation · Color · Melanin · Iridescence · Fossil bird

Kurzfassung Bei einer Feder aus der eozänen Messel Formation von Deutschland wurde eine originale strukturelle Färbung aus dicht gepackten Melanosomen nachgewiesen, die modernen irridisierenden Federn ähnlich ist, die Dünnschichtdiffraktion zeigen. Das Fossil selbst zeigt in seinem derzeitigen Zustand einen silbrigen Glanz, aber es ist unklar, durch welchen Mechanismus dieser entsteht. Mit Hilfe von Rasterelektronenmikroskopie, Elektronenstrahlmikroanalyse

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und doppelt fokussierter Ionenfeinstrahlmikroskopie untersuchen wir die Herkunft der glänzenden Färbung, die an den apikalen Hakenstrahlen auftritt. Ionenfeinstrahlmikroskopie stellt eine leistungsfähige Methode zur Untersuchung dreidimensionaler Nanostrukturen in Fossilien dar. Ergebnisse dieser Untersuchungsmethode zeigen, dass sowohl die abgeflachten, apikalen Hakenstrahlen, als auch die einzelnen Schichten aus Strukturmelanosomen, die mit denen heutiger Vogelfedern nahezu identisch sind, annähernd unversehrt überliefert sind. Ein Großteil der apikalen Hakenstrahlen ist unter einer dünnen Sedimentschicht erhalten, die aufgrund der Interferenz mit den Melanosomen zu dem silber glänzenden Farbeffekt führt. Dieser Effekt wird durch die irridisierende Färbung der Feder verstärkt, trat allerdings nicht im Originalzustand auf. Dies deutet darauf hin, dass die rötliche und grünliche Färbung, die typisch für Federn aus Messel ist, aufgrund von Ablagerungen auf der Oberfläche der einzelnen Melanosome zustande kommt.

Schlüsselwörter Außergewöhnliche Erhaltung · Farberhaltung · Melanin · Iridisieren · Fossile Vögel

Introduction

Distinct arrangements and morphologies of melanosomes can generate structural coloration and metallic iridescence in modern bird feathers by creating coherently scattered light (Prum 2006). Melanin is highly decay resistant and can survive with little alteration in fossils at least as old as the Jurassic (Glass et al. 2012). Many fossil feathers are preserved as remains of melanosomes, which are melanin-containing organelles (Vinther et al. 2008, 2010; Zhang et al. 2010). Additionally, melanosome shape and distribution offer a means of inferring ancient coloration and color patterns (Li et al. 2010, 2012; Clarke et al. 2010). Fossil feathers may preserve smooth sheets of melanosomes in arrangements similar to those that generate iridescence in modern birds (Vinther et al. 2010). The iridescent sheens in such feathers are created by so-called thin-film diffraction of a smooth layer of keratin above an equally smooth melanosome surface (Shawkey et al. 2006). The fossil feather examined here, from the Senckenberg Museum Frankfurt, SMF ME 3850, was collected from the famous Eocene Messel locality (~47 Ma) in Germany. It exhibits a conspicuous red hue that alternates in places with stripes of a silvery sheen in the barbules of the apical region (Fig. 1). Initially, the red hue was interpreted as an effect of the absorption of metal ions onto the surface of the eumelanosomes, which are rod-shaped and originally produce black and gray colors (Vinther et al. 2010). The fossil feathers in Messel vary from black to reddish and greenish in hue, which may indicate the presence of iron in different oxidation states. The silvery sheen was hypothesized to be a direct result of the arrangement of the fossil's originally iridescent melanosome sheets. The latter hypothesis was based on the spatial correlation between the sheets and the silvery sheen in the barbules of the distal part of the feather vane. In this case, such a silvery sheen would provide an easily detectable indication of iridescence in other fossil birds and in feathered dinosaurs.

Melanosomes are known to absorb metal ions in other contexts. Melanin granules in the squid *Sepia* have been shown to absorb metals such as iron, calcium, and magnesium without alteration of the melanosome macrostructure (Liu et al. 2004). Extant birds may accumulate metals such as calcium, zinc, copper, iron, and magnesium in their feather melanin (Niecke et al. 1999; McGraw 2008). Those metals are released in reducing conditions (Liu et al. 2004), and presumably also during diagenesis, with the removal of hydroxyl (–OH) and carboxyl (–COOH) functional groups that chelated the metals in the macromolecule (Riley 1997).

Here we investigate the mechanism giving rise to the silvery sheen in the Messel feather and test the hypothesis that the red hue is the result of diagenetic precipitation of metal ions, likely sourced from the melanosomes (Vinther et al. 2010). Investigating the mechanism of color production in the fossil, and any correlation between the preserved color and that of the original feather, requires a clear understanding of which components of the fossil remain on the part and counterpart when the shale is split. Furthermore, as compared with modern feathers, only the highly melanized components of the fossil feather are likely to survive decay (Goldstein et al. 2004). The appearance of the fossil may be affected by both the associated sediment matrix and the loss of the nonmelanized feather parts.

Methods

We investigated the Messel feather fossil SMF ME 3850 using a dual-beam focused ion beam scanning electron microscope (FIB-SEM) to image surface topography and concurrently ion-mill site-specific cross-sections (Schiffbauer and Xiao 2009, 2011) in order to document the three-dimensional nature of the exceptional preservation and elucidate the origin of the silvery sheen. We used FIB-SEM analysis and electron probe microanalysis (EPMA) to determine the chemical composition of the feather and surrounding sediment, and to investigate the origin of the reddish and greenish hues exhibited by some fossil feathers from the Messel Formation (Vinther et al. 2010, suppl. Figs. 1 and 2).

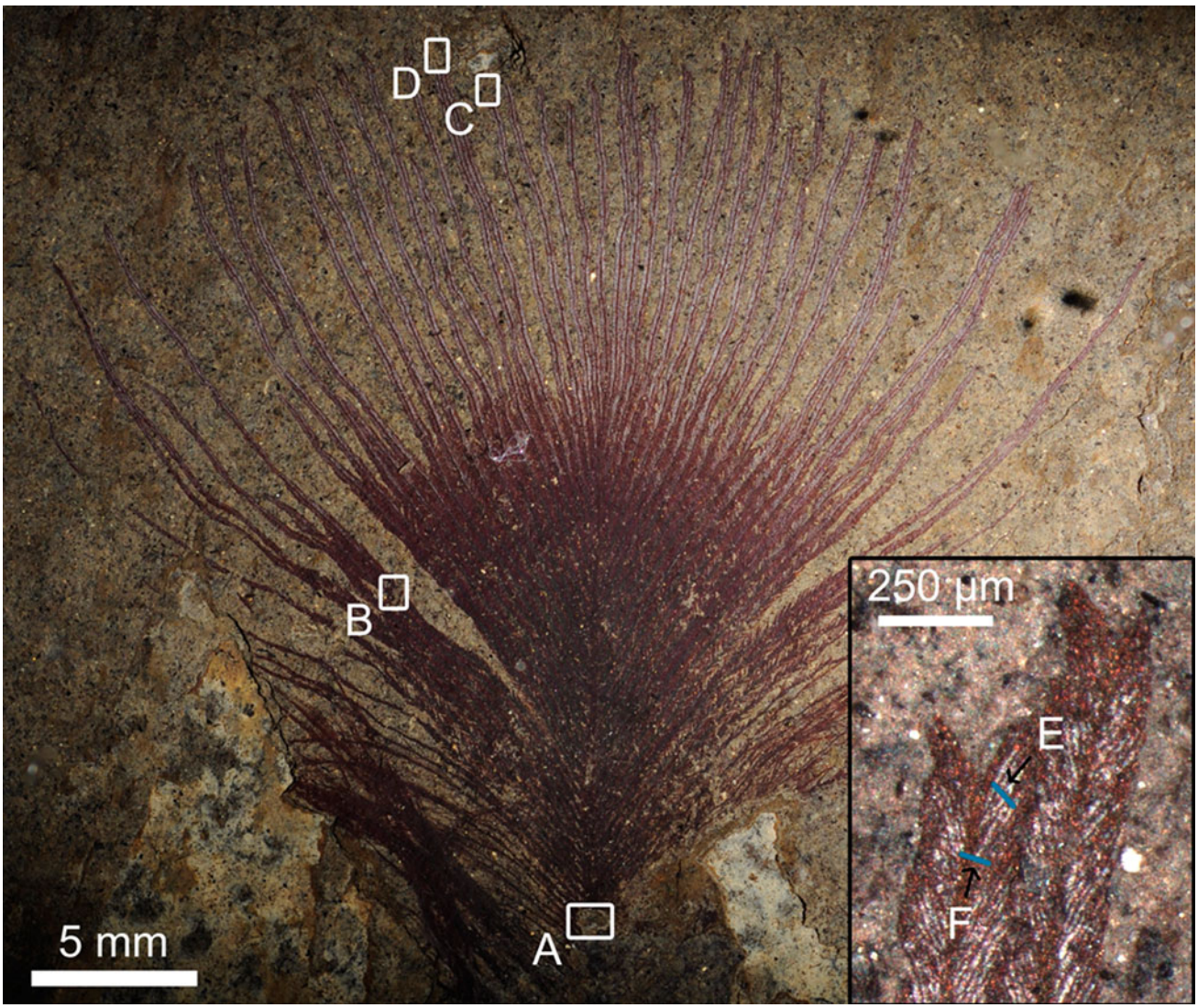

Fig. 1 *Color photo* of fossil SMF ME 3850 (main slab) showing the locations of each FIB-SEM cross-section. *Labeled boxes* correspond to subsequent figures. **a** Location of Fig. 2a–c. **b** Location of the basal barbule sample, Fig. 2d. **c** Location of Fig. 3. **d** Location of Fig. 4. Inset shows a detail of the apical barbs shown in Figs. 1d and 4. FIB-SEM cuts are marked in *blue*. *Arrows* indicate the direction of view. **e** Location and direction of FIB-SEM cut of Fig. 4a, b, e. **f** Location and direction of FIB-SEM cut of Fig. 4c, d

For environmental scanning electron microscopy (ESEM) and FIB-SEM milling, samples from the distal barbs/barbules, proximal barbs/barbules, and the rachis of the specimen were removed with a scalpel and mounted on standard aluminium stubs with carbon tape. Samples for ESEM (Philips XL 30) surficial analyses were Au sputter-coated for 25 s. Surficial elemental analyses were performed via EPMA using energy-dispersive X-ray spectroscopy (EDS) on a JEOL JXA-8530F hyperprobe operating at voltage of 15 keV with 40 ms dwell time and beam current of 5.033 nA. Prior to FIB-SEM analyses, the samples were lightly Au–Pd sputter-coated (approximately 5 nm thickness) in a Cressington 208HR high-resolution sputter coater. Combined surface–subsurface analyses were performed using an FEI Company Helios 600 Nanolab dual-beam FIB-SEM at the Virginia Tech Nanoscale Characterization and Fabrication Laboratory (Blacksburg, Virginia, USA), with electron imaging conditions at accelerating voltage of 5 keV and beam current of 86 pA. Initial FIB-SEM trench cuts used a gallium-ion beam accelerating voltage of 30 kV and current of 2.7 nA, and cross-sections were cleaned (to reduce curtaining/waterfall artifacts common for highly porous materials) with beam accelerating voltage of 30 kV and current of 2.7 pA (providing a smaller probe diameter for finer-scale milling purposes). Because the fossil is carbon rich compared with the siliceous host rock, FIB-SEM ion milling was facilitated by adding carbon-selective $MgSO_4 \cdot 7H_2O$ accessory

gas to the sample chamber. FIB-SEM analyses with atomic number (Z-contrast) backscatter imaging on a Zeiss Auriga 40 were also performed at the Zeiss factory in Oberkochen, Germany, to investigate the relative elemental composition of the melanosomes in cross-section.

Results

Structure of the feather

The symmetrical vane of this contour feather is 31 mm wide by 28 mm long and preserves approximately 50–60 barbs in the entire vane. The basal half of each barb forms a closed pennaceous vane of interlocking distal and proximal barbules. The distal half of the central barbs forms an open pennaceous portion of the feather vane, in which the barbules are flattened and do not interlock. Such an open pennaceous vane often occurs in contour feathers that have an ornamental function involving the display of structural colors (Lucas and Stettenheim 1972).

Rachis

Under light microscopy, the rachis appears as a flat, red region with no recognizable structure (Fig. 1). Secondary-electron imaging of the FIB-SEM cross-section through part of the rachis shows that aggregations of ~1-μm-long eumelanosomes are distributed in random orientations across the surface of the fossil (Fig. 2a), with no apparent organization in either packing or orientation. At its deepest, the layer of melanosomes extends 4–5 μm below the surface of the fossil (Fig. 2b). The layer is uneven (Fig. 2c), and in some parts of the section the packed melanosomes are less than 1 μm deep (Fig. 2b). The variation appears to be the result of the irregular splitting of the feather during separation of the part and counterpart.

Basal barbs and barbules

The barb rami and barbules close to the base of the feather are similar in appearance under light microscopy to the flat, red mass evident in the rachis (Fig. 1). Only their outlines and relative positions distinguish them as barbs and barbules. Electron imaging and FIB-SEM cross-sectioning show eumelanosomes identical in shape to those in the rachis in similarly random aggregations. On some small surface patches, the melanosomes are oriented in a single direction, but many other areas show melanosomes in varying orientations. In cross-section, the layer of melanosomes is uneven, ranging from 5–6 μm to less than 1 μm in thickness (Fig. 2d). Neither individual barb rami nor barbules can be identified in surface or cross-sectional view.

Apical barbs and barbules

The shapes of the barbule cross-sections and the organization of the melanosomes from near the apical tip of the feather both indicate that the obverse (or outer) surface of the feather is facing down into the slab and the reverse (or inner) surface of the feather is facing up. Depending on the precise location of the split of the feather between the slab and counterslab, the exposed surface of the specimen may reveal the inside of a barb ramus or barbule, or in some cases, the reverse surface of a barbule.

Under light microscopy the barb rami at the open pennaceous tip of the feather (Fig. 3a) are evident as a red mass, and the barbules appear as alternating red and silvery stripes (Vinther et al. 2010). Electron imaging allows the red and white areas of the fossil to be distinguished within the barb rami and barbules (Fig. 3b). Where melanosomes are exposed at the surface, regardless of their arrangement, the color is red (Fig. 3d, e). No melanosomes are visible where the color is silvery; the silvery regions appear similar to the host matrix surrounding the fossil in electron imaging (Fig. 3c, d).

FIB-SEM cross-sections reveal the three-dimensional structure of the barb ramus and barbule (Fig. 4). The preserved portion of the barb ramus resembles the cortex, or solid outer surface of the barb (Fig. 4c, d). The medullary layer of the ramus appears to have been separated with the counterslab. Within the ramus, melanosomes are loosely packed with random orientations (Figs. 3e, 4d, e). In cross-section the ramus is convex and broadly triangular, with the base of a distal barbule attached (Fig. 4d). The preserved cortex of the ramus is approximately 10 μm thick, and at the surface is approximately 36 μm wide (Fig. 4d).

In the two FIB-SEM cuts, the surface of the exposed barb ramus is a broad sheet of randomly oriented melanosomes. The melanosomes are well enough preserved to allow the outlines of individual barbule cells to be distinguished. In one cut (Fig. 4a, b) five complete distal barbules and part of a sixth are exposed, together with part of the ramus. In a second cut (Fig. 4c, d) four distal barbules, two proximal barbules, and part of the ramus are exposed. Apical barbules overlap adjacent basal barbules in an imbricated fashion.

The cross-sections of the barbs are long and narrow, with smooth, rounded outlines. Each cross-section is approximately 22 μm long and 3 μm wide at the center. The melanosomes on the obverse surface of each barbule appear to be organized in a smooth, closely packed layer which is darker under ESEM due to less charging or lower emission of secondary electrons from reduced edge effect (Fig. 3e). The melanosomes are oriented parallel to the surface of the feather, although they are not all aligned

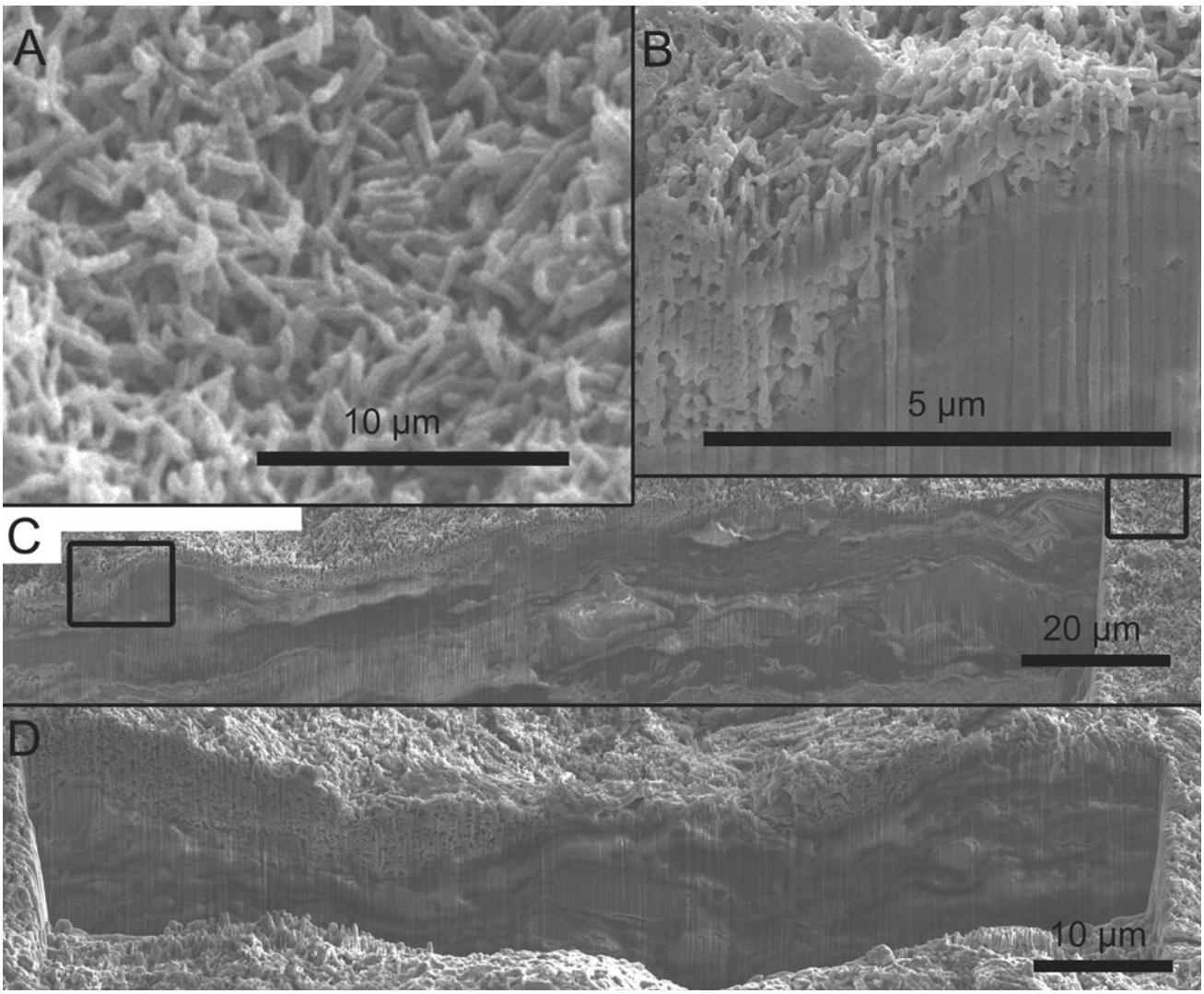

Fig. 2 ESEM imaging and FIB-SEM cross-section of fossil SMF ME 3850. **a** Detail of surface of rachis. **b** Detail of cross-section of rachis. **c** Rachis at location a in Fig. 1. *Black boxes* in **c** indicate locations of **a** and **b**. **d** Basal barbules at location b in Fig. 1

parallel to each other (Fig. 3e). Within the barbules, as well as on the exposed surface, this organization is not evident.

Elemental mapping

Electron probe microanalysis elemental maps showed a negligible difference in levels of magnesium and zinc in the fossil and matrix as mapped onto a photograph of the sampled region (only zinc figured, Fig. 5a, b). Calcium levels showed a similar pattern, except for higher concentrations around the edge of the fossil (Fig. 5c). Iron was present to varying degrees in the matrix, and high concentrations were present around the edge of the fossil, but iron concentrations were much lower in the red areas of the fossil (Fig. 5a, d). Sulfur was present in high concentrations only in areas where there was also a high concentration of iron, likely indicating the presence of pyrite (Fig. 5e). Carbon concentration was relatively high in the red areas of the fossil and patchy in the host rock matrix, but comparatively low in the white areas of the fossil (Fig. 5a, f). Aluminium, copper, and silicon were present in the matrix as well as in those parts of the fossil correlating with the silvery sheen, but at lower or negligible levels in the red section of the feather where melanosomes are exposed at the surface (Fig. 5a, g, h, i).

Discussion

Preservation of the feather

The long-held interpretation of the elongate bodies in fossil feathers as bacteria (e.g., Davis and Briggs 1995) was shown to be incorrect by Vinther et al. (2008), using a

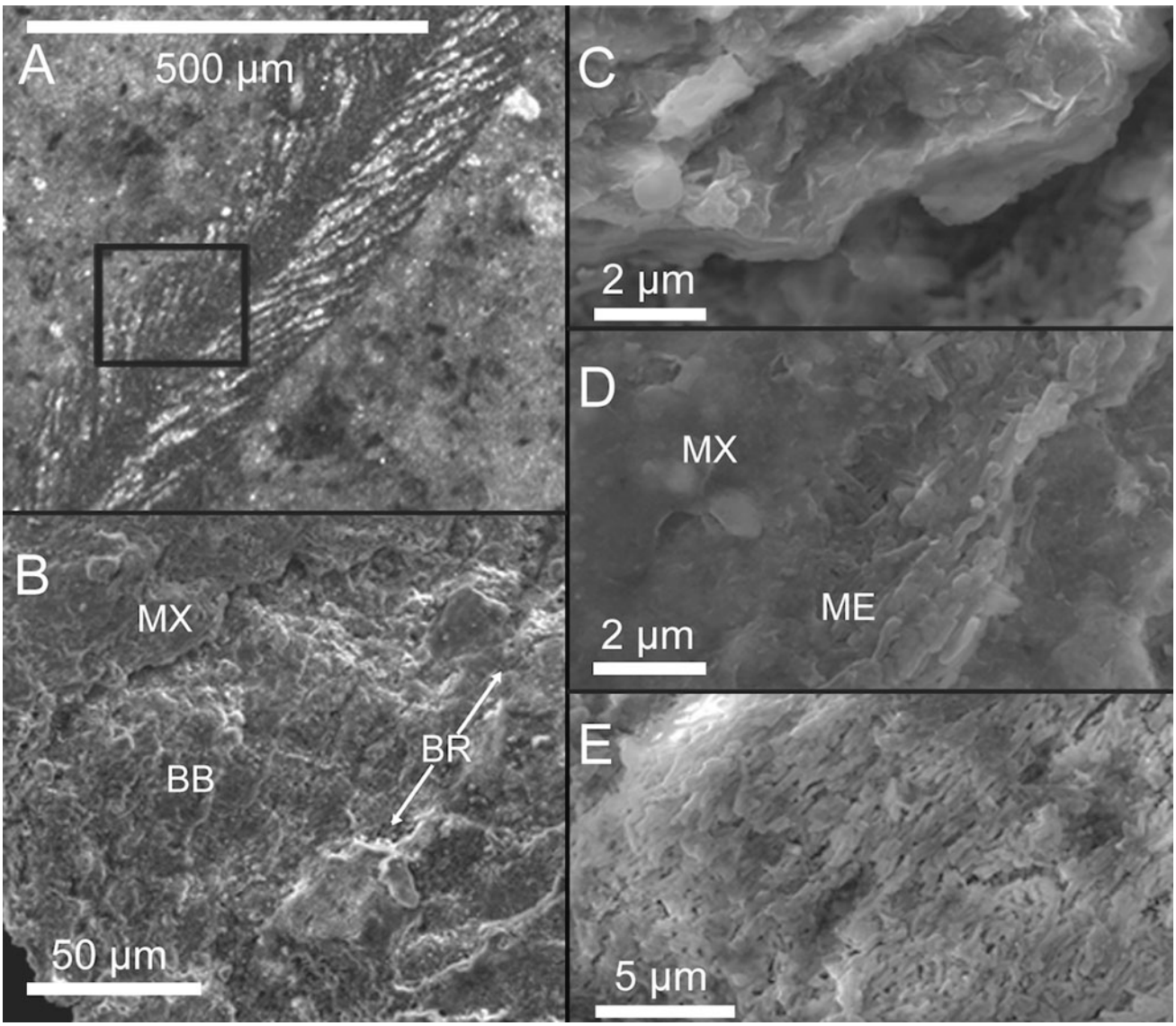

Fig. 3 An apical barb of fossil SMF ME 3850 at position d in Fig. 1. **a** Photograph of the section sampled, showing silvery pattern of the fossil. *Area* inside the *rectangle* is shown in ESEM images. **b** ESEM image of the entire sample within the *rectangle* showing barbules, matrix, and a barb ramus lying in the direction marked by *arrows*. **c** Matrix. **d** Barbules, showing exposed melanosome layer from a barbule and the surrounding matrix. **e** Barb ramus, showing dense region of loosely packed, aligned melanosomes. *BB* barbules, *BR* barb ramus, *ME* melanosomes, *MX* matrix

feather from the Cretaceous Crato Formation, and these structures are now recognized to be melanosomes. The arrangement of melanosomes in the Messel feather described here supports that interpretation; the smooth melanosome sheets are only observed on the dorsal surface of the distal barbules, corresponding to the iridescent part of the feather, and consistent with iridescent modern feathers. Melanosome-like microstructures in a pterosaur headcrest from Crato were recently interpreted as autolithified bacteria (Pinheiro et al. 2012). The higher levels of phosphorus and carbon revealed by EDS analysis of the microstructures in that specimen compared with the matrix, however, are consistent with a melanosome interpretation; apatite commonly occurs in association with fossilized melanosomes (e.g., in squid ink: Kear et al. 1995). The evidence of cellular division (Pinheiro et al. 2012, Fig. 2e) could equally be a result of simple juxtaposition of melanosomes. The microstructures in the Crato pterosaur headcrest may have been melanosomes that contributed to color banding used in display.

Many fossil feathers, especially those of dinosaurs from the Jurassic–Cretaceous of China, are compressed and condensed to the point where many details cannot be discerned (Foth 2012). In contrast, the low specific weight of

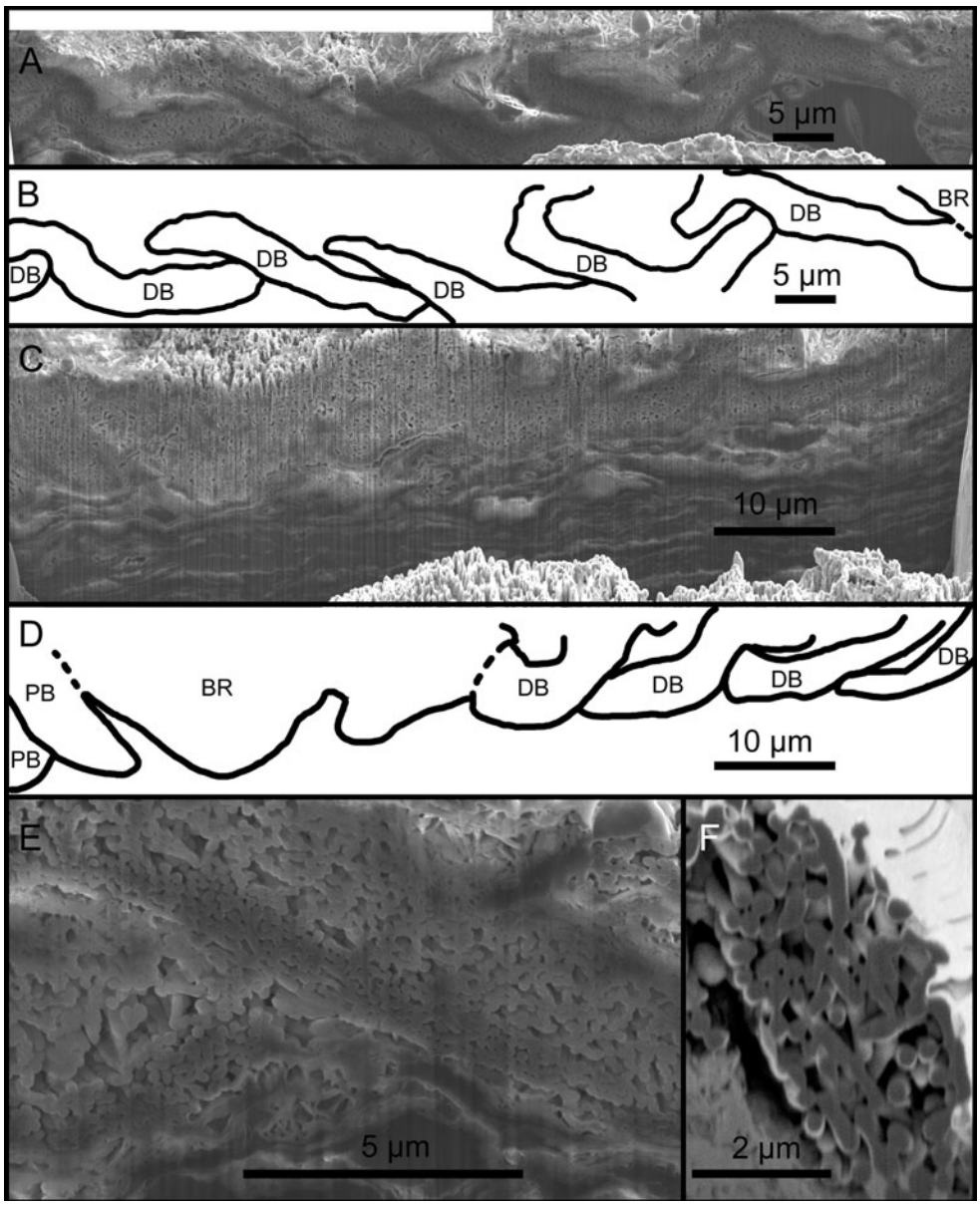

Fig. 4 FIB-SEM cross-sections of apical barbs of fossil SMF ME 3850. **a** Micrograph and **b** *sketched outline* of barb ramus and barbules corresponding to Fig. 1 location e. **c** Micrograph and **d** *sketched outline* of barb ramus and barbules corresponding to Fig. 1 location f. **e** Micrograph of densely packed layer of melanosomes in apical barbules. **f** Z-contrast backscatter microscopy image of FIB-SEM milled surface of fossil SMF ME 3850. Note the *lighter-colored* rims of the melanosomes, correlating to a higher mass elemental composition enveloping each melanosome. *DB* distal barbule, *PB* proximal barbule, *BR* barb ramus

the Messel Oil Shale and shallow burial depth may have contributed to the relatively low degree of compaction during diagenesis (Goth 1990; Felder and Harms 2004). The sample analyzed here, SMF ME 3850, provides a rare opportunity to study both the surface morphology and the three-dimensional structure of a fossil feather. Both excellent preservation and the use of FIB-SEM analysis allow us to observe features of the feather nanostructure.

The feather is preserved due to the resistance of melanosomes to bacterial decay (Goldstein et al. 2004), as well as the recalcitrant nature of melanin in diagenesis (Glass et al. 2012). The keratin has completely degraded in this fossil, which has led to some loss of the original feather microstructure, but the three-dimensional organization of the remaining eumelanosomes in the apical part of the feather allows for the observation of unprecedented anatomical details directly comparable to those of extant bird feathers. Mapping the location of FIB-SEM incisions onto a color photograph of the fossil (Fig. 1e, f) supports the identification of the rachis, barb rami, and barbules, and the

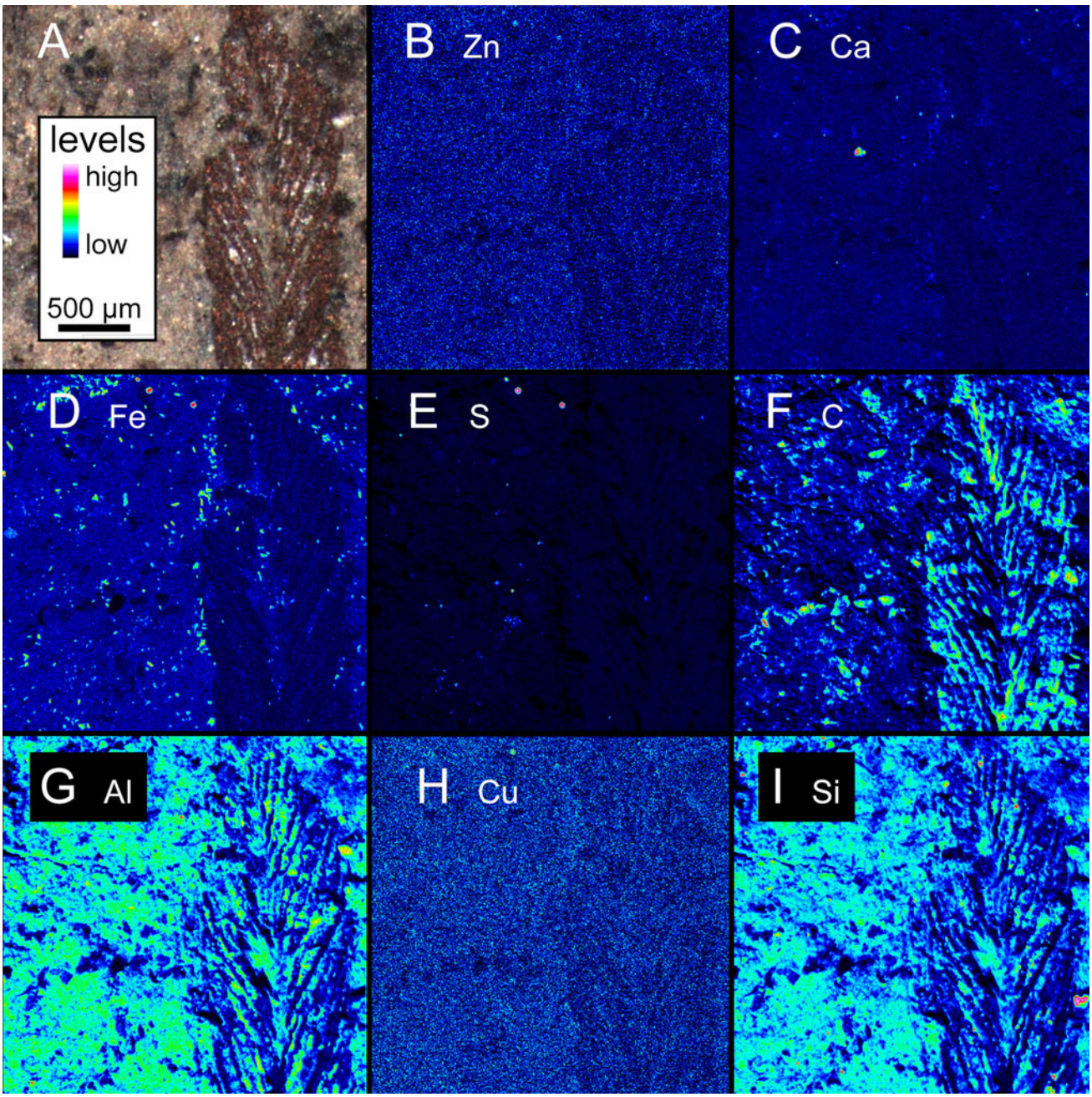

Fig. 5 EPMA elemental *maps* of apical barb of fossil SMF ME 3850. **a** *Photograph* of the area of the fossil corresponding to the elemental *maps*. **b** Zinc. **c** Calcium. **d** Iron. **e** Sulfur. **f** Carbon. **g** Aluminium. **h** Copper. **i** Silicon

reconstruction of their orientation in the fossil. FIB-SEM does not reveal the convex shape characteristic of the obverse side of the rachis in a modern feather (Lucas and Stettenheim 1972), probably due to degradation of the keratin leaving only the melanosome component. Distinct distal and proximal ledges on the barb rami where the bases of barbules insert, like those present on modern pennaceous bird feathers, are not visible. However, these structures may have been entirely keratinous and therefore not preserved. The apical barbules are partly buried in the sediment, but FIB-SEM reveals their three-dimensional morphology, which is slightly deformed only where they overlap. The cross-sections of the barbules are about seven times longer than they are wide, consistent with ratios for the base of a typical modern pennaceous barbule (Lucas and Stettenheim 1972). The absence of barbicels, or hooklets, is consistent with the open pennaceous structure at the distal tip of the feather. The rounded outline of the buried, obverse surface of the barb ramus, as well as the pattern of imbrication in the barbules and the position of

the structural color-producing melanosome layer on the counterpart (Vinther et al. 2010), indicate that the feather is preserved with the obverse or outer surface into the matrix. The excellent preservation of the barbules in the apical part of the feather can be ascribed to the dense packing of melanosomes in this region.

Origin of silvery sheen of distal barbules

EDS analysis via EPMA indicates that the composition of the silvery areas of the apical barbules is the same as that of the matrix. These silvery areas correspond to matrix visible between the red exposed areas of the barbules in ESEM analysis. FIB-SEM cross-sections reveal that matrix also is present between imbricated barbules below the surface of the fossil. The silvery sheen is evident only where matrix overlies the apical barbules.

We interpret the silvery sheen as a product of interference resulting from the light scattering at the interfaces of materials with different refractive indices, i.e., the melanosomes and the overlapping layer of sedimentary matrix. The thickness of the matrix layer is variable, but less than 6 μm, which is thin enough that the matrix is relatively transparent. Visible light passes through the thin layer of matrix and is backscattered by the melanosomes (Fig. 6). The silvery sheen is produced by the interference between light waves scattered backward at the surface of the matrix and at the surface of the underlying layer of melanin granules. Because the wedge of matrix overlying the melanosomes varies in thickness, all wavelengths of visible light are reinforced, producing broad-spectrum reflectance. Thus, the matrix overlying the barbules functions like a chirped single thin-film mirror, that is, a single thin-film mirror that varies in thickness and therefore reflects a range of wavelengths of light. In short, the sheen is a taphonomic artifact.

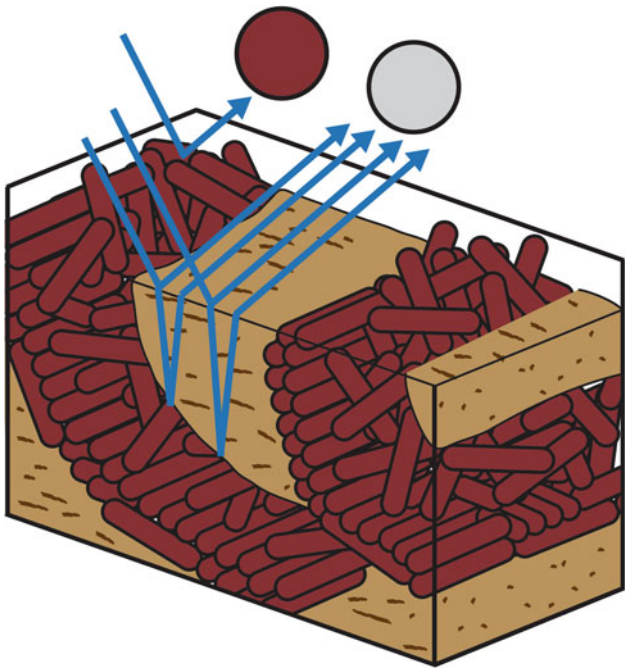

Fig. 6 Model of optical interference between light scattered by the surface of the matrix and the interface of the three-dimensional melanosome nanostructure. Different refractive indices of the air, melanosomes, and the partially overlapping layer of sedimentary matrix cause visible light to backscatter at the interfaces between materials. Because the layer of matrix overlying the melanosomes varies in thickness, all wavelengths of visible light are reinforced, producing broad-spectrum reflectance observed as a silvery sheen

The silvery color of the fossil could not be produced by the same anatomical mechanism behind the original structural color of the feather because the obverse surface that produced that structural color in the living feather is oriented downward into the matrix. The images of the superficial, structural color-producing melanosome layer of the barbules in Vinther et al. (2010) were taken from a small portion of the counterslab which contained an entire barbule where the obverse surface of the barbule was exposed. Although the densely packed melanosomes do not contribute directly to the production of the silvery sheen, they may increase the preservation potential of the intact barbules and the possibility that the imbricated structure will survive. When the fossil split near the reverse surface of the feather, the matrix between the imbricated barbules formed a thin wedge, one of the elements necessary to form an analog to a chirped single thin-film mirror. In contrast, the proximal barbules did not exhibit melanosome sheets nor do they preserve distinct barbules in cross-section or give rise to chirped single thin-film mirror iridescence. The extremely high fidelity of preservation, although rare, may not be unique to this fossil. Among 12 feathers from Messel examined using electron microscopy, 3 preserved melanosome sheets (Vinther et al. 2010) and 2 of those feathers preserved areas with a silvery sheen.

The red hue of the fossil

The red parts of the fossil are the exposed carbonaceous eumelanosomes. Atomic number (Z-contrast) selective backscatter imaging on a FIB-SEM milled surface (Fig. 4f) shows a higher signal on the surface of the melanosomes as compared with the core. This indicates a higher molecular weight elemental composition on and near the surface, which may represent a coating of iron minerals as originally posited (Vinther et al. 2010). While this assertion is not directly supported by the EPMA analyses, the outer coating potentially containing iron or other metals of higher atomic number is exceedingly thin, and therefore the concentration of these minerals may not be sufficient to be detected by EPMA or the X-ray signal may be

overwhelmed by bulk material directly under the coating. The varying red to green hues of other Messel fossil feathers also suggest that iron is the likely identity of the metal (Vinther et al. 2010).

Conclusions

FIB-SEM provides a powerful tool for studying photonic nanostructures in the fossil record, as illustrated by our study. Analysis of the three-dimensional structure preserved in SMF ME 3850 reveals the mechanism that generates the silvery sheen in the fossil. The coloration is an artifact of the high-quality preservation and almost perfectly intact barbules in the apical region. The color is not a direct result of the thin-film nanostructure of the barbules, which produced the iridescent structural color of the original feather. Instead, splitting of the fossil created a surface analogous to a chirped single thin-film mirror composed of matrix and eumelanosomes. The presence of this artifact indicates exceptional preservation, in this case due to the dense packing of the melanosomes that caused the original iridescent properties.

Analyses of fossil feathers from the Green River Formation, the Jehol Group, and the Xiagou Formation detected elevated copper levels compared with the surrounding matrix, which were interpreted as indicative of pigmentation (Wogelius et al. 2011). In contrast, EPMA analysis of the Messel feather investigated in this study revealed a lower concentration of copper in pigmented, melanosome-rich regions relative to the matrix, which might be due to other organic substances in the sediment matrix that also chelate copper, such as porphyrins and humic acids (Premovic et al. 2000).

The three-dimensional structure shown by FIB-SEM confirms the interpretation by Vinther et al. (2010) of a densely packed layer of melanosomes as remnants of nanostructure which created iridescent coloration in the original feather. The fossilized melanosomes have a thin coating of an element heavier than carbon, likely iron, causing the red coloration of the melanosomes exposed at the surface. Iridescence was previously inferred in fossil feathers from other localities based on individual melanosome shape (Li et al. 2012), but the preservation of nanostructures within a fossil feather has not been reported from localities other than the Messel Oil Shale. The unique three-dimensional preservation of this fossil, and potentially other Messel fossils, currently provides the best available opportunity to study the nanostructural morphology of fossil feathers.

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