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The early evolution of feathers: fossil evidence from Cretaceous amber of France

Vincent Perrichot^{1,*}, Loïc Marion², Didier Néraudeau³,
Romain Vullo³ and Paul Tafforeau⁴

¹*Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany*

²*Ecobio, UMR CNRS 6553, and ³Géosciences, UMR CNRS 6118, Université Rennes 1, 263 Avenue du Général Leclerc, 35042 Rennes, France*

⁴*European Synchrotron Radiation Facility, BP 220, 6 rue Jules Horowitz, 38043 Grenoble, France*

The developmental stages of feathers are of major importance in the evolution of body covering and the origin of avian flight. Until now, there were significant gaps in knowledge of early morphologies in theoretical stages of feathers as well as in palaeontological material. Here we report fossil evidence of an intermediate and critical stage in the incremental evolution of feathers which has been predicted by developmental theories but hitherto undocumented by evidence from both the recent and the fossil records. Seven feathers have been found in an Early Cretaceous (Late Albian, *ca* 100 Myr) amber of western France, which display a flattened shaft composed by the still distinct and incompletely fused bases of the barbs forming two irregular vanes. Considering their remarkably primitive features, and since recent discoveries have yielded feathers of modern type in some derived theropod dinosaurs, the Albian feathers from France might have been derived either from an early bird or from a non-avian dinosaur.

Keywords: feather evolution; early stages; Cretaceous amber; synchrotron; holotomography

1. INTRODUCTION

Feathers are complex integumental structures of a three-level branched structure composed of a rachis (primary shaft), barbs (secondary branches) and barbules (tertiary branches). Developmental theories propose that feathers evolved through a series of evolutionary novelties in the developmental mechanisms of the follicle and feather germ (Dyck 1985; Prum 1999; Chuong *et al.* 2000; Prum & Brush 2002). Recently, Xu (2006) has proposed a somewhat similar model but featuring a combination of transformations and innovations, and suggesting that tubular filaments and branching evolved before the appearance of the feather follicle. The recent discoveries of feathered dinosaurs from China support the evolutionary model based on developmental data, though additional data are needed to further understand the origin and structure of primitive feathers. Indeed, when neontological and palaeontological data illustrate almost all the series proposed by theories (Prum & Brush 2002; Xu 2006), transition remains particularly unclear before the stage III defined by Prum (1999), which is considered by Xu (2006) as probably the most critical stage of feather evolution in birds or non-avian dinosaurs. We recently discovered several isolated feathers fossilized in an Early Cretaceous amber of France, which display a primitive structure that illustrates the early formation of this critical stage. In addition to classical optical techniques, we used

X-ray synchrotron holotomography (Cloetens *et al.* 1999) to reveal finest details, confirming the possibilities of synchrotron investigation for studying amber inclusions (Tafforeau *et al.* 2006; Lak *et al.* in press).

2. MATERIAL AND METHODS

The amber piece was found in the quarry of Archingeay/Les-Nouillers, in Charente-Maritime (western France), which has already yielded numerous fossils, mainly insects (Perrichot 2004, 2005). It is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). In the regional stratigraphical section, this amber-bearing stratum corresponds to the subunit A1 and was dated as Late Albian (*ca* 100 Myr) by palynological studies (Néraudeau *et al.* 2002; Dejax & Masure 2005).

The feathers were originally fossilized in a single piece of amber, alongside 77 arthropods (see list in Perrichot 2004, table 2). The size of the entire amber piece was 4 × 3 × 2 cm. This piece was fragmented into 22 portions in order to separate inclusions for study. This preparation followed the method described by Perrichot (2004). The seven feathers are now isolated in a single portion of amber, and deposited in the Department of Earth History of the National Museum of Natural History in Paris, under the reference MNHN ARC 115.6.

Conventional imaging techniques using transmitted light microscope were first used but did not allow to bring all the information needed to assess precisely the morphology of the feathers. In order to reveal some critical structures in three dimensions, we used X-ray synchrotron phase imaging techniques on the ID19 beamline at the European Synchrotron Radiation Facility (ESRF, Grenoble, France). We performed

* Author and address for correspondence: Paleontological Institute, University of Kansas, Lindley Hall, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA (vincent.perrichot@neuf.fr).

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several propagation phase contrast microtomography and holotomography tests (Cloetens *et al.* 1999, 2006; Tafforeau *et al.* 2006; Lak *et al.* in press) using various configurations in order to define the optimal parameters to reveal the feathers clearly. As the feathers present a relatively large extension in regard to the size of each barb, it was necessary to combine high-resolution imaging with quite a large field of view. We used an optical magnification system coupled with a CCD FReLoN (Fast Readout Low Noise) camera (Labiche *et al.* 2007) providing an isotropic voxel size of 0.7 μm . In order to cover a large enough area of the amber piece, six scans of contiguous parts (two scans per line on three lines) were taken using local phase microtomography (propagation distance of 100 mm) in continuous acquisition mode (see Lak *et al.* in press) with a 30 keV monochromatic beam. Using 0.3 s of exposure time, 1500 projections were taken over 180°.

Being thin structures, feathers are very difficult to extract from these scans, so we used a single-distance holotomographic reconstruction of each scan after filtering of all the projection (subtraction of a blurred copy of the picture using a 10-pixel Gaussian filter), following the protocol described in Tafforeau *et al.* (2007). The data preparation allowed enhancement of the visibility of the feathers and other fine structures relative to larger ones. After correction of the strong ring artefacts (Tafforeau *et al.* 2006) on the reconstructed holotomographic slices, the six scans were assembled in order to obtain a single volume covering $1 \times 2 \times 3$ mm with a voxel size of 0.7 μm .

Owing to the large size of the data (40 Gb), a three-step segmentation protocol was used to limit the processing time. As the feathers appeared as white structures in the grey matrix of resin, the whole dataset was reduced by a linear factor of 8 (corresponding to a reduction by 512 of the volume) using binning by maximum. Each 5.6 μm voxel of the new volume was attributed the maximum value of all the corresponding 0.7 μm original voxels. That new volume was visualized and segmented in three dimensions using VGSTUDIO MAX v. 1.2 (Volume Graphics, Heidelberg, Germany) in order to obtain a rough extraction of the feathers. The binary segmentation mask was then exported, extrapolated to fit with the original dataset, and applied to it. The area containing the most visible feather was selected on that new volume and a fine segmentation was performed in order to prepare three-dimensional renderings.

3. RESULTS

Seven identical feathers are lying side by side in the amber piece (figure 1a) and very probably originate from a single individual. Like the rare fossil feathers previously known from amber, they are perfectly preserved, although probably incomplete in their basal part since there is no visible calamus. The tangle of these feathers, their three-dimensional disposition in amber, and numerous dust grains hinder the observation of some of them. The following description is mainly based on the three best visible. These are 2.3, 1.6 and 1.1 mm long as measured along the rachis. Filamentous, long and free barbs lacking barbules are inserted opposite to each other on each side of a rather flattened rachis and form two vanes (figure 2). The diameter of the rachis is constant, approximately 0.01 mm. The number of barbs is 40 per vane mm^{-1} of rachis; that is approximately 180 for the longest feather. Barbs are approximately 0.60 mm long near the basal part

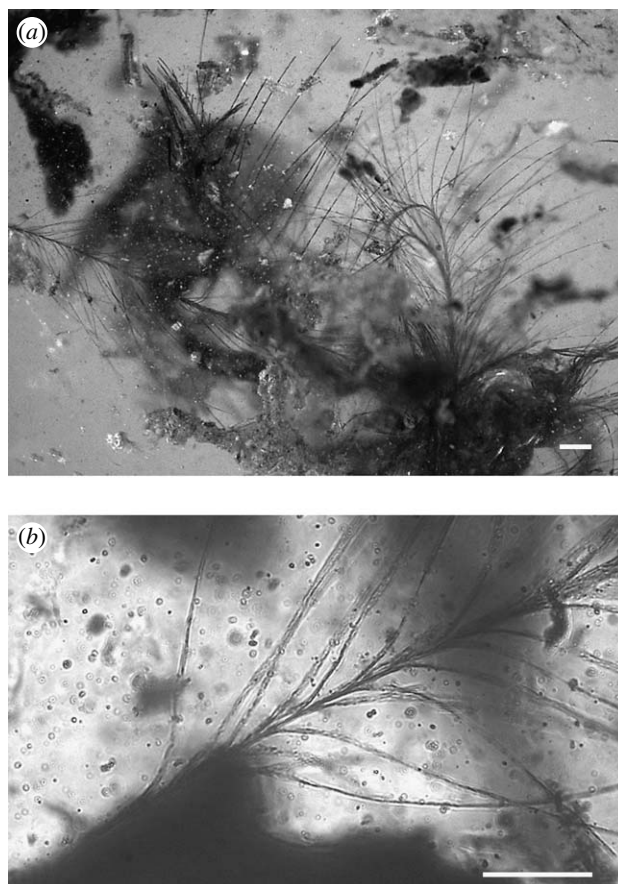


Figure 1. Fossil feathers from the Early Cretaceous amber of France (MNHN ARC 115.6): (a) seven feathers are preserved in a single piece of amber; (b) their excellent quality of preservation allows observation of fine structures using transmitted light microscope. Scale bars, 0.1 mm.

of the rachis, and 0.50 mm long near the distal tip. However, it is somewhat difficult to observe their point of insertion precisely, as they border the rachis before diverging, while their base is hidden by the more basal barbs (figures 1b and 2a,d). In fact, they fuse progressively to compose the rachis, and lack the complete fusion that is observed in the rachis of all other fossils and almost all modern feathers. The vanes observed on these feathers result from the insertion of barbs on the two opposite sides of the flattened rachis. These feathers are morphologically close to the down, ornamental or afterfeathers, and not to the contour, remiges or rectrices. However, they have a thick and long rachis, unlike classical down feathers whose barbs generally diverge from the very short apex of the rachis.

4. DISCUSSION

According to developmental theories, the rachis is the result of a complete fusion of the barbs, even in down feathers with a small basic rachis, and a planar form of feathers results from the helical growth of barb ridges within the follicle and interlocking between neighbouring barbs to create the vane (Dyck 1985; Griffiths 1996; Prum 1999; Chuong *et al.* 2000; Prum & Brush 2002; Xu 2006). A shaft consisting of incompletely fused, still distinguishable, partially superimposed barbs is not considered in feather evolution, although this stage would logically have existed with regard to the formation of feathers in the



Figure 2. Three-dimensional virtual reconstruction of one fossil feather in phase contrast microtomography: (a–c) long barbs form two vanes on each side of a relatively flattened shaft; (d) the shaft is flattened and composed by the still incompletely fused bases of the barbs, a stage in feather evolution that was hitherto unknown in fossil and recent records. Scale bars, 100 μm .

follicle. The structure observed in these specimens from French amber therefore represents the first fossil evidence of the intermediate stage between the very distinct stages II and IIIa defined by Prum (1999) in his theory of evolutionary diversification of feathers. Stage II is characterized by non-ramified barbs attached at their base to the calamus, without barbules. Stage IIIa corresponds to the appearance of a central shaft formed by the fusion of non-ramified barbs and the appearance of the planar form. Stage IIIb exhibits barbules without differentiation between basal or distal part of the feather, unlike in stage IV (figure 3). Similarly, the new fossils take place between stages II and III defined by Xu (2006), and more precisely correspond to the early phase of stage III. The present discovery, therefore, sheds new light on the idealized nature of the developmental stages of feather evolution. Indeed, with a long rachis appearing before the barbules, it emphasizes stage IIIb as unlikely and stage IIIa as more likely evolving after stage II. We prefer not to create a new stage for this morphology, as it merely illustrates a transition between two well-established stages rather than a distinct, stable stage. According to Prum (1999), Bock (2000) and Prum & Brush (2002), such

evidence for primitive feathers (excluding simple filaments or ‘protofeathers’) was hitherto desperately missing in the fossil record to augment theories on the origin of feathers.

Fossil feathers are essentially preserved as carbonized imprints in sedimentary rocks (Davis & Briggs 1995) and are rather rare in amber, even in abundant and rich Palaeogene ambers. The fossils we report here are only the sixth occurrence of feathers in Cretaceous amber, together with those from Lebanon (Schlee 1973; Schlee & Glöckner 1978), Myanmar (Grimaldi *et al.* 2002), Spain (Alonso *et al.* 2000; Delclòs *et al.* 2007) and the USA (Grimaldi & Case 1995). Further fossils mentioned from the Late Cretaceous ambers of Canada, Japan and Siberia (Kurochkin 1985; Grimaldi & Case 1995) have yet to be properly described or illustrated. Amber fossils are characterized by an exceptional quality of preservation that allows a detailed observation of all tiny structures. Those found in the Neocomian amber of Lebanon (Schlee & Glöckner 1978, fig. 6, pl. 3), the Aptian–Albian amber of Spain (Alonso *et al.* 2000, fig. 9.2; Delclòs *et al.* 2007, fig. 4N) and the Albian amber of Myanmar (Grimaldi *et al.* 2002, fig. 14e) clearly differ from the French fossils, featuring barbs and barbules organized in asymmetrical

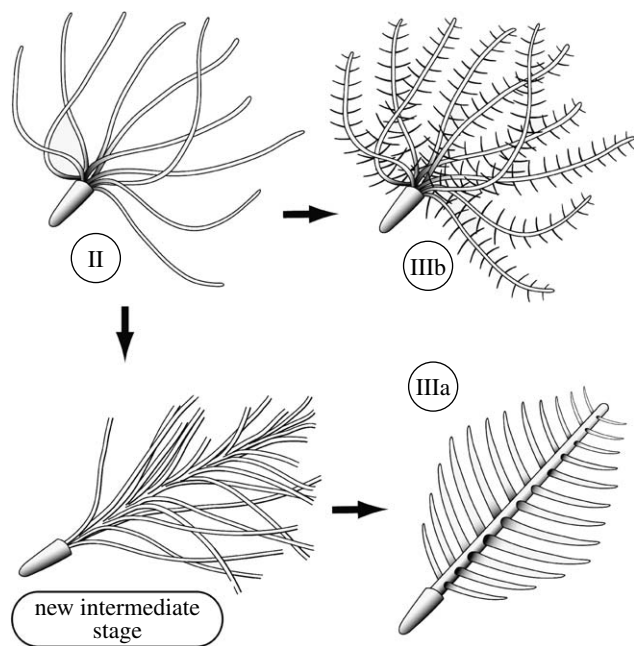


Figure 3. Feathers from French amber take place between the very distinct stages II and IIIa proposed in the developmental model of Prum (1999).

vanes, and thus similar to the contour feathers of stage IV of Prum's model (1999). Grimaldi & Case (1995) described a semiplume almost similar in aspect to our fossils, preserved in the Turonian amber of New Jersey, USA (Raritan-Magothy Formation, *ca* 90–94 Myr). However, it differs from the amber feathers from France by its larger size (7.5 mm long) and a cylindrical rachis decreasing in diameter from base to apex (Grimaldi & Case 1995, fig. 1).

In addition to the above-mentioned Spanish amber fossils, only two other feathers are mentioned in the Cretaceous of Europe, preserved as carbonized imprints: those from the Barremian limestones of Spain show a basal branching of filaments without apparent rachis (Sanz *et al.* 1988, fig. 1) and thus similar to stage II defined by Xu (2006); and those from the Santonian–Campanian of Slovenia display features of pennaceous feathers of stage IV, though barbules and hooklets are not visible but only inferred from the general morphology (Buffetaut *et al.* 2002, fig. 2).

Grimaldi & Case (1995) considered the semiplume from New Jersey as the oldest record of a bird in North America. However, feathers were still considered unique to birds at that time, and this is now known to be incorrect since the subsequent discovery of feathers in non-avian theropod dinosaurs in the Cretaceous of China (Chen *et al.* 1998; Xu *et al.* 1999*a,b*, 2000, 2001, 2003, 2004; Zhang & Zhou 2000; Ji *et al.* 2001, 2005; Norell *et al.* 2002; Xu & Zhang 2005). The oldest known birds, for example, *Archaeopteryx* from Germany and *Confuciusornis* from China, have modern-type feathers that are similar to those of extant birds, although they are significantly older (150–124 Myr) than the feathers from New Jersey and France. The latter have a much more primitive structure and are intermediate between the stages II and III of Prum (1999) and Xu (2006). They are also very distinct from the most derived feathers of stage V, which show asymmetrical vanes on

each side of the rachis and barbules. According to Prum & Brush (2002), filamentous feathers of stage II, with a tuft of barbs fused basally (such as modern down feathers), would have appeared alongside simple filaments, or protofeathers, in the theropod dinosaur *Sinosauropteryx* (145 Myr; Chen *et al.* 1998). However, the presence of such protofeathers in *Sinosauropteryx* remains unclear, being reinterpreted as collagen fibres by Lingham-Soliar *et al.* (2007). The presence of true feathers is less equivocal in some other theropods: the recently described *Pedopenna*, from China (Xu & Zhang 2005), shows long pennaceous feathers of stage IV attached to its legs. *Caudipteryx* and *Protarchaeopteryx*, described by Ji *et al.* (1998; see also Dyke & Norell 2005), also have pennaceous feathers of stage IV. Xu *et al.* (2000) and Norell *et al.* (2002) found dromaeosaurs (e.g. *Microraptor*) with modern feathers of stage V (remiges), a character that was hitherto considered to be unique to birds (Prum & Brush 2002) and now is recognized to have a more ancient origin among non-avian dinosaurs (Sereno 2004). *Jinfengopteryx*, though formerly assigned to an avialan bird (Ji *et al.* 2005), is more likely a troodontid with pennaceous feathers of stage IV (Xu & Norell 2006). Finally, Ji *et al.* (2001) and Xu *et al.* (2001) inferred the existence of a rachis in a pattern of branched barbs for the dromaeosaur *Sinornithosaurus* and a still unnamed Chinese theropod ('filaments jointed at their bases along a central filament' and 'filaments appearing to be around a central rachis', respectively). The morphology of the new fossils described herein, with a rachis forming 'primitive' vanes without barbules, is entirely consistent with the shafted feathers displayed by these two theropods. According to this, and to the current evolutionary model of increasing complexity in feather morphologies (Norell & Xu 2005; Xu 2006; Xu & Norell 2006; Zhang *et al.* 2006), the French amber feathers may thus belong to a non-avian theropod dinosaur. It is noteworthy that isolated teeth of troodontids were recovered from the amber deposit considered here (Vullo *et al.* 2007). Indeed, they were found in a slightly younger geological level of earliest Cenomanian age, located approximately 10 m above the amber-bearing level. Further teeth of troodontids and dromaeosaurids were also found in the same Cenomanian level from other nearby fossil localities of the Charentes region (Vullo *et al.* 2007). These two non-avian dinosaur clades are currently known to be feathered and are thus possibly related to the fossil feathers from France. But the poor early feather record still prevents a complete reconstruction of the distribution pattern of morphologies among non-avian coelurosaurs and basal birds, and the possibility that they are derived from an early bird cannot be excluded.

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