Filamentous Integuments in Nonavialan Theropods and Their Kin: Advances and Future Perspectives for Understanding the Evolution of Feathers

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5.1 Introduction

Among various vertebrate integumentary appendages, feathers are the most complex ones with a diversity of modern forms (Lingham-Soliar 2015; Lucas and Stettenheim 1972). How the complexity of various feather forms and their diverse functions originated and evolved has intrigued scholars from different disciplines (Brush 1972; Brush 2000; Chuong et al. 2003; Feo et al. 2015; Harris et al. 2005; Prum 1999; Prum and Brush 2002; Vinther et al. 2009; Xu and Guo 2009; Yu et al. 2002). Insights from avian integumentary anatomy and embryology, functional morphology, developmental biology, biochemistry, and some other disciplines have greatly improved our understanding of the origin and early evolution of feathers over the last few decades (Brusatte et al. 2014; Chuong et al. 2000, 2003; Xu and Guo 2009; Xu et al. 2014), but the most significant recent advances have been made in the field of paleontology, as a result of the discoveries of numerous nonavialan dinosaur fossils preserving feather-like structures or

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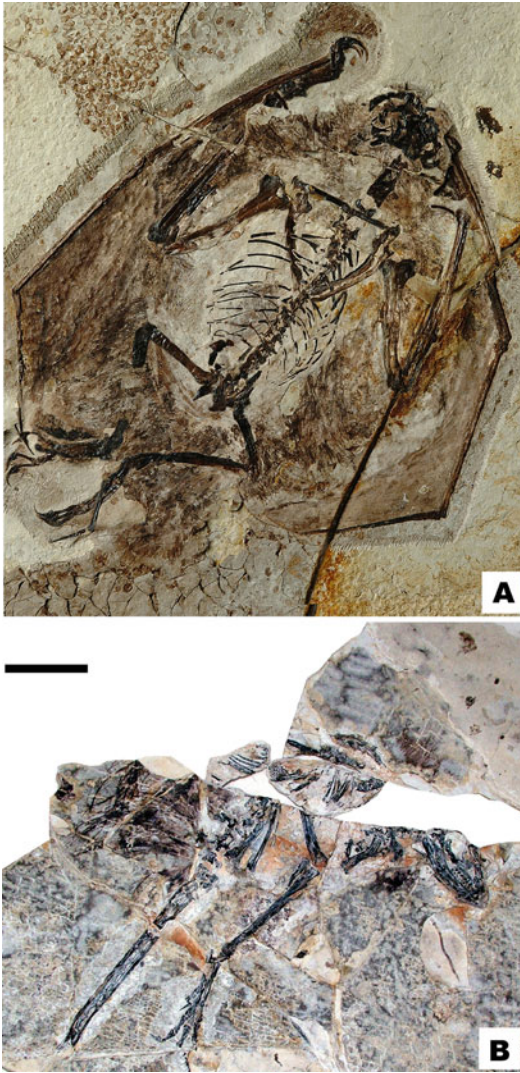e-mail: xuxing@ivpp.ac.cn

feathers from the Jurassic and Cretaceous beds of northeastern China (Godefroit et al. 2013a; Hu et al. 2009; Norell and Xu 2005; Xu and Guo 2009), Myanmar, Germany, Canada, and Russia (Godefroit et al. 2014; Göhlich and Chiappe 2006; Rauhut et al. 2012; Xing et al. 2016; Zelenitsky et al. 2012). The present chapter reviews the research on feathers or feather-like integumentary appendages in those recently uncovered, globally distributed fossils; highlights and discusses remaining controversies and problems in feather evolution; and proposes future directions in this important research area.

5.2 Filamentous Integuments Among Nonavialan Dinosaurs

Filamentous integuments of diverse morphologies are now known to be present in numerous nonavialan dinosaurs from several ornithischian groups, many nonavialan theropod groups (Norell and Xu 2005; Xu and Guo 2009; Xu et al. 2014), and even some pterosaurs as well (Kellner et al. 2010) (Figs. 5.1, 5.2, and 5.3). The morphologies of these structures range from single filaments to a range of more complex structures, including pennaceous feathers (Barrett et al. 2015; Xu and Guo 2009). Most of these filamentous integumental structures have been identified as early feathers, but their relationships to various modern feather morphologies are not

Fig. 5.1 Selected non-theropod avemetatarsalian fossils preserving filamentous integuments. (**a**) The anurognathid pterosaur *Jeholopterus*; (**b**) the heterodontosaurid ornithischian *Tianyulong*. Scale bars, 50 mm

2009; Xu et al. 2015), but these identifications cannot be confirmed given the lack of preservation of fine morphological features. More controversial is whether some filamentous integuments such as the mono-filamentous integuments seen in some ornithischians are feathers (Barrett et al. 2015) or some kind of feather homolog. Besides the overall poor documentation of the fine morphological details of the fossils of filamentous integument among nonavialan dinosaurs, one of the other lesser resolved issues in these early fossils includes the pattern of distribution of various filamentous structures across the body of these nonavialan dinosaurs and the functions of the diverse filamentous integuments (Xu and Guo 2009).

Nevertheless, at least 13 types of filamentous integumental structures have been reported among nonavialan dinosaurs (Table 5.1) (Xu and Guo 2009; Xu et al. 2010b). The common morphotypes include slender monofilamentous feathers (SMFIs), broad monofilamentous feathers (BMFIs), basally joining filamentous feathers (BJFFs), symmetrical open-vaned feathers (SOVFs), symmetrical close-vaned feathers (SCVFs), and asymmetrical close-vaned feathers (ASVFs). Other than those morphotypes, there are two other unusual forms. One is a proximally ribbon-like close-vaned feather (PRCVF), and the other is a rachis-dominant close-vaned feather (RDCVF). The PRCVFs have been argued to represent sheathed pin feathers (Foth 2012; Prum 2010), but some of their morphological features are not consistent with this identification (Xu et al. 2010a). It is possible that the long ribbon-like proximal portion represents a long calamus, and the PRCVFs are thus a type of calamus-dominant pennaceous feathers.

Several additional morphotypes seem to be present among the known fossil specimens, but are poorly represented in the fossil record. There are five morphotypes in this category: the basally joining shafted filamentous feathers (BJSFFs), the basally joining membranous-based filamentous feathers (BJMBFFs), the radially branched shafted filamentous feathers (RBSFFs), the bilaterally branched filamentous feathers (BBFFs), and the basally joining branched filamentous

well known because many of their morphological details are often either poorly preserved or have yet to be recovered (Barrett et al. 2015; Xu and Guo 2009). For example, barbules on the pennaceous morphotypes presumably are present in the pennaceous feathers of basal pennaraptorans (Foth et al. 2014), but their morphologies and even their presence have yet to be documented. Other morphotypes present in nonavialan dinosaurs are similar to the bristles and filoplumes of modern birds (Xu and Guo

Fig. 5.2 Selected non-pennaraptoran theropod fossils preserving filamentous integuments. (**a**) The compsognathid theropod *Sinosauropteryx*; (**b**) the therizinosauroid theropod *Beipiaosaurus*. Scale bars, 50 mm

feathers (BJBFFs). These less common morphotypes have been identified in some specimens of feathered dinosaurs (Xu and Guo 2009; Xu et al. 2015; Zhang et al. 2008), but the possibility that they are just preservation artifacts cannot be completely excluded.

SMFIs are known in several ornithischians such as the ceratopsian ornithischian *Psittacosaurus* (Mayr et al. 2002), the heterodontosaurid ornithischian *Tianyulong* (Zheng et al. 2009), and the ornithopod ornithischian *Kulindadromeus* (Godefroit et al. 2014), and some theropods such as the megalosaurid theropod *Sciurumimus (*Rauhut et al. 2012), possibly the ornithomimid theropod *Ornithomimus* (Zelenitsky et al. 2012), and possibly the likely compsognathid theropod *Juravenator* (Chiappe and Göhlich 2010). BMFIs are restricted to theropods and are known in the tyrannosauroid theoropod *Yutyrannus* (Xu et al. 2012), possibly the ornithomimid theropod *Ornithomimus*[1] (Zelenitsky

et al. 2012), and the therizinosauroid theropod *Beipiosaurus* (Xu et al. 2009). BJFFs are known in the ornithopod ornithischian *Kulindadromeus,* the dromaeosaurid theropod *Sinornithosaurus* (Xu et al. 2001), possibly the scansoriopterygid theropods *Epidexipteryx* (Zhang et al. 2008) and *Yi* (Xu et al. 2015), and the troodontid theropod *Anchiornis* (Hu et al. 2009). BJSFFs are present in *Sinornithosaurus* (Xu and Guo 2009), and SOVFs occur in a basal maniraptoran theropod (Xing et al. 2016). SCVFs are preserved in the oviraptorosaurian theropods *Protarchaeopteryx*, *Caudipteryx* (Ji et al. 1998; Zhou and Wang 2000; Zhou et al. 2000), and *Incisivosaurus*[2] (Xu et al. 2010b), the anchiornithine theropod *Anchiornis* and its kin (Godefroit et al. 2013a, b; Hu et al. 2009), the troodontid theropod *Jinfengopteryx* (Ji et al. 2005; Norell and Xu 2005; Xu and Norell 2006), and the

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[1] The pennaceous feathers inferred to be present in *Ornithomimus* are probably BMFFs based on the preserved morphology.

[2] STM4-1 and STM 22-6 were referred to *Similicaudipteryx* in the original description, but reexamination of the two specimens suggest that it is more proper to assign the two specimens to *Incisivosaurus* because the former closely resemble the latter in some dental features, which are unique to *Incisivosaurus*.
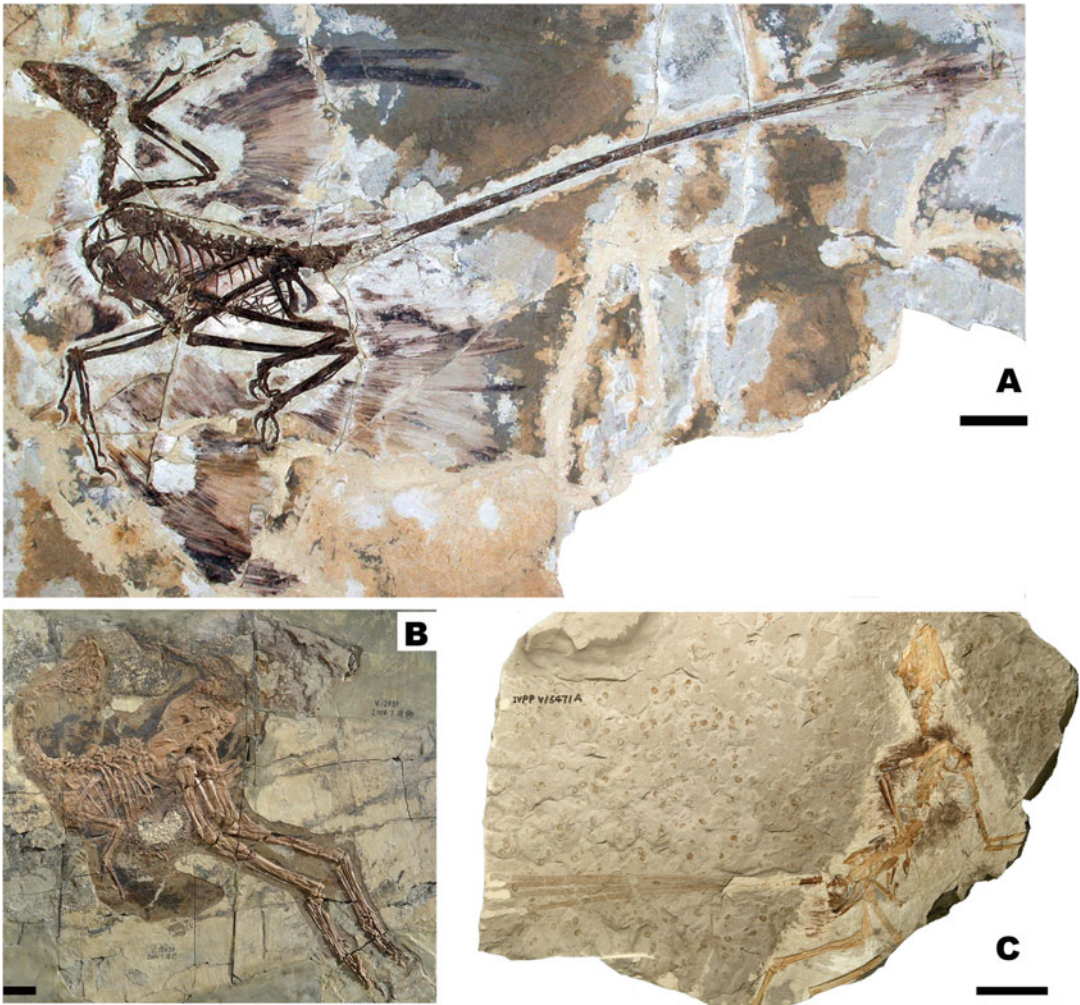
Fig. 5.3 Selected pennaraptoran theropod fossils preserving feathers. (**a**) The droameosaurid theropod *Microraptor*; (**b**) the oviraptorosaurian theropod *Caudipteryx*; (**c**) the scansoriopterygid theropod *Epidexipteryx*. Scale bars, 50 mm

dromaeosaurid theropods *Sinornithosaurus* (Ji et al. 2001) and *Microraptor* (Xu et al. 2003). ASVFs are known in *Microraptor* (Xu et al. 2003), the troodontid *Jianianhualong* (Xu et al. 2017), and the anchiornithine *Caihong* (Hu et al. 2018). PRCVFs are preserved in *Incisivosaurus* (Xu et al. 2010b), and RDCVFs have been found in *Epidexipteryx* (Zhang et al. 2008). RBSFFs occur in *Sinornithosaurus* (Xu et al. 2001), and BJBFFs were reported in *Yi* (Xu et al. 2015). Some filamentous feathers of several nonavialan dinosaurs might be referable to the morphotypes above, but cannot be confidently grouped with them at present. For example, some filamentous feathers of the compsognathid theropod *Sinosauropteryx* appear

to have a short quill and long barbs, and are possibly referable to RBSFFs, some filamentous feathers of the basal tyrannosauroid theropod *Dilong* appear to be BBFFs, some filamentous feathers of *Beipiaosaurus* might be RBSFFs, and the extremely short, filamentous elements reported to be associated with the alvarezsauroid theropod *Shuvuuia* (Schweitzer et al. 1999) might be SMFIs. All of these morphotype identifications need confirmation with better preserved fossils.

The patterns of distribution of some of these morphotypes across the dinosaurian body can be reconstructed confidently for some taxa. SMFIs cover most of the body of *Tianyulong* (Zheng et al. 2009) and *Kulindadromeus* (Godefroit

Table 5.1 Major filamentous integumentary structures found among nonavialan dinosaurs

Morphotype	Abbreviation	Definition
Slender monofilamentous integument	SMFI	Single slender filament
Broad monofilamentous integument	BMFI	Single broad filament
Basally joining filamentous feather	BJFF	Several filaments joined at their base without a central shaft
Symmetrical open-vaned feather	SOVF	A slender central shaft and open vanes of similar size on either side
Symmetrical close-vaned feather	SCVF	A thick central shaft and closed vanes of similar size on either side
Asymmetrical close-vaned feather	ASVF	A thick central shaft and closed vanes of different size on either side
Proximally ribbon-like close-vaned feather	PRCVF	A long ribbon-like proximal portion and a pennaceous distal portion
Rachis-dominant close-vaned feather	RDCVF	A hypertrophied rachis and a small/reduced pennaceous portion
Basally joining shafted filamentous feather	BJSFF	Multiple filaments joined at their bases on the distal end of a slender central shaft
Basally joining membranous-based filamentous feather	BJMBFF	Multiple parallel filaments joined at their base to a membranous structure
Radially branched shafted filamentous feather	RBSFF	Multiple filaments that branch radially along the length of a central filament
Bilaterally branched filamentous feather	BBFF	Multiple filaments that branch bilaterally along the length of a central filament
Basally joining branched filamentous feather	BJBFF	Several BJSFFs, RBSFFs, or BBFFs that are joined at their bases

et al. 2014), but they are restricted only to the middle portion of the tail in *Psittacosaurus* (Mayr et al. 2002). BMFIs are distributed over the skull, anterior neck, and posterior tail in *Beipiaosaurus* in a restricted pattern on its body (Xu et al. 2009), and they probably are present along the arm and posterior tail in *Yutyrannus* (Xu et al. 2012). The simply branched feathers such as BJFFs, BJSFFs, RBSFFs, or BBFFs seem to cover much of the body of *Sinosauropteryx* (Currie and Chen 2001) and *Yutyrannus* (Xu et al. 2012). One of the most unusual feather distribution patterns is the extensive feathering on the lower parts of the legs (and feet) of various theropods, including basal birds (Foth et al. 2014; Xu et al. 2003; Zheng et al. 2013). Flight feathers are typically only seen in forelimbs and tail of modern birds, but large SCVFs and ACVFs are present along the lower legs in a number of basal paravians, including basal birds, and in some cases even along the metatarsals (Foth et al. 2014; Xu et al. 2003; Zheng et al. 2013). Extensively feathered feet appear to be a plesiomorphic feature for Coelurosauria (Zheng et al. 2013).

5.3 Current Consensus on the Origin and Early Evolution of Feathers

The discoveries of various filamentous integuments in different nonavialan dinosaurs have provided significant new information on feather evolution (Chen et al. 1998; Ji et al. 1998, 2001; Norell and Xu 2005; Wellnhofer 2004; Witmer 2009a, b; Xu and Guo 2009; Xu et al. 2001, 2009, 2010b; Zhang and Zhou 2006). In combination with recent insights from developmental biology and other morphological aspects of modern feather diversity (Alibardi 2005; Brush 2000; Chuong et al. 2000; Evangelista et al. 2014; Feo et al. 2015; Foth 2011, 2012; Lin et al. 2013a, b; McNamara 2013; McNamara et al. 2013; Moyer et al. 2014; Prum 1999), these new data together have helped to reach some consensus in regard to the overall pattern of feather evolution.

In general, it is accepted now that the first feathers are simple, filamentous structures.

Feather complexity increased incrementally toward the origin of birds, and various feather types, including the highly complex flight feathers, appeared before the evolution of the earliest birds (Xu and Guo 2009; Xu et al. 2014).

Mapping these various filamentous integuments preserved as fossils onto a theropod phylogeny (Fig. 5.4), we can identify several stages in feather evolution: Stage I, the appearance of the filamentous morphology at least at the base of the Tetanurae (e.g., SMFIs in *Sciurumimus)*; Stage II, appearance of the primary branching morphology (e.g., barbs) and planar morphology at the base of the Coelurosauria (e.g., various branched filamentous feathers, including bilaterally branched feathers in the compsognathids and tyrannosauroids); Stage III, appearance of the secondary branching (i.e., plumulaceous barbules) and open vanes at the base of the Maniraptora (e.g., SOVFs in a basal maniraptoran preserved in the amber); Stage IV, appearance of closed vanes (pennaceous barbules) at the base of the Pennaraptora (e.g., SCVFs in several oviraptorosaurians and several deinonychosaurs); and Stage V, appearance of vane asymmetry at the base of Paraves (e.g., ACVFs in basal avialans and several deinonychosaurs). These evolutionary stages are consistent with the evolutionary stages inferred from developmental data derived from living birds, which include five major stages from an undifferentiated cylinder (stage I) to the pennaceous feathers with a closed vane (Prum 1999).

Besides the evolutionary sequence of major morphological features (above), some consensus also has been reached regarding the evolutionary sequence of the various functions of feathers. Locomotion (including flight), insulation, and display represent the three major functions exhibited among modern birds and their feathers, and various other functions also play important roles (Lucas and Stettenheim 1972; Prum and Brush 2002). Although certain morphological features of various feathers can be correlated with certain functions, these correlations are sometimes complex and weak. Nevertheless, functional inferences can be made based on the integumentary features, and they can be further strengthened if relevant osteological data and other lines of data converge on the same functional inference (Xu et al. 2011). For example, a coherent airfoil surface formed by close-vaned feathers may indicate a locomotory function if it is coincidently present in a long-armed theropod, an insulating layer formed by numerous slender filaments suggests an insulatory function, and display function can be achieved by striking colors, distinctive color patterns, or highly specialized shapes of various feathers. These three major functions all have been inferred to be present among nonavialan dinosaurs based on different lines of data (Chen et al. 1998; Evangelista et al. 2014; Feo et al. 2015; Han et al. 2014; Li et al. 2010, 2012, 2014; Xu and Guo 2009; Xu et al. 2014; Zhang et al. 2008).

Most researchers agree that the use of feathers for flight was the last major function that appeared out of the three major functions mentioned above (Ji et al. 1998), but that flight capability might have evolved early in paravian evolution instead of at the base of the Avialae or alternatively flight might have evolved even multiple times independently within the Paraves. This hypothesis suggests that even volant locomotion, a key feature previously used to define birds, is not restricted to birds (Brusatte et al. 2014; Xu and Guo 2009; Xu et al. 2003, 2011), and it is likely that feathers were exapted into a flight function from their initial uses for insulation and display/camouflage (Foth et al. 2014; Li et al. 2014; Xu and Guo 2009; Xu et al. 2009; Zhang et al. 2008, 2010). For example, a display function appeared early in coeluroaurian theropod evolution as indicated by the BMFIs in basal coelurosaurians such as *Yutyrannus* and *Beipiaosaurus* (Xu and Guo 2009; Xu et al. 2010b), and an insulatory function presumably
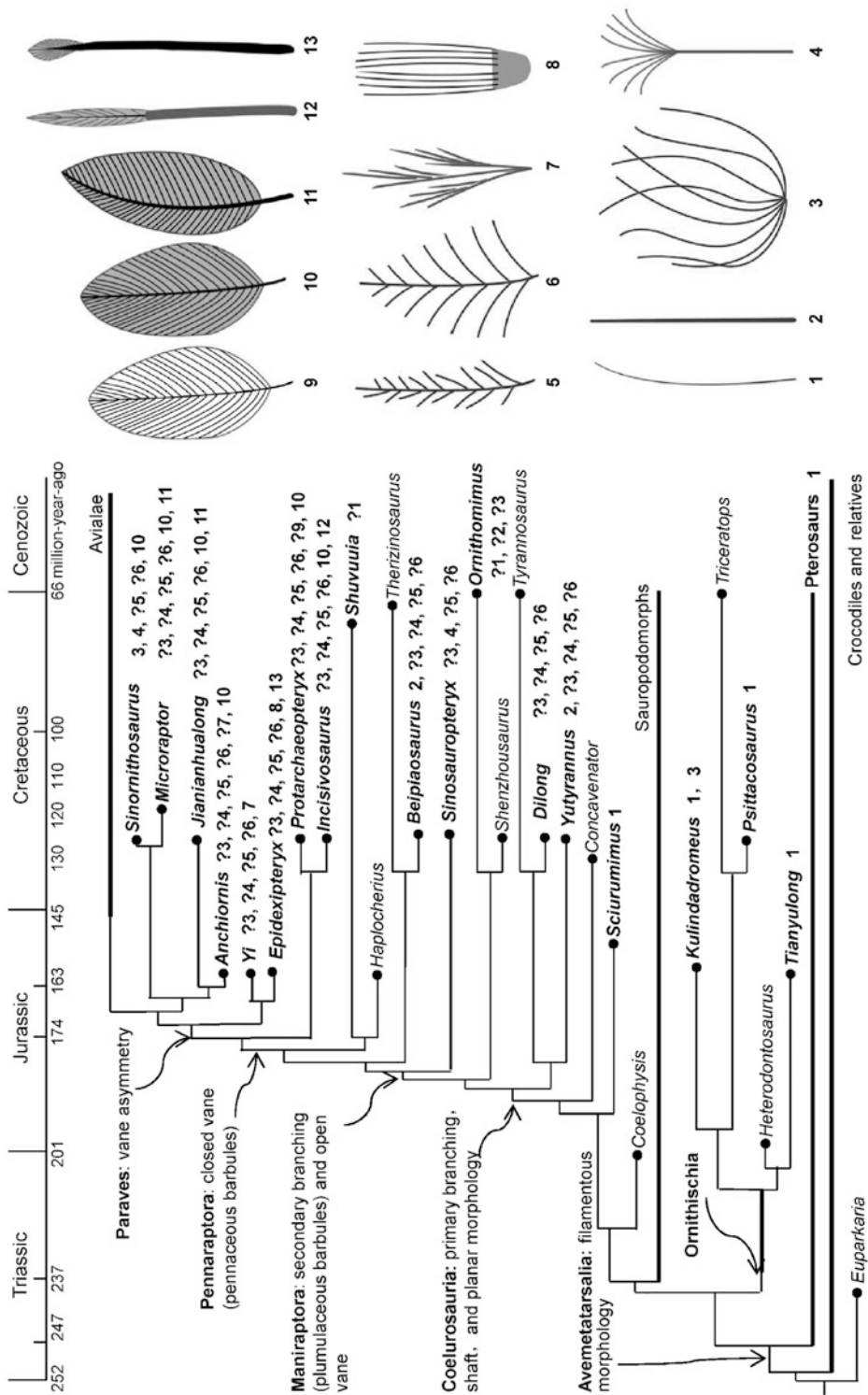
Fig. 5.4 Known feather-like or feather morphotypes across a simplified avemetatarsalian phylogeny. "?" indicates uncertainty regarding the presence of this particular morphotype in this group. 1, SMFF; 2, BMFF; 3, BJFF; 4, BJSFF; 5, RBSFF; 6, RBFF; 7, BJBFF; 8, BJMBFF; 9, SOVF; 10, SCVF; 11, ASVF; 12, PRCVF; 13, RDCVF

appeared early in tetanuran evolution (Rauhut et al. 2012), if not directly tied to the earliest feathers or feather-like structures.

5.4 Remaining Controversial/ Unresolved Issues in Feather Evolution

The evolutionary sequence of various feather morphologies occurring among different nonavialan dinosaurs is generally congruent with predictions based on a developmental model (Prum 1999). Along with that model, a clear evolutionary picture for feather origination and evolution is emerging, but there are still many remaining controversial and unresolved issues in feather evolution. For example, at what point in archosaurian phylogeny did the first feathers originate? How did the major microstructural features of feathers evolve? Did early feathers develop ontogenetically in the same way as modern feathers (from a follicle in a feather tract)? Did the major features of feathers appear incrementally in evolution, or did at least some appear simultaneously? And finally, what were the primary functions of various early feathers?

The discoveries of SMFIs in some theropods, several ornithischian groups and in some pterosaurs has led to the proposal of a hypothesis for feather origins in avemetatarsalians (Xu and Guo 2009; Xu et al. 2009; Zheng et al. 2009), suggesting that feathers represent a diagnostic feature of the Avemetatarsalia (a clade including both dinosaurs and pterosaurs). The alternative hypothesis, the theropod hypothesis for feather origin, suggests that feathers evolved only within Theropoda (Barrett et al. 2015). In this latter case, the SMFIs exhibited in some pterosaurs and ornithischians would have nothing to do with modern feathers, and they are just highly specialized integumentary appendages that evolved convergently in a closely related group. Whether the avemetatarsalian or the theropod hypothesis is more acceptable depends much on the identity (homology) of the SMFIs of

pterosaurs and ornithischians, and some exceptionally preserved pterosaurian fossils seem to provide strong evidence for the avemetatarsalian hypothesis (Yang et al. 2018).

Even though the avemetatarsalian hypothesis for the origin of feathers can be confirmed (or refuted) with additional specimens and data, the primary function for the first feathers remains unresolved. Clearly the earliest feathers were not used for flight purposes. While an insulatory function is plausible for the earliest and morphologically simplest feathers and feather-like structures, some morphological features seen among early feathers suggest that a display function is equally possible or even more likely. The SMFIs in *Tianyulong* and *Psittacosaurus* are long and rigid, and in the latter taxon have a limited distribution on the body. Furthermore, their density appears to be relatively low compared to that of the presumably insulative filamentous integumentary appendages in modern birds and mammals. Furthermore, the filamentous feathers in basal tetanurans are proportionally thick and fairly stiff in appearance (Currie and Chen 2001; Xu and Guo 2009). This rigidity suggests that display is a viable hypothesis for earliest function of feathers. The primary functions for some other types of feathers such as SCVFs and ACVFs also are debated. The SCVFs have been suggested to have performed various functions such as balancing during locomotion, aiding in the capture of insects, attracting females, or species signals among nonavialan dinosaurs. Among these functions, a display function has been favored more recently for the SCVFs of various basal pennaraptorans (Foth et al. 2014; Li et al. 2010) and even for the tail ACVFs of *Microraptor* (Li et al. 2012). While SCVFs in some basal paravians such as *Anchiornis* have been suggested to have functioned primarily for display (Foth et al. 2014; Li et al. 2010), they could have also been used in aerodynamic locomotion as indicated by coherent airfoil surfaces formed by the SCVFs, consistent with many other features that imply an aerodynamic function in basal paravians, including long and robust arms,

flight-adapted cerebral features, and significantly improved metabolism (Balanoff et al. 2013; Dececchi and Larrson 2013; Xu et al. 2014).

It is worthy of mention that a display function is particularly favored by melanosome data derived from several nonavialan theropod fossils (Li et al. 2010, 2012; Zhang et al. 2010). One study even suggests that melanosomes in wing feathers of *Archaeopteryx* might have strengthened *Archaeopteryx*'s feathers for flight (Carney et al. 2012). While the discoveries of fossilized melanosomes opened a new window into the Mesozoic ecosystems (Vinther et al. 2008), some other studies have cautioned the identification of microbodies preserved in fossils as fossilized melanosomes (Lindgren et al. 2015; Moyer et al. 2014). Nevertheless, no evidence has been presented so far to reject the identification of microbodies preserved in fossils as melanosomes. Fossilized melanosomes will continue to provide important data for us to understand various aspects of extinct animals and test different hypotheses regarding the primary functions and even biomechanics of early feathers.

Some uncertainties pertaining to feather evolution are the result of a lack of knowledge about the fine morphological features of various feathers or feather-like structures seen in nonavialan dinosaurs. For example, pennaceous barbules presumably are present in all close-vaned feathers of nonavialan theropods, but to date no direct evidence has been presented. The presence and morphologies of other types of barbules, such as plumulaceous barbules, also are poorly known among various feathers in nonavialan dinosaurs, resulting in a difficulty for the reconstruction of the evolutionary sequence of the rachis and related barbules. Compared to feathered dinosaur fossils from lacustrine deposits, feathers preserved in amber display much finer details which can be comparable to those in modern feathers (McKellar et al. 2011; Vincent 2008; Xing et al. 2016), but in most cases, these feathers are difficult to be placed phylogenetically, and thus their evolutionary implications are less than other larger phylogenetically constrained body fossils.

The lack of morphological details in some specimens also results in a key question remaining unresolved: the homologous relationships between some feather-like structures or various structures seen in the fossil feathers of nonavialan dinosaurs and those of modern feathers and their structures (Saitta et al. 2018). For example, it is not known whether the SMFIs and/or BMFIs are homologous to some types of modern feathers (e.g., the quill feathers in cassowaries (Prum 2005)) or to some parts of modern feathers such as the barbs or rachis. It is not known whether the membranous base of the BJMBFFs represents a type of structure absent among extant birds, or if it is homologous to certain parts of modern feathers (e.g., a large calamus), and we also do not know whether the ribbon-like portion of the PRCVFs are homologous to the tubular feather sheath of emergent feathers (Prum 2010) or to a long calamus of a unusual type of feather.

The developmental data from modern feathers have greatly improved our understanding of feather origin and diversification (Chu et al. 2014; Chuong et al. 2000, 2003, 2012; Jiang et al. 2011; Lin et al. 2013a, b; O'Connor et al. 2012; Prum 2005; Prum and Brush 2002; Widelitz et al. 2003; Wu et al. 2004; Yu et al. 2002; Yue et al. 2005, 2006, 2012) and in particular, recent data from fossil feathers (Norell and Xu 2005; Xu and Guo 2009; Xu et al. 2014) overall support the developmental model of the feather origin and evolution proposed by Prum (1999). However, the variable feathering in the tails of the tetanuran theropod *Juraventhat*, the ceratopsian ornithischian *Psittacosaurus*, and the early-diverging ornithischian *Kulindadromeus*, and in other parts of the body of some other dinosaurian taxa (e.g., the lower legs of the basal paravians, and the arms and tail of *Incisivosaurus* during different ontogenetic stages) suggests that there are some developmental differences between early feathers and modern feathers, and these early feathers seem to be less constrained and more flexible in some developmental features than modern feathers (Xu et al. 2010b). Consequently, while it is important to use developmental data from modern feathers to reconstruct the

evolutionary history of feathers, caution should be paid on such practices as the developmental features of feathers also evolved.

A better understanding of the origin and evolution of feathers requires a multidisciplinary approach. While new data from neontological morphology, developmental biology, and even comparative genomics have improved our understanding of the morphogenesis, development, and functions of feathers (Alibardi 2005; Chuong et al. 2000; Feo et al. 2015; Prum 2005; Seki et al. 2017), and additionally have provided broad insights into the evolution of feathers. However, it is important to emphasize here that the data from fossil specimens play a key role in reconstructing the evolutionary history of feathers by providing diverse morphological, developmental, phylogenetic, temporal, and other data not available from living species. Consequently, an increase in data from fossil feathers, derived from either the investigation of new fossil specimens or the application of new analytical or other techniques, will provide the final say in the ongoing research to develop an evolutionary model for feathers from their dinosaurian (or avemetatarsalian) origins to their modern diversity.

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