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The Earliest Feathers from the Lower Cretaceous Dabeigou Formation of North Hebei: Implications for the Early Evolution of the Jehol Biota

Qian Wu[1,2] | Qian-Nan Zhang[1,2] | Dang-Peng Xi[3]

[1]Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China | [2]University of Chinese Academy of Sciences, Beijing, China | [3]State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing, China

Correspondence: Qian-Nan Zhang (zhangqiannan@ivpp.ac.cn)

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1 | Introduction

1.1 | Yanliao to Jehol Biotas and Avian Origin

The origin and evolution of birds have long been a focal topic in paleontological research (Benton 2014). Over the past three decades, the Middle-Late Jurassic Yanliao Biota and Early Cretaceous Jehol Biota in Northeastern China have yielded an abundance of non-avian theropod dinosaur and early bird fossils, providing critical evidence for understanding avian origins and early evolutionary history (Zhou 2014; Xu et al. 2016, 2020; Sullivan et al. 2017). The Yanliao Biota, located across western Liaoning, northern Hebei, and southeastern Inner Mongolia, lasted from approximately 168 to 159 Ma, covering a period of about 10 million years (Xu et al. 2016). A variety of feathered theropods excavated from the Yanliao Biota document many transitional characteristics between non-avian theropods and birds. Notable examples include members of Anchiornithinae such as *Anchiornis* (Xu et al. 2009a), *Aurornis* (Godefroit et al. 2013a), *Caihong* (Hu et al. 2018), *Eosinopteryx* (Godefroit et al. 2013b), *Pedopenna* (Xu and Zhang 2005), *Serikornis* (Lefèvre et al. 2017), and *Xiaotingia* (Xu et al. 2011), as well as those of Scansoriopterygidae, for example, *Ambopteryx* (Wang et al. 2019), *Epidexipteryx* (Zhang et al. 2008b), and *Qi* (Xu et al. 2015). Although older than the Solnhofen limestone of Germany (Rietschel 1985; Wellnhofer et al. 2009), there are no definitive Aves fossils identified within the Yanliao Biota to date. The Jehol Biota, one of the most celebrated Early Cretaceous paleoecosys-

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tems, has produced numerous feathered non-avian theropods, many of which are closely related to birds. These include troodontids such as *Jianianhualong* (Xu et al. 2017) and *Jinfengopteryx* (Ji et al. 2005); dromaeosaurids like *Changyuraptor* (Han et al. 2014), *Microraptor* (Xu et al. 2000, 2003), *Sinornithosaurus* (Xu et al. 2001), *Wulong* (Poust et al. 2020), and *Zhenyuanlong* (Lü and Brusatte 2015); oviraptorosaurs such as *Caudipteryx* (Ji et al. 1998; Zhou and Wang 2000), *Incisivosaurus* (Xu et al. 2002, 2010), and *Protarchaeopteryx* (Ji et al. 1998); and more distantly related taxa including members of Therizinosauridae (Xu et al. 2009b; Pu et al. 2013), Compsognathidae (Ji and Ji 1996, 1997; Chen et al. 1998), and Tyrannosauroidea (Xu et al. 2004, 2012). Additionally, the Jehol Biota has contributed significantly to our understanding of early avian diversity, with taxa ranging from basal birds like *Confuciusornis*, *Jeholornis*, and *Sapeornis*, to abundant enantiornithines and basal ornithuromorphs (O'Connor 2020).

Due to volcanic activities and changes in depositional environment caused by the destruction of the North China Craton, there is a nearly 30-Ma time gap between the feathered Paraves of the Yanliao Biota and the early birds of the Jehol Biota (Xu et al. 2016). This temporal hiatus hinders our understanding of the evolution of some key avian characteristics, including the origin of modern contour feathers (Saitta et al. 2018). Stratigraphically, the Tiaojishan Formation of the Yanliao Biota is overlain by the Upper Jurassic Tuchengzi Formation and the volcanic rocks of the Zhangjiakou Formation, which underlie the Lower Cretaceous Dabeigou and Huajiying formations of the Jehol Biota (Xu et al. 2016). To date, only a few archosaur fossils have been reported from this period, notably *Chaoyangsaurus* (Zhao et al. 1999), *Xuanhuasaurus* (Zhao et al. 2006), and a dinosaur track (Lockley et al. 2006). The Huajiying Formation, located in the Sichakou Basin of Hebei Province, has produced the earliest Cretaceous fossil bird specimens worldwide (Yang et al. 2020). These fossils already exhibit the diversity of the major Mesozoic avian taxa, including basal pygostylians such as *Eoconfuciusornis* (Zhang et al. 2008a; Navalón et al. 2017); enantiornithines like *Cruralispennia* (Wang et al. 2017), *Eopengornis* (Wang et al. 2014), *Orienantius* (Liu et al. 2019), and *Protopteryx* (Zhang et al. 2000; Chiappe et al. 2019); and ornithuromorphs such as *Archaeornithura* (Wang et al. 2015). Therefore, exploring older strata, such as those of the Dabeigou Formation, is essential for uncovering more stem avian fossils. The Dabeigou Formation, underlying the Huajiying Formation, represents the lowest sedimentary strata of the Jehol Biota (Xu et al. 2016; Xi et al. 2019; Qin 2020), dating to approximately 135–130 Ma. It has yielded plenty of invertebrate fossils such as *Nestoria*, *Luanpingella*, and *Ephemeropsis* (Qin et al. 2017), as well as a few vertebrates, including "*Luanpingosaurus*" (Pang 1984), *Peipiaosteus* (Niu 2008), and *Regalerpeton* (Rong 2018). Notably, no theropod remains have been found to date within this unit.

Consequently, any discovery of feathered non-avian theropod or bird fossils in the Dabeigou Formation would provide critical insights into avian origin and evolution, as well as clarify the relationship between the Yanliao and Jehol biotas. Such findings could bridge the evolutionary gap and offer a more comprehensive understanding of the transition from non-avian theropods to early birds.

1.2 | Feather Categories in Non-Avian Theropod and Avian Fossils

Feathers are the distinctive integumentary structures of birds among living vertebrates (Zheng et al. 2012), and research on fossil feathers has long driven the study of fossil birds (O'Connor 2020). Indeed, over a century and a half ago, the discovery of a single feather led to the identification of *Archaeopteryx*, the oldest known bird (von Meyer 1861). Subsequent discoveries of more and more feathered dinosaur specimens have revealed that birds originated from theropod dinosaurs (Dyke and Kaiser 2011). At the same time, the shape and structure of feathers have undergone continuous changes and innovations during the evolution from theropod dinosaurs to birds (Foth and Rauhut 2020).

In extant birds, six main structural categories of feathers can be recognized, including contour feather, semiplume, down feather, filoplume, bristle, and powder feather (Zheng et al. 2012; Chatterjee 2015; Foth and Rauhut 2020). A contour feather can be further subdivided into remex (flight feather, including primary and secondary), rectrix (tail feather), and body contour feather (Chatterjee 2015). Additionally, developing feathers still encased in the feather shaft, known as pin feathers, exhibit some unique shapes during the growth process (O'Connor 2020). All these feathers together serve various functions, including aerodynamics, protection, thermal insulation, waterproofing, display, tactile sensation, and cleaning (Zheng et al. 2012; Foth and Rauhut 2020).

Many special integument or feather categories have been identified in feathered non-avian dinosaurs and early birds, including slender monofilamentous feathers (SMFIs), broad monofilamentous feathers (BMFIs), basally joining filamentous feathers (BJFFs), symmetrical open-vaned feathers (SOVFs), symmetrical close-vaned feathers (SCVFs), asymmetrical close-vaned feathers (ASVFs), proximally ribbon-like close-vaned feather (PRCVF), rachis-dominant close-vaned feather (RDCVF), basally joining shafted filamentous feathers (BJSFFs), basally joining membranous-based filamentous feathers (BJMBFFs), radially branched shafted filamentous feathers (RBSFFs), bilaterally branched filamentous feathers (BBFFs), basally joining branched filamentous feathers (BJBFFs), rachis-dominated feathers (RDFs), proximally wire-like part with a short filamentous distal tip (PWFDTs), scutellate scale filaments (SSFs), isolated bristle-like filaments (IBFs), and shaggy bifurcated contour feathers (SBCFs) (Wang et al. 2017; Xing et al. 2017, 2019; Saitta et al. 2018; Xu 2020). However, the overlap of feathers preserved on skeletal fossils often prevents accurate identification of morphology, leading to debates regarding the validity of new feather types. For instance, the presence of "protofeathers" in dinosaurs has been a contentious topic (Currie and Chen 2001; Mayr et al. 2002; Feduccia 2006; Lingham-Soliar et al. 2007, 2010).

Isolated feathers have been reported worldwide (Table 1). Due to the difficulty in determining their taxonomic affinity, their research significance has not received sufficient attention (Foth and Rauhut 2020). Consequently, detailed studies on isolated feathers are relatively limited (Perrichot et al. 2008), with notable exceptions such as those conducted on *Archaeopteryx* specimens

TABLE 1 | Record of Mesozoic dinosaurian feather and integument (modified from Davis and Briggs [1995] and Chiappe and Witmer [2002]).

Locality	Geological age	Depositional environment	Feather elements	Mode of preservation	Related species and taxa	Reference
Grassy Lake, southern Alberta, Canada	Late Cretaceous, Campanian	Terrestrial	Isolated feathers	Amber	Non-avian dinosaurs	Pike (1992); Chiappe and Witmer (2002); McKellar et al. (2008, 2011)
Taldysay, Kazakhstan	Late Cretaceous, Santonian—?Campanian	Estuarine	One contour feather	—	*Cretaaviculus sarysuensis*	Nessov (1992)
Kras region, southwestern Slovenia	Late Cretaceous, Santonian—Campanian	Lagoonal	Isolated feather	Carbonized residue		Buffetaut et al. (2002)
Hatanga River, northern Siberia, Russia	Late Cretaceous, Santonian	Terrestrial	Isolated feather	Amber		Kurochkin (1985); Nessov (1992); Chiappe and Witmer (2002)
Kuji, Japan	Late Cretaceous, Santonian	Terrestrial	Isolated feather	Amber		Grimaldi and Case (1995)
Southwest China	Late Cretaceous, Turonian—Santonian	Lacustrine	Feathers associated with skeleton	Carbonized residue	*Parvavis chuxiongensis*	Wang et al. (2014)
Tjulkeli, Kazakhstan	Late Cretaceous, upper Turonian—Coniacian	Estuarine	Isolated feather	—		Nessov (1992); Chiappe and Witmer (2002)
New Jersey, USA	Late Cretaceous, Turonian	Terrestrial	Isolated feathers	Amber		Grimaldi and Case (1995); Chiappe and Witmer (2002)
Alberta, Canada	Late Cretaceous	Fluvial	Filaments with skeletons	Carbonized residue	*Ornithomimus*	Zelenitsky et al. (2012)
Northeast Beirut, Lebanon	Late Cretaceous, Late Middle Cenomanian	Marine	Feathers with skeleton	Carbonized residue	*Enantiophoenix electrophyla*	Dalla Vecchia and Chiappe (2003); Cau and Arduini (2008)
Kachin State, Myanmar	Mid Cretaceous	Terrestrial	Isolated feathers and feathers associated with skeleton	Amber		Grimaldi et al. 2002; Xing et al. (2016, 2017, 2019, 2020)
Charente-Maritime, western France	Early Cretaceous, Late Albian	Estuarine	Isolated feathers	Amber		Perrichot et al. (2008)

(Continues)

TABLE 1 | (Continued)

Locality	**Geological age**	**Depositional environment**	**Feather elements**	**Mode of preservation**	**Related species and taxa**	**Reference**
Changma Basin, northwestern China	Early Cretaceous, Aptian	Lacustrine	Feathered skeleton and isolated feathers	Carbonized residue	*Feitianius*, *Gansus*	You et al. (2006); O'Connor et al. (2012, 2016)
Araripe Basin, northeastern Brazil	Early Cretaceous, Aptian	Lacustrine	Isolated feathers and feather with skeleton	Carbonized residues	Euenantiornithes	Martill and Frey (1995); Kellner (1996); Martill and Davis (2001); Sayão et al. (2011); de Souza Carvalho et al. (2015); Prado et al. (2016)
Ordos Basin, Inner Mongolia, China	late Early Cretaceous	Lacustrine?	Remiges associated with one skeleton	Carbonized residue	*Otogornis*	Dong (1993); Hou (1994); Li et al. (2008)
Las Hoyas, Spain	Early Cretaceous, Barremian	Lacustrine	Isolated contours feathers associated with skeletons	Carbonized residue	*Concornis, Eoaluavis*	Sanz et al. (1988, 1995, 1996); Sanz and Buscalioni (1992); O'Connor (2020)
Korumburra Group Koonwarra, Australia	Early Cretaceous, Barremian—Aptian	Lacustrine	Isolated semiplumes and body feathers	Carbonized residue		Waldman (1970); Chiappe and Witmer (2002)
Central Mongolia	Early Cretaceous	Lacustrine	Contour feather and feathers with skeleton	Carbonized residue	*Ambiortus, Holbotia*	Kurochkin (1985); Chiappe and Witmer (2002); Zelenkov and Averianov (2016)
Gurvan-Eren site, west Mongolia	Early Cretaceous, Barremian	Lacustrine	One remex, one rectrix, one down feather, several contour feathers	Carbonized residue		Kurochkin (1982, 1985); Chiappe and Witmer (2002)

(Continues)

TABLE 1 | (Continued)

Locality	Geological age	Depositional environment	Feather elements	Mode of preservation	Related species and taxa	Reference
Transbaikalia, Russia	Early Cretaceous, Hauterivian—Barremian	Lacustrine	Several contour feathers (one remex, body feathers)	Carbonized residue		Kurochkin (1985)
Jezzine, Lebanon	Early Cretaceous, Hauterivian	Terrestrial	Two contour feathers	Amber		Schlee (1973); Chiappe and Witmer (2002)
Jehol Biota, northeastern China	Early Cretaceous, Tithonian—?Berriasian	Lacustrine	Isolated feathers and feathers associated with skeleton	Carbonized residue	Stem birds, Enantiornithes, Ornithuromorpha, non-avian dinosaurs	Zhang et al. (2008); O'Connor (2020); Xu (2020)
La Pedrera de Mei locality, Sierra del Montsec, Spain	Early Cretaceous, Berriasian—Valanginian	Lacustrine	Isolated feathers and feathers associated with the skeleton	Carbonized residue	*Noguerornis*, enantiornithine hatchling	Chiappe and Lacasa-Ruiz (2002)
Kulinda Locality, Siberia, Russia	Middle to Late Jurassic	Lacustrine	Skeleton with scales and filamentous integuments	Carbonized residue	*Kulindadromeus*	Godefroit et al. (2014)
Solnhofen, Germany	Late Jurassic	Lagoonal	Isolated feather and feathers associated with the skeleton	Impression	*Archaeopteryx*	Rietschel (1985); Wellnhofer et al. (2009)
Karatau Range, Kazakhstan	Late Jurassic	Lacustrine	Isolated feathers	Carbonized residue	*Praeornis*	Rautian (1978); Dzik et al. (2010)
Yanliao Biota, northeastern China	Late Jurassic	Lacustrine	Remiges, covert, and rectrices associated with the skeleton	Carbonized residue	*Anchornis* and other non- avian dinosaurs	Xu et al. (2016)

(Carney et al. 2012; Kaye et al. 2019). However, isolated feathers can display the feather morphology more accurately than those found overlapping on the skeleton, making them highly valuable for studying the morphological evolution of feathers. Integrating information obtained from both feathered skeletal specimens and isolated feathers can provide important clues for the origins and evolution of birds. For example, it was in an isolated feather that the shaggy bifurcated contour feather of *Anchiornis* was identified (Saitta et al. 2018).

2 | Geological Settings

The Luanping Basin, located on the northern periphery of the North China Craton within the Yanshan belt, is a well-exposed Early Cretaceous active rift basin. Its formation is attributed to the uprising of asthenospheric materials along a lithospheric-scale tear fault, triggered by slab tearing of the subducting Paleo-Pacific plate (Wu et al. 2000; Wei et al. 2012; Zhu et al. 2020; Qin et al. 2024). The Lower Cretaceous strata in the Luanping Basin are completely preserved and form a relatively continuous, typical continental sequence. This stratigraphic succession serves as a basic stratigraphic framework for understanding contemporaneous fluvial-lacustrine deposits across North China (Tian et al. 2004; Wan et al. 2013; Xi et al. 2021).

The Lower Cretaceous sedimentary rocks exposed in the Luanping Basin consist of several formations, in ascending order: the Tuchengzi, Zhangjiakou, Dabeigou, Dadianzi, Xiguayuan, Nandian, and Qingshila formations (Tian et al. 2008; Wang and Ji 2009; Wang et al. 2013; Xi et al. 2021). These formations provide critical insights into the depositional environments and tectonic evolution of the region during the Early Cretaceous. The distribution of the Dabeigou Formation is limited to the area east of the Yanshan Fault Zone (Zhou et al. 2021). This formation is characterized by a high tuffaceous content, with the main lithology being grayish-green tuffaceous sandy conglomerates, sand shales, and marls (Qin et al. 2017).

The studied section exposes a well-developed sequence of the Dabeigou Formation, characterized by relatively high tuffaceous content and abundant *Nestoria* conchostracans. These features are consistent with the typical lithological and paleontological characteristics of this unit. In this region, the Dabeigou Formation is subdivided into three members (Qin et al. 2017). The lower member consists mainly of tuffaceous sandstones, transitioning upward into mudstones at its top. The second member is characterized by siliceous shales and mudstones interbedded with volcanic ash layers and is rich in conchostracan fossils. The upper member comprises siliceous mudstones dominated by ostracod assemblages and exhibits poorly developed bedding.

Within this sequence, the fossil-bearing horizon studied herein occurs as a dark gray, fossil-rich shale interval that yields abundant *Nestoria* and *Ephemeropsis*, some plant debris, bivalves, and ostracods, as well as rare feathers attributable to non-avian dinosaurs or early birds reported in this research. Based on lithology, fossil assemblage, and stratigraphic position, this fossiliferous horizon is confidently assigned to the middle member of the Dabeigou Formation.

Our field geological surveys confirm that the horizon is conformably underlain by volcanic rocks of the Zhangjiakou Formation and glutenites of the Tuchengzi Formation. At the uppermost exposure of the section, conglomerates diagnostic of the basal Dadianzi Formation are observed (Figure 1). No major erosional or depositional hiatus is evident at these contacts, supporting the interpretation of a continuous Early Cretaceous depositional system. The age of the fossil-bearing horizon is inferred to be approximately 132 Ma, based on regional stratigraphic correlation with dated sections of the Dabeigou Formation (Wang et al. 2015; Qin et al. 2017; Zhou et al. 2021). This horizon predates the Huajiying Formation in the Sichakou Basin and thus represents the earliest known physical fossil record of feathered theropods (including birds) within the Jehol Biota.

3 | Materials and Methods

The new specimens described here were recovered from the Lower Cretaceous Dabeigou Formation in Luanping, Hebei Province, Northeast China (Figure 1). These two isolated feathers were collected first-hand by the authors and other staff members from IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China) during fieldwork in 2020. Since then, they have been stored in the collection of IVPP.

The specimens are described in detail using standard comparative anatomical techniques. The terminology used in this research follows Lucas and Stettennheim (1972). SEM (scanning electron microscopy) imaging and EDS (energy-dispersive x-ray spectroscopy) mapping scan were conducted using a Merlin Compact ultra-high resolution field emission scanning electron microscope at IPC (Technical Institute of Physics and Chemistry, Chinese Academy of Science, Beijing, China). The SEM analyses were performed on an FEI Quanta 450 (FEG) operating at 20 kV under low vacuum conditions.

4 | Results

4.1 | Specimen IVPP V 33670

The pennaceous feather preserved on the slab and contour-slab exhibits a typical morphology, characterized by a stiff rachis and tightly interlocking barbules (Figure 2; Lucas and Stetttenheim 1972). The specimen is approximately 27 mm in length, with its widest part at the base (2.4 mm), gradually tapering upward, resulting in an aspect ratio of about 11.3 (Table 2). The rachis is slightly curved to one side (Figure 2A,E). The light color at the base indicates a hollow rachis (Figure 2D). The rachis is about 0.56 mm wide at the base, narrowing progressively toward the tip (Table 2). The calamus is not fully preserved.

The upper half of the vanes clearly displays a pennaceous structure (Figure 2A), with the leading and trailing vanes showing slight asymmetry (Table 2). Specifically, the leading vane is narrower than the trailing vane, with an asymmetry ratio (trailing vane width/leading vane width) of about 1.1. The lower barbs are

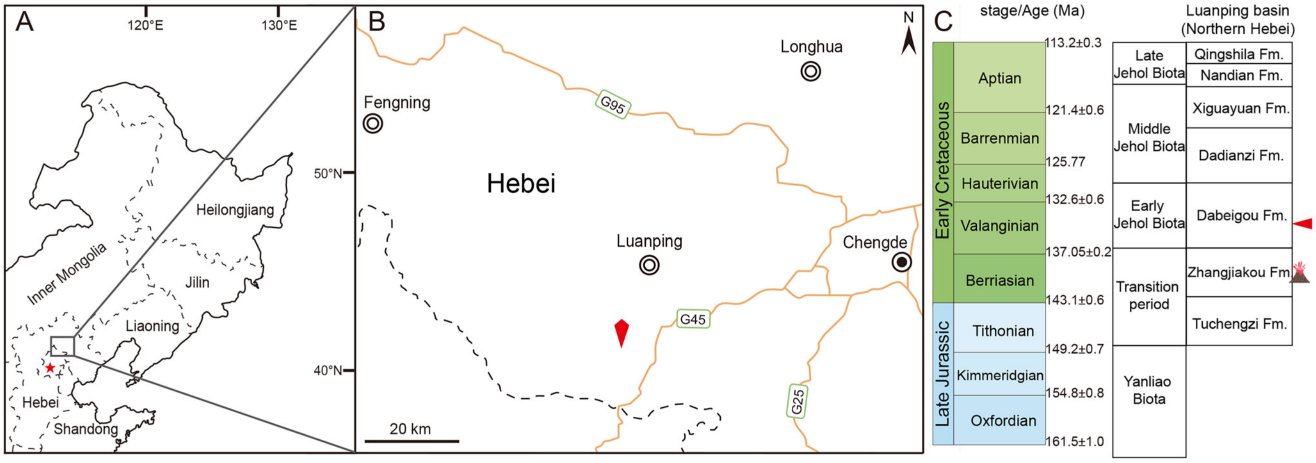

FIGURE 1 | Locality of the new specimens and stratigraphic context of their collection. (A) Northeastern China (red star for Beijing); (B) Luanping area (red arrow for fossil locality); (C) stratigraphic distribution (red arrow for fossil horizon, division of strata based on Tian et al. 2004).

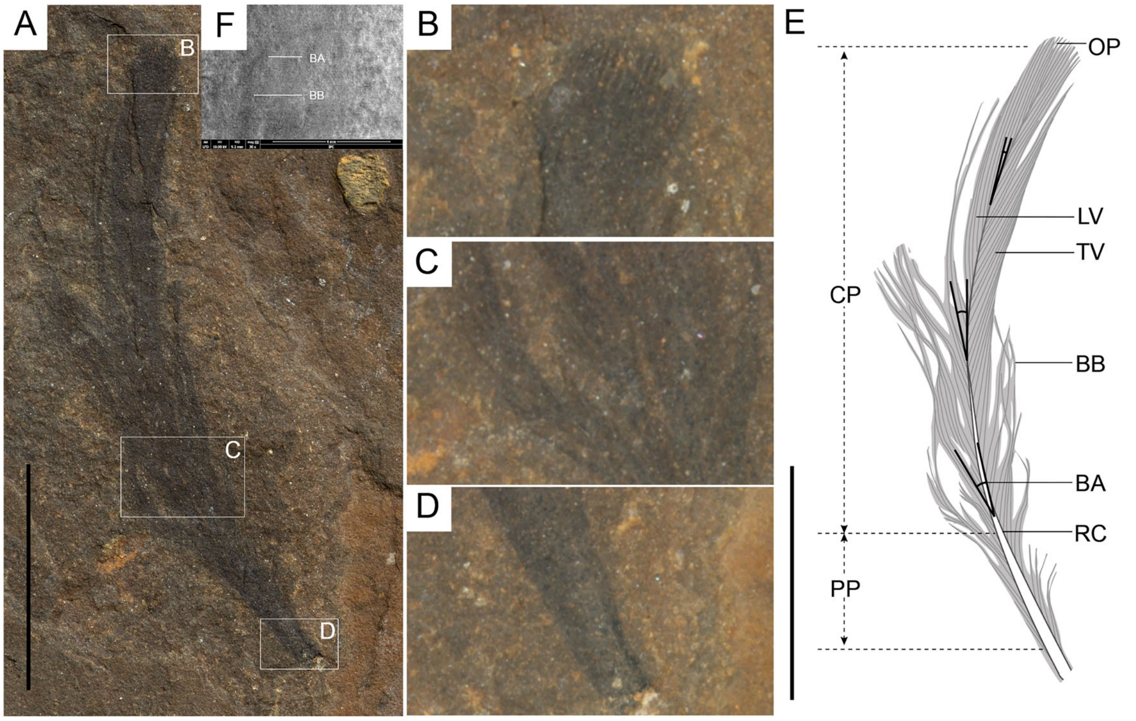

FIGURE 2 | Specimen IVPP V 33670. (A) Photo of the specimen; (B) detail of the open vane tip, as indicated by the upper white box in (A); (C) detail of the proximal plumulaceous portion, as indicated by the middle white box in (A); (D) the light color inside indicated the hollow proximal portion of the rachis, as indicated by the lower white box in (A); (E) interpretative drawing of the specimen; (F) SEM image showing the barb and barbule. BA, barb angle; BB, barb; CP, closed pennaceous vane; LV, leading vane; OP, open vane tip; PP, proximal plumulaceous; RC, rachis; TV, trailing vane. Scale bar = 1 cm.

dispersed from each other and do not form a closed pennaceous vane but instead exhibit a proximally plumulaceous appearance (Figure 2C). The tangled, soft barbs likely provided insulative function, which would be compatible with heat retention, possibly supporting elevated metabolic rates. In contrast, the middle to upper barbs are arranged in parallel and tightly packed sets, forming distinct pennaceous vanes (Figure 2A,E). This indicates the presence and interconnection of barbules, with the barb angle gradually decreasing from bottom to top (Table 2). The leading barb angle is consistently smaller than the trailing barb angle, with the asymmetry ratio (trailing /leading) increasing progressively (Table 2).

Based on its pennaceous morphology, slightly curved rachis, proximal plumulaceous region, closed vanes with open and round tips, IVPP V 33670 can be interpreted as a body contour type among the contour feathers, possibly from the lateral side of the bird's body (Chen et al. 2015) or as a covert feather from

TABLE 2 | Measurements of the specimen IVPP V 33670.

	Total	Tip (distal)	Upper 1/4	Middle	Lower 1/4	Proximal
Total length (mm)	27.095					
Width (mm)	2.398	1.825	2.371	2.387	2.398	
Rachis width (mm)					0.260	0.598
Leading vane width (mm)		0.900	1.111	1.133	1.021	
Trailing vane width (mm)		0.925	1.260	1.254	1.117	
Ratio of asymmetric (trailing/leading)		1.028	1.134	1.107	1.094	
Aspect ratio	11.299					
Leading barb angle			6.375	13.137	16.906	
Trailing barb angle			12.009	18.906	21.238	
Barb angle asymmetry (trailing/leading)			1.884	1.439	1.256	

the wing of a paravian theropod. A detailed analysis of the taxonomic affinity of the specimen is provided in the Discussion section. Such feathers would have served multiple functions such as protection, thermoregulation, individual identification, and aerodynamics (Zheng et al. 2012).

4.2 | Specimen IVPP V 33671

The specimen IVPP V 33671 does not conform to the typical morphology of extant feathers (Lucas and Stetttenheim 1972) but instead resembles the branched filaments observed in non-avian theropods (Perrichot et al. 2008; Xu 2020). The specimen is approximately 16 mm in length and 2 mm in width. Several rachises of varying lengths emanate from a common base, though the calamus is not preserved (Figure 3). All rachises are bent toward the same side (Figure 3A). The shorter rachises attached to the base are relatively slender (Figure 3C) and also bear branched barbs, resembling the afterfeather found in extant contour feathers (Lucas and Stetttenheim 1972; Stettenheim 2000).

Mesozoic afterfeathers are rarely documented in the literature, having been previously reported only in *Protopteryx* (Zhang et al. 2000) and as an isolated feather from the Santana Formation of the Araripe Basin (Lower Cretaceous), northeastern Brazil (Prado et al. 2016). Another type of integument featuring multiple radiating filaments has been described in the isolated feather of *Qi yi*, a member of Scansoriopterygidae (Xu et al. 2015). However, the randomly branched body integument of *Qi yi* is inconsistent with IVPP V 33671.

The barbs on the rachises are distributed on the same side and do not interlock to form a clear vane (Figure 3). These barbs are secondarily branched into barbules (Figure 3B); however, the thickness difference between barbs and barbules is not clearly defined, and the distribution of barbules on the barbs is uneven (Figure 3B), differing from the structure of extant feathers (Lucas and Stetttenheim 1972). Afterfeathers similarly possess branched barbs and barbules (Figure 3C). Due to preservation, the intersection between the rachis and the branches is not clear enough for precise measurement.

5 | Discussion

5.1 | Taphonomy of Feather Fossils

Both specimens are preserved as carbon films (Figure 4), a typical preservation mode for feathers among the five main types according to Davis and Briggs (1995): carbonized residues, bacterial autolithification, imprintation, amber, and coprolites. In the SEM observations, areas with carbon residues show cracking that does not exist in the surrounding sediment (Figure 4A,C). EDS analysis reveals that the carbon films have higher concentrations of C, Si, and O, while other elemental compositions do not significantly differ from those of the surrounding sediment (Figure 4E–G). At higher magnification, no typical melanosome structures are observed (Figure 4B,D).

Isolated feathers and feather-like integuments associated with skeletons have been discovered in a variety of depositional environments worldwide, including terrestrial, estuarine, lacustrine, fluvial, and marine settings (Davis and Briggs 1995; Chiappe and Witmer 2002) (Table 1). Most of these fossils are preserved as two-dimensional carbonized residues or impressions in limestone, shale, and claystone. Some found in amber have retained three-dimensional structures (Perrichot et al. 2008; Xu et al. 2016; Xing et al. 2017). Bacterial glycocalyx has been proposed to play an important role in feather preservation (Davis and Briggs 1995), while melanization is suggested to be a leading factor in the preservation of organic integuments in these fossils (Roy et al. 2019). In the Yixian Formation, which has yielded numerous beautiful Mesozoic birds and non-avian theropod specimens with various integument structures, volcanic activities in combination with less fluvial interference are supposed to have contributed to the preservation of soft tissues (Zhou and Zhang 2007; Jiang et al. 2017).

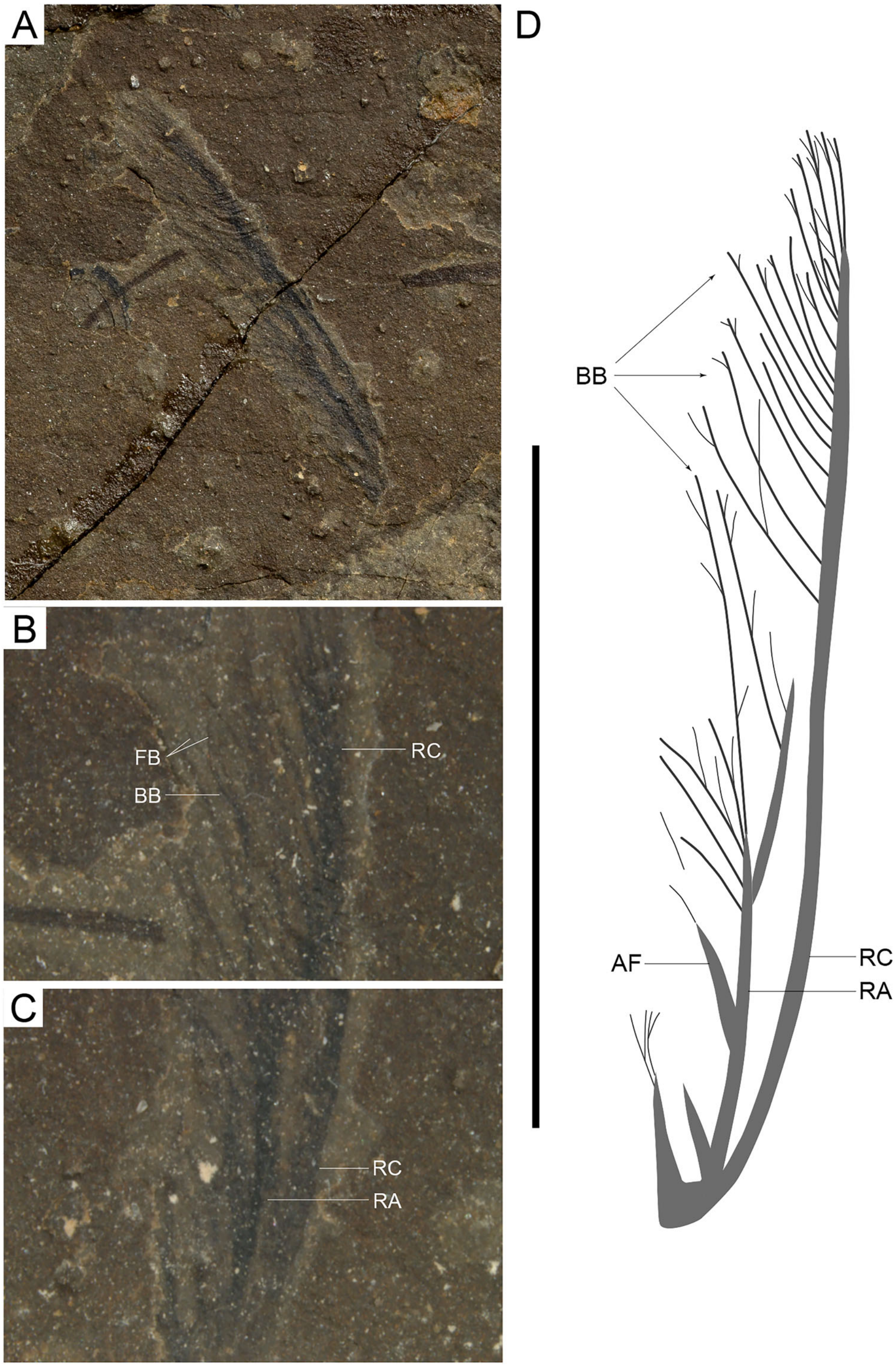

FIGURE 3 | Specimen IVPP V 33671. (A) Photo of the specimen; (B) magnification of (A), showing the rachis and forficate barbs; (C) magnification of (A), showing the rachis and rachis of afterfeather; (D) interpretative drawing of the specimen. AF, after feather; BB, barble; FB, forficate barbs; RA, rachis of afterfeather (aftershaft); RC, rachis. Scale bar = 1 cm.

Keratin, melanosomes, and fibril-like microstructures are preserved in many feather specimens, providing valuable information for reconstructing fossil animals. In the Yanliao and Jehol biotas, substantial evidence for the existence of melanosomes has been found, such as in *Anchiornis* (Lindgren et al. 2015) from the Tiaojishan Formation, *Eoconfuciusornis* from the Huajiying Formation (Pan et al. 2016), *Sinornithosaurus* from the Yixian Formation (Zhang et al. 2010), and other isolated feathers from the Jehol Biota (Zhang et al. 2010). In existing birds, melanosomes are embedded within keratin and cannot be directly observed using SEM (Moyer et al. 2014); unless the keratin is partially degraded, the melanosomes would not be exposed (Zhao et al. 2020). Experimental simulations have revealed that as temperature increases, barbules start to fuse, and feathers become

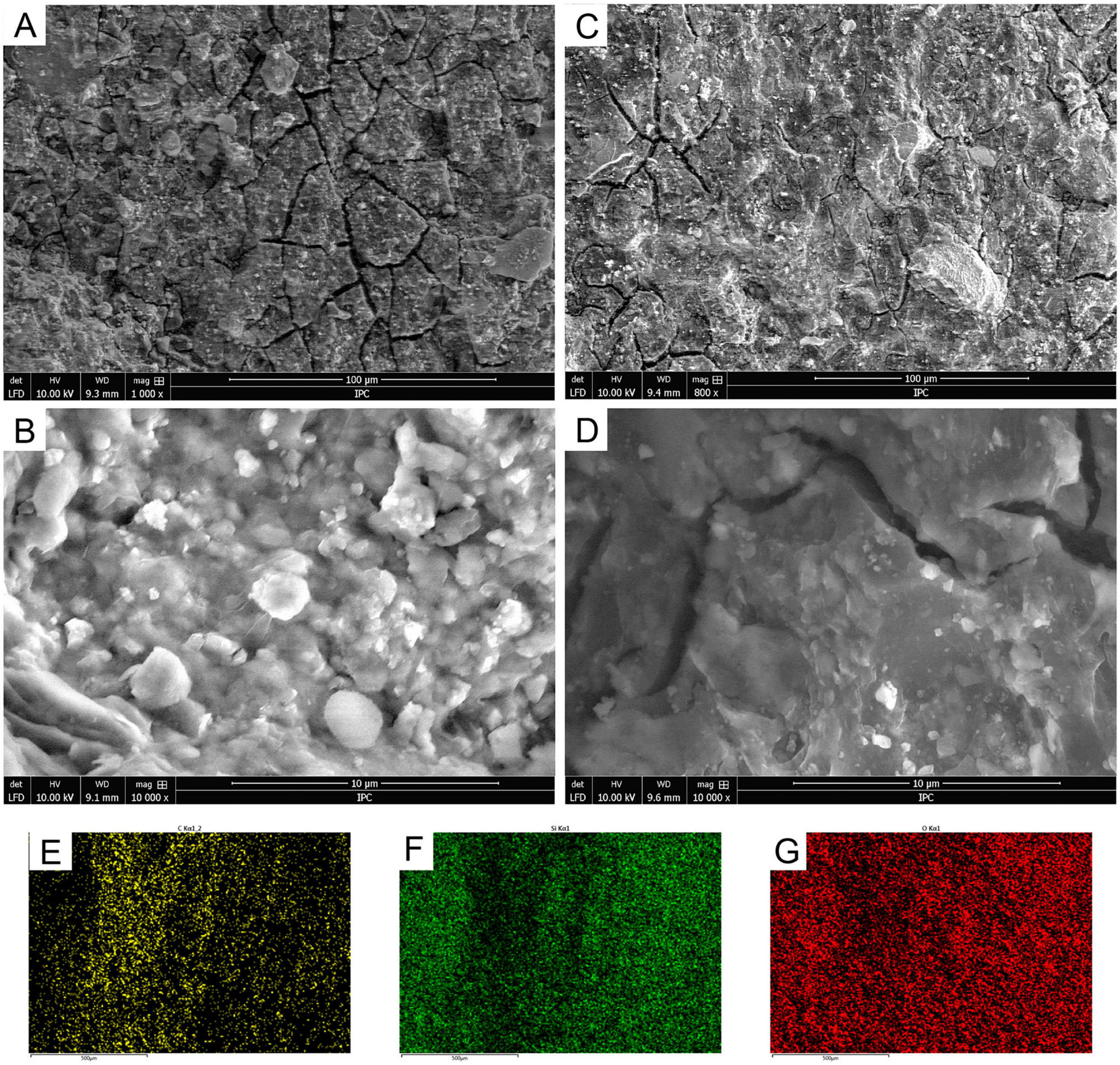

FIGURE 4 | SEM images of specimens IVPP V 33670 and IVPP V 33671, and EDS analysis of specimen IVPP V 33670. (A) SEM image of specimen IVPP V 33670, showing the crushed carbonic trace and the surrounding sediment; (B) magnification of (A); (C) SEM image of specimen IVPP V 33671, showing the crushed carbonic trace and the surrounding sediment; (D) magnification of (C); (E–G) EDS element mapping of specimen IVPP V 33670 in Figure 2F.

carbonized, leaving organic stains on the matrix (Roy et al. 2020; Zhao et al. 2020). If temperatures continue to rise, keratin will be partially destroyed, exposing the embedded melanosomes (Zhao et al. 2020). Under extremely high temperatures (over 300°C), only a negative impression remains on the matrix (Roy et al. 2020; Zhao et al. 2020).

The darker color of both specimens (Figures 2 and 3) suggests that they were not exposed to extremely high temperatures after they were buried, so there are still organic residues remaining. Under SEM observation, the original feathers of the two specimens are represented as crushed carbonized residues, which contain significantly higher concentrations of C, Si, and O compared to the surrounding sediment (Figure 4). High-magnification SEM observations do not reveal melanosomes, further indicating that the post-burial temperatures were relatively low (possibly below 250°C; Zhao et al. 2020), and the keratin has not been sufficiently degraded to expose the embedded melanosomes (Moyer et al. 2014; Zhao et al. 2020).

5.2 | Taxonomic Affinity of Specimen IVPP V 33670

According to the current findings, pennaceous feathers generally existed in pennaraptorans (Foth and Rauhut 2020) with few exceptions, while the integumentary structures described as "feathers" found in various dinosaurs are actually filaments and may be irregularly branched, examples including *Juravenator* (Chiappe and Göhlich 2010) and *Sinosauropteryx* (Chen et al. 1998; Currie and Chen 2001; Ji et al. 2007) of Compsognathidae, *Pelecanimimus* (Pérez-Moreno et al. 1994) of Ornithomimosauria, *Dilong* (Xu et al. 2004) and *Yutyrannus* (Xu et al. 2012) of Tyrannosauroidea, as well as some non-theropod dinosaurs, including *Kulindadromeus* (Godefroit et al. 2014), *Psittacosaurus* (Mayr et al. 2002, 2016), and *Tianyulong* (Zheng et al. 2009). Similar structures have also been observed in pterosaurs (Yang et al. 2019). However, these filaments lack rachis and vanes, which are typical characteristics of pennaceous feathers (Lucas and Stetttenheim 1972; Stettenheim 2000). Consequently, their morphologies are obviously different from our specimen (Figure 3). While there have been reports of pennaceous feathers in the ornithomimosaur *Ornithomimus* (Zelenitsky et al. 2012), this speculation is based on bone traces believed to be impressions of calami rather than direct evidence of feather structure. Therefore, we adopt a more conservative stance and consider that pennaceous feathers are primarily present in pennaraptorans.

Pennaraptora encompasses several clades, including Troodontidae, Dromaeosauridae, Oviraptoridae, Scansoriopterygidae, and Aves (Foth et al. 2014). Among these, troodontids, dromaeosaurids, and oviraptorids usually cover most of their body with shorter plumulaceous integuments, while larger pennaceous feathers are found on the back of the limbs and the tails (Lefèvre et al. 2020), as reported in *Anchiornis* (Hu et al. 2009; Longrich et al. 2012), *Caudipteryx* (Ji et al. 1998), and *Microraptor* (Xu et al. 2003). The plumulaceous structures covering the body surface exhibit various forms, ranging from single filaments (Stage I of feather evolution) to those branched from the base or rachis (Stage II or III of feather evolution) (Prum and Brush 2002) (Figure 5). Their pennaceous feathers are similar to those of birds, with shafts and parallel barbs forming closed or open vanes (Lefèvre et al. 2020). In some species considered capable of gliding flight, such as *Anchiornis* and *Microraptor*, these pennaceous feathers are asymmetrical and accompanied by smaller covert feathers, as in *Archaeopteryx* (Longrich et al. 2012). They also have a certain molting sequence similar to modern birds (Kiat et al. 2020). The troodontid *Caihong* has been reported to possess pennaceous body contours, but these are only distributed locally on the skull and neck, together with down-like body contours. Most of its body integuments remain simple, branched rather than forming vanes along the rachis (Hu et al. 2018).

Scansoriopterygids differ from other pennaraptoran theropods. Besides non-pennaceous plumulaceous structures covering the body, only ribbon-like feathers with central rachis and vanes have been found on the tail of *Epidexipteryx* (Zhang et al. 2008b). The nature of these unique feathers remains controversial, possibly representing pin feathers during development (Foth 2012). Notably, unlike other volant pennaraptorans, including birds, scansoriopterygids relied on membranous wings to fly (Wang et al. 2019), which might explain the absence of strong remiges on the limbs.

Among Mesozoic birds, it was originally widely believed that they had pennaceous feathers on the forelimbs, hindlimbs, and tails, while body feathers were also rachis-less down feathers similar to those of non-avian dinosaurs (O'Connor et al. 2012; Wang et al. 2014, 2015, 2017). However, along with the discoveries of new specimens and re-examinations of old materials, some controversies have begun to arise about the morphology of early bird body feathers recently (O'Connor 2020). Reports suggest that in *Archaeopteryx* (Foth et al. 2014) and some enantiornithines (Xu et al. 2016; Xing et al. 2017), body integuments are also pennaceous, with their down-like appearances resulting from taphonomic alterations (Foth 2012). Overlapping and small size of these body feathers, combined with the diagenetic alterations, make it difficult to identify rachis and vanes, which sparks debates about the recognition of morphological details (Kundrát 2004; Foth 2012; Saitta et al. 2018; Foth and Rauhut 2020).

The size of IVPP V 33670 is significantly smaller than the remiges and rectrices of early birds found in the overlying Huajiying Formation, such as in *Archaeornithura* (Wang et al. 2015), *Cruralispenni* (Wang et al. 2017), *Eoconfuciusornis* (Zhang et al. 2008a), *Eopengornis* (Wang et al. 2014), *Orienantius* (Liu et al. 2019), and *Protopteryx* (Zhang et al. 2000; Chiappe et al. 2019). However, it is longer than their supposed "down-like" body contours, indicating it belongs to an animal with a larger body size if it is a pennaceous body contour. Compared to other Mesozoic early birds and non-avian theropods found worldwide (Lefèvre et al. 2020; O'Connor 2020; Xu 2020), IVPP V 33670 is also smaller than their remiges and rectrices but comparable in size to the pennaceous feathers on the hindlimb of *Archaeopteryx* (Longrich 2006; Wellnhofer et al. 2009; Foth et al. 2014), coverts of *Anchiornis* (Longrich et al. 2012), feather-like contours on the femurs of *Microraptor* (Xu et al. 2000), major coverts on the forearms of *Zhenyuanlong* (Lü and Brusatte 2015), and feathers on the forelimbs of *Caudipteryx* (Ji et al. 1998). The slightly curved rachis and vane asymmetry are related to aerodynamic function (Carney et al. 2020). In conclusion, based on the current evidence, it is not yet possible to determine the precise taxonomic affinity of IVPP V 33670. However, its morphology is consistent with two interpretations presented in the descriptive section: It may represent a body contour feather from the lateral side of an early bird, or a covert feather from the wing of a non-avian paravian theropod. In either case, the specimen most likely derives from a volant paravian (Figure 5).

5.3 | The Earliest Theropod Remains of Jehol Biota

The most important fossils of the Jehol Biota occur in three key stratigraphic units: the 130.7 Ma *Protopteryx*-horizon of the Huajiying Formation, the 125 Ma Yixian Formation, and the 120 Ma Jiufotang Formation (the latter two forming the strictly-considered Jehol Group) (Pan et al. 2013). The Dabeigou Formation, dating back to 135–130 Ma, represents the earliest strata preserving the Jehol Biota (Xu et al. 2016; Xi et al. 2019; Qin 2020). This formation has previously yielded a few tetrapod specimens, such as "*Luanpingosaurus*" (Pang 1984; Wang 1986) and *Regalerpeton* (Rong 2018). The discovery of two isolated fossil feathers further confirms that the Dabeigou Formation has the potential for preserving terrestrial vertebrates. Given the specific horizon of those fossils, the existence of theropods represented by these feathers can be traced back to 132 Ma, predating the Huajiying Formation. It thus makes them the earliest known

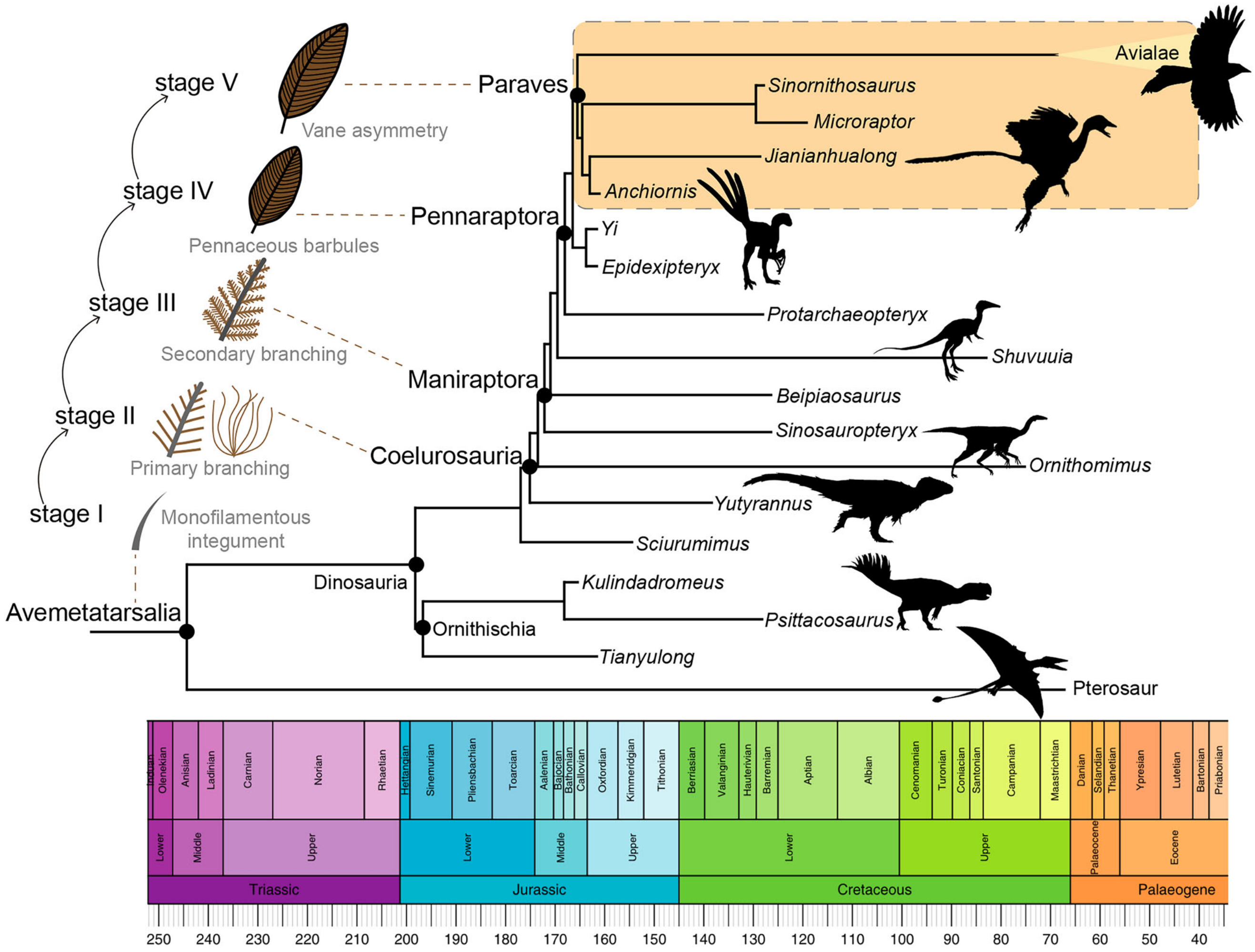

FIGURE 5 | Morphological evidence for the paravian affinity of IVPP V 33670 within the context of feather evolution (phylogenetic tree revised from Xu [2020]).

feathered theropod representatives of the Jehol Biota. This discovery enriches the terrestrial vertebrate fossil record of the Dabeigou Formation and provides new insights into the faunal composition of the Jehol Biota. It adds to the growing evidence that diverse vertebrate groups, including feathered paravians, were already present during the initial stages of this biota's development. Further excavations and integrated studies will be critical for refining our understanding of faunal turnover and ecosystem continuity across the Jurassic–Cretaceous transition.

6 | Conclusions

Here, we report the discovery of two isolated fossil feather specimens from the Dabeigou Formation in the Luanping Basin, Northern China. These feathers are preserved in shales as carbonaceous residues. Morphological comparisons indicate that the specimen IVPP V 33670 is referable to a non-avian theropod, whereas it is consistent with a paravian affinity (potentially even belonging to some early avian taxa), the first reports of these clades from within the Jehol Biota. SEM and EDS analyses did not reveal typical melanosomes in the carbonaceous residues of the specimens, indicating that these were not subjected to high temperatures after being buried, and consequently, the keratin has not been destroyed to expose the internal pigment body. The discovery of these specimens confirms the fossil preservation potential of the Dabeigou Formation and enriches the list of the vertebrate groups represented there. It also indicates that a complex ecosystem was already established during the early times of the Jehol Biota. These key findings help narrow the temporal and faunal gap between the Middle-Late Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota, extending the stratigraphic range of complex feathers-bearing pennaraptorans into the earliest Jehol deposits and reinforcing faunal continuity across the Jurassic–Cretaceous boundary in northeastern China.

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Conflicts of Interest

The authors declare no conflicts of interest.

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