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Praeornis sharovi Rautian, 1978 a fossil feather from the early Late Jurassic of Kazakhstan

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ABSTRACT

Since its original description as a feather belonging to a basal bird, the phylogenetic position of *Praeornis sharovi* was debated. It was considered as belonging to a bird, a cycad leaf, or as a ‘transitional’ integumentary structure between reptile scales and bird feathers. Recently, a basal enantiornithine bird was collected in Early Cretaceous beds of Brazil. This specimen shows very well-preserved rachis-dominated tail feathers with a very thick rachis and thick and rigid barbules. These features are present in *Praeornis*, suggesting that this fossil may be interpreted as the tail feather of a basal bird. In this way, *Praeornis* constitutes one of the oldest records of rachis-dominated feathers in the world. Rachis-dominated tail feathers, including that of *Praeornis* appear to be rigid paired structures not performed for aerodynamical purposes, suggesting that may be important in body balance.

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Introduction

The name *Praeornis sharovi* was coined by Rautian in 1978 on the basis of an isolated feather-like fossil. The specimen was originally found by the well-known paleontologist Aleksandr Grigorevich Sharov in 1971 in lower Upper Jurassic beds from Kazakhstan and was referred to it in a museum label as ‘*Praeornis*’. Later, this taxon was formally described by Rautian (1978) whom noted its remarkable peculiarities, including the absence of barbules, and consequently named the new ad hoc. bird Subclass Praeornithes. After Rautian (1978) publication, several authors doubted the animal affiliation of this supposed feather. Bock (1986), Doludenko et al. (1990), and Wellnhofer (2004) argued that the specimen was a cycad leaf, and Nesson (1992) proposed that it was even a synonym of the species *Cycadites sapportae*. In this regard, Kellner (2002) indicates that feather affinities cannot be corroborated for this fossil. However, Glazunova et al. (1991) presented SEM evidence indicating the avian nature of *Praeornis*, a criterion followed by Kurochkin (2001), whereas Dzik et al. (2010), concluded that this taxon represents a feather thanks to the presence of isotope composition. It is worthy to note that Dzik et al. (2010) based their analysis not on the holotype specimen but on a referred isolated feather coming from the same locality and stratum. This unambiguously supports the original interpretation of *Praeornis* as an animal keratinous integumental structure, and not as a plant leaf.

Probably, one of the main reasons of the debated *Praeornis* affinities was its large size, and the fact that it was found in lower Upper Jurassic deposits. At the time of the description of *Praeornis*

the Mesozoic bird record was mainly restricted to *Archaeopteryx* and the Latest Cretaceous toothed birds *Ichthyornis*, *Herperornis*, and its kin. In recent years the fossil record of Mesozoic birds has been dramatically increased mainly by the abundant record of China (Chiappe and Meng, 2016). More recently, a basal Enantiornithine was found in Early Cretaceous strata of Brazil (Carvalho et al. 2015a, 2015b). The specimen shows very well-preserved 3D tail feathers that allow to recognise and interpret several features of tail morphology in basal birds.

Because none of the previous authors compared *Praeornis* with the abundant evidence of fossil feathers coming from the Jurassic-Cretaceous deposits of China (Xu et al. 2010a; O’Connor et al. 2012) and Brazil (Carvalho et al. 2015a, 2015b) we think that a comparison may shed some light to *Praeornis* affinities. The aim of the present contribution is to discuss some aspects of *Praeornis* and to propose a new look at this controversial specimen.

Institutional abbreviations. PIN, Paleontological Institute of the Russian Academy of Sciences, Russia; UFRJ-DG Universidade Federal do Rio de Janeiro, Department of Geology collection, Brazil.

Locality and horizon

The holotype of *Praeornis sharovi* comes from the fossiliferous locality of Aulie, above the village Kasharata (formerly Mikhailovka) (Hecker 1948), Republic of Kazakhstan. The locality is famous due to the finding of the pterosaur *Sordes pilosus*, which preserved

integumental fibres (Sharov 1971; Unwin and Bakhurina 1994). Due to its important fossil findings, the locality was declared protected as a paleontological reserve (Galicky et al. 1968). The sediments that yielded *Praeornis* specimen belong to the top of the Karabastau Formation. This sedimentary unit was regarded by several authors as lower Upper Jurassic (Rasnitsyn and Zhang 2004; Vrsansky 2007), probably Oxfordian age (Zhang 2006).

Results

The holotype feather of *Praeornis sharovi* will not be described here, because it was described in great detail by previous authors (Rautian 1978; Kellner 2002; Dzik et al. 2010). Only main features and comments on important traits are made in some detail.

Dzik et al. (2010) reviewed in detail the specimen described by Rautian and pointed out the animal affinities for *Praeornis*. Dzik et al. (2010) and Sulej and Niedzwiedzki (2011) indicate that the specimen lacks any sign of vegetal structure and thus must be interpreted as a feather of an avian-like taxon. Furthermore, Dzik et al. (2010) referred to *Praeornis* another isolated structure coming from the same strata, although, due to some morphological differences are probably not the same taxon. Dzik et al. (2010) reported a ‘third vane’ on *Praeornis*, a feature that is not present in other known rachis-dominated feathers. However, this third vane was not observed by any previous author in the holotype specimen and is not visible from the photographs of the actual specimen. Since no living or fossil bird has three vanes on its feathers its presence in *Praeornis* seems unlikely.

Previous authors (e.g., Bock 1986; Wellnhofer 2004) considered that *Praeornis* was not a feather, mainly probably by its large size (the fragment of feather is nearly 15 cm. long) and ancient age. In fact, by that time, only sparse avian records were described for the Jurassic and only *Archaeopteryx* from Solnhofen (Germany) stands as a Jurassic avialan (Bock 1986). However, the recent finding of a large variety and abundance of fossil skeletons of avian and non-avian theropods having different feather kinds have been reported from Jurassic and Cretaceous China (O’Connor et al. 2012) and Brazil (Carvalho et al. 2015a, 2015b), and invites us to take a new look at *Praeornis*.

Probably, one of the most peculiar recent findings of Mesozoic fossil feathers are the very long ‘ribbon-like’ feathers. This consists on ‘rachis-dominated’ elongate tail rectrices (see Zhang et al. 2006, 2008; O’Connor et al. 2012). As for *Praeornis*, these feathers are usually described as modified pennaceous feathers, showing a ribbon-like proximal half and a barbed distal portion (Wang et al. 2014). Birds with ribbon-like feathers include some confuciusornithids, enantiornithines, and the enigmatic scansoriopterygids (Hou et al. 1996; Chiappe et al. 1999; Chiappe and Walker 2002; Zhang et al. 2008; Xu et al. 2010a, 2010b; but see Prum 2010).

Praeornis shares with rachis-dominated feathers the large size, very large, and transversely expanded rachis with a longitudinal midline groove, ovoidal cross-section of the scapus, and very thick and convex barbules on distal vane (Rautian 1978; see Chuong et al. 2003; O’Connor et al. 2012; Figure 1). Moreover, distal vane without barbules is a feature shared by *Praeornis* and rachis-dominated feathers (Chiappe et al. 1999; Zhang and Zhou 2000). The rachis-dominated rectrices are currently represented by two main morphotypes (see Xu et al. 2010b; O’Connor et al. 2012): one including the oviraptorosaur *Similicaudipteryx*, and the other including basal birds and scansoriopterygids. The complex proximal morphology of the rectricial feathers indicates that PIN 2585/32 is similar to the second morphotype, whereas in *Similicaudipteryx* there is not recognizable rachis and its scapus shows an abrupt wedge-like connection with the pennaceous distal end. It is worthy to mention that the supposed rachis-dominated feathers of *Similicaudipteryx* may be molting feathers (Prum 2010; Foth 2012; O’Connor et al. 2012). Within birds having rachis-dominated feathers, two different types can be distinguished: that present in Confuciusornithids and most Enantiornithes, in which the rachis is proximally naked, lacking any sign of barbs, and a second subtype present in pengornithids which show rachis-dominated rectrices having barbs along the entire rachis (O’Connor et al. 2012; Carvalho et al. 2015a) (Figure 2).

In this way, *Praeornis* cannot be distinguished by any character of its gross or detailed morphology from the rachis-dominated like feathers reported in several basal birds (O’Connor et al. 2012).



Figure 1. A, Holotype of *Cratoavis cearensis* (UFRJ-DG 031), B, Original illustration of *Praeornis* (modified from Rautian 1978).

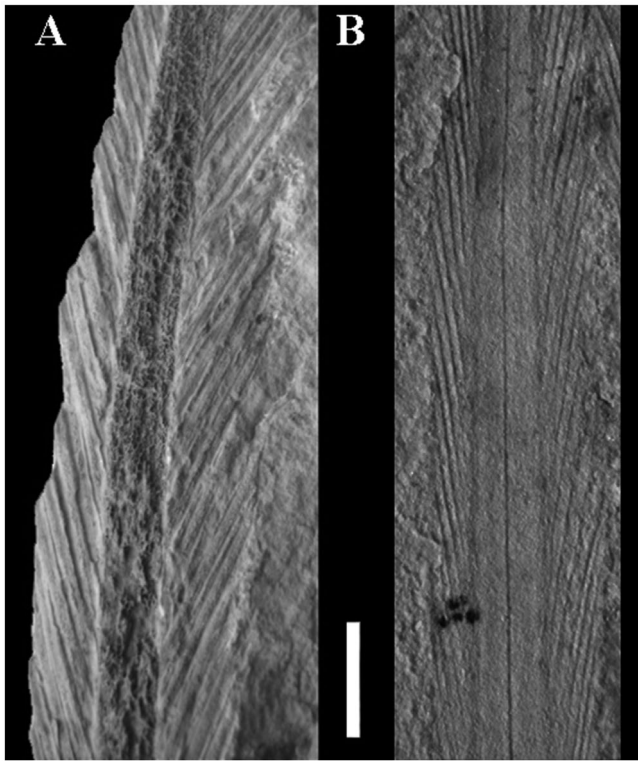


Figure 2. A–B, rectricial rachis-dominated tail feathers of A, *Praeornis sharovi* (PIN 2585/32, holotype), B, UFRJ-DG 031 Av, indeterminate Enantiornithes. Scale bar: A = 1 cm; B = 0.2 cm.

Discussion

Almost all known Early Cretaceous non-Ornithuromorpha pygostylians preserving feathers (i.e., confuciusornithids, enantiornithes), show an enigmatic kind of tail formed by a pair of elongate rectrices known as ‘ribbon-like’ or ‘rachis-dominated’ feathers, which are unknown in living birds (Prum 2010; Xu et al. 2010a; O’Connor et al. 2012). These feathers consist on a ribbon-like proximal half with a barbed distal portion, which contrasts with the morphology of *Sapeornis*, basal ornithuromorphs, some enantiornithines, which have a fan-shaped tail made up by a series of short rectrices, resembling that present in living birds (O’Connor et al. 2012). Basic anatomical aspects of the ribbon-like type feathers are still difficult to interpret. One of the main reasons is the absence of this kind of feather among living birds (O’Connor et al. 2012). In spite of different hypotheses regarding the structure of these feathers (e.g., Zhou and Zhang 2000; Zhang et al. 2008; Prum 2010; Xu et al. 2010a, 2010b; O’Connor et al. 2012), most authors concur that the rachis-dominated feathers are in agreement with the developmental mode of feather origins proposed by Prum (1999). On the contrary, some authors consider that feathers may have originated by differentiation of reptilian scales (Jones et al. 2000; Dzik et al. 2010; Sulej and Niedzwiedzki 2011). In this line of thought, Dzik et al. (2010) argued that *Praeornis* may be a link connecting reptilian scales from a *Longisquama*-like reptile with avian feathers. However, the recognition of *Praeornis* as a rachis-dominated rectricial feather argues against the evolutionary scenario proposed by Dzik et al. (2010) and Sulej and Niedzwiedzki (2011).

Since the discovery of ribbon-like elongate feathers in *Confuciusornis*, authors mostly agreed that such elongate

structures may be associated with sexual display or visual communication (Chiappe et al. 1999; Zhang and Zhou 2000; Clarke et al. 2006; Li et al. 2006; Zheng et al. 2007; Chiappe et al. 2008; Li et al. 2012; O’Connor et al. 2011; Padian and Horner 2011; O’Connor et al. 2012, 2013). In living birds with elongate forked tail, the rectrices change their angle of attack and angle of spread, and thus, the tail streamers retain an aerodynamic function (e.g., Balmford et al. 1994; Thomas 1997; Tubaro 2003). Furthermore, as early recognised, rachis-dominated feathers are sharply different from these tail feathers (Xu et al. 2010a, 2010b): in confuciusornithids and Enantiornithes the rachis-dominated rectrices are always preserved subparallel each other. They seem to be a rigid structure (Carvalho et al. 2015a, 2015b), having distal symmetrical vanes composed of very thick and probably rigid barbs. The very thick and rigid rachis and general morphology of this kind of tail feather indicate that it was not probably aerodynamical performed, and evidence at hand suggest that the paired rectrices may not spread as in living birds (Carvalho et al. 2015a, 2015b). This suggests, as proposed by previous authors (Choung et al. 2013), that rachis-dominated feathers may be not exclusively associated to the sexual display, but also could assist the body balance when the birds was perching, compensating the loss of weight due to the reduction of the long bony tail in ornithurine birds (Choung et al. 2013). Moreover, Hu and collaborators (2015) propose that these rigid structures could also work for stabilisation during trunk climbing.

With respect to taxa with intraspecific variation in the presence or absence of rachis-dominated feathers (e.g. *Confuciusornis*) and interpreted by some authors as the result of sexual dimorphism (Hou et al. 1996; Martin et al. 1998; Chiappe et al. 1999; Hou et al. 1999; but see Chiappe et al. 2008), may be alternatively interpreted as being the result of feather moulting. In numerous extant birds, when the feather moulting occurs in wings and tail, the change occurs in paired feathers, following bilateral symmetry (Owen and Ogilvie 1979). Considering that the rachis-dominated feathers are paired structures, the moulting should be simultaneous in both feathers. If the rachis-dominated feathers are indeed, important to the body balance when the bird is perching, the loss of these could imply that the behaviour of the bird should change and settle to its new condition, as occurs in many extant birds (e.g. Anseriformes, Phoenicopteriformes; Allen 1956; Salomonsen 1968; Palmer 1972; Fox and King 2011). However, more evidence is needed in order to sustain this hypothesis.

Documentation of a rachis-dominated feather from Kazakhstan expands the paleobiogeographic distribution of this kind of elongate tail feathers, up to now only reported from China, Spain and Brazil (e.g. Kellner 2002; Marugán-Lobón and Vullo 2011; Carvalho et al. 2015a, 2015b). Furthermore, the early Late Jurassic age of *Praeornis* posits it as one of the oldest findings of rachis-dominated feathers, together with similar-aged scansoriopterygids from China (Zhang et al. 2008).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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