HYPOTHESIS: AVIAN FLIGHT ORIGINATED IN ARBOREAL ARCHOSAURS GLIDING ON MEMBRANOUS WINGS

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The oldest feathers known to date have been found in archosaurs capable of flight. However, some of them (scansoriopterygids) flew by the use of a membrane rather than feathers. We therefore propose a new mechanism for the origin of avian flight by the use of membranous wings on both the forelimbs and the hindlimbs. It complements Beebe's (1915) prediction of the tetrapteryx stage. Paleontological and embryological evidence suggest that feathers are a modification of reptilian scales. Scansoriopterygids were covered mostly by down-like feathers which seemingly acted as thermal isolation rather than being adapted for flight. Certain early birds, including scansoriopterygids, possessed elongate shafted tail feathers, which were probably used principally for display and resembled elongate scales. We suppose that display is the primary function of early feathers, which were preadapted for thermal isolation and also flight. The body of theropods was covered mostly by typical reptilian scales, yet some ornithischian dinosaurs possessed filamentous integumentary structures which might have had a comparable

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display function. However, it is doubtful that these structures in dinosaurs were homologous with avian feathers. Early birds probably shared with theropod dinosaurs an incipient endothermy, which was inherited from their common ancestor in the Triassic Period.

Keywords: origins of avian flight, function of feathers, Scansoriopterygidae

Introduction

The origin and primary function of feathers have been debated for a long time (Holmgren 1955; Prum 1999). Currently, the prevailing view point on the origin of avian feathers is that they originated from filamentous integumentary structures found in some dinosaur fossils, which might constitute an adaptation for thermal isolation in endothermic cursorial theropods (Prum 1999; Makovicky and Zanno 2011; Chatterjee 2015). On the contrary, others suggest that feathers are a modification of reptilian scales (Dzik et al. 2010), whereas dinosaurs and early birds are thought to have been ectothermic (Ruben and Jones 2000; Feduccia 2012) and birds most likely not to be descendants of dinosaurs and instead to have evolved from arboreal forms of archosaurs (Czerkas and Feduccia 2014). Certain authors offer rather several alternatives for the origin of birds (James and Pourtless 2009) and the origin of feathers (Feduccia 2012). Most of the recent papers on the assembly of the avian body plan ignore non-dinosaur hypotheses for the origin of birds (e.g., Bhullar et al. 2012; Brusatte et al. 2014; Puttick et al. 2014; O'Connor and Zhou 2015; Nesbitt et al. 2017; Sullivan et al. 2017; Cau 2018) and archosaur species possessing unequivocal flight feathers are described as theropod dinosaurs (e.g., Hu et al. 2018; Rauhut et al. 2018).

However, only a mix of these two orthodox viewpoints can be sustained by biological data in the light of paleontological finds of the last decade. Herein, we discuss the available evidence on the origin of birds, archosaurian integumentary structures and thermal physiology. We propose a new mechanism for the origin of avian flight by the use of membranous wings at the very early stage, which complements Beebe's (1915) prediction of the tetrapteryx stage. Also, we provide a corrected reconstruction of the scansoriopterygid *Yi qi* (Xu et al. 2015) showing that it was capable of flight only if its membranous wings were also present on the hindlimbs.

The origin of avian flight

Important information relevant to the debate on the origin of avian flight may be provided by the archosaurian family Scansoriopterygidae, as it includes some of the earliest known flying maniraptorans (late Middle Jurassic–early Late Jurassic). Czerkas and Feduccia (2014) considered *Scansoriopteryx* an arboreal bird capable of parachuting or gliding, which would have represented the four-winged "tetrapteryx" stage of the avian evolution, as predicted by Beebe (1915). Interestingly, Czerkas and Feduccia (2014) noted that the body of *Scansoriopteryx* was covered solely by down-like feathers, which were composed of individual strands, and there were no indications of pennaceous feathers on the forelimb. The lack of preserved wing feathers in *Epidexipteryx* is also peculiar, but it had shafted elongate tail feathers (Zhang et al. 2008). The Early Cretaceous *Zhongornis haoae* may be closely related to scansoriopterygids (O'Connor and

Sullivan 2014). Interestingly, on the only known specimen of *Zhongornis* poorly preserved vaned feathers are visible solely on the tail and the manus (Gao et al. 2008).

The paradox of the apparent lack of flight feathers in scansoriopterygids was explained by the description of putative patches of membranous tissue and a long rod-like bone extending from each wrist in the scansoriopterygid *Yi*, which also had abundant down-like feathers (Xu et al. 2015). All known flying tetrapods, including both extinct and extant groups, possess a membrane for flight, as for example bats, flying squirrels and flying lizards (McGuire and Dudley 2011; Xu et al. 2015) It is intriguing to question whether birds are truly an exception to this rule. Notably, structures such as the contour feathers are far more complex than a membrane, so a membrane seems to be a simpler solution for the development of the ability to fly. In fact, a membrane (propatagium) is present in the forewings of extant birds (Brown et al. 1994) and contributes to avian flight by producing a significant part of the lift (Brown and Cogley 1996). Also, a membrane is present as a rudiment in the hindlimbs of certain baby birds (see Beebe 1915, fig. 10). One can therefore imagine that birds originated from archosaurs which used a membrane as the principal flight apparatus. If this is true, in the early avian evolution the membrane, still present in scansoriopterygids, was subsequently covered with contour feathers resulting in typical tetrapteryx forms such as *Anchiornis* (Hu et al. 2009) and *Microraptor* (Xu et al. 2003) (Fig. 1).

In flying objects the center of gravity must be located forward relative to the center of lift (wings) for good stability and maneuverability (Dizdarevic and Dizdarevic 2005). For this reason, scansoriopterygids probably represented the tetrapteryx body plan (Fig. 2), just like many other primitive birds did before shortening of the tail and reinforcement of the forewings (Beebe 1915).

The fossil feathers *Praeornis* from the Callovian–Oxfordian of Kazakhstan have a rachis and also three vanes (Dzik et al. 2010). The morphology of a three-vaned feather can be far more parsimoniously derived from a reptilian scale than from a simple filament, for example as in the scenario of such a transformation proposed by Dzik et al. (2010). Feathers are likely to be modified scales because during embryological development the feather sac represents the tip of a scale (Duerden 1922; Holmgren 1955). Given the presence of scale-like feathers on the tail of scansoriopterygids (Zhang et al. 2008), feathers hypothetically first appeared on the tail of early birds. Agnolin et al. (2017) noticed the similarity between *Praeornis sharovi* and rachis-dominated tail feathers of an enantiornithine bird, concluding that *Praeornis* may be interpreted as the tail feather of a basal bird. The down-like feathers composed mostly of individual strands, which covered the body of scansoriopterygids (Czerkas and Feduccia 2014) and probably acted as thermal isolation, would have been simplified from more complex vaned feathers like those present on their tail. The principal function of the elongate tail feathers in *Epidexipteryx* might have been display, as suggested by Zhang et al. (2008). Elongate tail feathers of various types were common in birds from the Cretaceous Period, such as for example the dromaeosaurid *Microraptor*, the basal bird *Jeholornis,* the confuciusornithiform *Confuciusornis*, and the enantiornithine *Eopengornis* (Sullivan et al. 2017). The flight feathers would also have evolved as a modification of the shafted display feathers. At some stage of the evolution of birds, the display tail feathers covered other body parts including the wings but it is uncertain when they acquired an aerodynamic value. The reason of the replacement of the membrane by feathers requires more study, but one possibility is the role of sexual selection.

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Praeornis is a pennaceous feather and it is coeval with scansoriopterygids, which apparently lacked feathers of this type. Comparable in age are also birds such as *Anchiornis* (Hu et al. 2009) and *Caihong* (Hu et al. 2018), which were equipped with flight feathers on both their forelimbs and hindlimbs. Therefore, scansoriopterygids can be ruled out as ancestors of the main lineage of birds. The common ancestor of sansoriopterygids (e.g. *Yi*) and more derived birds of the Late Jurassic (e.g. *Anchiornis*) likely differed from scansoriopterygids in having a longer tail and perhaps a shorter IV digit (Fig. 1).

The origin of birds and the integumentary structures of archosaurs

It can be pointed out that the late Middle Jurassic–early Late Jurassic birds were already diversified, including forms with a variety of flight apparatus types (a membrane, flight feathers). Thus, birds – here, defined as archosaurs equipped with feathers – would have evolved by the Early to Middle Jurassic. Some authors claim that scansoriopterygids and *Zhongornis* were not “birds” (Fostowicz-Frelik and O’Connor 2017) as in computerized cladistic analyses they are not recovered as members of the clade Aves (see Cau 2018). In fact, this is consistent with the viewpoint presented herein because we do not consider scansoriopterygids as direct ancestors of the main lineage of birds (Fig. 1). The bird-like maniraptorans and ornithomimosaurs of the Cretaceous age, which include common flightless forms, reveal little about bird origins regardless of whether they are considered as theropod dinosaurs or, alternatively, as non-dinosaur birds (Feduccia 2012). This standpoint may be inconsistent with the cladistic approach as certain maniraptorans of the Cretaceous Period, such as for example oviraptorosaurs, are cladistically

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recovered as more basal than the Jurassic scansoriopterygids (see Sullivan et al. 2017; Cau 2018). The Late Jurassic (Oxfordian) *Limusaurus* might possibly represent a secondarily flightless bird as well, due to its supposedly non-dinosaur hand anatomy and digestive physiology (Bajdek 2018). Secondarily flightless forms would have appeared at very early stages of the bird evolution and such bird forms can be easily mistaken for theropod dinosaurs (see Maryańska et al. 2002).

Remarkably, filamentous structures found in some theropod fossils can be easily mistaken for down feathers of flightless birds. It is debated whether these filaments represent a kind of integumentary structures of theropods or collagen fibers of decomposed skin (Feduccia et al. 2005; Smithwick et al. 2017). However, fossils show that the skin of dinosaurs was covered by reptilian scales, as seen for example in compsognathids (Chiappe and Gröhlich 2010) and tyrannosaurids (Bell et al. 2017). Filamentous integumentary structures have been found in some ornithischian dinosaurs, such as the heterodontosaurid *Tianyulong* (Zheng et al. 2009) and the ceratopsian *Psittacosaurus* (see Mayr et al. 2002). Since these structures were present mainly on the tail, whereas the whole body was covered by typical reptilian scales, it seems that their primary function was display rather than thermal isolation.

Elongate integumentary appendages of *Longisquama* from the Late Triassic are also thought by some researchers to be probably homologous with avian feathers (Jones et al. 2000). However, the function of the appendages and the phylogenetic position of *Longisquama* within diapsids are uncertain (Buchwitz and Voigt 2012). Because the limbs of *Longisquama* were short and the enigmatic appendages were placed along the dorsum, its body plan does not conform to that expected for the direct ancestor of birds.

If it is assumed that the enigmatic integumentary structures present in certain ornithischian dinosaurs and *Longisquama* were modified scales, and that avian feathers are modified scales too, one would say that they were homologous. On the other hand, all these structures most likely evolved from typical reptilian scales independently. Whereas true avian feathers are very complex structures and have probably evolved just once, simple thin elongate scales such as those encountered among ornithischians could have appeared multiple times in different lineages of reptiles (see James and Pourtless 2009).

Prum (1999) discussed several possible functions of filamentous integumentary structures in archosaurs, such as the thermal insulation, heat shielding, water repellency, communication, crypsis, and defense. Since the single-stranded feather-like structures which covered the body of scansoriopterygids are unlikely to have acted as a flight apparatus, it can be expected that they possessed an adaptive value of another kind (Czerkas and Feduccia 2014). For example, an incipient endothermy in dinosaurs and early birds has been suggested by researchers for a long time (e.g., Bakker 1975) but this issue is still a subject of controversy (see Feduccia 2012). The study of theropod and early avian gut contents, feces and gastric pellets suggests that both these groups were likely characterized by moderately high metabolic rates and hence likely an incipient endothermy (Bajdek 2018). Yet, the typical metabolic rates in theropods would have been a little lower than those of extant birds and mammals, which was suggested, among other clues, on the basis of the lack of respiratory turbinates (Ruben et al. 1998) and just moderately rapid digestive processes in theropods (Bajdek 2018). Remarkably, the evidence for an incipient endothermy in early birds is comparable to that for some Late Permian theriodont therapsids, which (a) were likely characterized by a relatively short food retention time in the gastrointestinal tract, as revealed by the study of fossil feces, and moreover (b) possibly had insulation in the form of hairs (Bajdek et al. 2016).

The arboreal and cursorial hypotheses for the origin of avian flight are still a subject of debate (Segre and Banet 2018). The model presented herein suggests that birds originated from arboreal forms of archosaurs that could spread the hindlimbs sideways for tree climbing and flight (Fig. 1). Currently, the vast majority of researchers argue that birds evolved from theropod dinosaurs (see Makovicky and Zanno 2011). However, several alternatives for the ancestral group of archosaurs have been proposed, including theropods, dinosauromorphs, crocodylomorphs, and “early archosaurs” (see James and Pourtless 2009). The dinosaur origin of birds is problematic due to the partially closed acetabulum in early birds such as *Anchiornis* and *Scansoriopteryx* (Czerkas and Feduccia 2014). The theropod hindlimbs had a fully upright stance and were clearly adapted for cursorial locomotion (Burnham et al. 2010; Czerkas and Feduccia 2014). For this reason, in this paper we have chosen to use a broader term “archosaur” to call the arboreal ancestor of birds (see also Bajdek 2018).

Conclusions

We propose that birds originated from tree-climbing archosaurs and probably passed through the stage of arboreal forms which glided on membranous wings. The membrane was present most likely on both the forelimbs and the hindlimbs. At some stage of early bird evolution the membrane was covered and replaced by feathers, resulting in “classical” tetrapteryx bird forms, which were predicted by William Beebe in 1915. Feathers probably evolved from reptilian scales and display is hypothetically the primary function of feathers, which were preadapted for thermal isolation and flight.

Author contributions

Piotr Bajdek conceived the idea of this work and wrote the manuscript.
Tomasz Sulej provided additional ideas and prepared the graphics.

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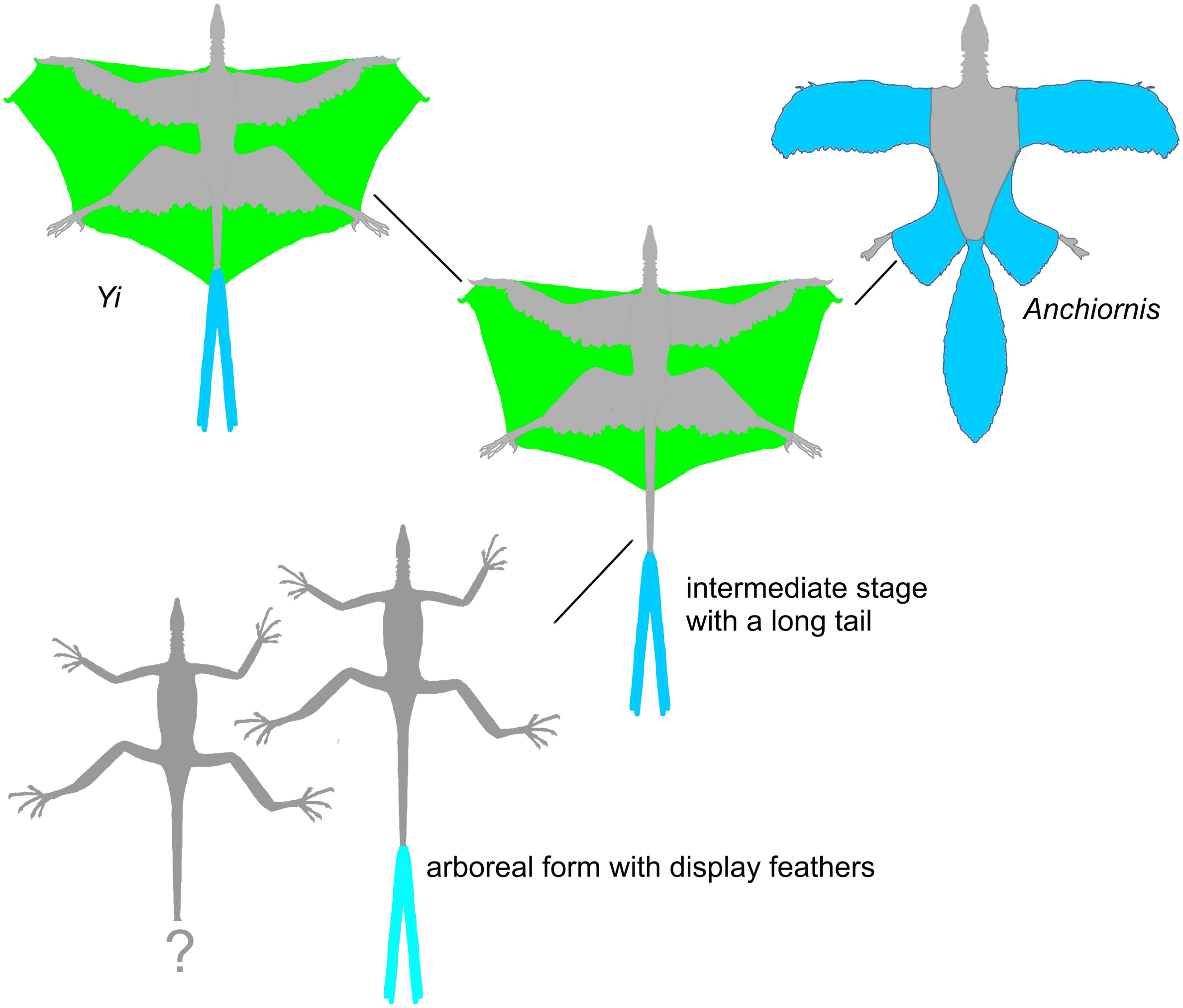

Fig. 1. Origin and early evolution of birds. Birds originated from tree-climbing archosaurs and passed through the stage of arboreal forms which glided on membranous wings. It is uncertain at which stage the tail feathers first appeared.

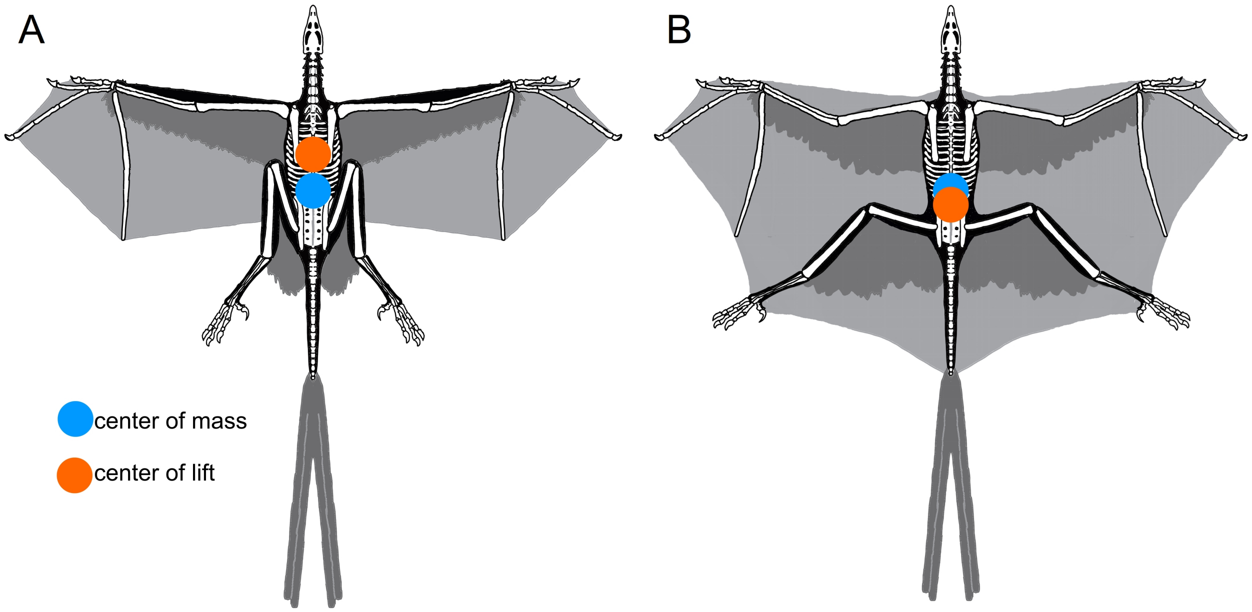

Fig. 2. Reconstructions of *Yi qi* showing the aerodynamic apparatus. Model proposed by Xu et al. (2015) **(A)** and a new model proposed herein **(B)**. Xu et al. (2015) provided three different alternatives for the construction of the front wing of *Yi* and only that one of the greatest extension of the membrane is reproduced (model A). Approximate positions of the center of mass (blue dots) and the center of lift (orange dots) are marked. Note that *Yi* was capable of flight only if the membrane was extended also on the hindlimbs, as the center of lift was located backward relatively to the center of mass (model B).