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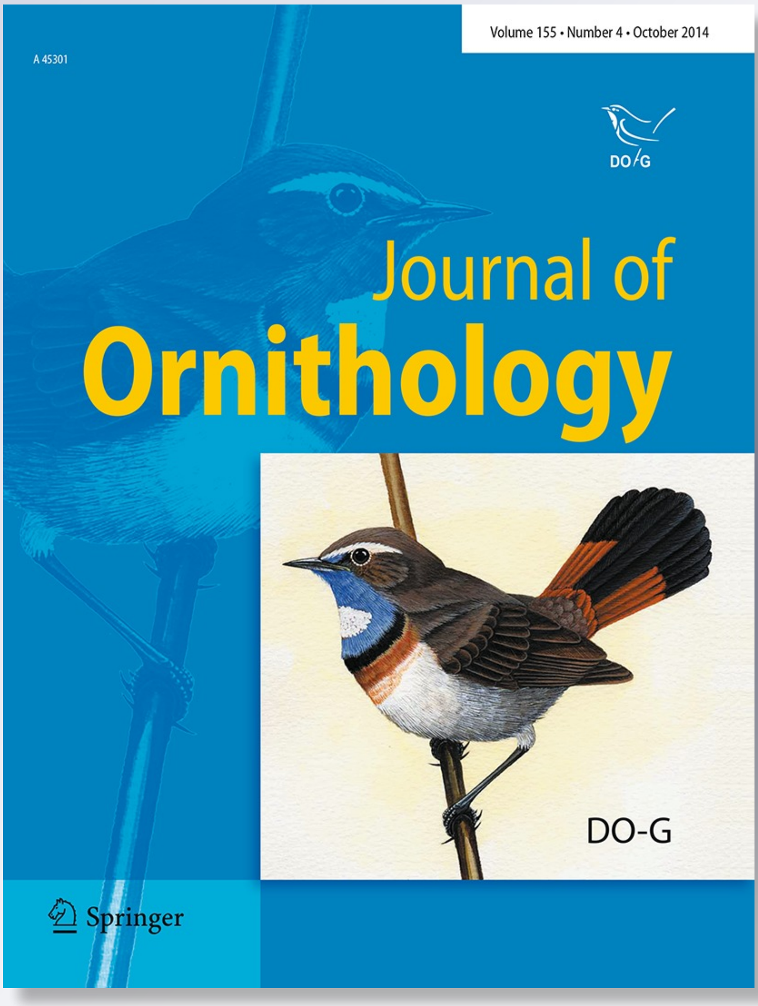

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ORIGINAL ARTICLE

Jurassic archosaur is a non-dinosaurian bird

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Abstract Re-examination utilizing Keyence 3D digital microscopy and low angled illumination of the fossil *Scansoriopteryx*, a problematic sparrow-size pre-*Archaeopteryx* specimen from the Jurassic Daohugou Biotas, provides new evidence which challenges the widely accepted hypothesis that birds are derived from dinosaurs in which avian flight originated from cursorial forms. Contrary to previous interpretations in which *Scansoriopteryx* was considered to be a coelurosaurian theropod dinosaur, the absence of fundamental dinosaurian characteristics demonstrates that it was not derived from a dinosaurian ancestry and should not be considered as a theropod dinosaur. Furthermore, the combination in which highly plesiomorphic non-dinosaurian traits are retained along with highly derived features, yet only the beginnings of salient birdlike characteristics, indicates that the basal origins of Aves stemmed from outside the Dinosauria and further back to basal archosaurs. Impressions of primitive elongate feathers on the forelimbs and hindlimbs suggest that *Scansoriopteryx* represents a basal form of "tetrapteryx" in which incipient aerodynamics involving parachuting or gliding was possible. Along with unique adaptations for an arboreal lifestyle, *Scansoriopteryx* fulfills predictions from the early twentieth century that the ancestors of birds did not evolve from dinosaurs, and instead were derived from earlier arboreal archosaurs which originated flight according to the traditional trees-down scenario.

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Zusammenfassung

Archosaurier aus dem Jura ist ein nicht-dinosaurischer Vogel

Eine erneute Untersuchung mittels Keyence-3D-Digitalmikroskopie und Dunkelfeldbeleuchtung des fossilen Scansoriopteryx, eines zweifelhaften sperlingsgroßen prä-Archaeopteryx-Beleges aus den jurassischen Daohugou-Schichten, liefert neue Hinweise, welche die weithin anerkannte Hypothese in Frage stellen, dass Vögel von Dinosauriern abstammen und sich der Vogelflug über laufende Formen entwickelte. Im Widerspruch zu früheren Deutungen, die Scansoriopteryx als Coelurosaurier, also einen theropoden Dinosaurier, betrachteten, zeigt das Fehlen grundlegender Dinosaurier-Eigenschaften, dass er nicht von Dinosauriervorfahren abstammt und somit auch nicht als theropoder Dinosaurier angesehen werden sollte. Außerdem deuten die in Kombination mit stark abgeleiteten Merkmalen erhaltenen deutlich plesiomorphen Nicht-dinosaurier-Eigenschaften bei gleichzeitig erst in Ansätzen vorhandenen vogelartigen Ausprägungen darauf hin, dass die tieferen Ursprünge der Aves außerhalb der Dinosaurier liegen und weiter zurück zu den basalen Archosauriern reichen. Abdrücke primitiver verlängerter Federn an den Vorder- und Hinterextremitäten legen nahe, dass Scansoriopteryx eine basale Form eines „Tetrapteryx"war, bei der beginnende Aerodynamik in Gestalt von Segel- oder Gleitflug möglich war. In Verbindung mit einzigartigen Anpassungen an eine baumbewohnende Lebensweise erfüllt Scansoriopteryx Vorhersagen aus dem frühen 20. Jahrhundert, die besagen, dass sich die Vorfahren der

Vögel nicht aus Dinosauriern entwickelten, sondern stattdessen von früheren baumbewohnenden Archosauriern abstammen, bei denen sich der Flug gemäß der traditionellen Baumtheorie entwickelte.

Introduction

The search for a suitable prototype for avian ancestry has intensified with the opening of the Chinese Lower Cretaceous Jehol Biota during the past two decades, but attention is now shifting to the older components of the Daohugou Biota of Jurassic age, considered variously as troodontid feathered dinosaurs or early birds (Feduccia 2012, 2013). Among the most intriguing, but still poorly understood, older elements are the scansoriopterygids, *Scansoriopteryx* (=*Epidendrosaurus*) (Czerkas and Yuan 2002; Zhang et al. 2002).

Previous interpretations from independent studies are in agreement that scansoriopterygids (*Scansoriopteryx*/*Epidendrosaurus* and *Epidexipteryx*) are more plesiomorphic than *Archaeopteryx* and are probably very close to the origin of birds (Zhang et al. 2008; Xu et al. 2010; Sullivan et al. 2014). These studies have also independently concluded that *Scansoriopteryx* was arboreal. However, there is disagreement as to what *Scansoriopteryx* should be regarded as either a coelurosaurian theropod dinosaur or an avian ancestor derived from non-dinosaurian archosaurs.

For more than three decades, since the discovery of *Deinonychus* and the use of cladistics employed towards deciphering dinosaurian phylogenetics and how birds are related to them, an essential criterion has been that bird-like dinosaurs were non-avian, primarily based on their obvious inability to fly and the assumption that they were not derived from volant ancestors. This non-avian status is crucial to the hypothesis that birds are derived from such dinosaurs represented by maniraptorans (dromaeosaurs, troodontids, oviraptorosaurids) in that their avian-looking characteristics are accounted for as exaptations which were not originally used for flight. Under this premise, the origin of birds supposedly evolved at least a rudimentary form of flight anatomy indirectly from behavior not associated with flight. As improbable as this might be, these non-avian forms then had to evolve into relatively tiny sizes in which the exaptations could eventually be co-opted into being used for flight (Padian and Chiappe 1998; Chiappe 2007). Furthermore, flight feathers, arguably the most complex of integumentary structures, had to then evolve aerodynamic capabilities from an implicitly non-aerodynamic cursorial lifestyle. As such, the dinosaurian scenario as ancestors of birds would have required the evolution of the most important avian characteristics necessary for flight essentially as exaptations, through a complex series of biophysically improbable events from a completely cursorial lifestyle. While not the only possible scenario for how birds evolved, the cursorial ground–up model has been firmly embraced by paleontologists using phylogenetic analyses to support their conclusions (Chiappe 2007).

Scansoriopteryx represents the opposite hypothesis in which birds are derived from non-dinosaurian archosaurs that were already small and had adapted to an arboreal lifestyle. Jumping, parachuting, and gliding are all predictable incipient stages of flight behavior, each totally adaptive, which are readily seen in some extant reptiles, as well as rarer examples in the fossil record, some of which date back to the Triassic or Upper Permian (McGuire and Dudley 2011; Frey et al. 1997). That the origin of birds would have involved some manner of jumping, parachuting, and gliding is substantiated by this re-examination of *Scansoriopteryx* and fulfills predictions from the early twentieth century that the ancestor of birds was a small, arboreal basal archosaur (Steiner 1918) and a “tetrapteryx” glider (Beebe 1915). The impressions of feathered wings in *Scansoriopteryx* are consistent with its basal level of avian status and provide important insights towards understanding how birds first achieved the ability to fly.

The non-dinosaurian and basal avian status of *Scansoriopteryx* presents challenges for phylogenetic interpretations which must account for maniraptorans having characteristics that appear to look avian. Either they are dinosaurs with exaptations of flight-related anatomy as interpreted within the constraints of cladistic analyses, or more likely that they are basal forms of secondarily flightless birds derived from birds which had at least some incipient ability to fly. Variations of this last option were proposed as early as the mid-1980s (Paul 2002; Olshevsky 1992), but have been largely ignored especially by phylogenetic analyses. As interpreted in this paper, the secondary flightless scenario necessitates that maniraptorans are not true theropods or dinosaurs because they would have been derived from birds more or less at the evolutionary level seen in *Scansoriopteryx*, or at a slightly more advanced stages. If so, then similarities linking maniraptorans to dinosaurs are mistaken interpretations due to convergence, examples of which are revealed by this re-examination of *Scansoriopteryx*.

While palaeontologists have in recent decades embraced the view that birds are derived from terrestrial theropod dinosaurs typified by the dromaeosaur *Velociraptor* (Chiappe 1999, 2007), and some still hold the view that flight was achieved from the biophysically improbable ground–up model and variations on that theme (Padian and Chiappe 1998; Burgers and Chiappe 1999; Dial 2003), most early workers favored evidence for a small, arboreal basal archosaur as the more logical interpretation for the ancestor

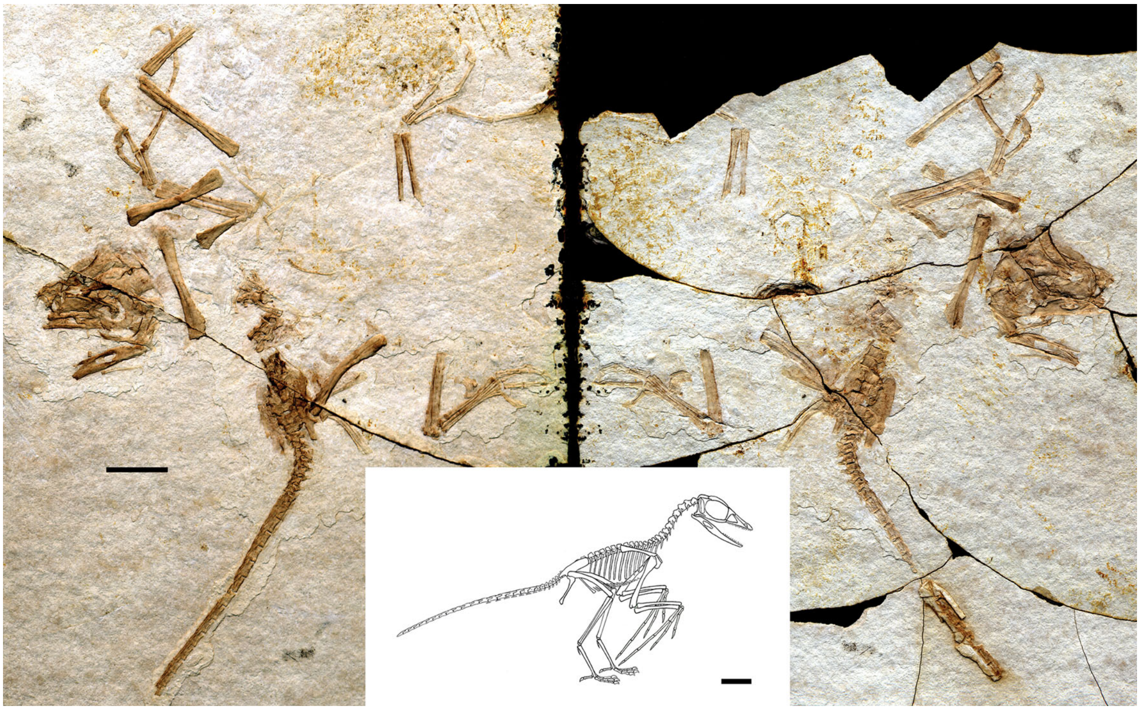

Fig. 1 *Left* mainslab of *Scansoriopteryx*; and *right* counterslab, shown slightly smaller than life size. *Scale bars* 1 cm. *Inset* skeletal reconstruction, approximately half life size (reconstruction, Stephen A. Czerkas)

of Aves, with the earliest types of birds having evolved flight, via the biomechanically beneficial gravity-assisted aerodynamics which are made possible in the trees–down model (Feduccia 2012), from small arboreal archosaurs. Abel (1911) suggested an extension of the arboreal hypothesis that both dinosaurs and birds descended from tree-climbing archosaurs. Regarding Abel's hypothesis, we make the distinction here that, even if dinosaurs and birds could have both been derived from arboreal archosaurs, they were separate lineages in which the dinosaurian lineage took on a cursorial lifestyle whereas the avian lineage maintained an arboreal lifestyle. While there is no evidence for an arboreal ancestor of dinosaurs, among the increasing number of arboreal-basal archosaurs is added *Scansoriopteryx*, a tiny animal from the Jurassic of China, that due to plesiomorphic skeletal characteristics qualifies as an archosaur (Fig. 1). But it does not have apomorphic skeletal characters which are essential in order to ally it with theropods, the Saurischia, or the more inclusive dinosaur designation.

Methods

The *Scansoriopteryx* fossil was inspected using a Keyence VHX-1000 digital microscope which made it possible to generate 3D imagery which, by rotating and inverting the images, generated the positive shape of the bones as compared to the natural molds of the bones in the fossil that preserve a negative shape. High resolution photographs were made using an Epson Scanner. Additional photography requiring low angle illumination was achieved with an Intralux 4000-1 positional lighting in conjunction with a Leica MS5 microscope combined with a digital camera by Sony. The identification number of the specimen of *Scansoriopteryx* from the Institute of Geology, Chinese Academy of Geological Sciences, for the specimen is: CAGS02-IG-gausa-1/DM 607.

Daohugou Biota

The famous Chinese Early Cretaceous Jehol and Jurassic Daohugou Biotas have opened a new window on life during that previously poorly known time period, and has particularly shed light on early avian evolution (Zhou et al. 2003; Sullivan et al. 2014). New discoveries support the hypothesis that the Daohugou Biota represents a transitional fauna with "archaic" Jurassic forms alongside new lineages evolving in situ, and immigrants which arrived following the end of East Asian isolation in the Lower Cretaceous (Barrett and Hilton 2006). More recently, discoveries of Jurassic rocks yielded a new element, composed primarily of four-winged gliders variously identified as troodontid theropods from preliminary cladistic analyses, or part of the early avian radiation, including

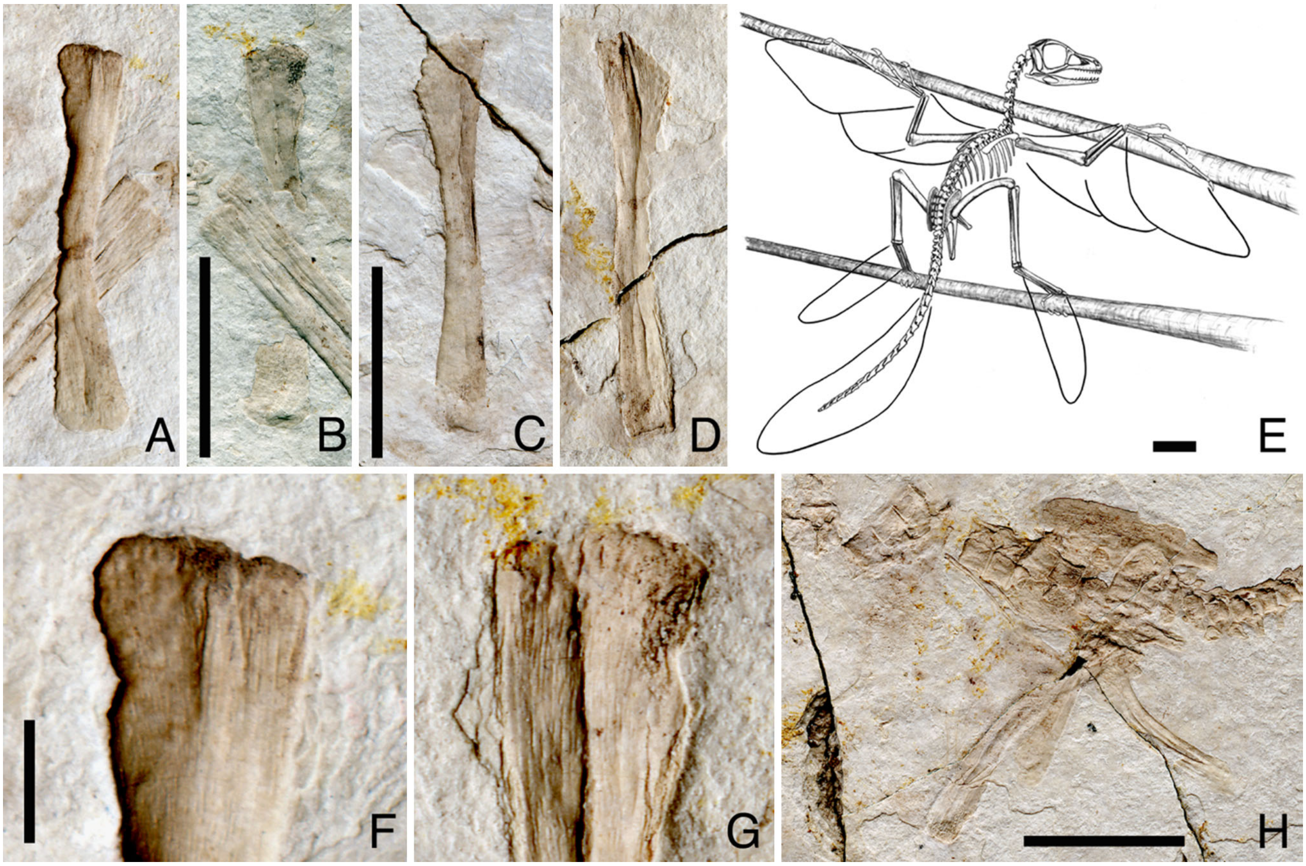

Fig. 2 **a**, **b** Right femur in anterior and posterior views. **c**, **d** Right (?) humerus ventral and dorsal views. **e** Skeletal reconstruction with area of flight feathers outlined. **f**, **g** Close-up of head of right femur in anterior and posterior views. **h** pelvis on counterslab. *Scale bars* (**a–e**, **h**) 1 cm, (**f**, **g**) 1 mm

particularly *Anchiornis* (Zheng et al. 2013). Whether interpreted as dinosaurs or early birds, they add support to the validity of the arboreal hypothesis for avian flight.

The specimen of *Scansoriopteryx* (Figs. 2, 3, 4), like its close ally *Epidexipteryx*, are from Daohugou, Inner Mongolia, and the Daohugou deposits, which arguably range widely in age from the Middle Jurassic to the Early Cretaceous, although radiometric dates range from 152 to 168 mya, from Middle to Late Jurassic. Recent work indicates that the Daohugou Formation represents the earliest stages of the Jehol Biota and belongs to the cycle of volcanism and sedimentation characterizing the Yixian Formation, but is Middle Jurassic age (Gao and Ren 2006; He et al. 2004; Liu et al. 2006; Wang et al. 2005). The age is nicely confirmed by more typical Jurassic fauna, as well as a four-winged glider *Pedopenna daohugouensis*, represented by a birdlike leg skeleton with feather impressions, which shows a basal affinity with troodontids from the Jurassic and the Lower Cretaceous microraptors (Xu and Zhang 2005).

Closely allied with *Scansoriopteryx* is a strangely feathered, pigeon-sized animal, *Epidexipteryx hui*. What is peculiar is its apparent lack of wing feathers, which may be due to preservational factors instead of actual biological development. Its skull is quite similar to that of *Scansoriopteryx*, the body quite bird-like, covered by down-like feathers and elongate ribbon-like feathers on a relatively short tail (Zhang et al. 2008). Somewhat similar feathers are known from some enantiornithine birds such as *Paraprotopteryx* and the more advanced *Protopteryx*, both of Lower Cretaceous age and clearly of avian status, indicating a continuum from *Scansoriopteryx* and *Epidexipteryx* to more advanced Aves. Phylogenetic analysis by Zhang et al. (2002) slots *Epidexipteryx* with *Epidendrosaurus* [=*Scansoriopteryx*], together forming a monophyletic Scansoriopterygidae, which was described as a rather bizarre lineage at the base of the Avialae. These forms also exhibit striking similarities to the oviraptorosaurids (including a short, high skull), considered here to be basal secondarily flightless birds (Maryańska et al. 2001). *Epidexipteryx* was described as lacking wing feathers therefore indicating a flightless condition which was considered to provide evidence that feathers evolved from some non-aerodynamic function. However, there are

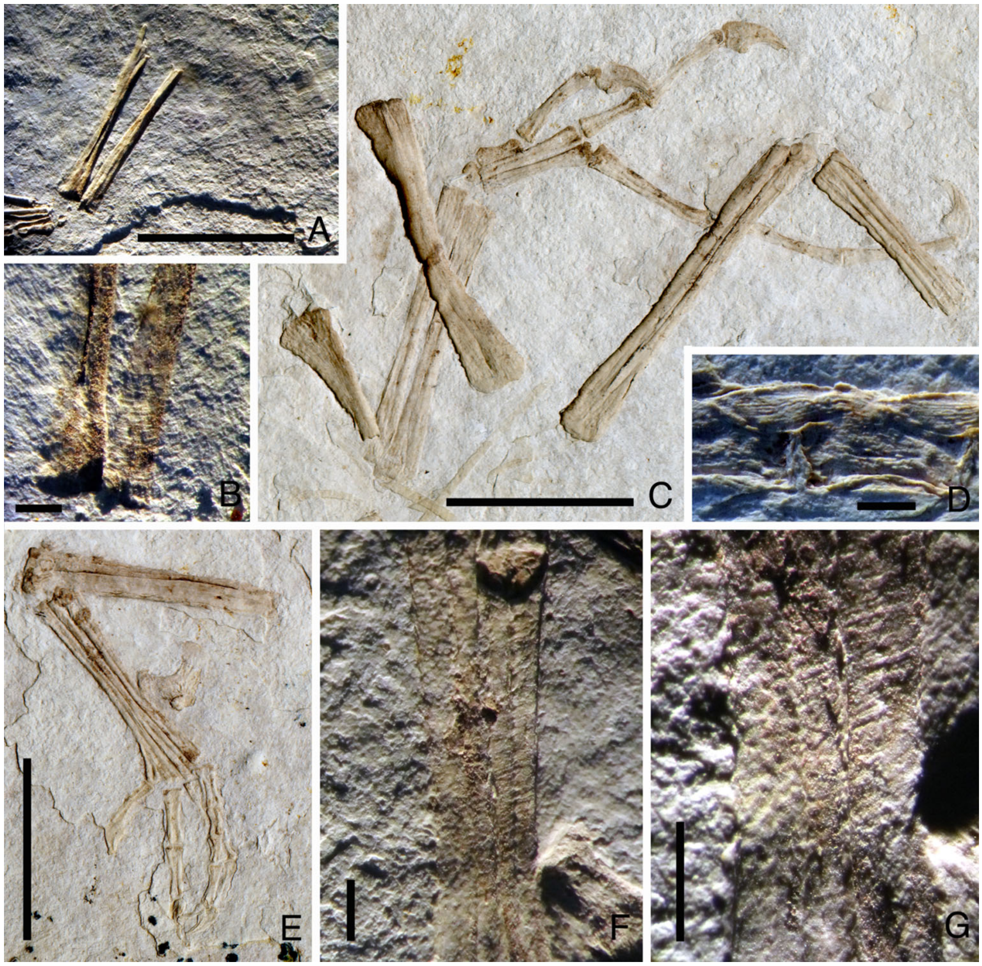

Fig. 3 **a** Left forearm and propatagium on mainslab; **b** close-up of radius and ulna with feather impressions on *left*, curved lines across bones on bottom half and different smoother texture pertaining to propatagium on *right*; **c** mainslab with right manus ventral surface overlain by distal half of scapula on *bottom left*, right femur on *left* over radius and ulna, left tibia/fibula and metatarsals on *right* over elongate third digit; **d** eleventh caudal vertebra on counterslab with prezygapophyses of eleventh and twelfth vertebra overlain by impressions of bony tendons as in dromaeosaurids; **e** right pes dorsal surface; **f** about half of mid-section of metatarsals to right pes showing scales on *left side* and feather shafts on *right*; **g** about one-fourth of mid-section to right pes with scales on *left side* and feather shafts on *right*. *Scale bar* (**a**, **c**, **e**) 1 cm, (**b**, **d**, **f**, **g**) 1 mm

examples in the Lower Cretaceous of birds such as the enantiornithine *Longipteryx chaoyangensis*, where specimens are known with preserved wing feathers, but others with body feathers and no wing feathers preserved (Feduccia 2013), so extreme caution must be exercised in drawing such conclusions that feathered wings did not exist. This is particularly so because the close and more primitive ally *Scansoriopteryx* does possess an avian wing with feathers well preserved on one forelimb but mostly lacking on the other.

Other authors have recognized the arboreal nature of all these tree-climbers, including *Scansoriopteryx* and *Epidexipteryx*, despite the absence of obvious wing feathers, but concluded that their arboreal lifestyles contradicted arguments supporting the cursorial or ground–up flight. Now, evidence for aerodynamic wings additionally lends support to the arboreal origin of avian flight (Chatterjee and Templin 2012).

Scansoriopterygids

While the first cladistic analysis placed scansoriopterygids within the Coelurosauria (Zhang et al. 2002), the analysis was preliminary, largely based on plesiomorphic characters and did not include a full set of relevant taxa including non-dinosaurian forms, nor were there salient theropod characters that have linked this small specimen with dinosaurs. The analysis was a largely phenetic grouping based on overall similarity; yet "Phylogenetic analysis has shown that *Epidendrosaurus* [*Scansoriopteryx*] is very close to the transition to birds" (Zhang et al. 2002, p 396).

Fig. 4 Section of mainslab to *Scansoriopteryx* with the manus and forearm preserved with impressions of feathers and propatagium directly associated. The area containing wing feathers and the propatagium are outlined in *red*. *A* propatagium, *B* isolated patch of feathers attributable to the pes, *C* tertials, *D* secondaries, *E* primaries. *Red lines* on pes indicate where impressions of feather shafts are located (see Fig. 2). *Scale bar* 1 cm. Image darkened to enhance detail (color figure online)

Paleontologists began to see the avian nexus: "it now seems that a curious form called *Epidendrosaurus* [=*Scansoriopteryx*] shares a few more synapomorphies with *Archaeopteryx* than other taxa do" (Padian and de Ricqlès 2009, p 270). A more extensive recent cladistics analysis placed *Scansoriopteryx* [=*Epidendrosaurus*] within Avialae, basal to archaeopterygids, which appears to be the consensus view today (Senter 2007; Xu et al. 2010). The generic names given the two known specimens, *Scansoriopteryx* ("climbing wing") and *Epidendrosaurus* ("upon tree lizard"), reflect the arboreal characters seen independently in the two descriptions, the former in reference to the tree-climbing adaptations of the manus. Its avian foot is apparent by its naturally articulated reversed first toe or hallux and recurved pedal claws, an adaptation exclusive to arboreal perching animals. Avian status is also seen in the gliding wing and wing feathers, the hand, and the semilunate carpal element which permits wing folding and extension. The most unusual feature is the extremely elongate outer finger, considered here to be digit IV as in Aves (Čapek et al. 2013). It is the longest manual digit whereas the middle digit in theropods is the longest.

The skull of the first specimen described (Czerkas and Yuan 2002) is imperfectly preserved in lacking the anterior portion of the upper and lower jaws and damage from the cracked matrix. Otherwise, bones of the skull are remarkably detailed considering their minute size. The skull in the specimen of *Epidendrosaurus* is not as complete but does have the anterior portion of mandibles and impressions of teeth. The skull of *Epidexipteryx* appears to bear a general resemblance, implying a close relationship. To a lesser extent, the skull of oviraptorosaurids (e.g., *Caudipteryx*) also appear to bear some similarities that extend to the basal enantiornithine *Eoenantiornis* (Zhou et al. 2005). However, caution should be made in making premature conclusions prior to a full description of the skull in *Scansoriopteryx*. The suggestion that *Zhongornis* is a non-avian theropod and is close or possibly an actual member of Scansoriopterygidae, instead of a bird (O'Connor and Sullivan 2014), is not supported by this paper. The original description of *Zhongornis* as being a bird (Gao et al. 2008) is supported here. Studies on the skull are ongoing but non-dinosaurian plesiomorphic characters have already been described regarding the morphology of the pterygoid and how it articulates with the quadrate (Czerkas and Yuan 2002).

Unlike theropod dinosaurs, invariably exhibiting a completely perforated and open acetabulum, *Scansoriopteryx* has a partially closed acetabulum, and no sign of a supra-acetabular shelf or an antitrochanter. Along with the mostly enclosed acetabulum indicated by the surface texture of the bone within the hip socket, the proximally oriented head of the femur is functionally concordant with a closed or partially closed acetabulum and with sprawling hindlimbs. There is additional phylogenetic evidence that the largely closed acetabulum was not directly inherited from dinosaurian ancestors with fully open acetabulae and subsequentially modified as a secondary reversal. The similar condition seen in *Anchiornis* (Hu et al. 2009) and *Microraptor* (personsal observations; Xu et al. 2000; Gong et al. 2012) with the partially open acetabulum in *Scansoriopteryx* creates a sequential phylogenetic pattern consistent with being inherited from non-dinosaurian archosaurs which had not yet achieved a fully upright stance as in dinosaurs (Fig. 2).

A fully perforated acetabulum is a sine qua non for dinosaurian status associated with major changes in posture and gait, by which a more upright posture and parasagittal stance is attained. Partially closed acetabulae are seen in basal archosaurs such as *Marasuchus* (*Lagosuchus*) which have not yet attained fully upright posture, and as noted in a number of the Chinese Jurassic early birds (some classified as troodontid theropods), such as *Anchiornis*, and even *Microraptor*, which are very close to the base of Aves and, like scansoriopterygids, also lack salient theropod characters. Significantly, unlike the typical dinosaurian manner as in theropods, the head of the femur is not offset from the shaft, again illustrating that scansoriopterygids had not yet attained fully upright posture. There was clearly no "piston in trough" dinosaurian joint, an integral part of an obligately bipedal posture and gait. An iliac supra-acetabular crest or shelf is a distinctively dinosaurian character associated with upright posture. However, modern birds independently evolved the uniquely avian, but functionally similar, antitrochanter, located lateral to the postero-dorsal rim of the acetabulum, making the avian hip joint unique among vertebrates (Hertel and Campbell 2007). *Archaeopteryx* and the avian oviraptorosaurids (*Caudipteryx*) have no structures that could be interpreted as an antitrochanter or a supra-acetabular shelf; the same is true of *Scansoriopteryx*.

The pubes of scansoriopterygids are directed forward, but unlike theropods the short length and proportions are suggestive of basal dinosauromorphs such as *Marasuchus* (Nesbitt et al. 2009; Langer et al. 2013). The ischium is large and the ilia are widely set apart; the pubic peduncle is very small and unexpanded, which is all unlike the theropod condition. Impressions of what appear to be elongate rod-like tendons, as in dromaeosaurids, are present along some of the elongate caudal vertebrae.

Scansoriopterygids have greater relative total arm length than any known theropod (Fig. 4). As with *Archaeopteryx*, the humerus is longer than its femur. Excluding the extra length due to the elongate outer digit, which would make the overall total arm length appreciably longer than in *Archaeopteryx*, the total length of the arm down to the distal end of the middle digit is slightly shorter than in *Archaeopteryx*. Despite being nearly equal to that of *Archaeopteryx*, the arm has different proportions, especially in regards to its much smaller deltopectoral crest and robust, slightly shorter radius and ulna, which represent a more basal plesiomorphic condition (Fig. 5). Another non-theropod feature involves the relative lengths of the manual proximal phalanges to the penultimate phalange in the long outer digit IV, in which the phalanges become progressively shorter distally rather than longer as in theropods. This progressive reduction of manual phalangeal length is plesiomorphic within Archosauria, and not characteristic of Theropoda. Theropods are united by having the middle manual digit, not the outer, as the longest. There are separate rodlike clavicles, so there is no furcula. The archosaurian scapula is expanded distally retaining the plesiomorphic condition similar to dinosauriformes, as in *Lewisuchus*, but differs in having a more narrow mid-shaft.

Because the bones in the fossil are preserved as negative shapes in natural molds which are exquisitely detailed, the recent re-examination of the tiny specimen using advanced Keyence 3D digital microscopy was extremely beneficial in that it provided a greatly enhanced view, revealing structures not clearly visible before and verifying interpretations of the natural contours of the bones. By inverting the imagery in the computer, it was possible to see the bones as if preserved in the positive form. This enabled confirmation of many otherwise equivocal aspects of the pelvis, forelimbs, hindlimbs, and tail. In conjunction with low angled illumination, impressions of elongate tendons along the longer distal caudal vertebrae were discovered (Fig. 3d). This suggests that the tail which overall has proportions similar to maniraptorans is possibly further aligned with dromaeosaurs.

The original description showed small patches of impressions pertaining to down-like feathers from parts of the animal including the skull, body, pelvis, and tail. These are typically short in length and similar to those of hatchling and nestling birds. Feather impressions covering more extensive areas were identified directly associated with the left forelimb. The feather impressions of the forelimbs are extensive and cover an area essentially equivalent to that of a fully mature developed wing (Fig. 4); however, the impressions are peculiar in that there are no indications of pennaceous vanes and instead are composed of long individual strands or filaments resembling hypertrophied down feathers. Such down-like feathers are atypical in the early ontogenetic development in modern birds, let alone those of more fully grown birds with equally long wing feathers. Given the level of feather experimentation with these basal birds, including *Epidexipteryx*, *Anchornis*, basal birds, and even extending into the enantiornithines such as the basal *Protopteryx*, variations of new feather types are not unexpected. These feathers are under study and will be described in detail in a later paper.

While not visible under ordinary lighting conditions, further microscopic examination under extremely low-angled, raking illumination has revealed that impressions of the elongate wing feathers continue onto the dorsal surface of the metacarpals on each manus. These appear to correlate with the calami of the feathers. As with the metacarpals, the dorsal surface of the pes was found to have a series of distinct strand-like markings extending along the length of the fourth metatarsal. These markings on the metatarsals suggest that the feathers were more numerous than in the hind-wings of *Microraptor*, *Anchiornis*, and other early birds (Xu et al. 2000; Hu et al. 2009; Zheng et al. 2013), and more closely resembles that of *Pedopenna* and those of the hind limb in *Epidexipteryx*. There are three dozen or more individual feathers stemming from along the metatarsals. Less distinct but

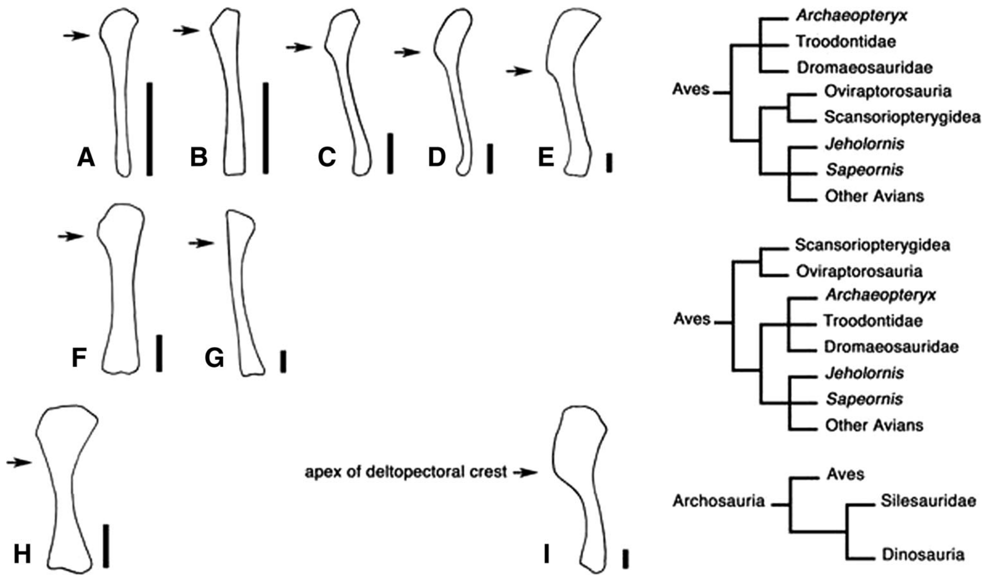

Fig. 5 Humeri with deltopectoral crest facing left, see *arrows* to follow development and convergence between Aves and Dinosauria. *A Scleromochlus*, and the basal bird lineage, Avemetatarsalia, which along with *B–E* depicts the progressive increase in size of the deltopectoral crest in basal avians; *F*, *G* non-dinosaurian silesaurids; *H* the archosauriform, *Euparkeria*; *I Eoraptor* which demonstrates the dinosaurian condition. *Scale bar* 1 cm. *A Scleromochlus*, the most basal known member of the bird-line archosaurs; *B Scansoriopteryx*, the most basal known member of Aves; *C Anchiornis*, a pre-*Archaeopteryx* bird; *D Archaeopteryx*; *E Jeholornis* (=*Shenzhouraptor*), a long-tailed toothed bird with powerful wings including the pronounced development of the deltopectoral crest which is the result of convergence to that in Dinosauria; *F Lewisuchus*, a dinosauriform and basal member associated with the non-dinosaurian silesaurids; *G Diodorus*, a silesaurid and non-dinosaurian sister-group to dinosaurs; *H Euparkeria*, a basal pre-archosaurian form previously believed to represent a generic ancestry that led towards birds and dinosaurs; *I Eoraptor*, one of the earliest known dinosaurs. On the *right* are three phylogenetic diagrams. The *upper* chart is based on that of Xu et al. (2010), which suggested an alternative interpretation which acknowledges that some groups of "non-avian theropods" could be basal members of Aves. The *middle* diagram follows this line of thought but modifies it by placing *Scansoriopteryx* as the most basal member of Aves. The *bottom* diagram represents Aves as a separate lineage derived from the Archosauria. Dinosauria and the non-dinosaurian Silesauridae are shown as sister groups, neither of which are directly related to Aves

otherwise similar markings are present on the third phalanx of digit III of the pes. As indicated by the feather impressions on the metacarpals, the similar markings on the pes indicate that, as with the forelimb, *Scansoriopteryx* was equipped with a feathered hind-wing. It is not known how far up the tibia/fibula this hind-wing may have gone, but it appears to have extended to the distal end of the phalanges just before the ungual on digit III. However, aside from the impressions on the metatarsals and phalanges, only a small patch from more distal portions of the feathers is exposed which may belong to the pes. Full extent of the hind wing remains speculative, but based on what is seen in the forelimb it may have been relatively substantial. No indications of scutate scalation are preserved, but there are impressions of small non-imbricating, reticulated scales visible along the opposite side of the pes along the second metatarsal.

The distal ends of the feathers from the manus are missing but must have reached beyond the outer edge of the rock in which the specimen is preserved. Based on the length of the secondary feathers on the forearm, the total length of the primary wing feathers is likely to have been somewhat longer than the manus itself, and probably approached that of wings in birds capable of flight. The strands, or barbs, that extend from the manus stem from along the metacarpals and from along the entire length of the outer, third digit. The middle digit in contrast does not appear to have had feathers that were as prominent as on the third finger. Instead, this digit that normally supports the primary feathers in birds, appears to have more weakly developed feathers, although their total length is not visible.

There are indications from where the feathers emanate below the ulna which suggest that a short patagium may have been present. Unlike most of the wing feathers, there appears to be a series of feathers that do not reach the bone itself. Instead, they appear to emanate slightly away from, and along the length of the ulna where upon the barbs spread from the calamus, resulting in V-shaped patterns. On the inner side of the forearm, there also appears to be a propatagium emanating from the wrist and along the radius of the left forelimb. While not unequivocal, these integumentary impressions strongly suggest that a propatagium was present. Along the distal end of the radius and ulna, there are continuous lines which curve around the wrist which pertain to soft body tissue. At this point, there is a transition of texture visible in which the elongate feathers are below the forearm and a smoother texture is above the forearm. There are only a few smaller and more typical down-like feathers scattered on this smoother surface which pertains to the propatagium membrane. The dramatic change in texture above the forearm to that from below the forearm is a strong indication that a propatagium was part of the bio-mechanical structure that formed the wings on the forelimbs in *Scansoriopteryx.* There is only one humerus preserved which may pertain to the right forelimb. However, there is enough area associated with the propatagium and the feathers, which are probably tertials, that belong to the space where the missing humerus would normally have been.

Short down-like feathers are preserved near the base of the tail. However, while it may be likely, it is unclear whether elongate down-like feathers similar to what is seen on the forelimb also existed on the tail. For most of the length of the tail, the feathers are not exposed and if present are still within the thin layers of matrix. There are a few indications exposed along the tail which suggest that feathers were present. These, however, are so incomplete that discerning what kind of feathers they are like is speculative. These feathers will require further study with enhanced microscopy, and hopefully new adult specimens will emerge to clarify feather structure in detail.

In sum, there are significant skeletal features of *Scansoriopteryx* which are unequivocally non-dinosaurian, including: acetabulum shallow and largely closed; head of femur lacks a distinctive neck and is instead more proximally oriented as in reptiles with sprawling limbs; supra-acetabular crest absent or with slight incipient development, unlike even the earliest Triassic dinosaurs; short, anteriorly directed pubic bones reminiscent of lagosuchid archosaurs; pubic peduncle very small and unexpanded; pubes lacking pubic foot; distal ends of pubes and ischia not fused; scapula expanded distally, retained from the archosaurian condition; outer manual digit longer than other digits (middle longest in theropods); outer metacarpal, digit IV, straight, robust and longer than the mid-metacarpal, digit III; and phalanges of manual digit IV progressively shorter distally (as in basal archosaurs). As an early bird, *Scansoriopteryx* conforms well with numerous unambiguous avian features, including elongate forelimbs, wing and hind-limb feathers, propatagium, semilunate carpal element, anisodactyl perching foot, tail with short anterior vertebrae, and arboreally adapted claws. It does not have characteristics that are mandatory to be considered dinosaurian, which indicates that it cannot have been derived from theropods, which even in early forms possessed a prerequisite suite of dinosaurian skeletal characters not present in *Scansoriopteryx*.

It is notable that the humerus in *Scansoriopteryx* (Fig. 5) resembles that in the non-dinosaurian dinosauromorph silesaurids, a sub-clade of archosaurs that evolved in the wake of the Permo-Triassic extinction, and also represented by Upper Triassic *Luntungutalia* and *Asilisaurus*, the two oldest well-preserved members of this sister-group that is outside Dinosauria (Peecook et al. 2013). But it is even more significant that the short deltopectoral crest so closely resembles that in *Scleromochlus* because this comparison takes the possible ancestry of *Scansoriopteryx* back to Avemetatarsalia and the base of the "bird-line" archosaurs (Benton 1999). *Scleromochlus* also makes an important comparison with *Scansoriopteryx* in that it has a closed acetabulum and femoral head that is more proximally oriented as in reptiles with sprawling limbs. As with the basal non-dinosaurian characteristics in *Scansoriopteryx*, including that of the pelvis and femur, the short delto-pectoral crest on the humeri continued to evolve in more derived forms which created a false dinosaurian appearance though convergence (see Fig. 4). Whereas the short length of the deltopectoral crest in silesaurids demonstrates a non-dinosaurian status, the relatively large delto-pectoral crest is significant in that it has been used to help identify possible basal dinosaurs, including *Nyasasaurus*, *Herrerasaurus*, and *Eoraptor* (Nesbitt et al. 2013). While not a member of the Silesauridae, the short delto-pectoral crest is a strong indication that *Scansoriopteryx* is not sufficiently derived to be considered a dinosaur. Instead, *Scansoriopteryx* represents a truly avian lineage that stemmed from a basal sister group outside that of Silesauridae and Dinosauria.

Discussion

Scansoriopterygids are small, arboreal archosaurs with feathered wings from the Jurassic which had plesiomorphous skeletons that do not have the salient characters necessary to be regarded as dinosaurs. Scansoriopterygids are not members of either Saurischia or the derived clade of carnivorous Theropoda, which birds have been largely thought to be derived from, based on phylogenetic analyses. Characteristics such as the structure of the deltopectoral crest of the humerus indicate affinities that have been attributed to Dinosauriformes, but it could be further argued that the lack of the offset articular head of the femur suggests an ancestry that predates Dinosauromorphs well into Ornithodira or Avemetatarsalia, if not further into more basal Archosauria. However, in contrast to its significant plesiomorphic characteristics, *Scansoriopteryx* does have sufficient avian characters to be considered as a basal bird, at a four-winged gliding stage in the evolution of flight. These extremely basal birds were clearly arboreal with the pes having a perching ability, and a climbing function made possible by the enlarged grasping range of the manual digits. Scansoriopterygids would certainly have been capable of climbing trees and branches but they may also have used their elongate manual digits to assist in landing safely in more of a quadrupedal manner similar to what is seen in many gliding lizards, in contrast to typical bipedal behavior in extant birds. Because the arboreal aspects in *Scansoriopteryx* are so basal in the development of flight, speculations as to how flight might have occurred through cursorial behavior are rendered unnecessarily complex and inappropriate. On a strictly cursorial animal, the elongate down-like filaments on the limbs and tail would not be as beneficial as in arboreal forms, but instead would be a hinderance if running were involved with the evolution of flight. Such a detrimental structure of feathers would not contribute to the progressive evolution of more aerodynamically derived feathers and instead would have inhibited such development among cursorial forms.

The discovery of scansoriopterygids fulfills two historical predictions: William Beebe's (1915) proposal that bird flight passed through a four-winged gliding "tetrapteryx" stage; and Hans Steiner and Gerhard Heilmann's hypothetical "proavis" avian ancestor, reconstructed in (1918) and (1926), respectively, as a small, arboreal archosaur. This non-dinosaurian aspect of the origin of birds directly affects the issue of dinosaur origins which has become more complicated due to non-dinosaurian characteristics within dinosauromorphs (Irmis 2011; Nesbitt 2011; Langer 2014). Recognizing that numerous sister groups and ghost lineages of non-dinosaur ancestors must have existed, and will need to be incorporated into the phylogeny for dinosaur origins, is further complicated by the removal of Aves, including basal secondarily flightless birds, from Dinosauria and maintaining their distinctly separate archosaurian/avian lineage. The origin of Aves is all the more complex because convergence with Dinosauria has obscured the true avian ancestry that, instead of being from within Dinosauria, is actually from non-dinosaurian archosaurs. Dromaeosaurs and troodontids with flight feathers should not be regarded as non-avian dinosaurs, because they are derived after *Scansoriopteryx* which makes them birds regardless of what degree of flight ability they might have possessed. This also indicates that larger flightless forms, including dromaeosaurs and other maniraptorans, are not simply precursors to extant birds but should be recognized as basal secondarily flightless birds. Instead of regarding Aves as a sub-Class derived from dinosaurs, *Scansoriopteryx* reinstates the validity of regarding Aves as a separate Class uniquely avian and non-dinosaurian.

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References

Abel O (1911) Die vorfahen der vogel und ihre lebensweise. Verh Zool-Bot Ges Wien 61:144–191

Barrett PM, Hilton JM (2006) The Jehol Biota (Lower Cretaceous, China): new discoveries and future prospects. Integr Zool 1:11–17

Beebe WA (1915) Tetrapteryx stage in the evolution of birds. Zoologica 2:39–52

Benton MJ (1999) *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. Philos Trans R Soc Lond B 354:1423–1446

Burgers P, Chiappe LM (1999) The wing of *Archaeopteryx* as a primary thrust generator. Nature 399:60–62

Čapek D, Metschler BT, Müller GB (2013) Thumbs down: a molecular-morphogenetic approach to avian digit homology. J Exp Zool B 322(1):1–1223

Chatterjee S, Templin RJ (2012) Palaeoecology, aerodynamics, and the origin of avian flight. In: Talent JA (ed) Earth and life, international year of planet earth. Springer, New York, pp 585–612

Chiappe LM (1999) Climbing *Archaeopteryx*? Archaeopteryx 15:109–112

Chiappe LM (2007) Glorified dinosaurs: the origin and early evolution of birds. Wiley, New York

Czerkas SA, Yuan C (2002) An arboreal maniraptoran from northeast China. Dinosaur Mus J 1:63–95

Dial KD (2003) Wing-assisted incline running and the evolution of flight. Science 299:402–404

Feduccia A (2012) Riddle of the feathered dragons. Yale University Press, New Haven

Feduccia A (2013) Bird origins anew. Auk 130:1–12

Frey E, Sues H-D, Munk W (1997) Gliding mechanism in the Late Permian reptile *Coelurosauravus*. Science 275:1450–1452

Gao K, Ren D (2006) Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-middle Jurassic age for the Daohugou beds. Acta Geol Sinica (English edn) 80:42–45

Gao CL, Chiappe LM, Ming QJ (2008) A new basal lineage of Early Cretaceous birds from China and its implications on the evolution of the avian tail. Palaeontology 51(4):775–791

Gong E-P, Martin LD, Burnham DA, Falk A, Hou L-H (2012) A new species of *Microraptor* from the Jehol Biota of northeastern China. Palaeoworld 21:81–91

He H, Wang XL, Zhou ZH, Zhu RX, Jin F, Wang F, Ding X, Boven A (2004) $^{40}Ar/^{39}Ar$ dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic age for the overlying Daohugou Beds. Geophys Res Lett 31:L20609

Heilmann G (1926) The origin of birds. Witherby, London

Hertel F, Campbell KE Jr (2007) The antitrochanter of birds: form and function in balance. Auk 124:789–805

Hu D, Hou L, Zhang L, Xu X (2009) Troodontid theropod from China with long feathers on the metatarsus. Nature 461:640–643

Irmis RB (2011) Evaluating hypotheses for the early diversification of dinosaurs. Earth Environ Sci Trans R Soc Edinb 101:397–426

Langer MC (2014) The origins of Dinosauria: much ado about nothing. Palaeontology 57(3):469–478

Langer MC, Nesbitt SJ, Bittencourt JS, Irmis RB (2013) Non-dinosaurian Dinosauromorpha. Geol Soc Lond Spec Publ 379:157–186

Liu Y, Liu Y, Ji S, Yang Z (2006) U–Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. Chin Sci Bull 51(21):2634–2644

Maryańska T, Osmólska H, Wolsan M (2001) Avialan status for Oviraptorosauria. Acta Palaeontol Polonica 47:97–116

McGuire JA, Dudley R (2011) The biology of gliding in flying lizards (genus *Draco*) and their fossil and extant analogs. Integr Comp Biol 51:983–990

Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull Am Mus Nat Hist 352:1–292

Nesbitt SJ, Irmis RB, Smith ND, Turner AH, Rowe T (2009) Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. J Vertebr Paleont 29:498–516

Nesbitt SJ, Barrett PM, Werning S, Sidor CA, Chairg AJ (2013) The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. Biol Lett 9:6. doi:10.1098/rsbl.2012.0949

O'Connor JK, Sullivan C (2014) Reinterpretation of the Early Cretaceous maniraptoran (Dinosauria: Theropoda) *Zhongornis haoae* as a scansoriopterygid-like non-avian, and morphological resemblances between scansoriopterygids and basal oviraptorosaurs. Vertebr Palasiat 52:3–30

Olshevsky G (1992) A revision of the parainfraclass Archosauria Cope, 1869, excluding the advanced Crocodylia. Mesoz Meand 2:1–268

Padian K, Chiappe LM (1998) The origin of birds and their flight. Sci Am 278:38–47

Padian K, de Ricqlès A (2009) L'origine et l'évolution des oiseaux: 35 années de progrèss. CR Palevol 8:257–280

Paul G (2002) Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds. Johns Hopkins University Press, Baltimore

Peecook BR, Sidor CA, Nesbitt SJ, Smith RMH, Steyer JS, Angielczky KD (2013) A new silesaurid from the upper Nta were Formation of Zanbia (Middle Triassic) demonstrates the rapid diversification of Silesauridae (Avemetatarsalia), Dinosauriformes). J Vertebr Paleontol 33(5):1127–1137

Senter P (2007) A new look at the phylogeny of coelurosauria (Dinosauria: Theropoda). J Syst Palaeontol 5(4):429–463

Steiner H (1918) Das problem der diastataxie des vogelflugels. Jena Z Naturwiss Ges 83:279–300

Sullivan C, Wang Y, Hone DWE, Wang Y, Xing X, Zhang F (2014) The vertebrates of the Jurassic Daohugou Biota of northeastern China. J Vertebr Paleontol 34(2):243–280

Wang X, Zhou Z, He H, Jin F, Wang Y, Zhang J (2005) Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. Chin Sci Bull 50:2369–2376

Xu X, Zhang F (2005) A new maniraptoran dinosaur from China with long feathers on the metatarsus. Naturwissenschaften 92(4): 173–177

Xu X, Zhou Z, Wang X (2000) The smallest known non-avian theropod dinosaur. Nature 408:705–708

Xu X, Ma QY, Hu DY (2010) Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian origins. Chin Sci Bull 55:1–7

Zhang F, Zhou Z, Xu X, Wang X (2002) A juvenile coelurosaurian theropod from China indicates arboreal habits. Naturwissenschaften 89:394–398

Zhang F, Zhou Z, Zing X, Wang X, Sullivan C (2008) A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. Nature 455:1105–1108

Zheng X, Zhou Z, Wang X, Zhang F, Zhang X (2013) Hind wings in basal birds and the evolution of leg feathers. Science 339: 1309–1312

Zhou Z, Barrett PM, Hilton J (2003) An exceptionally preserved Lower Cretaceous terrestrial ecosystem. Nature 421:807–811

Zhou Z, Chiappe LM, Zhang F (2005) Anatomy of the Early Cretaceous *Eoenantiornis buhleri* (Aves: Enantiornithes) from China. Can J Earth Sci 42:1331–1338