Article

The Avian Acetabulum: Small Structure, but Rich with Illumination and Questions

Alan Feduccia *

Posted Date: 3 November 2023

doi: 10.20944/preprints202311.0235.v1

Keywords: acetabulum; antitrochanter; archosaur; clade; convergence; dinosauriform; epigenesis, foramen acetabuli; gallinaceous; gallo-anseres; paedomorphosis; pelvis; supracetabular crest; synapomorphy

doi:10.20944/preprints202311.0235.v1

Article

The Avian Acetabulum: Small Structure, but Rich with Illumination and Questions

Alan Feduccia

Department of Biology, University of North Carolina, Chapel Hill, NC, 27584, USA; feduccia@bio.unc.edu

Abstract: That birds are maniraptoran theropod dinosaurs is now considered an evolutionary consensus. An "open" (i.e., completely, or substantially perforate) acetabulum is considered an important synapomorphy verifying the bird-dinosaur nexus. Here I present anatomical evidence from morphological aspects of the acetabulum and its important appurtenances, the supracetabular crest and the antitrochanter, that the hip anatomy differs substantially between dinosaurs and birds and for the current hypothesis of origins to be correct unlikely anatomical reversals would have been required. Given the thin bone of the acetabular walls and the varied tissue, both hard and soft, in the acetabular region and especially the lower part of the basin, it is apparent that many avian skeletons exhibit some anatomical loss of soft tissue and thin bone, some perhaps related to changes in gait, but also in part related to the dramatic trend in bone reduction associated with flight, especially in more advanced crown taxa. Many basal birds and early diverging neornithines tend to have a nearly closed or various levels of partially closed acetabula, thus rendering the current terms "open" or "closed" acetabula inaccurate; they should be modified or replaced.

Keywords: acetabulum; antitrochanter; archosaur; clade; convergence; dinosauriform; epigenesis; foramen acetabuli; gallinaceous; gallo-anseres; paedomorphosis; pelvis; supracetabular crest; synapomorphy.

1. Introduction

As early as Huxley [1]—and in a modern context Ostrom [2,3], Padian [4] and Gauthier [5]—the anatomy of the acetabulum and associated pelvic structures has been considered an important character linking dinosaurs and birds (Aves *sensu traditum* [6–8]; the "Avialae" of [5,9]). It remains so today [10,11] and considerable work has been expended on attempting to understand the transition from the putatively ancestral theropod locomotory system to that observed in extant birds (Neornithes) [12–20].

The acetabulum is a concave pelvic surface formed by the ilium, ischium and pubis which accommodates the head of the femur in tetrapods, providing pivotal ambulatory movement. The femoral head and acetabulum are each lined by an articular surface lubricated with a film of synovial fluid. Given the putative nexus of birds and dinosaurs, the morphology of the acetabulum took on new importance in bipedal vertebrates, specifically theropod dinosaurs and birds, but connectivity of acetabular morphology and function is still not fully understood. Triassic archosaurs such as *Lagosuchus* (synonymized with *Marasuchus* [21]), *Ticinosuchus*, etc., exhibit a closed acetabulum with a ventral foramen, and Late Triassic "rauisuchians" like *Postosuchus* exhibit an entirely theropodan pelvic anatomy, except for the acetabulum which is largely closed. Crocodilians, like other ancient archosaurs, have a closed acetabulum with an acetabular foramen, likewise seen in pterosaurs and humans. An open acetabulum is considered one of the most unchallengeable synapomorphies of dinosaurs and birds as opposed to stem dinosauromorphs and dinosauriforms that had not yet achieved fully upright posture and still exhibit a closed or partially closed acetabulum [22–24]. Many modern birds have a mainly open acetabulum; in others the walls of the basin are partially ringed by thin bone but covered by a fibrous sheet. The pit of the acetabulum is perforated by the foramen acetabuli at the confluence of the ilium, ischium, and pubis, located near the center of the basin. The rim of the acetabulum, the fibrocartilaginous labrum, is a white ring of cartilage lined by hyaline

doi:10.20944/preprints202311.0235.v1

cartilage, that provides an articulating surface for the femoral head, which has a pit (fovea) which receives the acetabular ligament. The deep floor is referred to as the acetabular fossa.

Despite this schematic characterization, it is more difficult adequately to assess acetabular morphology in extant birds than is generally realized. Preparatory methods used to produce skeletal collections in museums (e.g., defleshing with dermestid beetles, oxidation methods involving H_2O_2 and ammonia, chemical bleach and maceration) can damage or destroy fragile anatomical features. Fossils present even greater challenges to faithful preservation: the quality of the preserving sediment, microbial or micro-faunal destruction of soft tissue and thin bone, compaction and water-rock interaction, differential destruction from preservation diagenesis, and post-exposure weathering of the surviving fossilized material are all factors too easily forgotten. Taphonomic factors can obscure not only anatomical interpretation, as is clear from disputes on the identity and homology of fibrous or filament-like structures (still of unknown origin and function) in various theropod dinosaurs [25–37], but can also obscure phylogenetic signal in analyses which either are wholly reliant on morphological (particularly paleontological) data or which attempt to integrate data types, as illustrated by the problem of "stemward slippage" in attempts to understand the origin of major phyla [38–48]. Given the evolutionary tendency of birds toward reduction and thinning of bone, the avian skeleton (and especially the acetabulum) is particularly susceptible to taphonomic alteration or distortion during preparation for collections. It would therefore be unsurprising if important data might be overlooked in uncritical examination of fossil and museum material.

Spurred by these considerations, I here provide a new look at the argument that the hip joints of birds and dinosaurs are as similar as has been claimed for the past several decades. In addition to the perforation of the acetabulum with which we have been concerned thus far, there are two additional anatomical components that are of particular significance in this regard: (1) the formation and function of a supracetabular crest; and (2) the homology and function of the antitrochanter. Three sets of taxa must be evaluated to assess the distribution of these character states and thus critically to reexamine the familiar claim that birds have the hips (and legs) of theropod dinosaurs: first, basal archosaurs and basal dinosaurs, to establish the putatively ancestral condition for Aves; second, extant birds (Neornithes), to establish the derived avian condition; and finally, those basal avian forms that according to the best knowledge currently available from the fossil record have temporally and morphologically diverged the least from the primitive avian bauplan. This last group—basal birds—will be compared with unambiguously feathered "maniraptorans," i.e., Oviraptorosauria, Troodontidae, and Dromaeosauridae (together, with birds, constituting the Pennaraptora of recent authors). These taxa are universally considered to possess numerous derived avian character states [5,8,10,11,29,31,49–51], but significant disagreement has arisen regarding the phylogenetic interpretation of these data. While the pennaraptorans are typically considered to be primarily flightless nonavian theropods [52], others [10,51,53–59] have argued that some are secondarily flightless theropods derived from volant lineages; that they represent independent, parallel acquisitions of avian morphotypes in a general process of "ornithization" across some archosaur lineages [60]; that some pennaraptoran lineages independently acquired flight while remaining outside of Aves [61,62]; or that they are secondarily flightless birds that have been misidentified as theropods due to systemic homoplasy associated with flight loss and its developmental mechanisms [27,29–31,63–67].

Comparative morphological study is the primary basis for homology determination in all applications of phylogenetic analysis to paleontological data: analyses are obviously only as sound as the primary data upon which they are based. Accordingly, this paper will focus on the morphological and biofunctional level of investigation rather than the data-analytical; for problems with phylogenetic analyses of paleontological data in the dispute on the origin of birds the reader is referred to other works [29–31,50,68].

Note, furthermore, because of the range of fossil taxa under discussion in this review, the anatomical nomenclature adopted in the *Nomina Anatomica Avium* [69], although appropriate for Neornithes and Mesozoic birds, has not been used. The *Nomina Anatomica Avium*, like most modern avian anatomical references, portrays the standard *Gallus* (domestic chicken) and *Anas* (domestic duck) with fully open, dinosaurian acetabula, unlike the older images (Figure 1) which show the true anatomy with substantial medial acetabular walls.

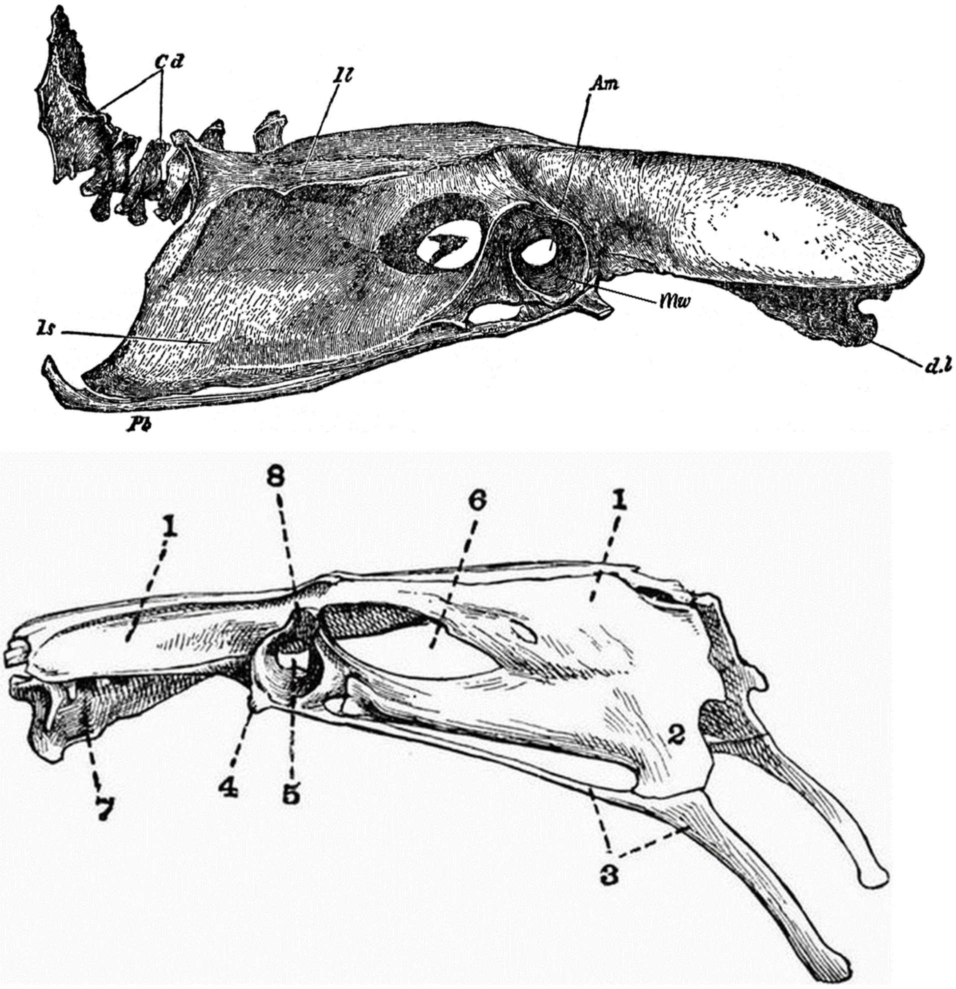


Figure 1. Pelves (Os coxae + Synsacrum, or innominate bone) of (upper) the domestic fowl *Gallus gallus* in right lateral view (see lowermost image for anatomical terms) and (below) the Mallard *Anas platyrhynchos* below in left lateral view. Note considerable medial "acetabular" walls (mw) surrounding the acetabular foramen (foramen acetabuli), whereas chickens are now typically incorrectly shown with a completely open acetabulum, as mentioned in the introduction, likely a result of presumed dinosaur ancestry. Abbreviations: 1, pre- and postacetabular ischium; 2, ilium; 3, pubis; 4, preacetabular tuberculum; 5, acetabulum with acetabular foramen, surrounded by medial "acetabular wall" (see mw in *Gallus* above; 6, ischiadic foramen; 7, intervertebral foramen; 8, antitrochanter). Images in the public domain.

Finally, the continued and illogical application of "phylogenetic nomenclature" [70], "phylonyms" [9], and the arbitrary redefinition of established taxon names necessitates the following nomenclatural clarifications. "Aves," as noted above, is used *sensu traditum*. "Archosauria" is here also used *sensu traditum* [71,72] and is therefore equivalent to the Archosauriformes of Nesbitt [73], Ezcurra [74], and de Queiroz et al. [9]. Chiappe [75–77] restricted "Ornithurae" from its historical usage (see discussions [78–80]) to a clade consisting only of the "the common ancestor of Hesperornithiformes and Neornithes plus all taxa descended from it" [77] (p. 205) (see also [81–83]); here the term is used in a more inclusive sense [7,29,78,79,84–87] in which it is equivalent to the "Ornithuromorpha" of Chiappe [88] and many recent phylogenetic analyses.

doi:10.20944/preprints202311.0235.v1

2. Hip joint morphology in basal Archosauria and Dinosauria

The acetabulum in Triassic archosaurs is a mostly closed, mainly imperforate structure that is structurally primitive, with the ilium, ischium and pubis adjoining each other at the lower part of the articular cavity [18,22,73,74,89,90]. The acetabular foramen arises at the junction between the pelvic bones and provides passage for the ligament that attaches to the femoral head. The surface of the acetabulum is somewhat uneven and exhibits a thick and strong rim for the attachment of the prominent white fibrocartilaginous collar, the labrum, bounded by an articular region, lined by hyaline cartilage. The transverse acetabular ligament, articulating with the head of the femur, parallels nutrient vessels to the hip joint. Most sauropsid acetabula have a small perforation in the pit of the eponymous basin. Basal archosaurs have a S-shaped femur with no in-turned head and without a well-developed upper rim (supra-acetabular crest) whereas dinosaurs have a relatively straight, vertically oriented femur with a fully in-turned head; the acetabulum is completely open with an upper bony rim over the hip socket known as the supraacetabular crest [91] that overhangs the acetabulum and distributes transmitted stresses and prevents unwanted excursions of the femur (Figure 2).

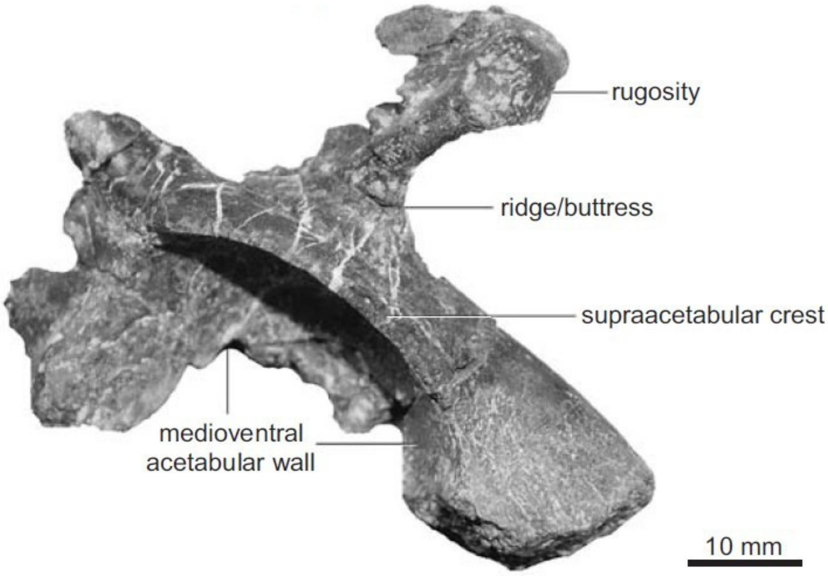
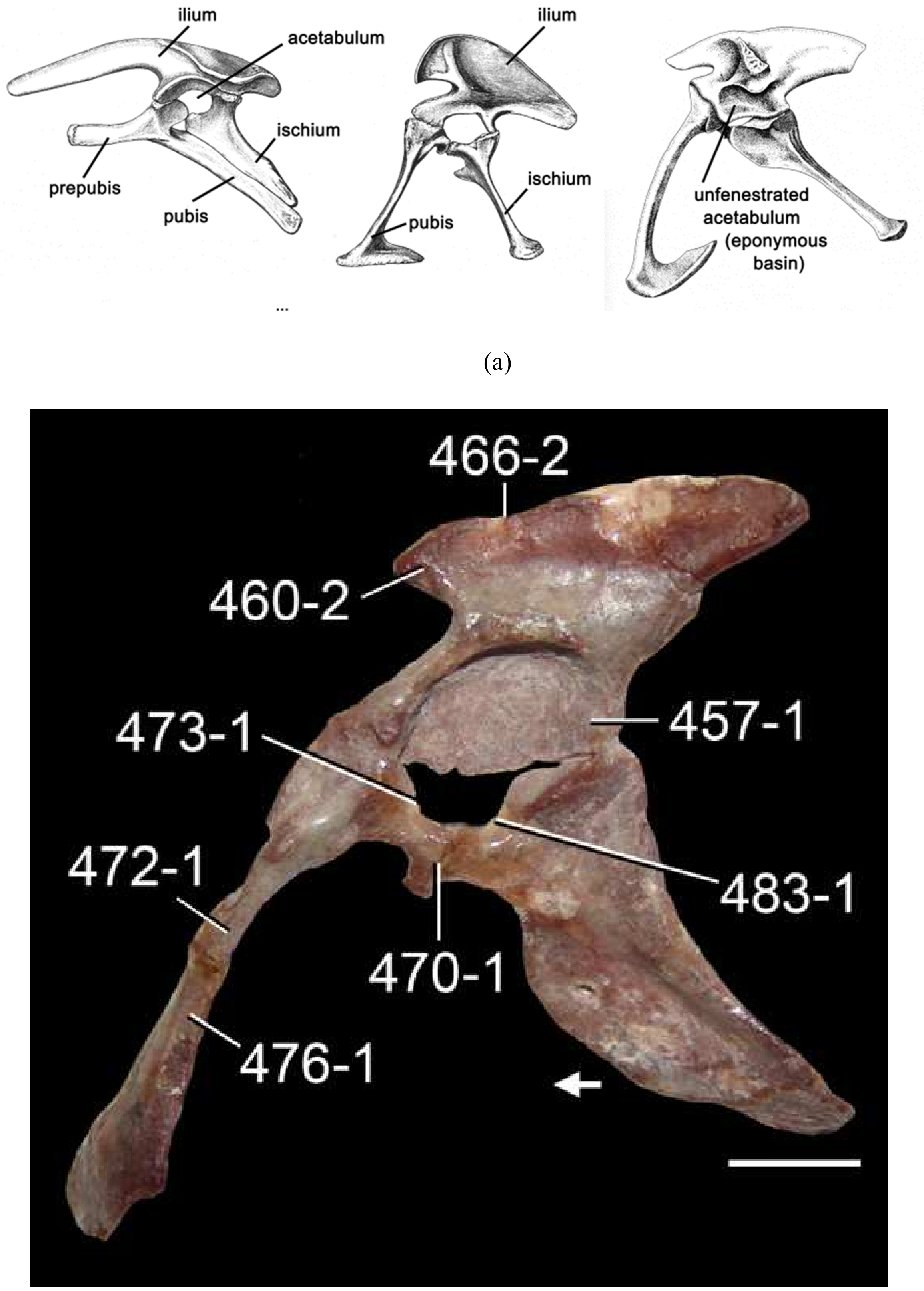


Figure 2. Late Triassic herrerasaurian dinosauriform *Caseosaurus crosbyensis* from New Mexico, illustrating the well-developed supra-acetabular crest characteristic of later dinosaurs. This feature, along with the avian antitrochanter, is absent in basal birds [91].

Among other modifications to the dinosaurian pelvis, femur, and axial skeleton, the combination of a vertically oriented femur with fully in-turned head articulating within a fully perforate acetabulum buttressed by a supracetabular crest allowed smooth pivoting of the hind limb about the hip joint, directly under the body, during the caudofemoralis-dominated excursion of the femur through the power and retracting strokes. It is a key morphofunctionally-integrated character complex in the “hip-driven” system of terrestrial locomotion, ancestral to archosaurs, whose biomechanical apogee is achieved in the striding, obligate cursorial bipedalism of theropod dinosaurs [12–19]. This character complex is already evident in *Lagosuchus* (Figure 3), is still more pronounced in silesaurids [92–94] and herrerasaurians (Figure 2) (note that there is some character discordance in Triassic dinosaurs, e.g., contrast the condition in *Pampadromaeus* [95] and *Eoraptor* [96]), and is fully established in primitive theropods. The condition in the large Jurassic tetanurine *Allosaurus* (Figure 3) may be taken as stereotypical of its development in Theropoda.

doi:10.20944/preprints202311.0235.v1



(a)

(b)

Figure 3. Mesozoic pelves: (a) compare, from left to right, pelves of *Stegosaurus*, an ornithischian; *Allosaurus* a saurischian theropod; and *Postosuchus*, a Triassic “rauisuchian” archosaur (note that aside from the open acetabulum in dinosaurs and the closure of the acetabulum in *Postosuchus* the pelves are otherwise quite similar; pelves modified from various sources); (b) pelvis of the dinosaurmorph

Lagosuchus. Abbreviations: 457-1: Acetabular antitrochanter present, 460-2: Preacetabular process of the ilium present, longer than 2/3 of its height, and not extending beyond the front edge of the pubic peduncle, 466-2: Concave dorsal margin of the iliac blade, 470-1: Pubis-ischium contact present and reduced to a thin proximal contact, 472-1: Total length of the pubis 3.94-4.87 times longer than the anteroposterior length of the acetabulum, 473-1: Recessed anterior and posterior portions of the acetabular margin of the pubis, 476-1: Rod-like, posteriorly curved pubic shaft, 483-1: The ischium's articular surfaces with the ilium and pubis are separated by a fossa [74].

A structure frequently homologized with the avian antitrochanter has been reported in many archosaurs [73,74] including basal dinosaurs [96–98], basal theropods and ceratosaurs [99–101], and a miscellany of coelurosaurs [16,102,103]. There is no osteological evidence that these structures are homologous: the avian antitrochanter forms primarily [69] or almost exclusively [90] from the ischium, whereas the so-called "antitrochanters" of these nonavian taxa are almost exclusively iliac in composition (see §3 for further discussion on the development and function of the antitrochanter). Moreover, while continuity of function is not a requirement of structural homology, it should be noted that putative "antitrochanters" of so great a range of taxa cannot possibly have performed the specialized mechanical role that the true antitrochanter does in extant birds as part of their peculiar hindlimb locomotory system [90,104]. Taxonomic distribution further argues against homology and thus against the soundness of applying avian anatomical terms to disparate structures that bear only superficial resemblance one to another.

Among Maniraptora, an antitrochanter has been reported in alvarezsaurs [105–108], therizinosauroids [11–109], oviraptorosaurs [112,113], troodontids [114], and dromaeosaurids [102,115–119*].* The putative "antitrochanters" of alvarezsaurs and therizinosauroids are iliac in composition and in the case of alvarezsaurs it is not even clear that they are articular structures [104]. The zeal for indiscriminate homologizing of osteological features sometimes extends to absurd levels: in *Mahakala*, for example, the femur is proposed to possess a "fossa articularis antitrochanterica" [*sic*] [120] (p. 42) (the authors meant "Facies articularis antitrochanterica")—a character state otherwise observed only in enantiornithines and ornithurines—even though *Mahakala* lacks an antitrochanter [120] (Figure 30b). With these preliminary clarifications made, pennaraptoran taxa in which an antitrochanter has been reported will be discussed further in §4.

3. Hip joint morphology in extant birds (Neornithes)

In Paleognathae, the acetabula are somewhat occluded, but some of the structural medial walls may be lost in preparation or handling; it is more open in *Apteryx*. Generally, one can see considerable occlusion in specimens of *Struthio* (Figure 4a), *Aepyornis*, and *Dromaius* (Figure 5). In the volant lithornithids and tinamous (Tinamiformes) the acetabulum appears partially closed (Figure 5b), conforming closely with *Gallus* and *Anas* (Figure 1), with bony walls of the basin but open at the bottom (in some fossils the bony interior has been lost). Lithornithids and tinamous have somewhat smaller antitrochanters and very limited supracetabular crests (Figure 5), if indeed the term is used correctly, because the structure of the so-called crest is about the same below and above the acetabulum; it is minimally a misnomer (the same is true of the mid-Jurassic *Anchiornis*, see §4). Antitrochanters are also evident in struthionids, rheas, kiwis and other "ratites" (Figs. 4a, 5f). Interestingly the acetabulum is partially or mainly closed in most ground-dwellers, unlike any putative dinosaurian relatives despite the presumed quasi-similarity in gait (Figure 5).

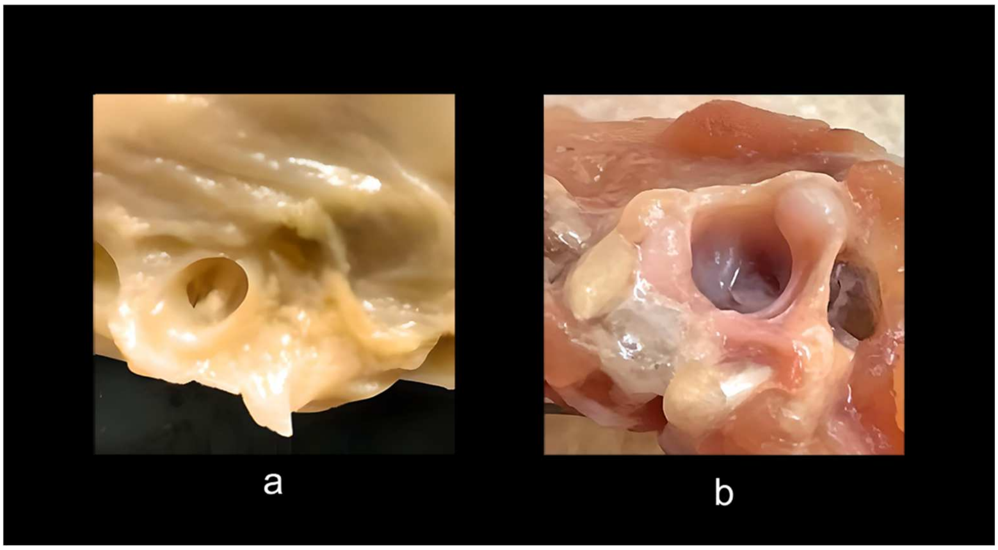


Figure 4. Acetabulum of (a) juvenile ostrich *Struthio camelus* (24-day old wet specimen, normal incubation 36-45 days; the specimen is fragile and preservative renders image with poor resolution) and (b) adult Scaled Quail *Callipepla squamata* showing acetabular closure and substantial medial wall, in left lateral view. Approximate diameter of the acetabulum in the *Struthio* and *Callipepla* specimens is approximately 3.5mm and 4.5mm respectively. Note the fully developed antitrochanter (at the upper right of the acetabulum) in the adult quail. (Author's specimens).

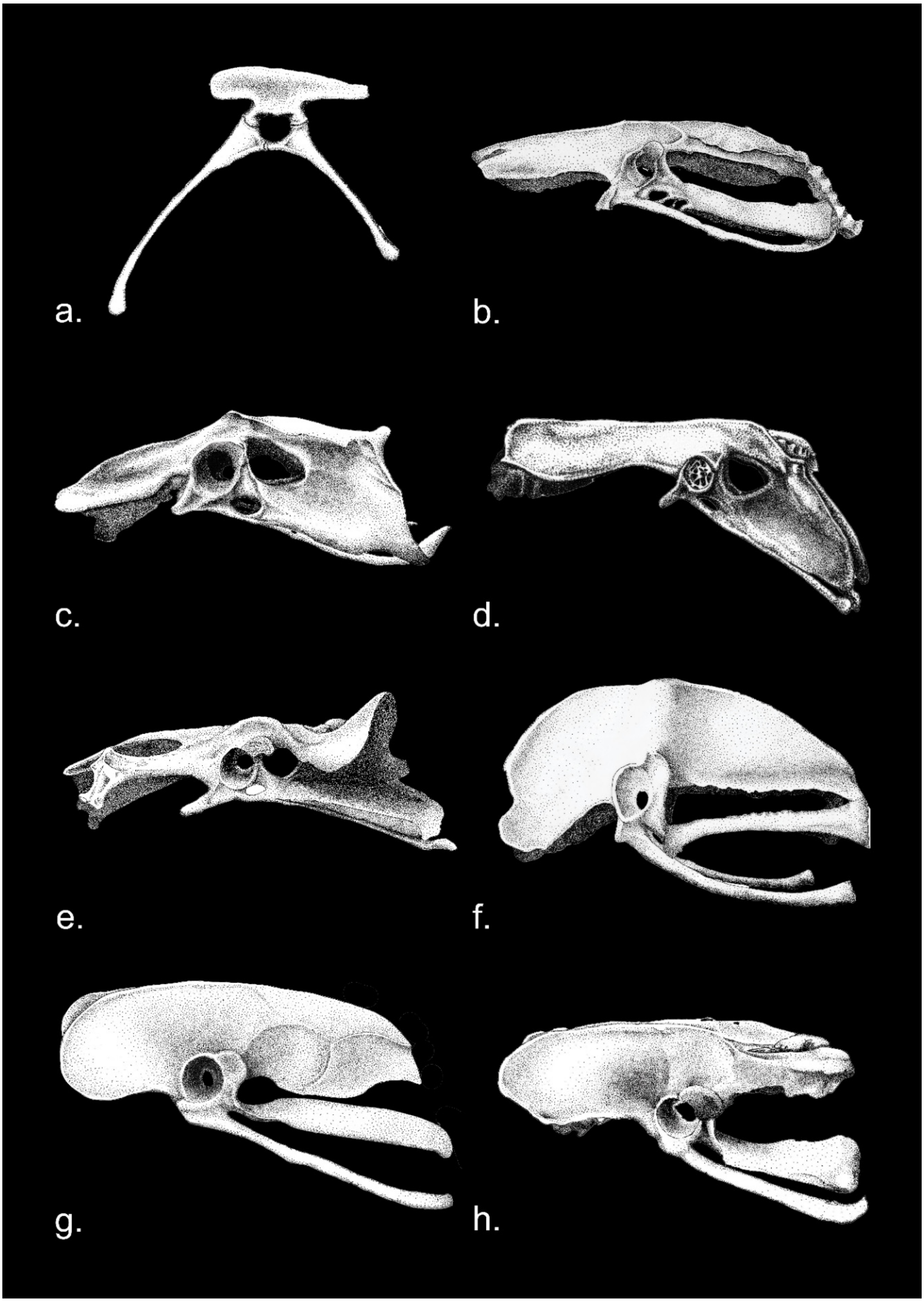


Figure 5. Pelvis of the basal theropod *Coelophysis* (a) compared to an array of primarily ground-dwelling birds: (b) Solitary Tinamou (*Tinamus solitarius*), (c) Wild Turkey (*Meleagris gallopavo*), (d) Japanese Quail (*Coturnix japonica*), (e) Greater Roadrunner (*Geococcyx californianus*), (f) Emu (*Dromaius novaehollandiae*), (g) Bush Moa (*Anomalopteryx didiformis*), and (h) Elephant Bird (*Aepyornis hildebrandti*). The avian acetabula show a range of closure from partial to nearly complete occlusion.

Note the contrast between the condition in these cursorial birds, which presumably should most closely approach the putatively ancestral theropod condition with respect to their acetabular morphology, and the condition in *Coelophysis*. Sources: drawing of *Coelophysis* provided by the late N. Colbert; tinamou drawn from photos provided by P. Houde; *Coturnix japonica* drawn from original photo from S. Mehta, interpreted by the author and artist K. Grow; *Dromaius* drawn from pelvis in author's collection; *Meleagris* drawn from photos in author's collection and photos; *Geococcyx* drawn from images and checked with specimen from the author's collection of zoo birds. Art by K. Grow.

In Neognathae the acetabulum is typically considered to be open, based usually on observation of skeletal preparations. The problem with this interpretation is illustrated by phasianid galliforms and particularly by the Japanese Quail (*Coturnix japonica*), a common model species for embryological study. Here the acetabulum is almost closed by lattice-like endochondral bone that is easily shattered in skeletal specimens [pers. obs.] (Figure 5d). There is some variation between taxa, and in two Scaled Quail (*Callipepla squamata*) carcass dissections and oxidation preparations, the acetabulum is largely closed by substantial medial bony walls about 2/3 the depth of the basin, with only a central foramen remaining [121] (compare with Figs. 4b and 5c-d). Preparation by oxidation method using 15 to 17% HO might be sufficient to disintegrate some of these interior bony walls in small specimens and they can be revealed only by careful dissection [121]. In examining chickens for biological studies, one sees that much of the anatomy within the acetabulum may have vanished in preparation, and many older specimens were processed with clorax that can easily disintegrate bone.

Surprisingly, chickens bred and prepared for human consumption provide further insight. Dissection of a common rotisserie-prepared chicken demonstrates that commercial chickens are going to market long before normal maturity in the wild. Such post-hatching chickens appear partially paedomorphic from post-hatching morphological characters; they are stuffed with food for about four to six weeks when they reach market size, without the skeleton fully formed, as evidenced by still developing epiphyses and considerable cartilage. On average the growth timing for such chickens is about 6 weeks or 42 days. In contrast, wild chickens, depending on the species, take 16 to 24 weeks, or 112 to 168 days to full maturity. One can see that this processing creates an form of induced paedomorphosis, which explains the large amounts of cartilage all over and incompletely fused and cartilaginous epiphyses (Fig 6). Studying these specimens provides a glimpse into their post hatching ontogeny, the epigenetic landscape at a stage of near completion. It is surprising, given the frequent characterization of birds as having—like dinosaurs—completely open acetabula, to discover that rotisserie specimens have partially closed acetabula with a perforation covered by soft tissue (Figure 6a). To make certain this observation was not anomalous, I studied and dissected 14 individuals of rotisserie chickens and two fully mature Poulet Rouge fowl (mature chickens that were farm raised with no additives including antibiotics). These acetabula had closed basin walls lined with bone and fibrocartilage with an acetabular membrane, and the acetabular ligament, which attaches to the femoral head, can be seen arising from a dimple covered by a strong fascia membrane in the lower upper part of the basin from the center, and connecting to the head of the femur (Figure 6b).

doi:10.20944/preprints202311.0235.v1

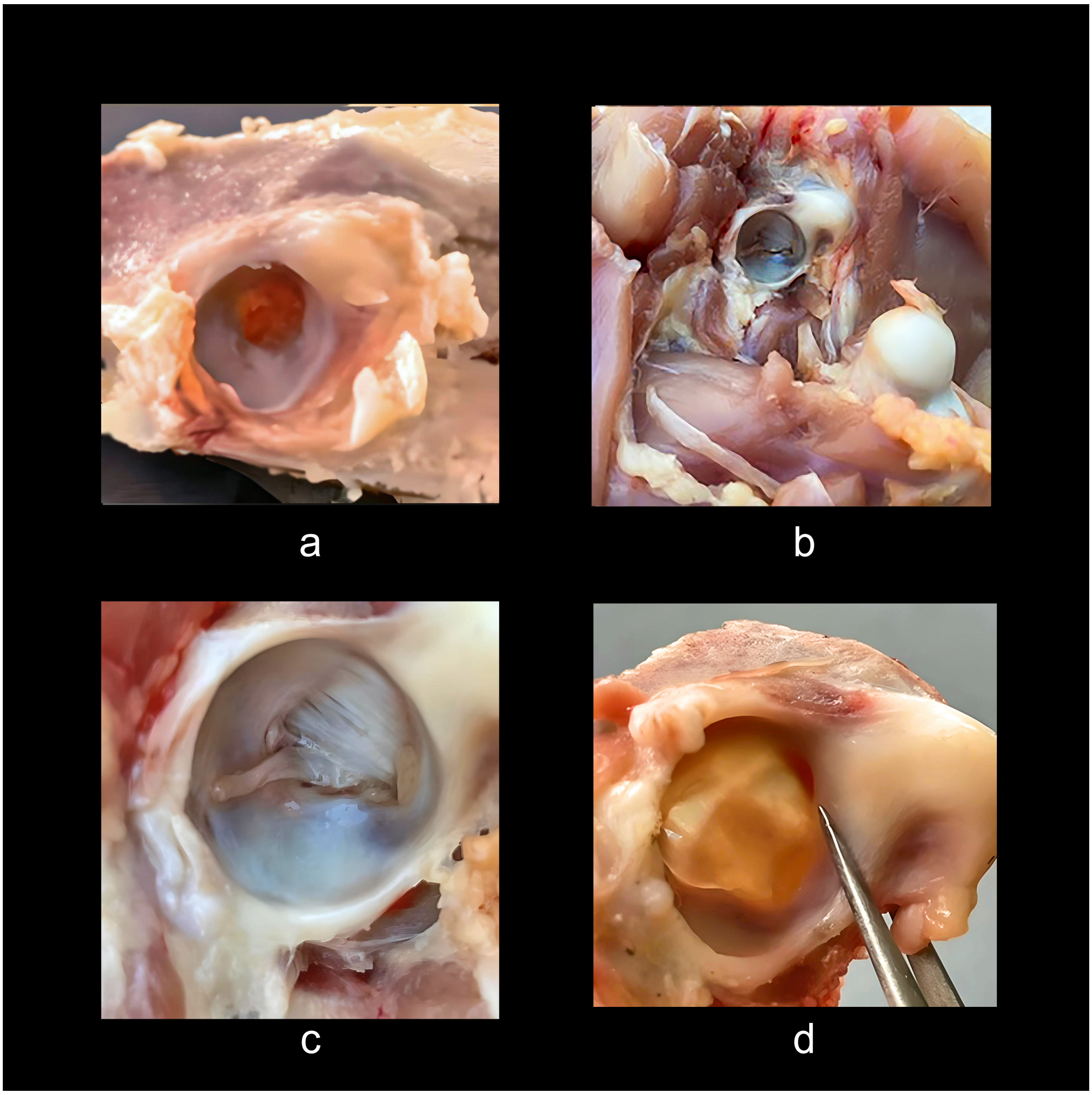


Figure 6. Acetabula of rotisserie chickens. These images show post-hatching additions, notably considerable cartilage and the antitrochanter: (a) a rotisserie chicken post-hatching, the acetabulum foramen near opening, showing considerable cartilage and an almost calcified antitrochanter; (b) Poulet Rouge fully mature chicken showing a mature ossified antitrochanter and femoral head; (c) mature Poulet Rouge showing white labrum surrounding the acetabular edge, ossified antitrochanter and femoral head (note the remnant of Ligamentum capitis femoris affixes to the femoral head, helping to stabilize the femur); (d) photo light shone from the base of the acetabulum shows the extent of medial bony walls and the basin of a fibrous sheet devoid of bone. Epiphyses of rotisserie specimens are entirely cartilaginous or in the process of transforming to endochondral bone. (Rotisserie chicken's acetabula approximately 10 mm; poulet rouge, 12 mm). Photos and dissections by the author.

Egawa et al. [122] argue that many anatomical landmarks in birds show developmental timing that parallels their phylogenetic order of acquisition, a Haeckelian interpretation, implying that the process of terminal addition may play a major role in ontogeny. Yet, so-called "terminal addition" is nothing more than the end of the epigenetic landscape whether in or out of the eggshell, and most vertebrates have considerable additions following hatching in birds, or birth in mammals (note especially marsupials where the premature fetus will finish much of its ontogeny within the marsupium with mouth attached to the nipples). In the case of quail, not only were the acetabula imperforate throughout embryogenesis, but even the adult acetabulum may be almost closed (Figure 5d). Egawa et al. [122] further suggested that a dinosaur-type perforated acetabulum arises from acetabular cartilage loss in chicken embryos. They linked acetabular perforation in "non-avian" dinosaurs and birds (represented in their study by *Struthio* and *Gallus*) with high susceptibility to bone morphogenetic protein (BMP) antagonists and Wnt ligands [122]. They point out that in non-archosauromorph sauropsids with unperforated adult acetabula the pelvic anlagen are not susceptible to the joint-secreted molecules, while in the transition to non-dinosaurian archosauromorphs with unperforated acetabula in the adult, the pelvic anlagen became susceptible to BMP antagonists but less susceptible to Wnt ligands, leading to no cartilage loss. Tsai and colleagues studied joint function and anatomy in the two extant archosaur clades, birds and crocodilians. Unsurprisingly, they demonstrated topologically and histologically similar articular soft tissues in the hip joints of both groups [123,124]. In all extant archosaurs the proximal femur has a hyaline cartilage core attached to its metaphysis via a fibrocartilaginous sleeve. Epiphyseal cartilage in extinct forms must therefore have been substantial [125,126]; loss of this epiphyseal cartilage in fossilization indicates that the preserved ends of bone in crown group archosaurs are almost certainly not joint surfaces [126] and this complicates functional inferences [123,124]. In a later study by Griffin et al. [20] the situation becomes more confused as the authors note that "The hip socket in *Coturnix* quail remained *imperforate* throughout embryonic development" [20] (p. 347) (my emphasis). On the same page they write that "…two derived avian states…resembled early ancestral/developmental morphologies (that is, instances of localized paedomorphosis): the broad, flat avian ischium resembled the *early embryonic and ancestral archosaurian* [my emphasis] condition more than it did the intermediate dinosaurian conditions." It should be noted in passing that while studies like those of Egawa et al. [122], Griffin et al. [20], and many others [127–130] exhibit a surprisingly Haeckelian recapitulationism, the data they provide are more reasonably interpreted in accordance with von Baer's embryological principles of simple conservativism of early embryos, without the orthogenetic implications of Haeckel's recapitulation of past ancestors. In the words of Paul Ehrlich and colleagues: "The resemblance of early vertebrate embryos is readily explained without resort to mysterious forces compelling each individual to reclimb its phylogenetic tree." [131, p. 66]. The avian antitrochanter is probably a neomorphic structure located lateral to the posterodorsal rim of the acetabulum of the pelvis (if so, the term "avian antitrochanter" would be a pleonasm); it is a striking feature in living birds, but evolved only relatively late, appearing as the center of gravity in birds shifted forward due to the enlargement of the flight musculature. This phylogenetically late addition comports with the fact that it appears late in embryology and upon hatching is still cartilaginous. The avian antitrochanter is unique among vertebrates, and a significant portion of the femur-pelvic articulation is located outside of the acetabulum. Hertel and Campbell [104] demonstrated that the antitrochanter-femur articulation transferred long-axis rotational movement of femur to pelvis [104]. This ridge, which is easily seen, lies above the acetabulum and is thickest just above the mid-portion of the depression. They concluded that this derived avian feature evolved as an aid in maintaining balance during bipedal locomotion [104]. It is a brace to prevent unwanted abduction of the hindlimb and to absorb stresses on the femur in locomotion. The term "antitrochanter" is a misnomer as its facet is not in opposition to the femur [104], and although it is believed to serve as a brace to control excessive abduction of the femur to pelvis, in specialized foot-propelled divers (Cretaceous hesperornithiforms, and post-K-Pg loons, and grebes), the antitrochanters are quite large compared to other birds (Figure 7), but the femora may project straight out from the sides of the pelvis at a 90° angle, fully abducted. Antitrochanter function in derived birds therefore clearly requires further investigation. Indeed, one would have to explain functionally why the antitrochanter should be basically similar in ratites and hesperornithiforms.

Figure 7. "Mesozoic diving dinosaurs" is now a commonly used but erroneous moniker for the hesperornithiforms. Shown are sacra of *Hesperornis* and *Parahesperornis*, large divers of the Late Cretaceous, in left lateral view showing nearly closed acetabula. Note also the prominent antitrochanters (arrows). Hesperornithiforms were capable of full lateral abduction of the hindlimbs during foot-propelled swimming (like loons and grebes), so the function of the antitrochanter in birds must extend beyond preventing excessive abduction of the femur. Images courtesy M. Everhart and the University of Kansas, Museum of Natural History, and University of Nebraska State Museum.

The newly described taxon Telluraves (also called land birds or core land birds), erected based on whole genome comparisons, includes primarily small arboreal birds which are all strong fliers and whose close relationships have long been recognized (like woodpeckers and passerines), but also (and more controversially) parrots, the diurnal birds of prey ("raptors"), and seriemas [8,132]. Most of these taxa exhibit fully open acetabula with greatly reduced medial walls, which might well be interpreted as a trend in modern birds to jettison all but essential "baggage," including bone, i.e., to reduce all anatomical structures that might hinder maximal flight efficiency. This possibility is further suggested by comparison with the condition in more primitive land birds, e.g., paleognaths, galliforms, and some cuculiforms (like the Greater Roadrunner, *Geococcyx californianus*) (many others, like bustards, gallinules, etc., are not shown here in this precursory work); in all these taxa there is still significant medial occlusion of the acetabulum (Figure 5), presumably both because the antitrochanter had developed (permitting the form of bipedal locomotion peculiar to birds) and because there was no additional selective benefit for further reduction of the bony acetabular walls. In turkey (*Meleagris*) there is major occlusion and some chachalacas (*Ortalis*) may have nearly complete acetabular occlusion. Interestingly, among those Telluraves which are or were primarily cursorial, cariamiforms like the extinct phorusrhacids (e.g., *Llallawavis* [133]) and extant seriemas (relicts of an older Neogene radiation [8,134]) exhibit considerable medial occlusion of the acetabulum.

4. The hip joint morphology of basal birds and pennaraptoran "maniraptorans"

The basal avian assemblage, stretching from the Late Jurassic to the Early Cretaceous, includes the archaeopterygids, *Chongmingia*, *Jinguofortis*, *Fukuipteryx*, *Cratonavis*, omnivoropterygids (="sapeornithids"), jeholornithids, and confucuisornithids [7,8,29,31,51,130,135–138]. Included in this group are taxa whose position is labile in phylogenetic analyses [139,140] but which are generally recovered near archaeopterygids as basal "Avialae," the most notable of which are the anchiornithids *Anchiornis*, *Xiaotingia*, *Eosinopteryx*, "*Aurornis*" (likely junior synonyms of *Anchiornis*) [141], and *Fujianvenator*, the oldest. *Rahonavis* [142] has variously been considered a basal bird or a dromaeosaurid [118,139,143]; it will here be discussed under the same heading as other basal birds. The phylogenetic interpretation of *Balaur*, described as either an aberrant dromaeosaurid [102,130,140,144,145] or a flightless basal bird [146–148], is unclear and its morphology is both bizarre and specialized; it will not be considered further here. *Zhongornis* was initially interpreted as a basal non-pygostylian bird [149] whereas other workers argue that it is a scansoriopterygid [150]. Scansoriopterygids were first described as tree dwellers (e.g., *Epidendrosaurus*, and *Scansoriopteryx*), but henceforth have almost universally been interpreted in reconstructions as ground-dwelling cursors, which is clearly incorrect; they were almost certainly trunk-climbers and gliders and they have closed acetabula. As the interpretation of scansoriopterygids is beyond the scope of this paper (see below), *Zhongornis* will not be discussed further here. *Zhongjianornis* was initially described as a basal bird [151] but further study has demonstrated that it is probably a basal ornithurine [152].

The "maniraptoran" taxa crucial to the dispute on the origin of birds are the pennaraptorans (as noted earlier). Accordingly, and for the sake of simplicity, it is the pelvic morphology of these taxa—the oviraptorosaurs, troodontids, and dromaeosaurids—that in the present paper will be compared with that of basal birds. The anatomy and phylogenetic interpretation of the enigmatic scansoriopterygids is too fraught a subject involving too many complexities to be addressed here and the reader is referred to previous work [29,31,153,154] that showed a definitive absence of diagnostic dinosaurian characters.

(a). Basal birds.—In archaeopterygids the acetabulum is medially occluded, as is clearest from the London specimen [155] (figs. 29-31) (see also [118]), and neither an antitrochanter nor a supracetabular crest are developed, as is most clearly shown by the London, Berlin, Eichstätt and Munich specimens ([155] (figs. 29-31); [156] (figs. 5.83, 5.110 and 5.113); [157] (fig 3a)) (see also Figure 8d).

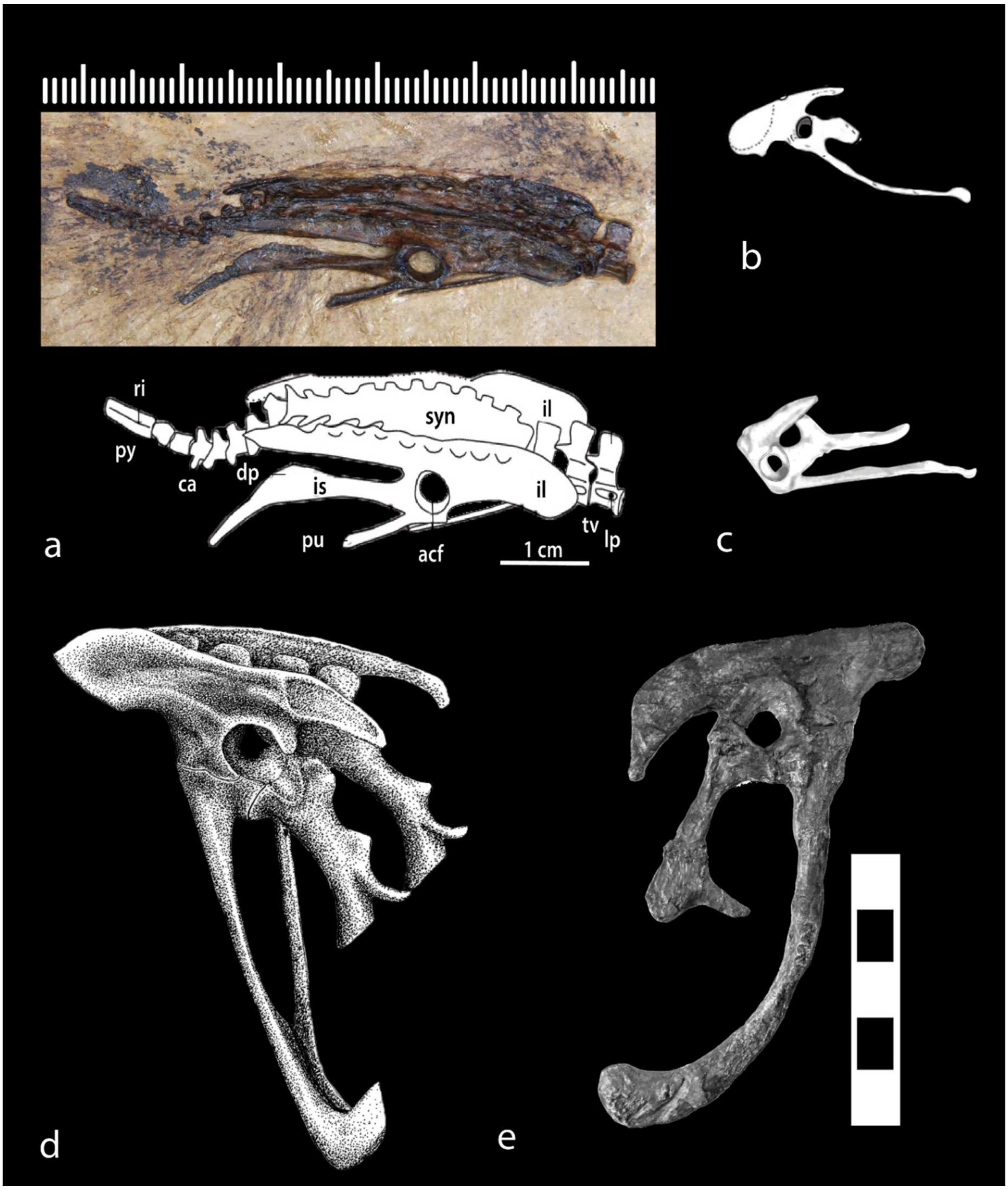


Figure 8. Pelves of Mesozoic birds showing medial acetabular walls: (a) Early Cretaceous ornithurine *Gansus* [237]; (b) Early Cretaceous enantiornithine *Qiliania* [238] and (c) *Pterygornis* [239] (note the medial walls in these forms); (d) Late Jurassic *Archaeopteryx* showing expansive medial walls (image composite, primarily after P. Wellnhofer, based on the Munich specimen, with details from the London, Berlin and Eichstätt specimens); (e) *Microraptor*, similar to *Archaeopteryx*, the Early Cretaceous four-wined bird-like glider (dromaeosaur) (note the descending bony walls of the acetabulum). *Microraptor* photo courtesy D. Burnham. Art by K. Grow.

Agnolin and Novas [115] (Figure 3B) interpreted a slight swelling on the posteroventral rim of the acetabulum in the Berlin specimen as an antitrochanter, but this interpretation seems incorrect because: (1) it is positioned on the posteroventral rim of the acetabulum, whereas the avian antitrochanter is posterodorsal to the acetabulum [69,90,104]; it is composed solely of the ilium, while the avian antitrochanter is composed of both ischium and ilium [69,90,104] and (3) a comparable structure is not seen in the pelvis of other specimens. Note that in those archaeopterygid specimens that are preserved on their backs (or partially rotated onto their backs), as in the London, "Thermopolis" [158], and 11th skeletal exemplars [147], the hind limbs splay markedly (although the ilia are barely preserved in the "Thermpolis" specimen, the femora are not disarticulated, or at least well within their in-life range of motion; the same is true of the 11th specimen, where the ilia are also poorly preserved). Death posture in an articulated, or largely articulated, skeleton corresponds to range of motion in life and in theropods, a sprawling orientation, even postmortem, is mechanically prevented so long as the femora, with their strongly inturned heads, remain in articulation [116,159]. It is therefore unsurprising that the femoral head of archaeopterygids is not fully inturned (despite repeated claims to the contrary) as was already clear from the Eichstätt specimen [160] (Figure 11a,b) (see also [155], (figs. 36-42)). Wellnhofer [156] stated that in the "Thermopolis" specimen the femoral head is fully inturned, but this is incorrect: the putative head of the right femur in this specimen is a calcite deposit or other obscuring piece of matrix, an interpretation confirmed by the fact that it does not fluoresce under UV light [156] (Figure 5.130). Similarly, in the Daiting specimen, the femoral head is clearly not fully inturned [161] (Figure 32). Although Paul (2002) claims that a supracetabular crest is present in archaeopterygids, it is absent in the London, Berlin, Eichstätt and Munich specimens (Figure 8d) (compare with [90] (Figure 1B-E) and see also [162]); the only particular indication of such a structure is in the large Solnhofen specimen (with the most robust hindlimbs among the archaeopterygid material), which may in fact belong to a separate genus *Wellnhoferia* [156,161,163,164].

Anchiornithids are closely allied with archaeopterygids: "*Anchiornis huxleyi* shared derived features with avialans […] Morphological comparisons strongly suggest *Anchiornis* is more closely related to avialans than to deinonychosaurians or troodontids. *Anchiornis huxleyi* exhibits many conservative paravian features, and closely resembles *Archaeopteryx* and other Jurassic paravians…" [141] (p. 4). The acetabulum in *Anchiornis* is partially occluded by substantial medial bony walls ([165] (Figure 4c); [141] (Figure 32); D. Burnham, pers. comm.) (Figure 9). A weak though clearly demarcated crest is present above the acetabulum ([165] (Figure 4c); [141] (Figure 32)), but it is not broad and is more like a reinforcement rim, as it proceeds down the sides of the acetabular circle; but like basal birds there is no antitrochanter homologous to that of later birds.

Figure 9. Femora and right pubis of *Anchiornis*, with hip joint partially visible due to taphonomic displacement of proximal femur, showing part of the expansive bony medial acetabular wall (arrow). Image courtesy R. Pei.

There appears to be neither a well-developed supracetabular crest nor an antitrochanter in *Xiaotingia* [166] (Figure 2c) or "*Aurornis*" [146] (figs. 2c-d) (if "*Aurornis*" is a valid taxon and not a junior synonym of *Anchiornis*, as noted earlier), but these taxa are likely all anchiornithids. The situation in the recently described *Fujianvenator* is also uncertain because there is no clear view of details of the acetabulum, but the specimen is very close anatomically to *Anchiornis*. There is little reason to believe that *Anchiornis* and *Fujianvenator* could not have been volant or near-volant and in most aspects they morphologically qualify as basal birds. Note that seriamas (Cariamidae), terrestrial birds with reduced wings and long-legs (South American counterparts of African secretarybirds) are still able fliers, and both roost and build their nests in trees.

The ilia and ischia are not preserved in *Chongmingia* [136]. The condition in *Jingufortis* is unclear: the acetabulum is obscured by the synsacrum, but the ilium appears to lack a supracetabular crest or antitrochanter [137] (Figure S4). The acetabulum of *Fukuipteryx* is open, but there does not appear to be either a supracetabular crest or antitrochanter [138] (Figure 5d). The acetabulum of *Cratonavis* appears to be mostly perforate (with perhaps slight medial occlusion) but there is neither a supracetabular crest nor antitrochanter [130] (extended data Figure 3a-b). *Rahonavis* has a fully perforate acetabulum, a small antitrochanter, and poorly developed supracetabular crest [142] (Figure 29).

The incongruent distribution and parallel development of character states among basal birds is a serious obstacle to evolutionary interpretation and phylogenetic reconstruction at all levels of the basal avian radiation crownward of the archaeopterygids and those archaic taxa closely related to the archaeopterygids reviewed above [8,29,51]. Omnivoropterygids (e.g., *Sapeornis*, *Kompsornis*), jeholornithids (e.g., *Jeholornis*) and confuciusornithids (e.g., *Confuciusornis, Eoconfuciusornis*) are usually compressed into their slabs and the hip joints in these taxa are often not fully visible or well preserved. In other cases, specimens seem to provide conflicting data: for example, some specimens of *Sapeornis* seem to show at least partial medial occlusion of the acetabulum, whereas others appear to show substantial perforation [167] (figs. 8a-b) and the actetabulum of "*Shenshiornis*," probably a junior synonym of *Sapeornis*, a good flier, is completely perforate [168] (Figure 4c). A small antitrochanter may be present in confuciusornithids ([169] which incorrectly characterized confuciusornithids as terrestrial birds; contrast with [170,171]). Confuciusornithids lack a supracetabular crest [169–171], and both omnivoropterygids and jeholornithids lack supracetabular crests and antitrochanters ([167,172]; [168] (Figure 4c); [173] (Figure 4D)).

The situation in basal birds is perhaps reciprocally illuminated by consideration of some more derived Cretaceous taxa (Figure 8a-c). Thus, in both the amphibious ornithurine *Gansus* (Figure 8a) and enantiornithines like *Qiliana* and *Pterygornis* (Figs. 8b-c), all flying birds, the acetabula are mostly perforate but nevertheless exhibit bony walls extending slightly into the acetabular basin (in the more archaic enantiornithines there is substantially greater closure of the acetabulum than in ornithurines *contra* [174]; in some, like *Sinornis*, the closure seems extensive [80] (Figure 8.4A-B). Interestingly, the poorly known Amazonian herbivorous river bird, the Hoatzin (*Opisthocomus hoazin*), has a similar acetabulum with reduced medial walls [pers. obs.]. Significant medial occlusion—and evidence of taphonomic destruction—is also evident in the flightless ornithurine *Patagopteryx* [175] (Figure 13.11c), which is often (though perhaps spuriously) recovered as a basal ornithurine (or "ornithuromorph") [130,152,175–178]. This medial occlusion persists in the hesperornithids *Hesperornis* and *Parahesperornis* (Figure 7), highly adapted flightless foot-propelled divers with pachyostotic bones like penguins (the same condition is observed in *Baptornis* [179] (Figure 5a); it is interesting in this regard to note that *Natovenator*, an at least semiaquatic dromaeosaur that appears to have been adapted for efficient swimming, is reported to have a "small" acetabulum [180]. Partial medial occlusion of the acetabulum continues to be observed in taxa close to Neornithes (e.g., *Iaceornis*, the pelvis of which was assigned to *Apatornis* by Marsh [181]) [83] (pp. 46-52 and Figure 15), though not in *Ichthyornis* [182] (Figure 25). As noted in §3, the acquisition of an antitrochanter is a phylogenetically late development, apparent only in the enantiornithines and ornithurines [8,90,104,174]. In both enantiornithines and ornithurines, the maintenance of balance in obligately bipedal locomotion is linked to the presence of an antitrochanter [104] and the late phylogenetic acquisition of this character state, in addition to persisting medial occlusion of the acetabulum and the absence of a supracetabular shelf in basal birds, is consistent with the argument that the acquisition of obligate bipedalism in birds (with the forelimbs fully decoupled from the hindlimbs during locomotory excursion) occurred only after they had first passed through a "tetrapteryx" stage [29,31,65,66].

(b) "Non-avian pennaraptoran maniraptorans."—Character conflict indicative of both parallelism and mosaicism are even more significant a source of interpretive difficulties when considering the morphology of the pennaraptorans; it is responsible for significant disagreements about the relationships of paravian taxa [29,31,51,115,139,140;162]. Foremost among these is disagreement on the monophyly of both Deinonychosauria and Dromaeosauridae: both taxa have recently been recovered as paraphyletic. Some analyses recover troodontids either as more closely related to Aves than to dromaeosaurids or farther removed from Aves than a clade ("Eumanirpatora") of dromaeosaurids *sensu stricto* and "averaptorans" (unenlagiids, microraptorines, and anchiornithids); likewise, some analyses recover microraptorines and unenlagiids as successive outgroups to Aves rather than clustering with more "typical" dromaeosaurids like the familiar *Deinonychus* and *Velociraptor* [51,139,140;162]. For the determination of homology and character state polarity special reference must be given to those pennaraptoran taxa that are basal to their respective clades, but character conflict alone interferes with the reliable reconstruction of the phylogenetic relationships of these taxa, as does the possibility of systemic interference with phylogenetic signal from the profound morphological transformations induced by loss of flight. Reliance on simple tabulations of step count

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 3 November 2023 doi:10.20944/preprints202311.0235.v1

difference between constrained and unconstrained trees [52] to determine whether the most basal members of pennaraptoran clades have been correctly resolved by parsimony analysis of current data matrices is naïve and takes no account of statistical significance of differences in tree populations [50]. These difficulties preclude obvious answers and will be reflected in the brief comparative survey below.

Oviraptorosaurs uniformly display fully perforate acetabula, but the distribution of the supracetabular crest and antitrochanter is unclear and their interpretation difficult. Caudipterygids lack supracetabular crests and antitrochanters ([183] (pl. VI); [184] (pl. III); [185] (Figure 5)), as is also the case in caenagnathoids (i.e., caenagnathids and oviraptorids) ([186] (Figure 6a); [187] (Figure 4L); [188] (figs. 24-25); [189] (Figure 2k); [190] (Figure 7)). *Avimimus portensosus*, however, possesses an ischial antitrochanter that therefore appears homologous with that in birds ([112]; [191] (Figure 4c)). Funston et al. [191], nevertheless, report a new species, *Avimimus nemegtensis*, that lacks an antitrochanter. Since it is not clear why a single genus should be polymorphic for this character state, it is difficult to interpret this character conflict. It should perhaps be noted that embryonic oviraptorosaur material preserved close to hatching, as well as neonate oviraptorosaurs, do not reveal an antitrochanter ([192] (figs. 3,10); [193] (Figure 7); [194] (Figure 1)), suggesting that, as in enantiornithines and ornithurines, the antitrochanter in *Avimimus portentosus* appeared only late in ontogeny. Yet as the material from *Avimimus nemegtensis* appears to be equivalent in ontogenetic age to *Avimimus portentosus*, it remains difficult to explain why this latter taxon—if it has been correctly referred to *Avimimus*—lacks an antitrochanter. It is possible that despite its topological similarity to the condition in birds, the structure in *Avimimus portentosus* was independently acquired and is nonhomologous.

Troodontids have fully perforate acetabula, although the condition in crucial taxa, like *Jianianhualong* and *Jinfengopteryx*, is unclear [195,196]; they lack supracetabular crests [114]. Makovicky and Norell [114] reported an iliac "antitrochanter" in troodontids. If correct, this structure would not be homologous with the avian condition, but as *Daliansaurus* [197] (Figure 10a), *Gobivenator* [198] (Figure 2n), and *Sinovenator* [199] (Figure 1f) all lack an antitrochanter, there is reason to doubt the attribution of the structure to troodontids in the first instance.

Dromaeosaurids, in the comparative context of this review, must be considered in three discrete phenotypic clusters until the monophyly or paraphyly of the group has been more concretely determined: microraptorines, unenlagiids, and the "typical" taxa like *Deinonychus* and *Velociraptor* (including those forms which exhibit trends toward larger body size). The halszkaraptorines are apparently specialized semiaquatic forms and can therefore be bracketed from the present overview. The microraptorine pelvis is a very close match with that of *Archaeopteryx*, including medial occlusion of the acetabulum (Figure 8d,e.) and absence of either a strong supracetabular crest or antitrochanter (Figure 8e) ([120] (Figure 31]; [200] (Figure 2); [201] (Figure 24); [202] (Figure 1c)). Interestingly, the acetabulum of *Hesperonychus* opens dorsolaterally, which would enable it to abduct the hindlimbs in splayed fashion as in other gliders like *Microraptor*, which no doubt abducted feathered hindlimbs to provide airfoils [202]. Yet *Microraptor* is almost universally depicted in reconstructions flying with the legs drooping beneath the animal [203], which is contrary to the biomechanics of gliding animals, all of which splay their hindlimbs out in flight. The *Microraptor* hindlimb could not have evolved asymmetric, aerodynamic flight feathers if positioned beneath the animal. It is therefore unsurprising that the femoral head exhibits medial offset in *Microraptor* [200] (Figure 8). There is significant medial occlusion of the acetabulum in unenlagiids, there is no supracetabular crest (or it is at best weakly developed) and there is no antitrochanter ([204] (Figure 2c); [205] (Figure 7.1)). In *Bambiraptor* the acetabulum shows partial medial occlusion, the supracetabular crest is at best only weakly developed, and a clearly demarcated antitrochanter, as opposed to some posterodorsal thickening of the iliac acetabular margin associated with the ischiadic peduncle, is not evident [206] (Figure 3.26). In *Deinonychus* [207] (Figure 64) and *Velociraptor* ([208] (figs. 11-12); [209] (figs. 17a,18)) the supracetabular crest remains weak and a clearly demarcated antitrochanter is absent, while in *Velociraptor* the acetabulum continues to exhibit medial occlusion.

5. Discussion

Partial closure of the acetabula and absence of an antitrochanter in early birds (the partial closure persists, as has been seen, in many modern birds), is surprising; it appears to be inconsistent with the persistent assertion that these taxa had developed obligate bipedalism like their presumed theropod ancestors. That some pennaraptoran "maniraptorans" (notably the microraptorines and troodontids) also exhibit partial closure of the acetabulum and an absence of an antitrochanter is a further incongruity in that these taxa should exhibit "typical" theropod pelvic girdle modifications for terrestrial cursoriality. Of course, partial or even full closure of the acetabulum does not of itself entail that an archosaur was incapable of bipedalism (at least facultatively) or of maintaining a parasagittal gait: poposauroids [210–214] and rauisuchids like *Postosuchus* [215] were fully parasagittal and obligately bipedal, and obligately quadrupedal ornithischians in which the acetabulum secondarily exhibits either partial (e.g., ceratopsids) or full occlusion (e.g., ankylosaurs) still held their femora erect rather than splayed [216,217]. Compsognathids are "prototypical" small theropods [218] yet they lack a supracetabular crest or antitrochanter [218–220] and still appear to have been obligately bipedal cursors (for an alternative view, see [51,221,222]). To give only one more example, although they appear to have been ideally suited for arboreal trunk climbing and their pelvic osteology (as reviewed above) suggests that they were not obligately bipedal (let alone cursorial), nevertheless microraptorines may have been opportunistically piscivorous and capable of hunting lakeshore environments [223,224]. In many cases, there is not a simple correspondence between gross anatomy and behavior (yet we also know that early birds were already experimenting with a range of trophic specializations, as indicated by evidence for granivory, folivory,frugivory in omnivoropterygids and jeholornithids [8,29,51,225,226]). The cumulative anatomical picture for a given range of taxa and its integration with supplementary data permitting behavioral and ecological inferences is necessary. It is in this context that the evidence presented here on the pelvic osteology of early birds and "pennaraptoran" maniraptorans reinforces the conclusion that, particularly when the abductive ability permitted to the hindlimb by this pelvic osteology is considered, the first birds—and at taxa like the microraptorines—were not terrestrial cursorial bipeds, like theropods, but trunk-climbing gliders [29,31,227].

These data obviously have a definitive bearing on the evolution of flight, which has been a crucial issue for the current consensus since the 1970s. Obligate bipedalism is erroneously considered the standard locomotory pattern of all early birds for one reason: according to cladistic analyses birds are living dinosaurs and one must accommodate the cladogram. This unfortunate turn has forced the acceptance of implausible hypotheses for everything from the origin of flight to the origin of feathers since the mid-1980s. The basic problem is quite simple: if one accepts a theropod as the ancestral bauplan, we are immediately faced with the need to explain how an obligately bipedal reptile with a massive, broad pelvic region, and arms half the length of the hind limbs, with very small hands with short digits, could have been transmuted by natural selection into the avian anatomical condition see in early birds such as the Jurassic anchiornithids and archaeopterygids, with relatively small narrow pelves, fore-limbs twice the length of the hindlimbs, elongate gracile digits, and hand claws characteristic of trunk-climbing mammals and birds (e.g., woodpeckers). In contrast to an improbable "gravity-resisted" ground up scenario for the origin of flight, the "gravity-assisted" trees down scenario would allow an organism to take advantage of the cheap gravity available from high places (and small size) so that the animal could produce drag to help break the fall. In this scenario even the smallest mechanisms to break the fall can be explained in microevolutionary terms, each stage being selectively advantageous. Despite innumerable suggestions, a satisfactory explanation of a how a terrestrial theropod could take flight has yet to appear. Padian [228] argued, following the so-called WAIR (wing-assisted inclined running) model [229], that this curious behavior could provide such a mechanism. Accordingly, newly hatched dinosaurs flapped incipient wings to scale steep inclines, jumping off logs., rocks or small hills when evading predators, and somehow began to fly. The WAIR model animal is among the most highly derived hill-running quail, the Chukar partridges (*Alectoris chukar*), that flap their wings, running inclined surfaces to achieve stability and height. In other words, those promoting WAIR are using as a model a highly specialized bird that was already endowed with massive flight musculature. In this case the wings push the bird towards the steep slope. Thus, WAIR is little more than a unique crown galliform locomotor specialization, not appropriate for the origin of flight in avian ancestors largely devoid of any advanced pectoral anatomy [230]. In contrast, The much simpler "gravity-assisted" trees-down narrative is the likely way practically all land vertebrates acquired flight: first jumping and parachuting, then gliding from trees to the bottom of trees, and climbing back (energetically the most efficient manner of locomotion [231]), and finally developing lift and thrust, gliding and eventually flapping flight. This scenario comports with the anatomical structure of early birds which were likely not obligately bipedal, but capable of substantial abduction for tree climbing [227].

It is perhaps because of this anatomical and behavioral pathway toward the evolution of avian flight and the assembly of the neornithine body plan that bipedalism in birds differs fundamentally from bipedalism in all other archosaurs, and it is belatedly being realized that modern birds are not quite the well-behaved ordinary parasagittal or planar bipeds that they have long been considered [104,232]. Yet the peculiar way in which birds manage bipedalism is what one would expect if birds started their evolutionary trajectory toward obligate bipedalism from a different starting point than the system employed to such success by dinosaurs. It is just as significant that the pennnaraptorans (oviraptorosaurs, troodontids, and dromaeosaurs), the apparently basal exemplars of which tend to exhibit a remarkable number of avian characters (including, but not limited to, a semilunate carpal, avian pennaceous feathers, an aerodynamic flight hand, closed or partially closed acetabulum, and archosaurian Mesozoic bird teeth and vertical tooth replacement with characters not unlike those from *Archaeopteryx* to *Hesperornis* and *Ichthyornis*, and extending back to more basal archosaurs), also show evidence of derivation from forms not unlike basal birds in their pelvic osteology and the locomotory habits that can be inferred from this osteology. This is a logical explanation for the surprising persistence of medial occlusion of the acetabulum in many pennaraptorans and the absence, in most, of either well-defined supracetabular crests or antitrochanters. These data are also consistent with the extensive hindlimb plumage observed in microraptorines [29,31,51,233]; if *Jinfengopteryx* is in fact a basal troodontid [140,234] (but see discussions in [115,139,162]) then troodontids also primitively exhibited a "tetrapteryx" bauplan. Taken together, these data suggest that ancestral pennaraptorans fundamentally differed from theropods in their locomotory strategies. As is so often the case upon critical comparative examination of pennaraptoran morphology, the pelvic data that have been reviewed in this paper underscore the question: are these "theropods" actually "hidden birds" [29,31,50,235]

6. Conclusion

The goal of this precursory investigation into the form and function of the avian acetabulum and its appurtenant structures is to provide a template for further investigation while emphasizing some of the more convincing biomechanical conclusions enumerated in this essay. The avian acetabulum and its adjunct structures, the supracetabular crest and antitrochanter, could not have been transmuted from truly dinosaurian ancestors as we know them, and the additional sophistications that presumably control movement of the femur could have arisen only well after avian origins. For birds and allies to be direct descendants of dinosaurs with complete or partially occluded acetabular basins and devoid of a supracetabular crest equivalent to that of dinosaurs would require any number of evolutionary reversals, which would require special pleading. In early birds and allies, the hindlimbs could be abducted and this would facilitate tree-climbing, as elaborated by the late Derek Yalden [236] (see also [227]). Although the well-known and now classic *Archaeopteryx* and *Microraptor* are almost universally depicted as terrestrial cursors, their hip anatomy and highly recurved manual and pedal claws (like climbing mammals and woodpeckers) argues strongly for arboreality and splayed hind-limb wings in flight, as advocated by their perceptive early describers. Further investigation of hip anatomy provides another much-needed detail to our ever-growing knowledge of avian evolution.

Funding: This research received no external funding.

Data Availability Statement: No new data were created.

Acknowledgments: I thank Rui Pei for permission to use photographs of *Anchiornis*; David Burnham, for sharing first-hand knowledge of the pelves of *Microraptor* and *Anchiornis* from specimens observed at the Shandong Museum, and for providing 18 photos; Peter Houde for providing photos of pelves of 3 species of *Lithornis* (lithornithids) and 4 genera of tinamous; Zhiheng Li for providing information on *Jeholornis* and *Sapeornis*; and Lindsey Fortnash for sharing her osteological collection and photos of pelves. Study of hundreds of bird skeletons through the years was made possible by kind access to the skeletal collections at the University of Michigan's Museum of Zoology, Bird Division (courtesy Robert Storer); and the Smithsonian's National Museum of Natural History (courtesy Storrs Olson). For comments on earlier drafts of this paper, I thank Frances C. James and John A. Pourtless IV; the latter also granted permission to incorporate unpublished manuscript material in the current paper. Kaysia Grow skillfully prepared the figures, and especially the art for Figure 5. Lastly, I thank Emma Li for encouraging submission of this paper and John A. Pourtless IV for editorial assistance.

Conflict of Interest: The author declares no conflict of interest.

References

1. Huxley, T.H. On the animals which are most nearly intermediate between birds and reptiles. The Annals and Magazine of Natural History **1868**, *2*, 66-75.
2. Ostrom, J.H. *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.* **1976**, *8*, 91-182.
3. Ostrom, J.H. The Question of the Origin of Birds. In *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*; Schultze, H.-P., Trueb, L., Eds.; Cornell University Press: Ithaca, NY, USA, 1991; pp. 467-484, IBSN 0-8014-2497-6.
4. Padian, K. Macroevolution and the origin of major adaptations: vertebrate flight as a paradigm for the analysis of patterns. In *Proceedings of the Third North American Paleontological Convention*; Mamet, B.L., Copeland, M.J., Eds. Business and Economic Service: Toronto, CA, 1982; Volume 2, pp. 485-489.
5. Gauthier J.A. Saurischian monophyly and the origin of birds. *Mem. Calif. Acad. Sci.* **1986**, *8*, 1-55.
6. Chiappe, L.M. Enantiornithine (Aves) tarsometatarsi and the avian affinities of the Late Cretaceous Avisauridae. *J. Vertebr. Paleontol.* **1992**, *12*, 344-350.
7. Feduccia, A. *The Origin and Evolution of Birds*, 2nd ed.; Yale University Press: New Haven, CT, USA, 1999; ISBN 0-300-07861-7.
8. Mayr, G. *Avian Evolution: The Fossil Record of Birds and its Paleobiological Significance*; Wiley: Chichester, UK, 2017; ISBN 9781119020769.
9. De Queiroz, K.; Cantino, P.D.; Gauthier, J.A., Eds. *Phylonyms: A Companion to the PhyloCode*; CRC Press: Boca Raton, FL, USA, 2020; ISBN 978-1-138-33293-5.
10. Paul, G.S. *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*; Johns Hopkins University Press: Baltimore, MD, USA, 2002; ISBN 0-8018-6763-0.
11. Makovicky, P.J.; Zanno, L.E. Theropod Diversity and the Refinement of Avian Characteristics. In *Living Dinosaurs: The Evolutionary History of Birds*; Dyke, G., Kaiser, G., Eds. Wiley-Blackwell: Hoboken, NJ, USA, 2011; pp. 9-29, ISBN 978-0-470-65666-2.
12. Gatesy, S.M. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* **1990**, *16*, 170-186.
13. Gatesy, S.M. Functional evolution of the hind limb and tail from basal birds to theropods. In *Functional Morphology in Vertebrate Paleontology*; Thomason, J.J., Ed.; Cambridge University Press: Cambridge, UK, 1995; pp. 219-234, ISBN 9780521629218.
14. Gatesy, S.M. Locomotory Evolution on the Line to Modern Birds. In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds. University of California Press: Berkeley, CA, USA, 2002; pp. 432-447, ISBN 0-520-20094-2.
15. Carrano, M.T. Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, in vivo strains, and bone morphology. *Paleobiology* **1998**, *24*, 450-469.
16. Farlow, J.O.; Gatesy, S.M.; Holtz, Jr., T.R.; Hutchinson, J.R.; Robinson, J.M. Theropod locomotion. *Amer. Zool.* **2000**, *40*, 640-663.
17. Hutchinson, J.R.; Gatesy, S.M. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology* **2000**, *26*, 734-751.

18. Hutchinson, J.R. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zool. J. Linn. Soc.* **2001**, *131*, 123-168, doi: 10.1006/zjls.2000.0254.
19. Hutchinson, J.R.; Allen, V. The evolutionary continuum of limb function from early theropods to birds. *Naturwissenschaften* **2009**, *96*, 423-448, doi: 10.1007/s00114-008-048-3.
20. Griffin, C.T.; Botelho, J.F.; Hanson, M.; Fabbri, M.; Smith-Paredes, D.; Carney, R.M.; Norell, M.A.; Egawa, S.; Gatesy, S.M.; Rowe, T.B.; Elsey, R.M.; Nesbitt, S.J.; Bhullar, B.-A.S. The developing bird pelvis passes through ancestral dinosaur conditions. *Nature* **2022**, *608*, 346-352, doi: 10.1038/s41586-022-04982-w.
21. Agnolin, F.L.; Ezcurra, M.D. The validity of *Lagosuchus talampayensis* Romer, 1971 (Archosauria, Dinosauriformes), from the Late Triassic of Argentina. *Breviora* **2019**, *565*, 1-21, doi: 10.3099/0006-9698-565.1.1.
22. Charig, A.J. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In *Studies in Vertebrate Evolution: Essays Presented to F. R. Parrington*; Joysey, K.A., Kemp, T.S., Eds. Oliver and Boyd: Edinburgh, UK, 1972; pp. 121-155, IBSN 9780050021311.
23. Sereno, P.C.; Arcucci, A.B. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *J. Vertebr. Paleontol.* **1994**, *13*, 385-399.
24. Sereno, P.C.; Arcucci, A.B. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *J. Vertebr. Paleontol*. **1994**, *14*, 53-73.
25. Lingham-Soliar, T. Evolution of birds: ichthyosaur integumental fibers conform to dromaeosaur protofeathers. *Naturwissenschaften* **2003**, *90*, 428-432, doi: 10.1007/s00114-003-0448-x.
26. Lingham-Soliar, T. The dinosaurian origin of feathers: perspectives from dolphin (Cetacea) collagen fibers. *Naturwissenschaften* **2003**, *90*, 563-567, doi: 10.1007/s00114-003-04837.
27. Feduccia, A.; Lingham-Soliar, T.; Hinchliffe, J.R. Do feathered dinosaurs exist? Testing the hypothesis on neontological and paleontological evidence. *J. Morphol.* **2005**, *266*, 125-166, doi: 10.1002/jmor.10382.
28. Lingham-Soliar, T.; Feduccia, A., Wang, X. A new Chinese specimen indicates that "protofeathers" in the Early Cretaceous theropod dinosaur *Sinosauropteryx* are degraded collagen fibers. *Proc. R. Soc. B* **2007**, *274*, 1823-1829, doi: 10.1098/rspb.2007.0352.
29. Feduccia, A. *The Riddle of the Feathered Dragons: Hidden Birds of China*; Yale University Press: New Haven, CT, USA, 2012; ISBN 978-0-300-16435-0.
30. Feduccia, A. Bird origins anew. *Auk* **2013**, *130*, 1-12, doi: 10.1525/auk.2013.130.1.1.
31. Feduccia, A. *Romancing the Birds and Dinosaurs: Forays in Postmodern Paleontology*; BrownWalker: Irvine, CA, USA, 2020; ISBN 978-1-59942-606-8.
32. Foth, C. On the identification of feather structures in stem-line representatives of birds: evidence from fossils and actuopalaeontology. *Paläontol. Z.* **2012**, *86*, 91-102, doi: 10.1007/s12452-011-0111-3.
33. Rauhut, O.W.M; Foth, C.; Tischlinger H.; Norell, M.A. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 11746-11751, doi: 10.1073/pnas.1203238109.
34. Godefroit, P.; Sinitsa S.M.; Dhouailly, D.; Bolotsky, Y.L.; Sizov, A.V.; McNamara M.E.; Benton, M.J.; Spagna, P. A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. *Science* **2014**, *345*, 451-455, doi: 10.1126/science.1253351.
35. Godefroit, P.; Sinitsa, S.M.; Cincotta, A.; McNamara, M.E.; Reshetova, S.A.; Dhouailly, D. Integumentary Structures in *Kulindadromeus zabaikalicus*, a Basal Neornithischian Dinosaur from the Jurassic of Siberia. In *The Evolution of Feathers: From Their Origin to the Present*; Foth, C., Rauhut, O.W.M., Eds.; Springer Nature: Cham, CH, 2020; pp. 47-65, ISBN 978-3-030-27223-4.
36. Smith, N. A.; Chiappe, L.M.; Clarke, J.A.; Edwards, S.V; Nesbitt, S.J.; Norell, M.A.; Stidham, T.A.; Turner, A.; van Tuinen, M.; Vinther, J.; Xu, X. Rhetoric vs. reality: A commentary on "Bird Origins Anew" by A. Feduccia. *The Auk: Ornithological Advances* **2015**, *132*, 467-480, doi: 10.1642/AUK-14-203.1.
37. Xu, X. Filamentous Integuments in Novavialan Theropods and Their Kin: Advances and Future perspectives for Understanding the Evolution of Feathers. In *The Evolution of Feathers: From Their Origin to the Present*; Foth, C., Rauhut, O.W.M., Eds.; Springer Nature: Cham, CH, 2020; pp. 67-78, ISBN 978-3-030-27223-4.
38. Sansom, R.S.; Gabbott, S.E.; Purnell, M.A. Non-random decay of chordate characters causes bias in fossil interpretation. *Nature* **2010**, *463*, 797-800, doi: 10.1038/nature/08745.

39. Sansom, R.S.; Gabbott, S.E.; Purnell, M.A. Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and the implications for the vertebrate fossil record. *Proc. R. Soc. B* **2011**, *278*, 1150-1157, doi: 10.1098/rspb.2010.1641.
40. Sansom, R.S.; Willis, M.A. Fossilization causes organisms to appear erroneously primitive by distorting evolutionary trees. *Sci. Rep.* **2013**, *3*, 2458:1-5, doi: 10.1038/srep02545.
41. Murdock, D.J.E.; Gabbott, S.E.; Mayer, G.; Purnell, M.A. 2014. Decay of velvet worms (Onychophora), and bias in the fossil record of lobophodians. *BMC Evol. Biol.* **2014**, *14*, 222:1-10, doi: 10.1186/s12862-014-0222-z.
42. Nanglu K.; Caron J.-B.; Cameron, C.B. Using experimental decay of modern forms to reconstruct the early evolution and morphology of fossil enteropneusts. *Paleobiology* **2015**, *41*, 460-478, doi: 10.107/pab.2015.11.
43. Sansom, R.S. Bias and sensitivity in the placement of fossil taa resulting from interpretations of missing data. *Syst. Biol.* **2015**, *64*, 256-266, doi: 10.1093/sysbio/syu093.
44. Sansom, R.S.; Gabbott, S.E.; Purnell, M.A. Atlas of vertebrate decay: a visual and taphonomic guide to fossil interpretation. *Palaeontology* **2013**, *56*, 457-474, doi: 10.1111/pala.12037.
45. Sansom, R.S. Preservation and phylogeny of Cambrian ecdysozoans tested by experimental decay of *Priapulus*. *Sci. Rep.* **2016**, *6*, 32817:1-12, doi: 10.1038/srep32817.
46. Briggs, D.E.G.; McMahon, S. The role of experiments in investigating the taphonomy of exceptional preservation. *Palaeontology* **2016**, *59*, 1-11, doi: 10.1111/pala.12219.
47. Asher, R.J.; Smith, M.R. Phylogenetic signal and bias in paleontology. *Syst. Biol.* **2022**, *71*, 986-1008, doi: 10.1093/sysbio/syab072.
48. Reeves, J.C.; Sansom R.S. Multivariate mapping of ontogeny, taphonomy and phylogeny to reconstruct problematic fossil taxa. *Proc. R. Soc. B* **2023**, *290*, 20230333:1-12, doi: 10.1098/rspb.2023.0333.
49. Padian, K.; Chiappe, L.M. The origin and early evolution of birds. *Biol. Rev.* **1998**, *73*, 1-42.
50. James, F.C.; Pourtless, IV, J. A. Cladistics and the origin of birds: a review and two new analyses. *Ornithol. Monogr.* **2009**, *66*, 1-78, doi: 10.1525/om.2009.66.1.1
51. Chatterjee, S. *The Rise of Birds: 225 Million Years of Evolution*; Johns Hopkins University Press: Baltimore, MD, US, 2015; ISBN 978-1-4214-1590-1.
52. Hartman, S.; Mortimer, M.; Wahl, W.R.; Lomax, D.R.; Lippincott, J.; Lovelace, D.M. A new paravian dinosaur from the Late Jurassic of North America supports a late acquisition of avian flight. *PeerJ* **2019**, *e7247*, 1-51, doi: 10.7717/peerj.7247
53. Lü, J.; Dong, Z.; Azuma, Y.; Barsbold, R.; Tomida, Y. Oviraptorosaurs compared to birds. In *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*; Zhou, Z., Zhang, Z. Eds.; Science Press: Beijing, CN, 2002; pp. 175-189, ISBN 9787030105516.
54. Maryańska, T.; Omsólska, H.; Wolsan, M. Avialan status for Oviraptorosauria. *Acta Paleontol. Pol.* **2002**, *47*, 97-116.
55. Persons, IV, W.S.; Currie, P.J. Dragon tails: convergent caudal morphology in winged archosaurs. *Acta Geol. Sin-Engl.* **2012**, *86*, 1402-1412.
56. Sorkin, B. Aerial ability in basal Deinonychosauria. *Bull. Gunma Mus. Natu. Hist.* **2014**, *18*, 21-34.
57. Sorkin, B. Scansorial and aeriability in Scansoriopterygidae and basal Oviraptorosauria. *Hist. Biol.* **2021**, *31*, 3202-3214, doi: 10.1080/08912963.2020.185518.
58. Hutson, J.D.; Hutson, K.N. An examination of forearm bone mobility in *Alligator mississippiensis* (Daudin, 1802) and *Struthio camelus* Linnaeus, 1758 reveals that *Archaeopteryx* and dromaeosaurs shared an adaptation for gliding and/or flapping. Geodiversitas **2015**, *37*, 325-344, doi: 10.5252/g2015n3a3.
59. Hutson, J.D.; Hutson, K.N. Retention of the flight-adapted avian finger-joint complex in the Ostrich helps identify when wings began evolving in dinosaurs. *Ostrich* **2018**, *89*, 173-186, doi: 10.2989/00306525.2017.1422566.
60. Kurochkin E.N. Parallel evolution of theropod dinosaurs and birds. *Entomol. Rev.* **2006**, *86*, S45-58, doi: 10.1134/S0013873806100004б.
61. Dececchi, T.A.; Larsson, H.C.E.; Pittman, M.; Habib, M.B. High flyer or high fashion? A comparison of flight potential among small bodied paravians. *Bull. Am. Mus. Nat. Hist.* **2020**, *440*, 295-320.
62. Pei, R.; Pittman, M.; Goloboff, P.A.; et al. Potential for powered flight neared by most close avialan relatives, but few crossed its thresholds. *Curr. Biol.* **2020**, *30*, 1-14, doi: 10.1016/j.cub.2020.06.105.
63. Czerkas, S.A.; Zhang, D.; Li, J.; Li, Y. Flying dromaeosaurs. In *Feathered Dinsoaurs and the Origin of Flight*; Czerkas, S.J., Ed; Dinosaur Museum: Blanding, UT, USA, 2002; pp. 127-135, ISBN 1-932075-01-1.
64. Feduccia, A. Birds are dinosaurs: Simple answer to a complex problem. *Auk* **2002**, *119*, 1187-1201.

65. Martin, L.D. A basal archosaurian origin for birds. *Acta Zoolog. Sin.* **2004**, *50*, 978-990.
66. Martin, L.D. Origins of avian flight—a new perspective. *Oryctos* **2008**, *7* 45-54.
67. Feduccia, A.; Czerkas, S.A. Testing the neoflightless hypothesis: propatagium reveals flying ancestry of oviraptorosaurs. *J. Ornithol.* **2015**, *156*, 1067-1074, doi: 10.1007/s1007/s10336-015-1190-9.
68. Pourtless, IV, J.A. Skepticism, the critical standpoint, and the origin of birds: a partial critique of Havstad and Smith (2019). *Biol. Philos.* **2022**, *37*, 57:1-19, doi: 10.1007/s10539-022-09887-6.
69. Baumel, J.J.; King, A.S.; Breazile, J.S.; Evans, H.E.; Vanden Berge, J.C., Eds. *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd ed.; Nuttal Ornithological Club: Cambridge, MA, USA, 1993; ISBN 9781877973345.
70. Cantino P.D.; de Queiroz K. *International Code of Phylogenetic Nomenclature (PhyloCode) Version 6*; CRC Press: Boca Raton, FL, USA, 2020; ISBN 978-1-138-332829.
71. Benton, M.J., Clark, J.M. Archosaur phylogeny and the relationships of the Crocodylia. In *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*; Benton, M.J., Ed.; Clarendon Press: Oxford, UK, 1988; pp. 295-338, ISBN 9780198577058.
72. Benton, M.J. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philos. Trans. R. Soc. B* **1999**, *354*, 1423-1446.
73. Nesbitt, S.J. The early evolution of archosaurs: relationships and the origin of major clades. *Bull. Am. Mus. Nat. Hist.* **2011**, *352*, 1-292.
74. Ezcura, M.D. The phylogenetic relationships of basal archosauromorphs , with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* **2016**, 4:e1778:1-385, doi: 10.7717/peerj.1778.
75. Chiappe, L.M. Cretaceous avian remains from Patagonia shed new light on the early radiation of birds. *Alcheringa* **1991**, *15*, 333-338.
76. Chiappe, L.M. The first 85 million years of avian evolution. *Nature* **1995**, *378*, 349-355.
77. Chiappe, L.M. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithines and *Patagopteryx deferrariisi*. *Münchner Geowiss. Abh. A* **1996**, *30*, 203-244.
78. Martin, L.D. The origin and early radiation of birds. In *Perspectives in Ornithology*; Brush, A.H., Clark, Jr., G.A., Eds; Cambridge University Press: New York, NY, USA, 1983; pp. 291-338, ISBN 978-0-521-24857-0.
79. Martin, L.D. The beginning of the modern avian radiation. *Travaux et Documents des Laboratoires de Géologie de Lyon* **1987**, *99*, 9-19.
80. Sereno, P.C.; Rao, C.; Li, J. *Sinornis santensis* (Aves: Enantiornithes) from the Early Cretaceous of Northeastern China. In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds; University of California Press: Berkeley, CA, USA, 2002; pp. 184-208, ISBN 0-520-20094-2.
81. Padian, K.; Hutchinson, J.R.; Holtz, Jr., T.R. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *J. Vertebr. Paleontol.* **1999**, *19*, 69-80.
82. Clarke, J.A., Norell, M.A. The Morphology and Phylogenetic Position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. *Am. Mus. Novit.* **2002**, *3387*, 1-46.
83. Clarke, J.A. Morphology, phylogenetic taxonomy, and systematics of *Ichythyornis* and *Apatornis* (Avialae: Ornithurae). *Bull. Am. Mus. Nat. Hist.* **2004**, 286, 1-179.
84. Feduccia, A. Mesozoic aviary takes form. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 5-6, doi: 10.1073/pnas.0509970102.
85. Hou Hou, L.; Martin, L.D.; Zhou, Z.; Feduccia, A.; Zhang, F. A diapsid skull in a new species of the primitive bird *Confuciusornis*. *Nature* **1999**, *399*, 679-682.
86. Zhou, Z.; Zhang, F. Discovery of an ornithurine bird and its implications for Early Cretaceous avian radiation. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 18998-19002, doi: 10.1073/pnas.0507106102.
87. Zhou, Z.; Zhang, F. Mesozoic birds of China—a synoptic review. *Front. Biol. China* **2007**, *2*, 1-14, doi: 10.1007/s11515-007-0001-y.
88. Chiappe, L.M. Basal Bird Phylogeny: Problems and Solutions. In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds; University of California Press: Berkeley, CA, USA, 2002; pp. 448-472, ISBN 0-520-20094-2.
89. Romer, A. *The Osteology of the Reptiles*; University of Chicago Press: Chicago, IL, USA, 1956; ISBN 9780226724911
90. Naples, V.L.; Martin, L.D.; Simmons, J. The pelvis in early birds and dinosaurs. In *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*; Zhou, Z., Zhang, Z. Eds.; Science Press: Beijing, CN, 2002; pp. 203-210, ISBN 9787030105516.

91. Baron, M.G.; Williams, M.E. A re-evaluation of the enigmatic dinosauriform *Caseosaurus crosbyensis* from the Late Triassic of Texas, USA and its implications for early dinosaur evolution. *Acta Palaeontol. Pol*. **2018**, *63*, 129-145, doi: 10.4202/app.00372.2017
92. Dzik, J. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *J. Vertebr. Paleontol.* **2003**, *23*, 556-574, doi: 10.1671/A1097.
93. Peecook, B.R.; Sidor, C.A.; Nesbitt, S.J.; Smith, R.M.H.; Steyer, J.S.; Angielczyk, K.D. A new silesaurid from the upper Ntawere Formation of Zambia (Middle Triassic) demonstrates the rapid diversification of Silesauridae (Avemetatarsalia, Dinosauriformes). *J. Vertebr. Paleontol.* **2013**, *33*, 1127-1137, doi: 10.1080/02724634.2013.755991.
94. Martz, J.W.; Small, B.J. Non-dinosaurian dinosauromorphs from the Chinle Formation (Upper Triassic) of the Eagle Basin, northern Colorado: *Dromomeron romeri* (Lagerpetidae) and a new taxon, *Kwanasaurus williamparkeri* (Silesauridae). *PeerJ* **2019**, e7551:1-71, doi: 10.7717/peerj.7551.
95. Langer, M.C.; McPhee, B.W.; Marsola, J.C.dA.; Roberto-da-Silva, L.; Cabreira, S.F. Anatomy of the dinosaur *Pampadromaeus barberenai* (Saurischia—Sauropodomorpha) from the Late Triassic Santa Maria Formation of southern Brazil. *PloS ONE* **2019**, *14*, e0212543:1-64, doi: 10.1371/journal.pone.0212543.
96. Sereno, P.C.; Martínez, R.N.; Alcober, O.A. Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). *J. Vertebr. Paleontol.* **2013**, *32(s1)*, 83-179, doi: 10.1080/02724634.2013.820113.
97. Langer, M.C. Basal Saurischia. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 25-46, ISBN 978-0-520-25408-4.
98. Pacheco, C.; Müller, R.T.; Langer, M.; Pretto, F.A.; Kerber, L.; Dias da Silva, S. *Gnathovorax cabreirai*: a new early dinosaur and the origin and initial radiation of predatory dinosaurs. *PeerJ* **2019**, e7963:1-23, doi: 10.7717/peerj7963.
99. Tykoski, R.S.; Rowe, T. Ceratosauria. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 47-70, ISBN 978-0-520-25408-4.
100. Pol, D.; Rauhut, O.W.M. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proc. Roy. Soc. B* **2012**, *279*, 3170-3175, doi: 10.1098/rspb.2012.0660.
101. Marsola, J.C.A.; Bittencourt, J.S.; Butler, R.J.; Da Rosa, A.A.S.; Sayão, J.M.; Langer, M.C. A new dinosaur with theropod affinities from the Santa Maria Formation, south Brazil. *J. Vertebr. Paleontol.* **2018**, *38*, e1531878:1-25, doi: 10.1080/02724634.2018.1531878.
102. Turner, A.H.; Makovicky, P.J.; Norell, M.A. A review of dromaeosaurid systematics and paravian phylogeny. *Bull. Am. Mus. Nat. Hist.* **2012**, *371*, 1-206.
103. Brusatte, S.L.; Lloyd, G.T.; Wang, S.C.; Norell, M.A. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Curr. Biol*. **2014**, *24*, 2386-2392, doi: 10.1016/j.cub.2014.08.034.
104. Hertel, F.; Campbell, Jr., K.E. The antitrochanter of birds: form and function in balance. *Auk* **2007**, *124*, 789-805, doi: 10.1093/auk/124.3.789
105. Perle A.; Chiappe, L.M.; Barsbold, R.; Clark, J.M.; Norell, M.A. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. *Am. Mus. Novit.* **1994**, *3105*, 1-29.
106. Novas, F.E. Anatomy of *Patagonykus puertai* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **1997**, *17*, 137-166, doi: 10.1080/02724634.1997.10010959.
107. Chiappe, L.M.; Norell, M.A.; Clark, J.M. The Cretaceous, Short-Armed Alvarezsauridae *Mononykus* and Its Kin. In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds; University of California Press: Berkeley, CA, USA, 2002; pp. 87-120, ISBN 0-520-20094-2.
108. Lee, S.; Park J.-Y.; Lee Y.-N.; Kim, S.-H., Lü, J.; Barsbold, R.; Tsogtbaatar, K. A new alvarezsaurid dinosaur from the Nemegt Formation of Mongolia. *Sci. Rep.* **2019**, 9:15494:1-12, doi: 10.1038/s41598-019-52021-y.
109. Clark, J. M.; Maryańska, T.; Barsbold, R. Therizinosauroidea. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 151-164, ISBN 978-0-520-25408-4.
110. Zanno, L.E. Osteolgy of *Falcarius utahensis* (Dinosauria: Theropoda): characterizing the anatomy of basal therizinosaurs. *Zool. J. Linn. Soc.* **2010**, *158*, 196-230, doi: 10.1111/j.1096-3642.2009.00464.x.
111. Liao, C.-C.; Zanno, L.E.; Wang, S.; Xu, X. Postcranial osteology of *Beipiaosaurus inexpectus* (Theropoda: Therizinosauria). *PloS ONE* **2021**, *16*, e0257913:1-28, doi: 10.1371/journal.pone.0257913.
112. Kurzanov S.M. New data on the pelvic structure of *Avimimus*. *Paleont. Jour.* **1983**, *4*, 115-116.

113. Osmólska, H.; Currie, P.J.; Barsbold, R. Oviraptorosauria. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 165-183, ISBN 978-0-520-25408-4.
114. Makovicky, P.J.; Norell, M.A. Troodontidae. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 184-195, ISBN 978-0-520-25408-4.
115. Agnolin, F.L.; Novas, F.E. Unenlagiid theropods: are they members of the Dromaeosauridae (Theropoda, Maniraptora)? *An. Acad. Bras. Cienc.* **2011**, *83*, 117-162.
116. Lü, J.; Brusatte, S.L. A large, short-armed, winged dromaeosaurid (Dinosauria: Theropoda) from the Early Cretaceous of China and its implications for feather evolution. *Sci. Rep.* **2015**, 5:11775:1-11, doi: 10.1038/srep11775.
117. Gianechini, F.A.; Makovicky, P.J.; Apesteguía, S.; Cerda, I. Postcrainal skeletal anatomy of the holotype and referred specimens of *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín 2005 (Theropoda, Dromaeosauridae), from the Late Cretaceous of Patagonia. *PeerJ* **2018**, 6:e4558:1-84, doi: 10.7717/peerj4558.
118. Forster, C.A.; O'Connor, P.M.; Chiappe, L.M.; Turner, A.H. The osteology of the Late Cretaceous paravian *Rahonavis ostromi* from Madagascar. *Palaeontol. Electron.* **2020**, *23*, a29:1-75, doi: 10.26879/793.
119. Novas, F.E.; Agnolín, F.L.; Motta, M.J.; Egli, F.B. Osteology of *Unenlagia comaheunsis* (Theropoda, Paraves, Unenlagiidae) from the Late Cretaceous of Patagonia. *Anat. Rec.* **2021**, *304*, 2741-2788, doi: 10.1002/ar.24641.
120. Turner, A.H.; Pol, D.; Norell, M.A. Anatomy of *Mahakala omnogovae* (Theropoda: Dromaeosauridae), Tögrögiin Shiree, Mongolia. *Am. Mus. Novit.* **2011**. 3722, 1-66.
121. Mehta, S.; Guha, K.; Shalini, S.; Kumar, C. Gross anatomical studies on the os-coxae and synsacrum of Japanese quail (*Coturnix coturnix japonica*). *Indian J. Vet. Anat.* **2014**, *26*, 126-127.
122. Egawa, S.; Saito, D.; Abe, G.; Koji, T. Morphogenetic mechanism of the acquisition of the dinosaur-type acetabulum. *R. Soc. Open Sci.* **2018**, *5*, 180604:1-12, doi: 10.1098/rsos.180604.
123. Tsai, H.P.; Holliday, C.M. Articular soft tissue anatomy of the archosaur hip joint: structural homology and functional implications. *J. Morphol.* **2015**, *276*, 601-30, doi: 10.1002/jmor.20360.
124. Tsai, H.P.; Middleton, K.M.; Hutchinson, J.R.; Holliday, C.M. Hip joint articular soft tissues of non-dinosaurian Dinosauromorpha and early Dinosauria: evolutionary and biomechanical implications for Saurischia. *J. Vertebr. Paleontol*. **2018**, *38*, e1427583, doi: 10.1080/02724634.2017.1427593.
125. Benton, M.J. *Dinosaurs Rediscovered: How a Scientific Revolution is Rewriting History*; Thames and Hudson: New York, NY, USA, 2020; ISBN 9780500052006.
126. Holliday, C.M.; Ridgely, R.C.; Sedlmayr, J.C.; Witmer, L.M. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. *PloS ONE* **2010**, *5*, e13120:1-16, doi: 10.1371/journal.pone.0013120.
127. Bhullar, B.-A.S.; Hanson, M.; Fabbri, M.; Pritchard, A.; Bever, G.S.; Hoffman, E. How to Make a Bird Skull: Major Transitions in the Evolution of the Avian Cranium, Paedomorphosis, and the Beak as a Surrogate Hand. *Integr. Comp. Biol.* **2016**, *56*, 389-403, doi: 10.1093/icb/icw069.
128. Botelho, J.F.; Smith-Paredes, D.; Soto-Acuña, S.; O'Connor, J.; Palma, V.; Vargas, A.O. Molecular development of fibular reduction in birds and its evolution from dinosaurs. *Evolution* **2016**, *70*, 543-554, doi: 10.1111/evo.12882.
129. Smith-Paredes, D.; Núñez-León, D.; Soto-Acuña, S.; O'Connor, J.; Botelho, J.F.; Vargas, A.O. Dinosaur ossification centres in embryonic birds uncover developmental evolution of the skull. *Nat. Ecol. Evol.* **2018**, *2*, 1966-1973, doi: 10.1038/s41559-018-0713-1.
130. Decoupling the skull and skeleton in a Cretaceous bird with unique appendicular morphologies. *Nat. Ecol. Evol.* **2023**, *7*, 20-31, doi: 10.1038/s41559-022-01921-w.
131. Ehrlich, P.R.; Holm, R.W.; Parnell, D. *The Process of Evolution*; McGraw-Hill: New York, NY, USA, 1963; ISBN 0070191336.
132. Yuri, T.; Kimball, R.T.; Harshman, J.; et al. Parsimony and model-based analyses of indels in avian nuclear genes reveal congruent and incongruent phylogenetic signals. *Biology* **2013**, *2*, 419-444, doi: 10.3390/biology2010419.
133. A new Mesembriornithinae (Aves, Phorusrhacidae) provides new insights in the phylogeny and sensory capabilities of terror birds. *J. Vertebr. Paleontol.* **2015**, *35*, e912656:1-18, doi: 10.1080/02724634.2014.912656.
134. A Well-Preserved Partial Skeleton of the Poorly Known Early Miocene Serieam *Noriegavis santacruensis*. *Acta Paleontol. Pol.* **2013**, *60*, 589-598, doi: 10.4202/app.00011.2013.

135. O'Connor, J.; Chiappe, L.M.; Bell, A. Pre-modern Birds: Avian Divergences in the Mesozoic. In *Living Dinosaurs: The Evolutionary History of Birds*; Dyke, G., Kaiser, G., Eds. Wiley-Blackwell: Hoboken, NJ, USA, 2011; pp. 39-114, ISBN 978-0-470-65666-2.
136. Wang, M.; Wang, X.; Wang, Y.; Zhou, Z. A new basal bird from China with implications for morphological diversity in early birds. *Sci. Rep.* **2016**, *6*, 19700:1-12, doi: 10.1038/srep19700.
137. A new clade of basal Early Cretaceous pygostylian birds and developmental plasticity of the avian shoulder girdle. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 10708-10713, doi: 10.1073/pnas.1812176115.
138. Imai, T.; Azuma, Y.; Kawabe, S.; Shibata, M.; Miyata K.; Wang, M.; Zhou, Z. An unusual bird (Theropoda, Avialae) from the Early Cretaceous of Japan suggests complex evolutionary history of basal birds. *Commun. Biol.* **2019**, *2*, 399:1-11, doi: 10.1038/s42003-019-0639-4.
139. Agnolin, F.L.; Motta, M.J.; Egli, F.B.; Lo Coco, G.; Novas, F.E. Paravian Phylogeny and the Dinosaur-Bird Transition: An Overview. *Front. Earth Sci.* **2019**, *6*, 252:1-28, doi: 10.3389/feart.2028.00252.
140. Pittman, M.; O'Connor, J.; Field, D.J.; Turner, A.H., Ma, W.; Makovicky, P.J.; Xu, X. Pennaraptoran Systematics. *Bull. Am. Mus. Nat. Hist.* **2020**, *440*, 7-36.
141. Pei, R.; Li, Q.; Meng, Q.; Norell, M.A.; Gao, K.-Q. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of northeastern China. *Bull. Am. Mus. Nat. Hist.* **2017**, *411*, 1-66.
142. Forster, C.A.; Sampson, S.D.; Chiappe, L.M.; Krause, D.W. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* **1998**, *279*, 1915-1919, doi: 10.1126/science.279.5358.1915.
143. Pittman, M.; Xu, X., Eds. Pennaraptoran Theropod Dinosaurs Past Progress and New Frontiers. *Bull. Am. Mus. Nat. Hist.* **2020**, *440*, 1-353.
144. Csiki, Z.; Vremir, M.; Brusatte, S.L.; Norell, M.A. An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 15357-15361, doi: 10.1073/pnas.1006970107.
145. Brusatte, S.L.; Vremir, M.; Csiki-Sava, Z.; Turner, A.H.; Watanabe, A.; Erickson, G.M.; Norell, M.A. The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria, Theropoda) from the Late Cretaceous of Romania. *Bull. Am. Mus. Nat. Hist.* **2013**, *374*, 1-100.
146. Godefroit, P.; Cau, A.; Dong-Yu, H.; Escuillié, F.; Wenhao, W.; Dyke, G. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* **2013**, *498*, 359-362, doi: 10.1038/nature12168.
147. Foth, C.; Tischlinger, H.; Rauhut, O.W.M. New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature* **2014**, *511*, 79-82, doi: 10.1038/nsature13467.
148. Cau, A.; Brougham T.; Naish, D. The phylogenetic affinities of the Late Cretaceous Romanian theropod *Balaur bondoc* (Dinosauria, Maniraptoran): dromaeosaurid or flightless bird? *PeerJ* **2015**, e1032:1-36, doi: 10.7717/peerj.1032.
149. Gao, C.; Chiappe, L.M.; Meng, Q.; O'Connor, J.K.; Wang, X.; Cheng, X.; Liu, J. A new basal lineage of Early Cretaceous birds from China and its implications on the evolution of the avian tail. *Palaeontology* **2008**, *51*, 775-791, doi: 10.1111/j.1475-4983.2008.00793.x.
150. O'Connor, J.K.; Sullivan, C. Reinterpretation of the Early Cretaceous maniraptoran (Dinosauria, Theropoda) *Zhongornis haoae* as a scansoriopterygid-like non-avian, and morphological resemblances between Scansoriopterygids and basal oviraptorosaurs. *Vert. PalAs.* **2014**, *52*, 3-30.
151. Zhou, Z.; Zhang, F.; Li, Z. A new Lower Cretaceous bird from China and tooth reduction in early avian evolution. *Proc. Roy. Soc. B* **2010**, *277*, 219-227, doi: 10.1098/rspb.2009.0885.
152. O'Connor, J.K.; Zhou, Z. A redescription of *Chaoyangia beishanensis* (Aves) and a comprehensive phylogeny of Mesozoic birds. *J. Syst. Palaeontol.* **2013**, *11*, 889-906, doi: 10.1080/14772019.2012.690455.
153. Czerkas, S.A.; Yuan, C. An arboreal maniraptoran from Northeast China. In *Feathered Dinsoaurs and the Origin of Flight*; Czerkas, S.J., Ed; Dinosaur Museum: Blanding, UT, USA, 2002; pp. 63-95, ISBN 1-932075-01-1.
154. Czerkas, S.A.; Feduccia, A. Jurassic archosaur is a non-dinosaurian bird. *J. Ornithol.* **2014**, *155*, 841-851, doi: 10.1007/s10336-014-1098-9.
155. Martin, L.D. Mesozoic Birds and the Origin of Birds. In *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*; Schultze, H.-P., Trueb, L., Eds.; Cornell University Press: Ithaca, NY, USA, 1991; pp. 485-540, IBSN 0-8014-2497-6.
156. Wellnhofer, P. Archaeoptery*: The Icon of Evolution*; Verlag Dr. Friedrich Pfeil: München, DE, 2009; ISBN 978-3-89937-108-6.

157. Schwarz, D.; Kundrát, M.; Tischlinger, H.; Dyke, G.; Carney, R.M. Ultraviolet light illuminates the avian nature of the Berlin *Archaeopteryx* skeleton. *Sci. Rep.* **2019**, *9*, 6518:1-11, doi: 10.1038/s41598-019-42823-5.
158. Mayr, G.; Pohl, B.; Hartman, S.; Peters, D.S. The teneth skeletal specimen of *Archaeopteryx*. *Zool. J. Linn. Soc.* **2007**, *149*, 97-116, doi: 10.1111/j.1096-3642.2006.00245.x.
159. Burnham, D. *Archaeopteryx*—a re-evaluation suggesting an arboreal habitat and an intermediate stage in the *trees down* origin of flight. *N. Jb. Geol. Paläont. Abh.* **2007**, *245*, 33-44, doi: 10.1127/0077-7749/2007/0245-0033.
160. Wellnhofer, P. Das fünfte Skelettexemplar von *Archaeopteryx*. The fifth skeletal example of *Archaeopteryx*. *Palaeontogr. A* **1974**, *147*, 169-216.
161. Kundrát, M.; Nudds, J.; Kear, B.P.; Lü, J.; Ahlberg, P. The first specimen of *Archaeopteryx* from the Upper Jurasic Mörnsheim Formation of Germany. *Hist. Biol.* **2019**, *31*, 3-63, doi; 10.1080/08912963.2018.1518443.
162. Agnolin, F.; Novas, F.E. *Avian Ancestors: A Review of the Phylogenetic Relationships of the Theropods Unenlagiidae, Microraptoria,* Anchiornis, *and Scansoriopterygidae*; Springer: Dordrecht, NL, 2013; ISBN 978-94-007-5636-6.
163. Elzanowski, A. A new genus and species for the largest specimen of *Archaeopteryx*. *Acta Paleontol. Pol.* **2001**, *46*, 519-532.
164. Elzanowski, A. Archaeopterygidae (Upper Jurassic of Germany). In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds. University of California Press: Berkeley, CA, USA, 2002; pp. 129-159, ISBN 0-520-20094-2.
165. Xu, X.; Zhao, Q.; Norell, M.; Sullivan, C.; Hone, D.; Erickson, G.; Wang, X.; Han, F.; Yu, G. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chin. Sci. Bull.* **2009**, *54*, 430-435, doi: 10.1007/s11434-009-0009-6.
166. Xu, X.; You, H.; Han, F. An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* **2011**, *475*, 465-470, doi: 10.1038/nature10288.
167. Zhou, Z.; Zhang, F. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can. J. Earth Sci.* **2003**, *40*, 731-747, doi: 10.1139/E03-011.
168. Hu, D.; Li, L.; Hou, L.; Xu, X. A New Sapeornithid Bird from China and Its Implications for Early Avian Evolution. *Acta Geol. Sin-Engl.* **2010**, *84*, 472-482, doi: 10.1111/j.1755-6724.2010.00188.x.
169. Chiappe, L.M.; Ji, S.; Ji, Q.; Norell, M.A. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. *Bull. Am. Mus. Nat. Hist.* **1999**, *242*, 1-89.
170. Martin, L.D.; Zhou, Z.; Hou, L.; Feduccia, A. *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. *Naturwissenschaften* **1998**, *85*, 286-289.
171. Zhou, Z.; Hou, L. The Discovery and Study of Mesozoic Birds in China. In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds. University of California Press: Berkeley, CA, USA, 2002; pp. 160-183, ISBN 0-520-20094-2.
172. Zhou, Z.; Zhang, F. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* **2002**, *418*, 405-409, doi: 10.1038/nature00930.
173. O'Connor, J.K.; Sun, C.; Xu, X.; Wang, X.; Zhou, Z. A new species of *Jeholornis* with complete caudal integument. *Hist. Biol.* **2012**, *24*, 29-41, doi: 10.1080/08912963.2011.552720.
174. Chiappe, L.M., Walker, C.A. Skeletal Morphology and Systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds. University of California Press: Berkeley, CA, USA, 2002; pp. 240-267, ISBN 0-520-20094-2.
175. Chiappe, L.M. Osteology of the Flightless *Patagopteryx deferrariisi* from the Late Cretaceous of Patagonia (Argentina). In *Mesozoic Birds: Above the Heads of Dinosaurs*; Chiappe, L.M., Witmer, L.M., Eds. University of California Press: Berkeley, CA, USA, 2002; pp. 281-316, ISBN 0-520-20094-2.
176. You, H.-L.; Lamanna, M.C.; Harris, J.D.; et al. A Nearly Modern Amphibious Bird from the Early Cretaceous of Northwestern China. *Science* **2006**, *312*, 1640-1643, doi: 10.1126/science.1126377.
177. Wang, M.; Zheng, X.; O'Connor, J.K.; Lloyd, G.T.; Wang, X.; Wang, Y.; Zhang, X.; Zhou, Z. The oldest record of ornithuromorpha from the early cretaceous of China. *Nat. Commun.* **2015**, *6*, 6987:1-9, doi: 10.1038/ncomms7987.
178. O'Connor, J.K.; Zelenkov, N.V. The Phylogenetic Position of *Ambiortus*: Comparison with Other Mesozoic Birds from Asia. *Paleontol. J.* **2013**, *47*, 1270-1281, doi: 10.1134/S0031030113110063.
179. Martin, L.D.; Tate, Jr., J. The Skeleton of *Baptornis advenus* (Aves: Hesperornithiformes). *Smithson. Contrib. Paleobiol.* **1976**, *27*, 35-66.

180. Lee, S.; Lee, Y.-N.; Currie, P.J.; Sissons, R.; Park, J.-Y.; Kim, S.-H.; Barsbold, R.; Tsogtbaatar, K. A non-avian dinosaur with a streamlined body exhibits potential adaptations for swimming. *Commun. Biol.* **2022**, *5*, 1185:1-9, doi: 10.1038/s42003-022-04119-9.
181. Marsh, O.C. Odontornithes, a Monograph of the Extinct Toothed Birds of North America. *Report of the United States Geological Exploration of the Fortieth Parallel* **1880**, *7*, 1-201.
182. Benito, J.; Chen, A.; Wilson, L.E.; Bhullar, B.-A.S.; Burnham, D.; Field, D.J. Forty new specimens of *Ichthyornis* provide unprecedented insight into the postcranial morphology of crownward stem group birds. *PeerJ* **2022**, *10*, e13919:1-134, doi: 10.7717/peerj.13919.
183. Zhou, Z.-H.; Wang, X.-L.; Zhang, F.-C.; Xu, X. Important features of *Caudipteryx*—evidence from two nearly complete new specimens. *Vert. PalAs.* **2000**, *38*, 241-254.
184. Zhou, Z.-H.; Wang, X.-L. 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. *Vert. PalAs.* **2000**, *38*, 111-127.
185. Qiu, R.; Wang, X.; Wang, Q.; Li, N.; Zhang, J.; Ma, Y. A new caudipterid from the Lower Cretaceous of China with information on the evolution of the manus of Oviraptorosauria. *Sci. Rep.* **2019**, *9*, 6431:1-10, doi: 10.1038/s41598-019-42547-6.
186. Currie, P.J.; Russell, D.A. Osteology and relationships of *Chirostenotes pergracilis* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada. *Can. J. Earth Sci.* **1988**, *25*, 972-986.
187. Smith, D. The Type Specimen of *Oviraptor philoceratops*, a Theropod Dinosaur from the Upper Cretaceous of Mongolia. *N. Jb. Geol. Paläont. Abh.* **1992**, *186*, 365-388.
188. Balanoff, A.M.; Norell, M.A. Osteology of *Khaan meckennai* (Oviraptorosauria: Theropoda). *Bull. Am. Mus. Nat. Hist.* **2012**, *372*, 1-77.
189. Funston, G.F.; Tsogtbaatar, C.; Tsogtbaatar, K.; Kobayashi, Y.; Sullivan, C.; Currie, P.J. A new twi-fingered dinosaur sheds light on the radiation of Oviraptorosauria. *R. Soc. Open Sci.* **2020**, *7*, 201184:1-15, doi: 10.1098/rsos.201184.
190. Rhodes, M.W.; Funston, G.F.; Currie, P.J. New material reveals the pelvic morphology of Caenagnathidae (Theropoda, Oviraptorosauria). *Cretac. Res.* **2020**, *114*, 104521, doi: 10.1016/j.cretres.2020.104521.
191. Funston, G.F.; Mendonca, S.E.; Currie, P.J.; Barsbold, R. Oviraptorosaur anatomy, diversity and ecology in the Nemegt Basin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2018**, *494*, 101-20, doi: 10.1016/j.palaeo.2017.10.023.
192. Norell, M.A.; Clark, J.M.; Chiappe, L.M. An Embryonic Oviraptorid (Dinosauria: Theropoda) from the Upper Cretaceous of Mongolia. *Am. Mus. Novit.* **2001**, *3315*, 1-17.
193. Weishampel, D.B.; Fastovsky, D.E.; Watabe, M.; Varricchio, D.; Jackson, F.; Tsogtbaatar, K.; Barsbold, R. New oviraptorid embryos from Bugin-Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *J. Vertebr. Paleonol.* **2008**, *28*, 1110-1119, doi: 10.1671/0272-4634-28.4.1110.
194. Lü, J.; Currie, P.J.; Xu, L.; Zhang, X.; Pu, H.; Jia, S. Chicken-sized oviraptorid dinosaurs from central China and their ontogenetic implications. *Naturwissenschaften* **2013**, *100*, 165-175, doi: 10.1007/s00114-012-1007-0.
195. Xu, X.; Currie, P.; Pittman, M.; Xing, L.; Meng, Q.; Lü, J.; Hu, D.; Yu, C. Mosaic evolution in an asymmetrically feathered troodontid dinosaur with transitional features. *Nat. Commun.* **2017**, *8*, 14972:1-12, doi: 10.1038/ncomms14972.
196. Ji, Q.; Ji, S.; Lü, J.; You, H.; Chen, W.; Liu, Y.; Liu, Y. First avialian bird from China. *Geol. Bull. China* **2005**, *24*, 197-210.
197. Shen, C.; Lü, J.; Liu, S.; Kundrát, M.; Brusatte, S.L.; Gao, H. A New Troodontid from the Lower Cretaceous Yixian Formation of Liaoning Province, China. *Acta Geol. Sin-Engl.* **2017**, *91*, 763-780, doi: 10.1111/1755-6274.13307.
198. Tsuihiji, T.; Barsbold, R.; Watabe, M.; Tsogtbaatar, K.; Tsogtbaatar, C.; Fujiyama, Y.; Suzuki, S. An exquisitely preserved troodontid theropod with new information on the palatal structure from the Upper Cretaceous of Mongolia. *Naturwissenschaften* **2014**, *101*, 131-142, doi: 10.1007/s00114-014-1143-9.
199. Xu, X.; Norell, M.A.; Wang, X.-L.; Makovicky, P.J.; Wu, X.-C. A basal troodontid from the Early Cretaceous of China. *Nature* **2002**, *415*, 780-784.
200. Gong, E.-P.; Martin, L.D.; Burnham, D.A.; Falk, A.R.; Hou, L.-H. A new species of *Microraptor* from the Jehol Biota of northeastern China. *Palaeoworld* **2012**, *21*, 81-91, doi: 10.1016/j.palwor.2012.05.003.
201. Hwang, S.H.; Norell, M..A.; Ji, Q.; Gao, K. New Specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *Am. Mus. Novit*. **2002**, *3381*, 1-44.

202. Longrich, N.R.; Currie, P.J. A microraptorine (Dinosauria—Dromaeosauridae) from the Late Cretaceous of North America. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 5002-5007, doi: 10.1073/pinas.0811664106.
203. Brusatte, S.L. A Mesozoic aviary. *Science* **2017**, *335*, 792-794, doi: 10.1126/science.aal2397.
204. Novas, F.E.; Puerta, P.F. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* **1997**, *387*, 390-392.
205. Novas, F.E. Avian Traits in the Ilium of *Unenlagia comahuensis* (Maniraptora, Avialae). In *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*; Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L., Eds. Indiana University Press: Bloomington, IN, USA, 2004; pp. 150-166, ISBN 0-253-34373-9.
206. Burnham, D. New Information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana. In *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*; Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L., Eds. Indiana University Press: Bloomington, IN, USA, 2004; pp. 67-111, ISBN 0-253-34373-9.
207. Ostrom, J.H. Osteology of *Deinonychus antirrhopus*, an Unusual Theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.* **1969**, *30*, 1-165.
208. Norell, M.A.; Makovicky, P.J. Important Features of the Dromaeosaurid Skeleton: Information from a New Specimen. *Am. Mus. Novit.* **1997**, *3215*, 1-28.
209. Norell, M.A.; Makovicky, P.J. Important Features of the Dromaeosaurid Skeleton II: Information from Newly Collected Specimens of *Velociraptor mongoliensis*. *Am. Mus. Novit.* **1999**, *3282*, 1-45.
210. Nesbitt, S. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bull. Am. Mus. Nat. Hist.* **2007**, *302*, 1-84.
211. Bates, K.T.; Schachner, E.R. Disparity and convergence in bipedal archosaur locomotion. *J. R. Soc. Interface* **2012**, *9*, 1339-1353, doi: 10.1098/rsif.2011.0687.
212. Gauthier, J.A.; Nesbitt, S.J.; Schachner, E.R.; Bever, G.S.; Joyce, W.G. The Bipedal Stem Crocodilian *Poposaurus gracilis*: Inferring Function in Fossils and Innovation in Archosaur Locomotion. *Bull. Peabody Mus. Nat. Hist.* **2011**, *52*, 107-126, doi: 10.3374/014.052.0102.
213. Farlow, J.O.; Schachner, E.R.; Sarrazin, J.C.; Klein, H.; Currie, P.J. Pedal Proportions of *Poposaurus*: Convergence and Divergence in the Feet of Archosaurs. *Anat. Rec.* **2014**, *297*, 1022-1046, doi: 10.1002/ar.22863.
214. Schachner, E.R.; Irmis, R.B.; Huttenlocker, A.K.; Sanders, K.; Cieri, R.L.; Nesbitt, S.J. Osteology of the Late Triassic Bipedal Archosaur *Poposaurus gracilis* (Archosauria: Pseudosuchia) from Western North America. *Anat. Rec.* **2020**, *303*, 874-917, doi: 10.1002/ar.24298.
215. Weinbaum, J.C. Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha), from the Upper Triassic of the United States. *Geol. Soc. Spec. Publ.* **2013**, *379*, 525-553, doi: 10/1144/SP379.7.
216. Vickaryous, M.K.; Maryańska, T.; Weishampel, D.B. Ankylosauria. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 363-392, ISBN 978-0-520-25408-4.
217. Dodson, P.; Forster, C.A.; Sampson, S.D. Ceratopsidae. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmólska, H., Eds; University of California Press: Berkeley, CA, USA, 2004; pp. 494-513, ISBN 978-0-520-25408-4.
218. Xing, L.; Miyashita, T.; Wang, D.; Niu, K.; Currie, P.J. A new compsognathid theropod dinosaur from the oldest assemblage of the Jehold Biota in the Lower Cretaceous Huajiying Formation, northeastern China. *Cretac. Res.* **2020**, *107*, 104285, doi: 10.1016/j.cretres.2019.104285.
219. Ostrom, J. The Osteology of *Compsognathus longipes* Wagner. *Zitteliana* **1978**, *4*, 73-118.
220. Currie, P.J.; Chen, P.-J. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Can. J. Earth Sci.* **2001**, *38*, 1705-1727, doi: 10.1139/cjes-38-12-1705.
221. Chatterjee, S.; Templin, R.J. Feathered Coelurosaurs from China: New Light on the Arboreal Origin of Avian Flight. In *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*; Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L., Eds. Indiana University Press: Bloomington, IN, USA, 2004; pp. 251-281, ISBN 0-253-34373-9.
222. Chatterjee, S.; Templin, R.J. Palaeoecology, Aerodynamics, and the Origin of Avian Flight. In *Earth and Life: Global Biodiversity, Extinction Intervals and Biogeographic Perturbations Through Time*; J.A., Ed. Springer: Dordrecht, NL, 2012; pp. 585-612, ISBN 978-94-024-0491-3.
223. Xing, L.; Persons, IV, W.S.; Bell, P.R.; Xu, X.; Zhang, J.; Miyashita, T.; Wang, F.; Currie, P.J. Piscivory in the feathered dinosaur *Microraptor*. *Evolution* **2013**, *67*, 2441-2445, doi: 10.1111/evo.12119.

224. Kim, K.S.; Lim, J.D.; Lockley, M.G.; Xing, L.; Kim, D.H.; Piñuela, L.; Romilio, A.; Yoo, J.S.; Kim, J.H., Ahn, J. Smallest known raptor tracks suggest microraptorine activity in lakeshore setting. *Sci. Rep*. **2018**, *8*, 16908:1-10, doi: 10.1038/s41598-018-35289-4.
225. Hu, H.; Wang, Y.; McDonald, P.G.; et al. Earliest evidence for fruit consumption and potential seed dispersal by birds. *eLife* **2022**, *11*, e74751:1-19, doi: 10.7554/eLife.74751.
226. Wu, Y.; Ge, Y.; Hu, H.; Stidham, T.A.; Li, Z.; Bailleul, A.M.; Zhou, Z. Intra-gastric phytoliths provide evidence for folivory in basal avialans of the Early Cretaceous Jehol Biota. *Nat. Commun.* **2023**, *14*, 4558:1-7, doi: 10.1038/s41467-023-40311-z.
227. Burnham, D.A.; Feduccia, A.; Martin, L.D.; Falk, A.R. Tree climbing—a fundamental avian adaptation. *J. Syst. Palaeontol.* **2011**, *9*, 103-107, doi: 10.1080/1477s019.2010.522201.
228. Padian, K. Evolutionary insights from an ancient bird. *Nature* **2018**, *557*, 36-37, doi: 10.1038/d41586-018-04780-3.
229. Dial, K.P. Wing-Assisted Incline Running and the Evolution of Flight. *Science* **2003**, *299*, 402-404, doi: 10.1126/science.1078237.
230. Kuznetsov, A.N.; Panyutina, A.A. Where was WAIR in avian flight evolution? *Biol. J. Linn. Soc.* **2022**, *137*, 145-156, doi: 10.1093/biolinnean/blac019.
231. Norberg, U.M. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*; Springer: Berlin, DE, 1990; ISBN 978-3-642-83850-7.
232. Kambic, R.E.; Roberts, T.J.; Gatesy, S.M. Long-axi rotation: a missing degree of freedom in avian bipedal locomotion. *J. Exp. Biol.* **2014**, *217*, 2770-2782, doi: 1242/jeb.101428.
233. Xu, X.; Zhou, Z.; Wang, X.; Kuang, X.; Zhang, F.; Du, X. Four-winged dinosaurs from China. *Nature* **2003**, *421*, 335-340, doi: 10.1038/nature01342.
234. Pol, D.; Goloboff, P.A. The Impact of Unstable Taxa in Coelurosaurian Phylogeny and Resampling Support Measures for Parsimony Analyses. *Bull. Am. Mus. Nat. Hist.* **2020**, *440*, 97-115.
235. James, F.C. How many dinosaurs are birds? *BioScience* **2021**, *71*, 991-994, doi: 10.1093/biosci/biab060.
236. Yalden, D.W. Forelimb Function in *Archaeopteryx*. In *The Beginnings of Birds: Proceedings of the International* Archaeopteryx *Conference Eichstätt 1984*; Hecht, M.K., Ostrom, J.H., Viohl, G., Wellnhofer, P., Eds. Freunde des Jura-Museums Eichstätt: Willibaldsburg, DE, 1985; pp. 91-97, ISBN 3-9801178-0-4.
237. Wang, Y.-A.; O'connor, J.K.; Li, D.Q.; You, H.-L. New information on postcranial skeleton of the Early Cretaceous *Gansus yumenensis* (Aves: Ornithuromorpha). *Hist. Biol.* **2016**, *28*, 666-679, doi: 10.1080/08912963.2015.1006217.
238. Ji, S.A.; Atterholt, J.; O'Connor, J.K.; Lamanna, M.C.; Harris, J.D.; Li, D.-Q.; You, H.-L.; Dodson P. A new, three-dimensionally preserved enantiornithine bird (Aves: Ornithothoraces) from Gansu Province, north-western China. *Zool. J. Linn. Soc.* **2011**, *162*, 201-219, doi: 10.1111/j.1096-3642.2010.00671.x.
239. Wang, M.; Li, Z.; Zhou, Z. Insight into the growth pattern and bone fusion of basal birds from an Early Cretaceous enantiornithine bird. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 11470-11475, doi: 10.1073/pnas.1707237114.