

Article

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

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Abstract: The idea 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 the acetabulum and its important appurtenances, the supracetabular crest and the antitrochanter, that hip anatomy differs substantially between dinosaurs and birds. 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 partially closed acetabula, thus rendering the current terms “open” or “closed” acetabula inaccurate; they should be modified or replaced. Given new evidence presented here, the relationship of “dinosaurs” and birds must be re-evaluated.

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



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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 many studies have attempted to chart 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 descent of birds from theropod dinosaurs, the morphology of the acetabulum took on new importance, but the connectivity of acetabular morphology and function is still not fully understood. Triassic archosaurs such as *Lagosuchus* (synonymized with *Marasuchus* [21]), *Ticinosuchus*, and others 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. Crocodylians, 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, but in others, the walls of the basin are partially ringed by thin bone 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 cartilage that provides an articulating surface for the femoral head, which has a pit (fovea) that receives the acetabular ligament. The deep floor is referred to as the acetabular fossa.

Despite this schematic characterization, it is more difficult to adequately 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 H₂O₂ 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 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 composition and homology of fibrous or filament-like structures in various theropod dinosaurs [25–37] but can also obscure phylogenetic signals in analyses that 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 the 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 reexamine the familiar claim that birds have the hips (and legs) of theropod dinosaurs: first, basal archosaurs and 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. Whereas the pennaraptorans are typically considered to be primarily flightless nonavian theropods [52], others [10,51,53–59] have argued that some are secondarily flightless (“neoflightless”) 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: obviously, analyses are 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. The reader is referred to other works [29–31,50,68] for a review of problems with phylogenetic analyses of paleontological data in the dispute on the origin of birds.

Given the range of taxa discussed 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 *Gallus* (domestic chicken) and *Anas* (domestic duck) with fully open, dinosaurian acetabula, unlike older images (Figure 1), which show substantial medial acetabular walls.

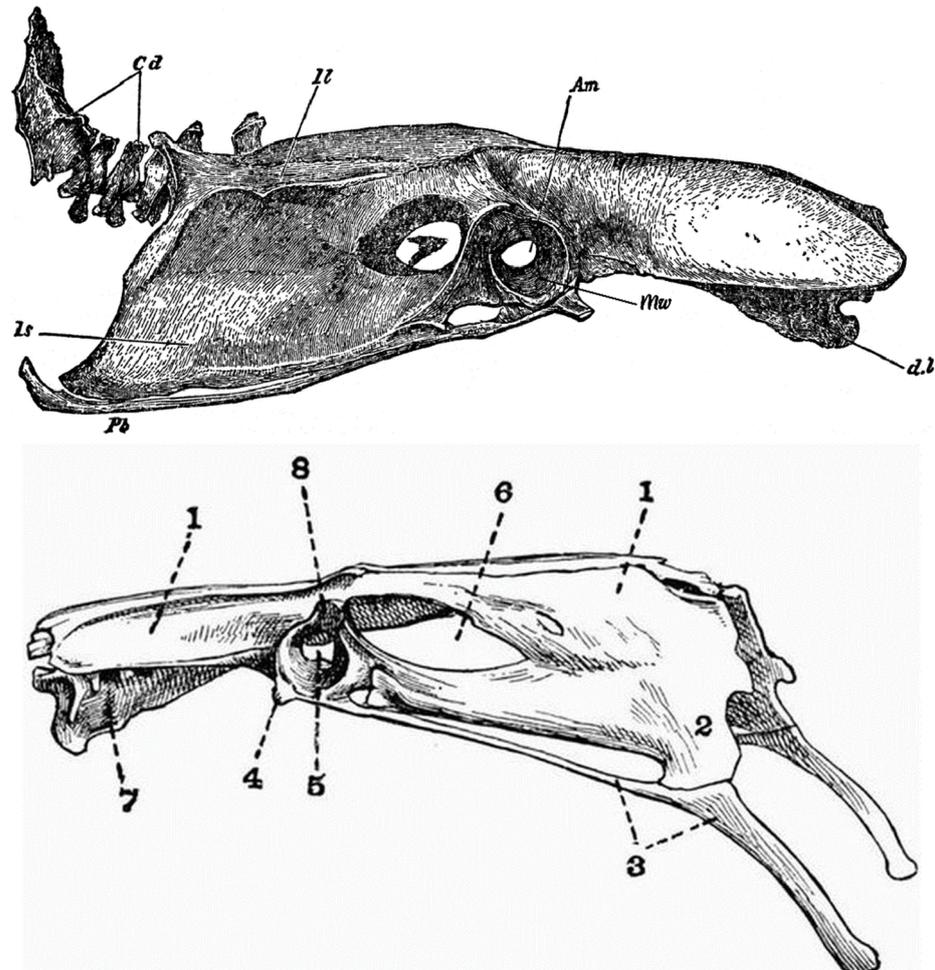


Figure 1. Pelves (Os coxae + Synsacrum, or innominate bone) of (upper) right lateral view of the domestic fowl *Gallus gallus*; below, Mallard *Anas platyrhynchos* in left lateral view. (See lower image for anatomical terms). Note considerable medial “acetabular” walls (mw) surrounding the acetabular foramen (foramen acetabuli). 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). *Gallus*, *Encyclopaedia Britannica*, 1911; *Anas*, *The Vertebrate Skeleton*, Cambridge Press, 1897; public domain.

The continued 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 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 [78–80] to a clade consisting only of “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 phylo-

genetic analyses. For ease of reference, Table 1 provides brief (and taxonomically informal) characterizations of the major subdivisions of Archosauria that are relevant to this review.

Table 1. Archosauria and some of its major taxonomic subdivisions. Taxa are informally characterized for readers unfamiliar with archosaur taxonomy. For detailed discussions, readers are invited to consult the References. Abbreviations: mya, million years ago.

Taxon	Comments
Archosauria	“Ruling reptiles”, Archosauria arose in the late Permian (~298–251 mya), diversified in the aftermath of the end-Permian extinction, and dominated terrestrial ecosystems in the Mesozoic (~251–65 mya). They include birds, crocodylians, dinosaurs, pterosaurs (flying reptiles), and many other related forms.
Crurotarsi	All those archosaurs are more closely related to extant crocodylians than they are to other archosaurs (Crurotarsi are often, but misleadingly, called “Pseudosuchia”). They are characterized by their complex ankle configuration and were extraordinarily diverse, particularly in the Triassic (~251–201 mya), and during this time, they often approximated dinosaur morphotypes through parallelism or convergence. Crocodylians are the only forms to have survived the end-Cretaceous extinction event.
Dinosauromorpha	Dinosaurs and a variety of successively related outgroup taxa, like <i>Lagosuchus</i> and silesaurids, are the subject of intense study and continuing fossil discoveries. Relationships among dinosauromorph taxa remain in flux.
Dinosauria	The exact taxonomic composition and interrelationships of the major dinosaurian lineages have been debated in recent years. Dinosaurs include theropods, sauropods (like <i>Apatosaurus</i>), and ornithischians (like <i>Triceratops</i>). They dominated terrestrial ecosystems from the Late Triassic to the end of the Cretaceous.
Theropoda	The familiar carnivorous (though some may have secondarily shifted diet) dinosaurs, ranging in size from the diminutive compsognathids to the gigantic tyrannosaurids.
Maniraptora	A group of theropods erected during the 1980s and crucial to discussions on the origin of birds: they include five major subgroups (Therizinosauroidea, Alvarezsauria, Oviraptorosauria, Dromaeosauridae, and Troodontidae) and, putatively, Aves. The most birdlike taxa currently classified as theropods belong to the Maniraptora.
Pennaraptora	Those maniraptorans, viz. Oviraptorosauria, Dromaeosauridae, and Troodontidae possess unambiguously pennaceous feathers.
Aves	Birds, including the Jurassic archaeopterygids, several lineages of basal forms (most discovered in China in the past three decades), and the enantiornithines and ornithurines (including living birds).
Enantiornithes	“Opposite birds” are a remarkably diverse group, fully volant, that constitute the major radiation of Cretaceous land birds. Their pectoral girdle and tarsometatarsus are constructed differently from those of ornithurine birds, indicating parallel refinement of the flight apparatus during early avian history.
Ornithurae	All those birds are more closely related to extant birds (Neornithes) than they are to Enantiornithes. They appear to have been the less speciose radiation of Cretaceous land birds, perhaps marginalized by enantiornithine success.
Neornithes	Extant birds, from paleognaths like “ratites” to neognathous songbirds.

2. Hip Joint Morphology in Basal Archosauria and in Dinosauria

The acetabulum in Triassic archosaurs is a mostly closed or 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 (i.e., reptiles—including birds—and their related amniote stem forms) acetabula have a small perforation in the pit of the eponymous basin. Basal archosaurs have an S-shaped femur with no in-turned head and without a well-developed upper rim (supracetabular 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 supracetabular crest [91] that overhangs the acetabulum and distributes transmitted stresses and prevents unwanted excursions of the femur (Figure 2).

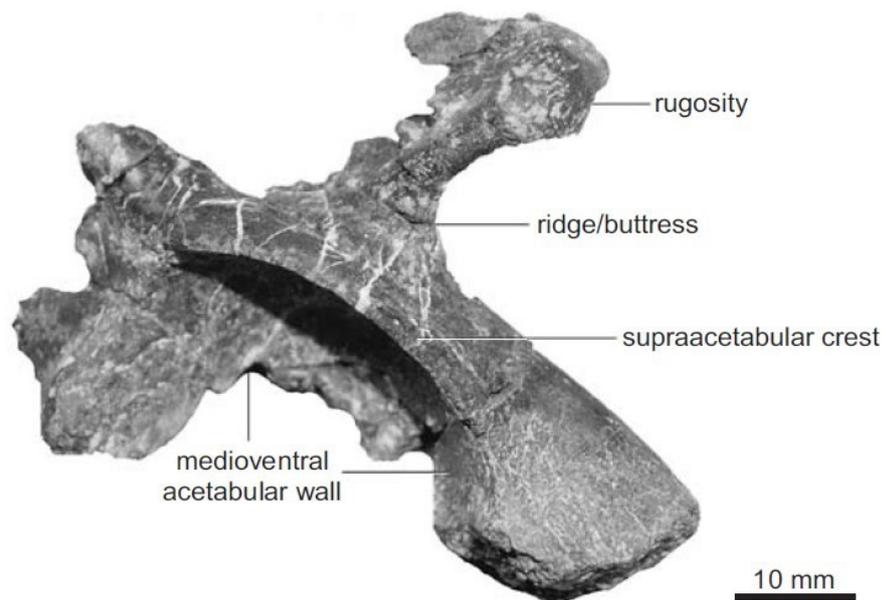
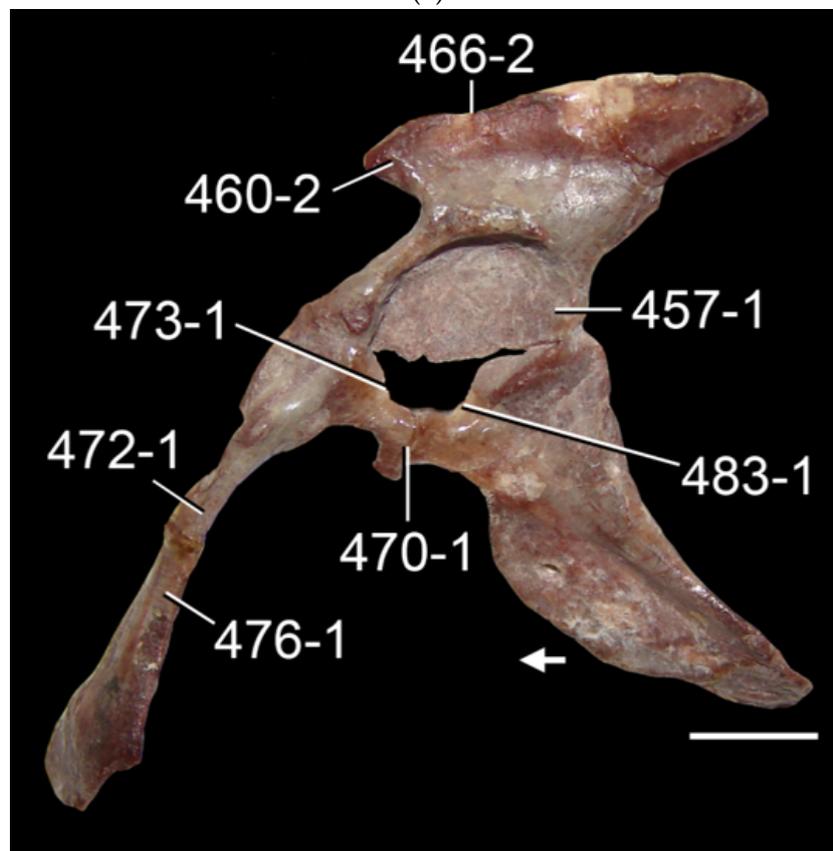
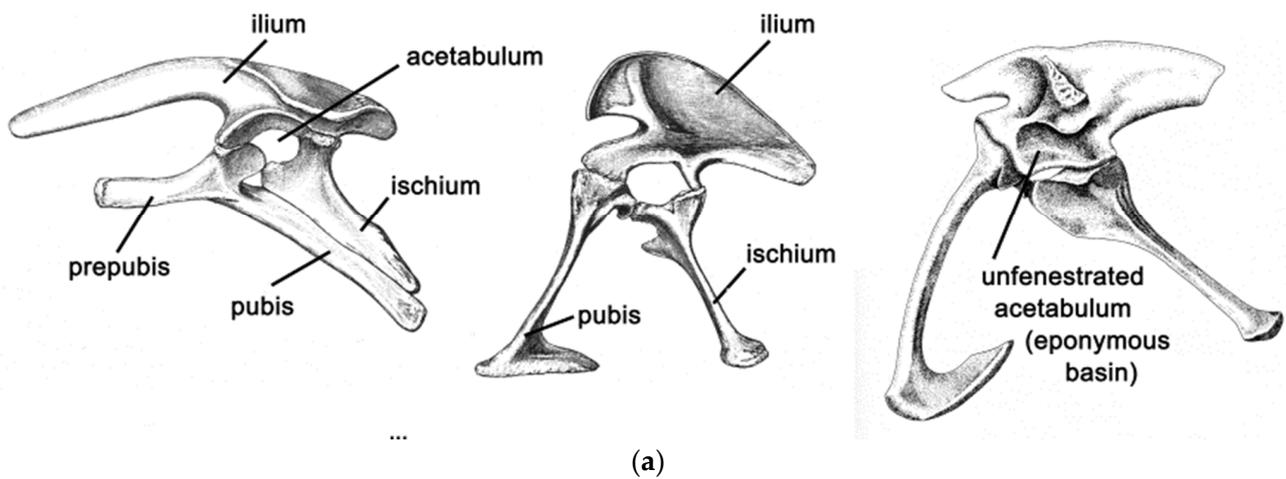


Figure 2. Late Triassic herrerasaurian dinosauriform *Caseosaurus crosbyensis* from New Mexico, illustrating the well-developed supracetabular crest characteristic of later dinosaurs [91]; use, CC by 4.0.

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) and 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.

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 Section 3 for further discussion on the development and function of the antitrochanter). Moreover, while continuity of function is not a requirement of 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 to one another.



(b)

Figure 3. Mesozoic pelves: (a) compare, from left to right, pelves of *Stegosaurus*, an ornithischian; *Allosaurus*, a saurischian theropod (both from varied sources); 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) (modified from [31]); (b) pelvis of the dinosaurmorph *Lagosuchus* (modified from [74], used under CC by 4.0 license). 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. (*Postosuchus*, courtesy S. Chatterjee).

Among Maniraptora, an antitrochanter has been reported in alvarezsaurs [105–108], therizinosauroids [109–111], 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 the dromaeosaurid *Mahakala*, for example, the femur is proposed to possess a “fossa articularis antitrochanterica” [*sic*] [120] (p. 42) (the authors presumably meant “Facies articularis antitrochanterica”)—a character state otherwise observed only in enantiornithines and ornithurines—even though *Mahakala* lacks an antitrochanter [120]. With these preliminary clarifications made, pennaraptoran taxa in which an antitrochanter has been reported will be discussed further in Section 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. Generally, one can see considerable occlusion in specimens of *Struthio* (Figure 4a), *Aepyornis*, and *Dromaius* (Figure 5); it is more open in *Apteryx*. 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. Antitrochanters are also evident in struthionids, rheas, kiwis, and other “ratites” (Figures 4a and 5f). Interestingly, the acetabulum is partially or mainly closed in most ground-dwellers, unlike any putative dinosaurian relatives despite the presumed similarity in gait (Figure 5).

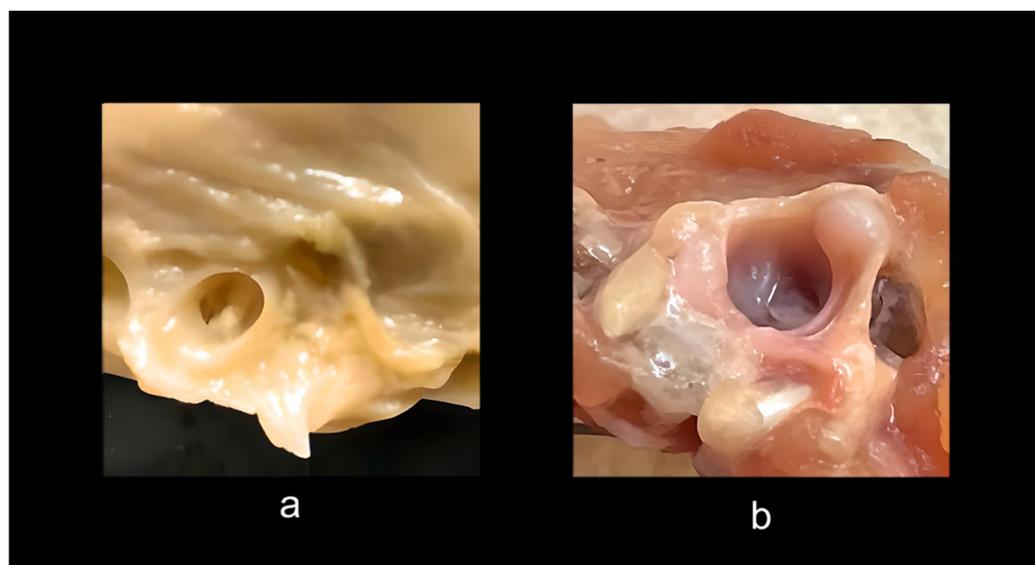


Figure 4. Acetabulum of (a) juvenile ostrich *Struthio camelus* (24-day old wet specimen, normal incubation 36–45 days; the specimen is fragile and preservative renders image with poor resolution), and (b) adult Scaled Quail *Callipepla squamata* showing acetabular closure and substantial medial wall,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

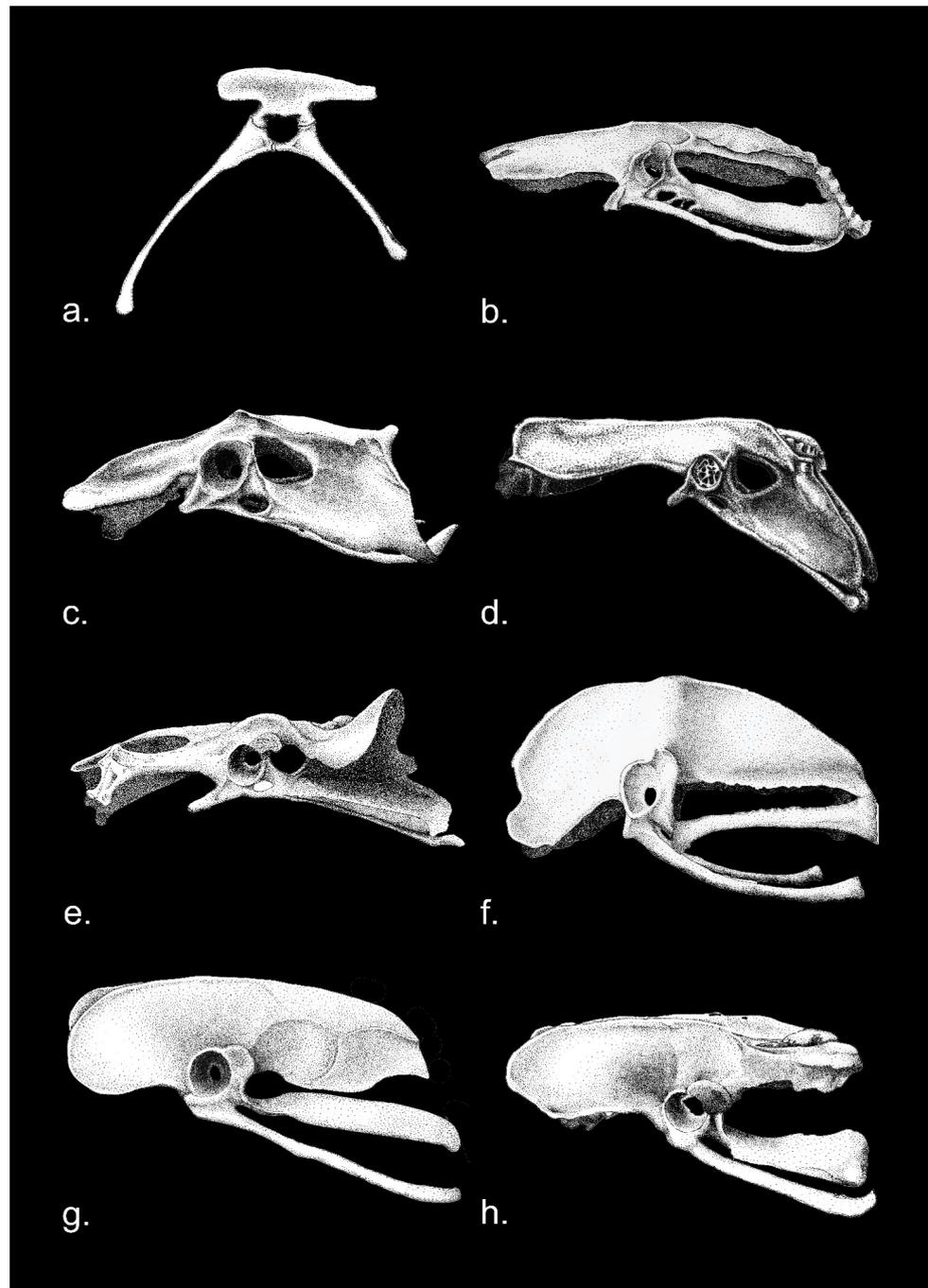


Figure 5. Pelvis of the basal theropod *Coelophysis* (a) compared to an array of primarily ground-dwelling birds: (b) Solitary Tinamou (*Tinamus solitarius*), (c) Wild Turkey (*Meleagris gallopavo*), (d) Japanese Quail (*Coturnix japonica*), (e) Greater Roadrunner (*Geococcyx californianus*), (f) Emu (*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 an original photo from S. Mehta, interpreted by the author; *Dromaius* drawn from the pelvis in the author's collection; *Meleagris* drawn from photos in the author's collection and photos; *Geococcyx* drawn from images and checked with specimen from the author's collection. 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 Figures 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 4 to 6 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 a form of induced paedomorphosis, which explains the large amounts of cartilage all over and incompletely fused and cartilaginous epiphyses (Figure 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).

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 a 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, whereas 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 crocodylians). 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, so epiphyseal cartilage in extinct forms would have been substantial [125,126]. The loss of this epiphyseal cartilage in fossilization, therefore, indicates that the preserved ends of the 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 confusing 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 state and that of ancestral archosaurian* [my emphasis] condition more than it did the intermediate dinosaurian conditions.” It should be noted in passing that although 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 principles of simple conservatism 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 reascend 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 femoral-pelvic articulation is located outside of the acetabulum. Hertel and Campbell [104] demonstrated that the antitrochanter-femur articulation transfers long-axis rotational movement of the femur to the 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, modern 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.

The newly described taxon Telluraves (arboreal land birds or core land birds), erected from whole genome comparisons, includes small arboreal birds that 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*). 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 were or are 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.

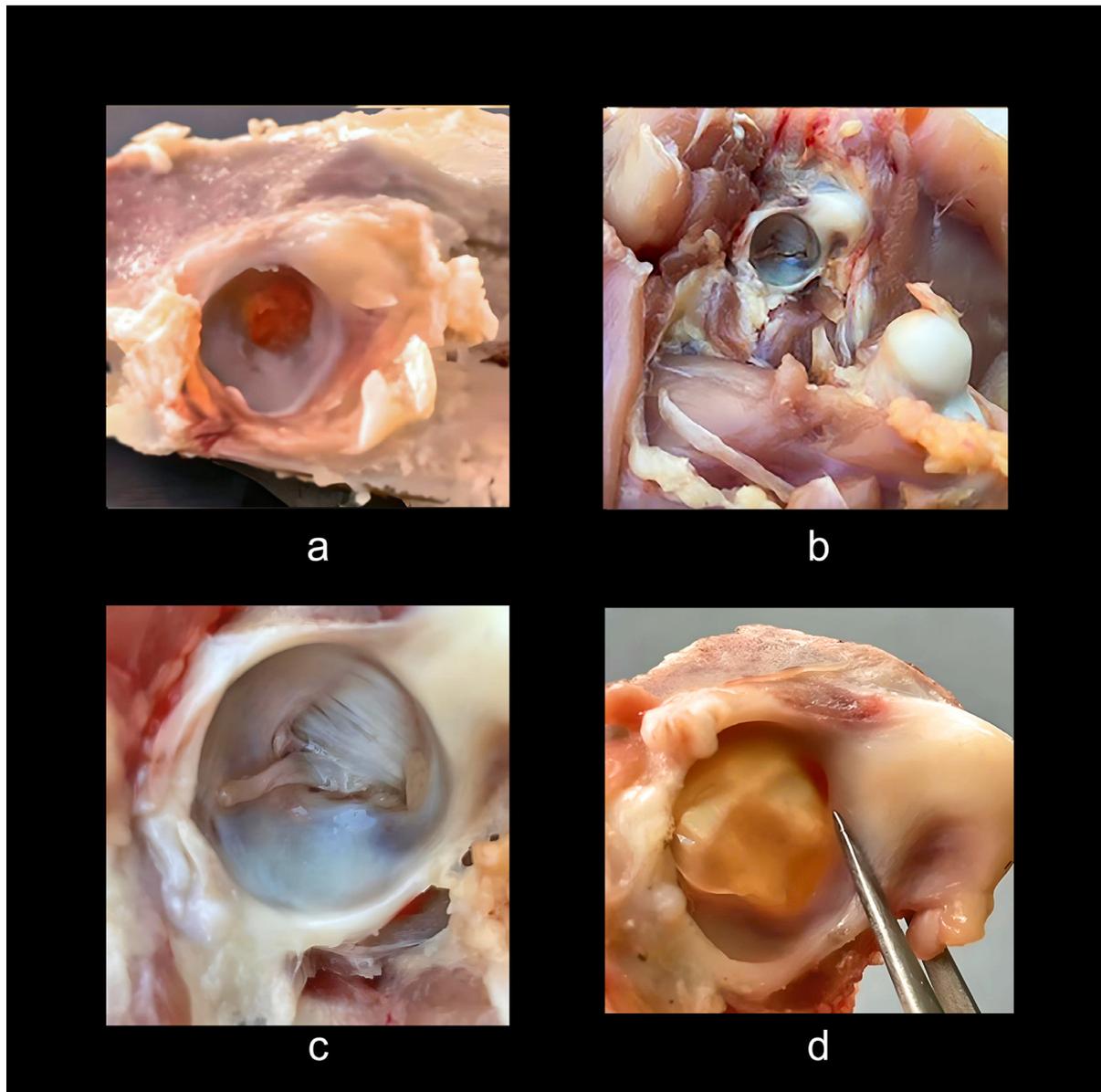


Figure 6. Acetabula of rotisserie chickens. These images show post-hatching additions, notably considerable cartilage, and the antitrochanter: (a) rotisserie chicken post-hatching, the acetabulum foramen near the opening, showing considerable cartilage and an almost calcified antitrochanter; (b) Poulet 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 into endochondral bone. (Rotisserie chicken acetabula, approximately 10 mm; Poulet Rouge, 12 mm). Photos and dissections by the author.



Figure 7. Sacra of *Hesperornis* (above) and *Parahesperornis* (below), large divers of the Late Cretaceous, in left lateral view showing nearly closed acetabula. Often called diving dinosaurs, the acetabula show that they are definitively not allied with dinosaurs. 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. *Hesperornithiforms* are often termed diving dinosaurs, but given their acetabula anatomy this designation is erroneous. Images courtesy M. Everhart and the University of Kansas, Museum of Natural History, and University of Nebraska State Museum. Scale cm.

4. The Hip Joint Morphology in Basal Birds and in Pennaraptora

The basal avian assemblage, ranging from the Late Jurassic to the Early Cretaceous, includes the archaeopterygids, *Chongmingia*, *Jinguoformis*, *Fukuipteryx*, *Cratonavis*, omnivoroptyergids (=“sapeornithids”), jeholornithids, and confuciusornithids [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, 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 others argue that it is a scansoriopterygid [150]. Scansoriopterygids were first described as tree dwellers (e.g., *Epidendrosaurus* and *Scansoriopteryx*) but henceforth have

often 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. 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 [29,31,151,152] that showed a definitive absence of diagnostic dinosaurian characters. *Zhongornis* will not be discussed further here. *Zhongjianornis* was initially described as a basal bird [153], but further study suggests that it is a basal ornithurine [154].

The maniraptoran taxa most important 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.

(a). *Basal birds*.—In archaeopterygids the acetabulum is medially occluded, as is clearest from the London specimen [155] (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 ([155–157]).

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, whereas the avian antitrochanter is composed exclusively or principally from the ischium [69,90,104] and (2) 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 “Thermopolis” specimen, the femora are not disarticulated, and are within their natural 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 a 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] (see also [155]). 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]. Similarly, in the Daiting specimen, the femoral head is not fully inturned [161]. 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].

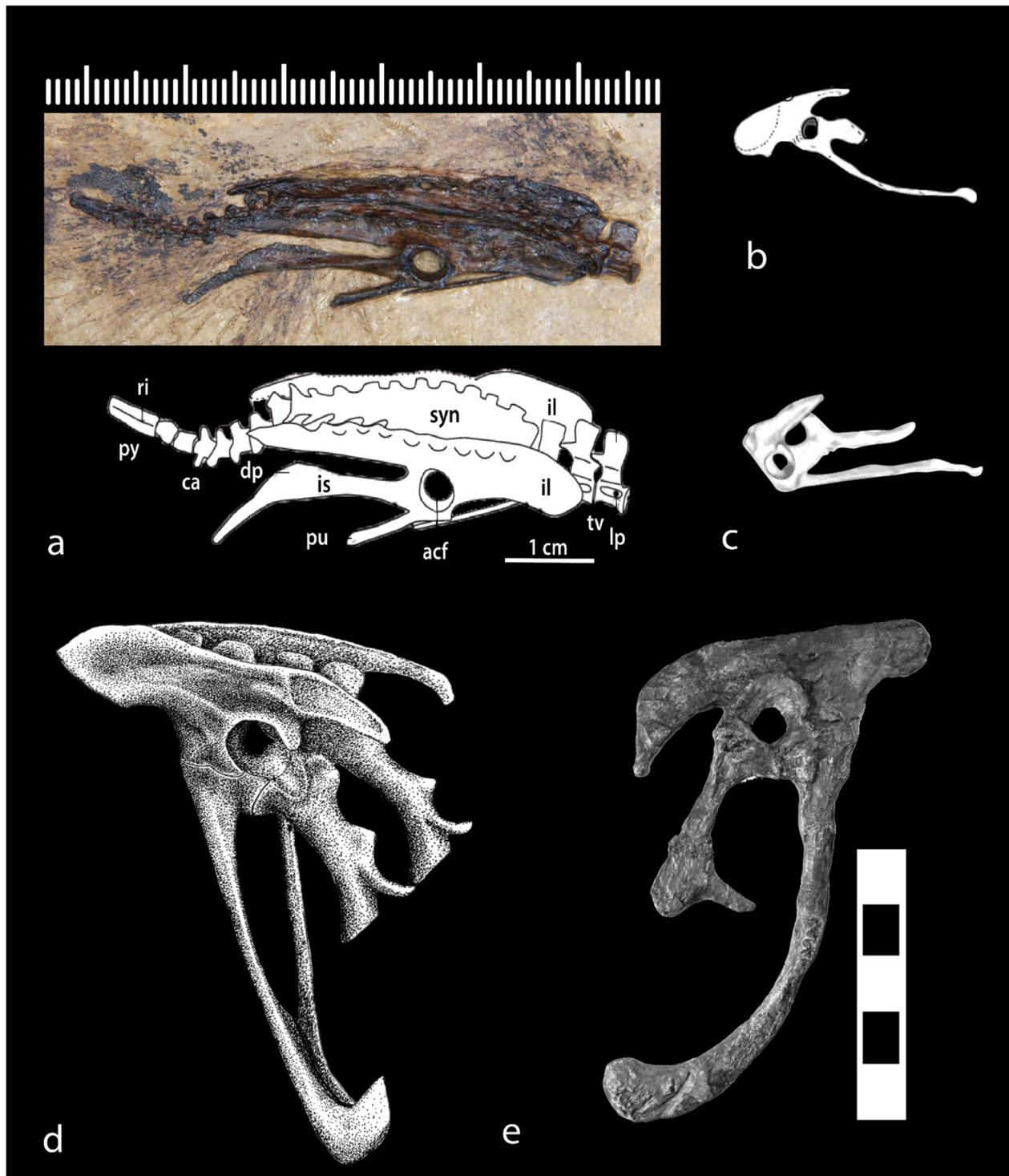


Figure 8. Pelves of Mesozoic birds showing medial acetabular walls: (a) photograph and interpretive drawing of Early Cretaceous ornithurine *Gansus* [165]; (b,c) Early Cretaceous sparrow-size enantiornithines, (b) *Qiliania* [166]; (c) *Pterygornis* [167]; (d) Late Jurassic *Archaeopteryx* (image composites of varied sizes, primarily after P. Wellnhofer, based primarily on the Munich specimen, with details from the London, Berlin, and Eichstätt specimens); (e) *Microraptor*, the Early Cretaceous four-winged bird-like glider (dromaeosaur), considered by many an early bird. (*Microraptor* photo courtesy D. Burnham); scale cm for e Art by K. Grow.

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.” [141] (p. 4). The acetabulum in *Anchiornis* is partially occluded by substantial medial bony walls ([168] (Figure 4c); [141]; D. Burnham, pers. comm.) (Figure 9). A weak though clearly demarcated crest is present above the acetabulum ([168] (Figure 4c); [141]), but it is not broad and is more like a reinforcement rim, as it proceeds down the sides of the acetabular circle. As in basal birds, there is no antitrochanter.

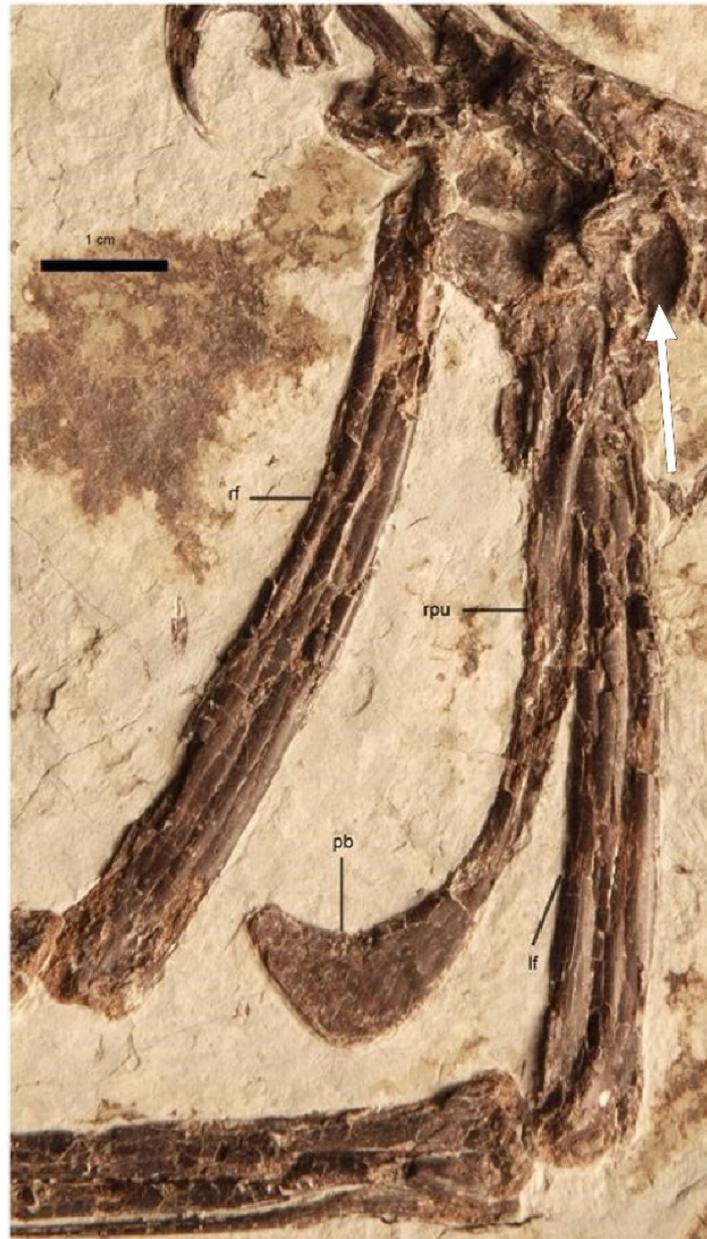


Figure 9. Femora and right pubis of *Anchiornis*, with the hip joint partially visible due to taphonomic displacement of the proximal femur, showing part of the expansive bony medial acetabular wall (arrow). Abbreviations: lf; left femur; pb, pubic boot; rf, right femur; rpu, right pubis. Image courtesy R. Pei.

There appears to be neither a well-developed supracetabular crest nor an antitrochanter in *Xiaotingia* [169] (Figure 2c) or “*Aurornis*” [146] (Figure 2c,d) (if “*Aurornis*” is a valid taxon and not a junior synonym of *Anchiornis*), but these taxa are likely all anchiornithids. The

situation in the recently described *Fujianvenator* is also uncertain, 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 seriemas (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]. 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 and poorly developed supracetabular crest; the purported antitrochanter, however, is iliac in origin [142].

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 taxa closely related to the archaeopterygids [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 [170] (Figure 8a,b) and the acetabulum of “*Shenshiornis*”, probably a junior synonym of *Sapeornis*, is completely perforate [171] (Figure 4c). A small antitrochanter may be present in confuciusornithids ([172], which incorrectly characterized confuciusornithids as terrestrial birds; contrast with [173,174]). Confuciusornithids lack a supracetabular crest [172–174], and both omnivoropterygids and jeholornithids lack supracetabular crests and antitrochanters ([170,175]; [171] (Figure 4c); [176] (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 *Qiliania* and *Pterygornis* (Figure 8a–c), 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* [177]; 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* [178], which is often (though perhaps spuriously) recovered as a basal ornithurine (or “ornithuromorph”) [130,152,178–181]. 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* [182] (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 [183]. 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 [184]) [83] (pp. 46–52), though not in *Ichthyornis* [185]. In both enantiornithines and ornithurines, the maintenance of balance in obligately bipedal locomotion is linked to the presence of an antitrochanter [104]. The phylogenetically late 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) *Pennaraptora*.—Character conflict indicative of both parallelism and mosaicism is 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 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 the 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 is difficult. Caudipterygids lack supracetabular crests and antitrochanters ([186] (pl. VI); [187] (pl. III); [188] (Figure 5)), as is also the case in caenagnathoids (i.e., caenagnathids and oviraptorids) ([189] (Figure 6a); [190] (Figure 4L); [191]; [192] (Figure 2k); [193] (Figure 7)). *Avimimus portentosus*, however, possesses an ischial antitrochanter that, therefore, appears homologous with that in birds ([112]; [194] (Figure 4c)). Funston et al. [194], 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 ([195] (Figures 3 and 10); [196] (Figure 7); [197] (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 perforated acetabula, although the condition in crucial taxa, like *Jianianhualong* and *Jinfengopteryx*, is unclear [198,199]. 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* [200] (Figure 10a), *Gobivenator* [201] (Figure 2n), and *Sinovenator* [202] (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); [203] (Figure 2); [204] (Figure 24); [205] (Figure 1c)). Interestingly, the acetabulum of *Hesperonychus* opens dorsolaterally, which would enable it to abduct the hindlimbs in a splayed fashion as in other gliders like *Microraptor*, which no doubt abducted feathered hindlimbs to provide airfoils [205]. Yet, *Microraptor* is often depicted flying with the legs drooping beneath the animal [206], 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 the *Microraptor* [203] (Figure 8). There is significant medial occlusion of the acetabulum in unenlagiids, no supracetabular crest (or it is at best weakly developed), and no antitrochanter [207] (Figure 2c); [208]. In *Bambiraptor*, the acetabulum shows partial medial occlusion, the supracetabular crest is 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 [209]. In *Deinonychus* [210] (Figure 64) and *Velociraptor* [211] (Figures 11 and 12); [212] (Figures 17a and 18), the supracetabular crest remains weak, a clearly demarcated antitrochanter is absent, and in *Velociraptor* the acetabulum continues to exhibit medial occlusion.

5. Discussion

Partial closure of the acetabula and absence of an antitrochanter in early birds is surprising, for it is inconsistent with the persistent assertion that these taxa had developed obligate bipedalism like their presumed theropod ancestors. That some pennaraptorans (notably the microraptorines and troodontids) also exhibit partial closure of the acetabulum and lack 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 [213–217] and rauisuchids like *Postosuchus* [218] 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 [219,220]. Compsognathids are “prototypical” small theropods [221], yet they lack a supracetabular crest or antitrochanter [221–223] and still appear to have been obligately bipedal cursors (for an alternative view, see [51,224,225]). 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 [226,227]. In many cases, there is not a simple correspondence between gross anatomy and behavior (yet we also know that early birds were experimenting with a range of trophic specializations, as indicated by evidence for granivory, folivory, and frugivory in omnivoropterygids and jeholornithids [8,29,51,228,229]). The cumulative anatomical picture for a given range of taxa and its integration with supplementary data is necessary for sound behavioral and ecological inferences. It is in this context that the evidence presented here on the pelvic osteology of early birds and pennaraptorans reinforces the conclusion that, particularly when the abductive ability permitted to the hindlimb is considered, the first birds—and at least taxa like the microraptorines—were not terrestrial cursorial bipeds, like theropods, but trunk-climbing gliders [29,31,230]. This would be consistent with arguments that (at least some of) these taxa are “neoflightless” theropods, whose immediate ancestors underwent transformations in the theropod locomotory system (perhaps because of a shift to arboreality) [10,51,53–59]. Yet these data are also consistent with the argument that they are misidentified birds and, like them, are instead descended from more basal, arboreal archosaurs that had yet to acquire the theropod system of obligately bipedal locomotion [27,29–31,63–67]. Homoplasy-driven character conflict confounds morphological

interpretations and necessarily precludes facile assessment of alternative hypotheses or overreliance on the results of phylogenetic analyses.

Nevertheless, the data reviewed here are a further indication, supplementing the discovery of a “tetrapteryx” stage in early avian evolution, that obligate bipedality in birds is a secondary, phylogenetically later acquisition, only fully refined in the Cretaceous. This is fundamentally incompatible with the argument—advanced since Huxley, championed by Ostrom, repeated ad infinitum—that the obvious reason birds are obligate bipeds and that they never passed through an evolutionary phase in which all four limbs were integrated into the flight mechanism, is that birds are descended from obligate bipeds, viz. theropods. This neat, tidy, almost irresistible line of argumentation (buttressed, so it has seemed to many, by phylogenetic analyses) has motivated and continues to motivate fruitless efforts to provide a biologically (or even biophysically) coherent, epistemologically sound explanation for the origin of avian flight in a terrestrial, gravity-resisted context (of which WAIR—wing-assisted incline running [231,232]—is but the latest forlorn example [29–31,233]). None of this is now consistent with available fossil evidence, or, as this paper has labored to show, even by a closer consideration of the morphology of neornithine birds. These data instead suggest that the reason bipedalism in birds differs fundamentally from bipedalism in all other archosaurs (belated recognition that modern birds are not quite the well-behaved “ordinary” parasagittal or planar bipeds that they have long been considered continues to grow [104,234]) is that 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 pennaraptorans (oviraptorosaurs, troodontids, and dromaeosaurs)—whose (apparently) basal exemplars exhibit a remarkable number of derived avian characters—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 [29,31,51,235]; if *Jinfengopteryx* is, in fact, a basal troodontid [140,236] (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” [29,31,50,237].

6. Conclusions

The hypothesis that birds are maniraptoran theropod dinosaurs, despite the certitude with which it is proclaimed, continues to suffer from unaddressed difficulties [29–31,50,237]. This paper has reviewed the evidence for yet another such difficulty and presented evidence consistent with alternatives to that hypothesis. It is believed that careful study of neglected areas of avian anatomy, or reexamination of areas long thought to be understood, will yield further such difficulties, and it is hoped that this paper will be an encouragement toward such efforts. Until problems like those discussed here—and many others that continue to be dismissed either by appeal to “consensus” or through overconfidence in the results of phylogenetic analysis of morphological data—have satisfactorily been resolved, skepticism toward the current consensus and continued investigation of alternative hypotheses are needful for the promotion of critical discourse in vertebrate phylogenetics and evolutionary biology.

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