

Scapular orientation in theropods and basal birds, and the origin of flapping flight

PHIL SENTER



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Basal birds such as *Archaeopteryx* and *Confuciusornis* are typically portrayed as flapping fliers. However, here I show that shoulder joint orientation in these animals prevented elevation of the humerus above the dorsum, thereby preventing use of the recovery stroke, an important part of flapping flight. In members of the clade Ornithothoraces, which includes extant birds and the extinct avian clade Enantiornithes, the shoulder joint is reoriented to permit elevation of the humerus above the dorsum, permitting flapping flight. Although basal birds may have glided, flapping flight began significantly later in avian evolution than has been thought.

Key words: Theropoda, Aves, *Archaeopteryx*, flight, flapping flight.

Phil Senter [phil.senter@lsc.edu], Department of Math and Science, Lamar State College at Orange, 410 Front Street, Orange, Texas 76630, United States.

Introduction

Researchers have long debated whether basal birds such as *Archaeopteryx* were powered flyers. Arguments from feather morphology (Feduccia and Tordoff 1979), osteology (Olson and Feduccia 1979; Feduccia 1993), muscle orientation (Ruben 1991; Rayner 2001), muscle power output (Ruben 1991), and kinematics (Ruben 1991; Brugers and Chiappe 1999) have been used to support the hypothesis that such animals were capable of flapping flight. On the other hand, arguments from feather morphology (Speakman and Thomson 1993), osteology (Ostrom 1976; Vasquez 1992; Ostrom et al. 1999), muscle orientation (Ostrom 1976; Ostrom et al. 1999; Speakman 1993), and muscle power output (Speakman 1993) have also been used to support the opposite hypothesis: that these animals were incapable of flapping flight. All these arguments are moot if the glenoids (shoulder sockets) of basal birds were oriented in such a manner that the humerus could not be raised above the dorsum for the recovery stroke, an important part of flapping flight (Jenkins 1993; Poore et al. 1997). Here, I present evidence that indicates that the glenoids of basal birds were oriented in just such a manner.

In non-avian dinosaurs, the scapula is positioned laterally to the ribcage, widely separated from the vertebral column, with the flat costal surface facing medially; this orients the glenoid so that it faces ventrally (Fig. 1). In extant birds (Jenkins 1993) and in fossil ornithothoracine birds (Elzansowski 1981; Norell and Clarke 2001; Sanz et al. 2004) the scapula has rotated about its long axis 90° from its orientation in non-avian dinosaurs; the scapula lies dorsal to the ribcage with the glenoid (shoulder socket) facing laterally (Figs. 2D, 3D). This change in orientation allows the avian humerus to be elevated above the dorsum during the recovery

stroke (Jenkins 1993; Poore et al. 1997) (Fig. 2D). In contrast, scapular orientation in non-avian dinosaurs prevents elevation of the humerus higher than about half-mast (Gishlick 2001; Carpenter 2002; Senter and Robins 2005) (Fig. 2B, C), which precludes use of the full recovery stroke, hence precludes flapping flight. During fast flight, many birds use a low-amplitude wingbeat that involves a recovery stroke of lesser magnitude than that used in slow flight (Rayner 2001). However, even during fast flight with a low-amplitude wingbeat, the recovery stroke still involves significant elevation of the humerus above the dorsum (Rayner 2001). Therefore, the inability of non-avian dinosaurs to raise the humerus higher than half-mast prevented them from employing powered flight.

The orientation of the scapula in birds basal to the clade Ornithothoraces (e.g., *Archaeopteryx* and *Confuciusornithidae*) has been debated. These animals are often portrayed with scapulae that lie dorsal to the vertebral column so that the glenoids face laterally, as in extant birds (Ostrom 1976; Martin 1983; Paul 1988; Jenkins 1993; Hou et al. 1996). However, some authors have opined that in basal birds the scapula occupies the typical theropod position with the glenoid oriented ventrally (Bakker and Galton 1974; Tarsitano and Hecht 1980). Here, these contrary opinions are treated as conflicting hypotheses, and conditions in articulated specimens of non-avian dinosaurs and ornithothoracine birds are used to generate predictions for the two hypotheses.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York City, New York, USA. BMNH, The Natural History Museum, London, United Kingdom. IGM, Mongolian Institute of Geology, Ulaan Baatar, Mongolia. IVPP, Institute of Vertebrate Paleontology and Paleo-

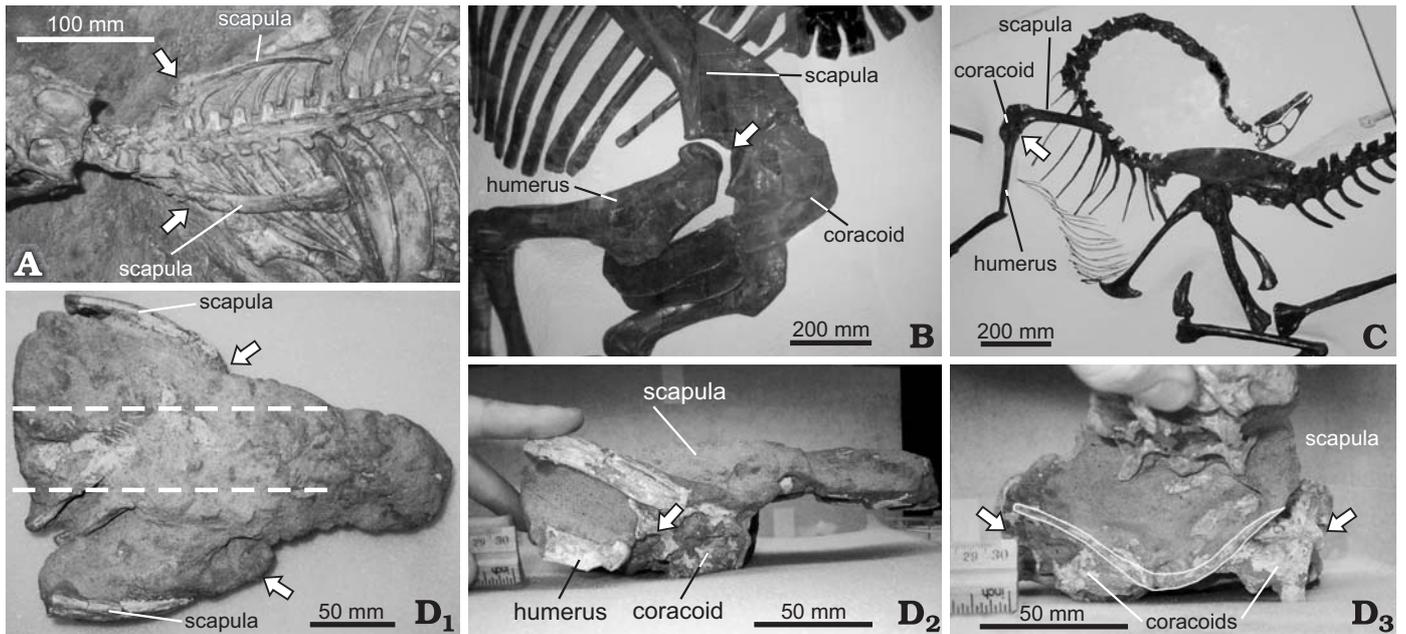


Fig. 1. Scapular position and glenoid orientation in articulated skeletons of non-avian dinosaurs, with glenoids indicated by arrows. **A.** Dorsal view of the ornithischian dinosaur *Psittacosaurus mongoliensis*, AMNH 6254, showing lateral position and wide spacing of scapulae. **B.** Lateral view of the ornithischian dinosaur *Centrosaurus apertus*, AMNH 5351, showing ventral orientation of glenoid and position of glenoid anteroventral to ribcage. **C.** Lateral view of the ornithomimid theropod dinosaur *Struthiomimus altus*, AMNH 5339, showing position of glenoid anteroventral to ribcage. **D.** The deinonychosaurian theropod dinosaur *Velociraptor mongoliensis*, IGM 100/976, in dorsal (**D₁**), right lateral (**D₂**), and anterior (**D₃**) views, with the furcula outlined in white for clarity, showing that the scapulae are widely spaced, laterally positioned, and exhibit ventrally oriented glenoids, as in other dinosaurs. Broken white lines in (**D₁**) indicate lateral extremities of vertebral column.

anthropology, Beijing, China. LH, Las Hoyas collection, Universidad Autónoma de Madrid, Madrid, Spain; NGMC, National Geological Museum of China, Beijing, China. PVSJ, Museo de San Juan, San Juan, Argentina; SAM, South African Museum, Cape Town, South Africa; TMM, Texas Memorial Museum, Austin, Texas, USA.

Materials and methods

I observed several articulated dinosaur and skeletons at various museums (cited below with accession numbers), some of which are illustrated in Figs. 1 and 3. Observations from those specimens were supplemented with data from other articulated specimens illustrated in the literature (cited below).

The influence of glenoid morphology and orientation on humeral range of motion was examined by manually manipulating bones and casts of the specimens illustrated in Fig. 2A–C; the resulting data were supplemented with data from previous such studies (Gishlick 2001; Carpenter 2002; Senter and Robins 2005). As in previous studies (Gishlick 2001; Carpenter 2002; Senter and Robins 2005), joint surfaces were presumed to represent the limits of motion. Horizontal metal bars, padded with foam rubber and clamped to chemistry ring stands, were used to pose the humerus for photography, and tracings of the photographs were superimposed to illustrate range of motion (see also Carpenter 2002; Senter and Robins 2005) (Fig. 2).

Avian and non-avian theropod furculae were observed in specimens at various museums. The angle between the furcular arms was measured with a protractor, using my own photographs of personally observed specimens and published photos of other specimens (specimens and literature listed in Table 1).

Data, hypotheses, and predictions

During the decay process in extant birds, in the absence of scavenging by large animals, the pectoral girdle usually remains attached to the thorax until after the head, neck, and femur have detached (Davis and Briggs 1998). Even after scavenging by large animals, the avian head and neck usually detach from the thorax before or at the same time as the pectoral girdle (Oliver and Graham 1994). Therefore, if the decay process in extant birds resembles that of fossil birds and non-avian dinosaurs, it stands to reason that the pectoral girdle is in its natural position in an articulated fossil bird or dinosaur skeleton that retains the head and neck in articulation.

Numerous articulated dinosaur skeletons that are preserved on their sides retain heads, necks, and femurs. Such specimens show that the glenoid is anteroventral to the ribcage and that the scapular blade is lateral to the ribcage. Articulated ornithischian skeletons that show this include specimens of *Heterodontosaurus tucki* (AMNH 28471, cast of SAM K 1332), *Othnielia rex* (Galton 1983), *Thescelosaurus*

edmontonensis (Sternberg 1940), *Parasaurolophus walkeri* (Parks 1922), “*Procheneosaurus praeceps*” (AMNH 5340), *Corythosaurus casuarius* (AMNH 5240, AMNH 5338), *Anchiceratops longirostris* (Lull 1933), *Centrosaurus nasicornis* (AMNH 5351), and *Styracosaurus albertensis* (AMNH 5376) (Fig. 1). In saurischian skeletons, the vertebral column usually curls dorsally after death. Even so, the glenoid remains anteroventral to the ribcage. Articulated saurischian skeletons, preserved on their sides, that show this include specimens of *Eoraptor lunensis* (TMM 43451-2 [cast of PVSJ 512]), *Camarasaurus lentus* (Glimore 1925), *Gorgosaurus libratus* (Lambe 1917), *Compsognathus longipes* (Bidar et al. 1972; Ostrom 1978), *Huaxiagnathus orientalis* (Hwang et al. 2004), *Sinosauropteryx prima* (Currie and Chen 2001), *Scipionyx samniticus* (Dal Sasso and Signore 1998), *Ornithomimus edmonticus* (Parks 1928), *Struthiomimus altus* (AMNH 5339), *Sinornithomimus dongi* (Kobayashi et al. 1999), *Caudipteryx zoui* (Zhou et al. 2000), and *Khaan mckennai* (IGM 100/1127) (Fig. 1C). The fact that the glenoid remains anteroventral to the ribcage in these specimens, even after the vertebral column has curled dorsally, indicates that the pectoral girdle has remained attached to the vertebral column and has been dragged dorsally along with it, keeping the glenoid approximately in its natural position relative to the ribcage (Fig. 1C).

Articulated dinosaur skeletons preserved on their backs or bellies are less common, but do occur. Salient examples include specimens of the ornithischians *Edmontosaurus annectens* (AMNH 5060) and *Psittacosaurus mongoliensis* (AMNH 6254), and the saurischian *Velociraptor mongoliensis* (IGM 100/976). These show that the scapular blades are widely separated from the vertebral column and lie laterally to the ribcage, so that the glenoids are rather far apart; the flat costal surface of the scapular blade faces medially and the glenoid faces ventrally (Fig. 1A, D₁).

Deinonychosaurs, the saurischian dinosaurs most closely related to birds (Clark et al. 2002; Senter et al. 2004), are often depicted with scapulae oriented in extant avian fashion: lying along the vertebral column dorsal to the ribcage, with the glenoid dorsal to the ribcage and facing laterally (Paul 1988; Sanz et al. 2004). However, articulated specimens of the deinonychosaur *Velociraptor mongoliensis* that are preserved in three dimensions show that even in these animals the scapula and glenoid are oriented in typical dinosaurian fashion (Norell and Makovicky 1999; Achenbach 2003) (Fig. 1D). These specimens and an articulated specimen of the deinonychosaur *Microraptor zhaoianus* (Hwang et al. 2002) also confirm that the scapulae are as widely spaced in deinonychosaurs as they are in other non-avian dinosaurs. According to a recent study (Carpenter 2002), even the scapulae of the non-avian theropod *Unenlagia comahuensis*, which were previously thought to be oriented like those of ornithothoracine birds (Novas and Puerta 1997), more likely exhibited typical dinosaurian orientation.

Oviraptorid theropods have also been depicted with scapulocoracoids oriented in extant avian fashion (Paul 1988).

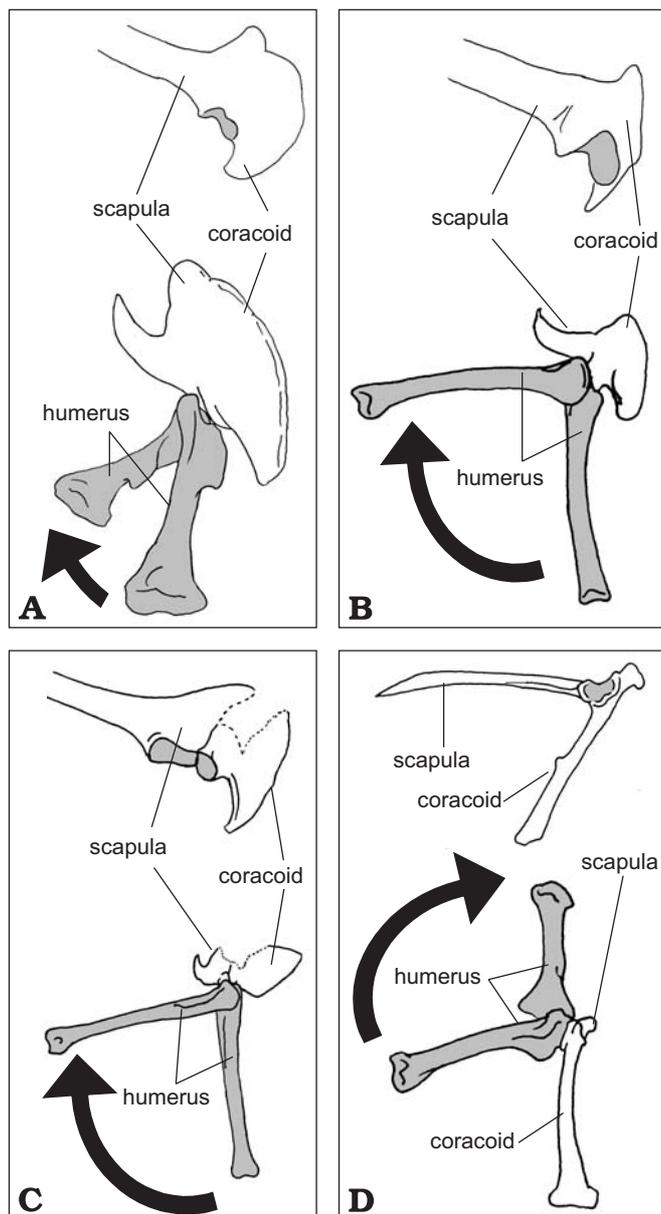


Fig. 2. Right scapulocoracoid in lateral view (above in each figure, with glenoid shaded) and scapulocoracoid + humerus in anterior view (below, with humerus shaded and shown in full elevation and depression) of non-avian theropod dinosaurs and an extant bird, in anterior view. **A.** The theropod dinosaur *Acrocanthosaurus atokensis*, modified from Senter and Robins (2005). **B.** The ornithomimosaurian theropod *Archaeornithomimus asiaticus*, AMNH 6567. **C.** The deinonychosaurian theropod *Bambiraptor feinbergi*, AMNH 30556 (left elements, reversed). **D.** European starling, *Sturnus vulgaris*, modified from Jenkins (1993) and Poore et al. (1997). Note that maximum humeral elevation is higher in theropods with an extension of the glenoid floor onto the lateral surface of the scapula (*Archaeornithomimus*, *Bambiraptor*) than in the more basal theropod (*Acrocanthosaurus*), but the humerus still cannot be elevated higher than a subhorizontal position.

However, an articulated skeleton of the oviraptorid *Ingenia yanshini*, preserved in three dimensions, shows that the scapulae lie along the lateral sides of the ribcage, widely separated, with glenoids oriented ventrally, as in other non-avian dinosaurs (Larson and Rigby 2005).

As noted by previous authors (Norell and Makovicky 1999), the bony floor of the deinonychosaurian glenoid exhibits a slight extension onto the lateral surface of the scapula, which gives the glenoid more lateral exposure than in more basal theropods. This is also true in other derived coelurosaurian theropod taxa, including ornithomimosaurs (AMNH 6567: *Archaeornithomimus asiaticus*) and *Tanycolagreus* (Carpenter et al. 2005). Previous studies have shown that such glenoid morphology allows the humerus of the derived coelurosaurs *Deinonychus* (Gishlick 2001) and *Tanycolagreus* (Carpenter's [2002] "cf. *Coelurus*") (Carpenter 2002) to be elevated to a subhorizontal position; in contrast, in the more basal theropods *Coelophysis* and *Allosaurus*, in which the glenoid floor lacks the lateral extension, humeral elevation is much more limited (Carpenter 2002). My own manual skeletal manipulations—using methods similar to those of Carpenter (2002)—confirm the finding that the slight lateral extension of the glenoid floor allows the humerus to be elevated to a subhorizontal position in derived coelurosaurs (*Archaeornithomimus*, *Bambiraptor*), and that humeral elevation is limited in more basal theropods (*Acrocanthosaurus*), which lack the glenoid floor extension (Fig. 2A–C). However, even with the slight extension onto the lateral surface of the scapula, the glenoid in derived coelurosaurs still faces predominantly ventrally, and the humerus cannot be elevated higher than the dorsum (Gishlick 2001; Carpenter 2002) (Fig. 2).

In contrast to the condition in non-avian dinosaurs, the scapulae of ornithothoracine birds lie close to the vertebral column, dorsal to the ribcage, with the flat costal surface of the scapular blade facing ventrally; in this position, the glenoid faces laterally (Figs. 2D, 3D), allowing the humerus to be elevated high above the dorsum (Jenkins 1993; Poore et al. 1997) (Fig. 2D). Numerous articulated fossils preserved on their backs and bellies confirm that the scapulae are closely spaced, lying close to the vertebral column, in fossil ornithothoracines that retain heads and necks. Examples include specimens of the Mesozoic birds *Gobipteryx minuta* (Elzanowski 1981), *Protopteryx fengningensis* (Zhang and Zhou 2000), *Eoalulavis hoyasi* (LH 13500a), *Vescornis hebeiensis* (Zhang et al. 2004), and *Apsaravis ukaana* (Norell and Clarke 2001), the Cenozoic bird *Prefica* sp. (Feduccia 1999), and roller-like Cenozoic birds from Messel (Peters 1992) (Fig. 3D).

Articulated avian fossils preserved on their sides and retaining the head and neck are less common, but a few exist and confirm that the scapulae remain dorsal to the ribcage in fossil ornithothoracines, even if the vertebral column has bent dorsally after death. Examples include specimens of the Cenozoic birds *Palaeotis weigelti*, *Messelornis cristata* (Peters 1992), *Gallinuloides wyomingensis*, and *Rhynchoaeites messelensis* (Feduccia 1999).

The differences in scapular orientation between non-avian theropods and ornithothoracine birds are related to the morphology of the furcula. In both groups, the tips of the furcula articulate with a region of the scapulocoracoid that is in the vicinity of the glenoid; this region is the acromion pro-

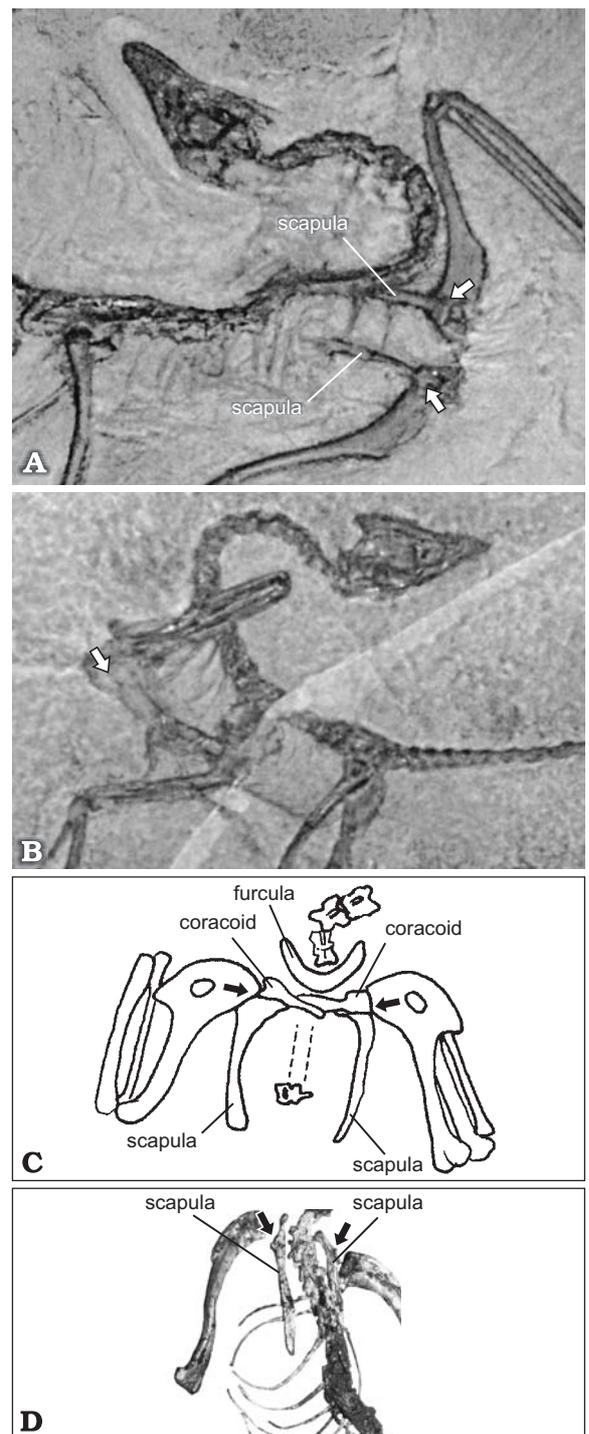


Fig. 3. Articulated skeletons of Mesozoic birds, showing scapular position and glenoid orientation, with glenoids indicated by arrows. **A.** AMNH cast of "Berlin specimen" of *Archaeopteryx lithographica*, showing that the glenoids are anteroventral to the ribcage. The unnatural position of the left humerus above the glenoid is an artifact of dislocation of the left shoulder. **B.** AMNH cast of the "Eichstätt specimen" of *Archaeopteryx lithographica*, showing that the glenoid is anteroventral to the ribcage. **C.** *Confuciusornis sanctus* in dorsal view, showing wide spacing and lateral position of scapulae, with lateral extremities of vertebral column (extrapolated from dimensions of disarticulated dorsal vertebrae) represented by a pair of broken lines. Modified from Chiappe et al. (1999). **D.** The enantiornithine bird *Eoalulavis hoyasi*, LH 13500a, in dorsal view, showing close spacing and dorsal position of scapulae.

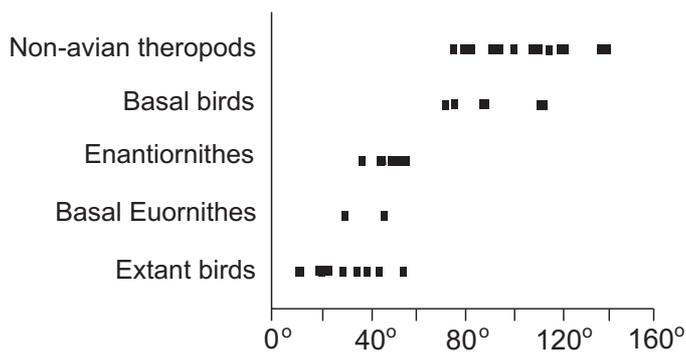


Fig. 4. Angles between furcular arms in non-avian theropods and birds. Data sources listed in Table 1.

cess of the scapula in non-avian theropods (Chure and Madsen 1996; Norell and Makovicky 1999) and is the acroracoid process of the coracoid in ornithothoracine birds (Ostrom 1976). In ornithothoracine birds, the angle between furcular arms is small (Fig. 4), which makes the furcula narrow, allowing the scapulae to approach the midline. In non-avian theropods, the angle between the furcular arms is large (Figs. 1D₃, 4), which makes the furcula wide, preventing the glenoids from approaching the midline and relegating the scapulae to a lateral position along the ribcage (Hwang et al. 2002; Larson and Rigby 2005; *Velociraptor mongoliensis*: IGM 100/976) (Fig. 1D₃).

These data allow the delineation of two hypotheses and their respective predictions, regarding scapular orientation in basal birds:

Hypothesis 1.—The scapulae of basal birds were oriented in typical dinosaurian fashion.

Prediction 1: In articulated specimens of basal birds preserved on their sides, the glenoids lie anteroventral to the ribcage.

Prediction 2: In articulated specimens of basal birds preserved on their backs or bellies, the scapulae are widely spaced, and lie far from the vertebral column.

Prediction 3: The angle between the furcular arms of basal birds is large.

Hypothesis 2.—The scapulae of basal birds were oriented in typical ornithothoracine bird fashion.

Prediction 1: In articulated specimens of basal birds preserved on their sides, the glenoids lie dorsal to the ribcage.

Prediction 2: In articulated specimens of basal birds preserved on their backs or bellies, the scapulae are closely spaced, and lie close to the vertebral column.

Prediction 3: The angle between the furcular arms of basal birds is small.

Testing of the hypotheses

There are six known specimens of the basal bird *Archaeopteryx lithographica* (Senter and Robins 2003). Of these, the “Berlin specimen” (Dames 1884) and the “Eichstätt speci-

Table 1. Raw data used for Fig. 4. For photographs taken by the author, the specimen’s accession number is given. For photographs from the literature and websites, the citation is given.

Taxon	Angle between furcular arms	Source of photo
Non-avian theropods:		
<i>Albertosaurus sarcophagus</i>	100°	Makovicky and Currie 1998
<i>Allosaurus fragilis</i>	120°, 120°, 120°, 121°, 135°, 140°	Chure and Madsen 1996
<i>Bambiraptor feinbergi</i>	75°	AMNH 30556
<i>Citipati osmolskae</i>	92°	Clark et al. 1999
<i>Daspletosaurus torosus</i>	106°, 110°	Makovicky and Currie 1998
Deinonychosauria indet.	119°	NGMC 91
<i>Heyuannia huangi</i>	80°	Lü 2002
<i>Khaan mckennai</i>	80°, 81°	IGM 100/1002, IGM 100/1127
<i>Microraptor zhaoianus</i>	80°, 83°, 91°	Czerkas et al. 2002; Hwang et al. 2002
<i>Oviraptor philoceratops</i>	95°	AMNH 6517
<i>Protarchaeopteryx robusta</i>	119°	NGMC 2125
<i>Scipionyx samniticus</i>	115°	Dal Sasso and Signore 1998
<i>Velociraptor mongoliensis</i>	114°	IGM 100/976
Basal birds:		
<i>Archaeopteryx lithographica</i>	90°	BMNH R 37001
<i>Changchengornis hengdaoziensis</i>	88°	Ji et al. 1999
<i>Confuciusornis sanctus</i>	72°, 75°, 88°	Peters 1996; Chiappe et al. 1999
<i>Sapeornis chaoyangensis</i>	111°, 112°	Zhou and Zhang 2003
Enantiornithes:		
<i>Concornis lacustris</i>	48°	LH 2814
<i>Eoalulavis hoyasi</i>	36°	LH 13500
<i>Iberomesornis romerali</i>	56°	LH 022R
<i>Longipteryx chaoyangensis</i>	49°	Zhang et al. 2001
<i>Noguerornis gonzalezi</i>	56°	Lacasa-Ruiz 1989
<i>Protopteryx fengningensis</i>	55°	Zhang and Zhou 2000
<i>Sinornis santensis</i>	43°, 52°	Sereno and Rao 1992; Zhou 1995
Basal Euornithes:		
<i>Archaeovolans repatriatus</i>	29°	Czerkas and Xu 2002
<i>Yanornis martini</i>	45°	IVPP 12558
Extant birds:		
<i>Alca torda</i>	22°	Bodies to Bones 2002
<i>Alle alle</i>	21°	Bodies to Bones 2002
<i>Ara chloroptera</i>	40°	Wageningen University and Research Centre Experimental Zoology Group 2004
<i>Corvus corone</i>	20°	Tibor 2004
<i>Lagopus lagopus</i>	22°	Bodies to Bones 2002
<i>Larus marinus</i>	38°	Bodies to Bones 2002
<i>Mitu mitu</i>	20°	AMNH 519
<i>Passer domesticus</i>	13°	Tibor 2004
<i>Phalacrocorax carbo</i>	33°	Wageningen University and Research Centre Experimental Zoology Group 2004
<i>Pica pica</i>	19°	Tibor 2004
<i>Streptopelia decaocto</i>	10°	Tibor 2004
<i>Sturnus vulgaris</i>	20°	Tibor 2004
<i>Sula bassana</i>	55°	Wageningen University and Research Centre Experimental Zoology Group 2004
<i>Tetrao tetrix</i>	43°	Bodies to Bones 2002
<i>Tetrao urogallus</i>	28°	Bodies to Bones 2002

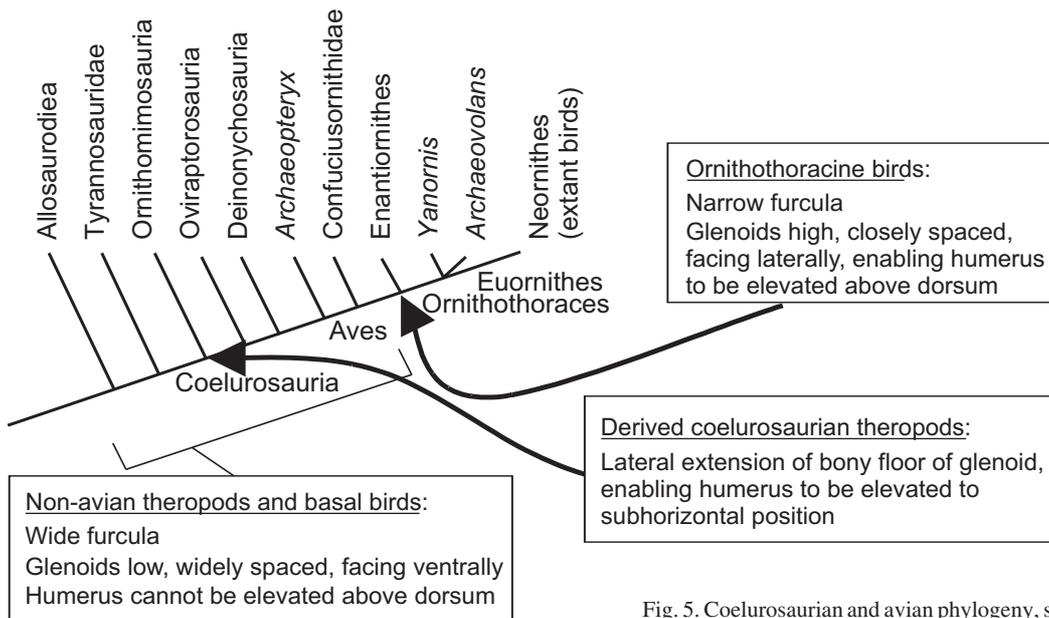


Fig. 5. Coelurosaurian and avian phylogeny, showing evolution of shoulder features.

men” (Wellnhofer 1974) are the only two that retain a sufficiently articulated head and neck to evaluate scapular position. Both are preserved on their sides and exhibit glenoids that lie anteroventral to the ribcage (Dames 1884; Wellnhofer 1974) (Fig. 3A, B). This satisfies Prediction 1 of Hypothesis 1. The holotype of the basal bird *Wellnhoferia grandis* is also articulated, retains the head and neck, and is preserved on its side. Its glenoids are also anteroventral to the ribcage (Elżanowski 2001), satisfying Prediction 1 of Hypothesis 1. The basal bird *Confuciusornis sanctus* is known from several articulated specimens preserved on their backs or bellies; in these, the scapulae are widely spaced, some distance from the vertebral column (Chiappe et al. 1999) (Fig. 3C), which satisfies Prediction 2 of Hypothesis 1. The angle between the furcular arms in basal birds is large, broadly overlaps the range for non-avian theropods (Fig. 4), and does not overlap the range for ornithothoracine birds (Fig. 4), which satisfies Prediction 3 of Hypothesis 1.

Conclusion

All of the predictions of Hypothesis 1 are satisfied, whereas none of the predictions of Hypothesis 2 are satisfied. Hypothesis 1 is therefore supported by the evidence, and Hypothesis 2 is not. The scapulae of basal birds were therefore oriented in typical dinosaurian fashion, and not in typical ornithothoracine fashion.

Discussion

Four arguments have previously been advanced in favor of Hypothesis 2. However, all four arguments are based on in-

correct assumptions and have yielded an incorrect conclusion. One such argument involved reconstructions of muscle orientations and depended on an interpretation of a bony prominence on the coracoid of *Archaeopteryx* and non-avian theropods (commonly called the “biceps tubercle”) as an origin for the biceps brachii (Ostrom 1976). However, it is now known that the bony prominence in question is a site of convergence between the origins of three muscles, none of which is the biceps brachii (Carpenter 2002).

According to the second argument, the 90° bend in the coracoid of *Archaeopteryx* provides evidence that the scapula was dorsal to the ribcage, with the glenoid facing laterally (Martin 1983). However, a 90° bend also occurs in the coracoids of deinonychosaurian theropods (Xu et al. 1999; Hwang et al. 2002), in which the scapula lies lateral to the ribcage with the glenoid facing ventrally (Hwang et al. 2002; Achenbach 2003) (Fig. 1D).

According to the third argument, the vertebral column of the “Berlin specimen” of *Archaeopteryx* has moved dorsally without dragging the scapulae with it, leaving the scapulae in their original position relative to the slab (Jenkins 1993). In this position, they appear to have originally been dorsal to the ribcage (Fig. 3A). However, as shown above, scapulae are dragged dorsally as the vertebral column moves dorsally in both ornithothoracine birds and non-avian theropods; in the latter the appearance that the dorsally dragged scapulae were originally dorsal to the vertebral column (Fig. 1C) is an artifact of the dragging. It stands to reason that the same was true for the “Berlin specimen” of *Archaeopteryx*. Heads and necks detach before or along with the pectoral girdle during the decay process in extant birds (Oliver and Graham 1994; Davis and Briggs 1998). Therefore, the fact that the heads and necks of the “Berlin” and “Eichstätt” specimens of *Archaeopteryx* have not detached suggests that the pectoral girdle has not detached either.

According to the fourth argument, overlap between the scapular blades and the proximal ends of the ribs in the holotype of *Wellnhoferia grandis* demonstrates that its scapulae were dorsal to the ribcage (Jenkins 1993). However, only the tips of the scapulae overlap the proximal ends of the ribs in that specimen. The same is true for most articulated non-avian theropod skeletons (Osborn 1916; Ostrom 1978; Dal Sasso and Signore 1998; Zhou et al. 2000; Currie and Chen 2001) (Fig. 1C), including deinonychosaurs that are preserved in three dimensions with the scapulae lateral to the ribcage (Achenbach 2003). Furthermore, the glenoids lie anteroventral to the ribcage in the *Wellnhoferia* holotype (Elżanowski 2001), as in non-avian theropods and unlike fossil ornithothoracine birds that are preserved on their sides (Feduccia 1999). Hypothesis 2 is therefore not supported by available evidence.

In addition to the four arguments listed above, there are three articulated fossil skeletons in which scapular orientation appears to contradict the conclusion reached here. However, in all three cases, the scapula is not in its original position. One such case is the holotype of the troodontid coelurosaur *Mei long* (Xu and Norell 2004). In this specimen, the scapulae lie atop the ribcage, which appears to confirm Prediction 1 of Hypothesis 2 for coelurosaurs, thereby supporting the idea that in derived non-avian coelurosaurs the scapula exhibited typical ornithothoracine orientation. However, the specimen is dorsoventrally flattened, and its ribs all lie in the same plane. The scapulae actually lie on the lateral surfaces of the ribs, which have rotated dorsally due to the flattening of the specimen. Moreover, the glenoids remain widely spaced, as in other non-avian dinosaurs and in contrast to ornithothoracine birds. The tips of the scapulae approach the proximal ends of the ribs, just as they presumably did as they lay to the sides of the ribcage before the flattening, as in non-avian dinosaur skeletons preserved on their sides (Osborn 1916; Ostrom 1978; Dal Sasso and Signore 1998; Zhou et al. 2000; Currie and Chen 2001). Therefore, the scapulocoracoids of *Mei long* were oriented as in other non-avian dinosaurs, and the appearance to the contrary is an artifact of dorsoventral flattening.

The second skeleton that appears to contradict the conclusion reached here is the “Munich specimen” of *Archaeopteryx*. The specimen is mostly articulated, preserved on its side, and one glenoid is higher than the ribcage (Wellnhofer 1993). However, the other glenoid is far ventral to the dorsal margin of the ribcage (Wellnhofer 1993). Also, the fact that the distal end of each scapula is lower on the ribcage than the glenoid is (Wellnhofer 1993), demonstrates that both scapulae have rotated and moved far from their natural positions. Furthermore, cranial disarticulation in the specimen suggests that decay is at too late a stage to infer that the pectoral girdle is in its original position.

The third skeleton that appears to contradict the conclusion reached here is that of the holotype of *Iberomesornis romerali* (Sanz and Bonaparte 1992). This ornithothoracine bird appears to have a scapula that exhibits the typical non-avian dinosaur orientation, as the glenoid is anteroventral to the rib-

cage (Sanz and Bonaparte 1992). However, the head and neck have detached, and the scapula is displaced, having been dragged along with the proximal end of the humerus, which has broken off and rotated ventrally. The scapula was originally in the typical ornithothoracine position.

Birds basal to the clade Ornithothoraces exhibit typical coelurosaurian morphology of the glenoid and humeral head (Ostrom 1976; Jenkins 1993). We can therefore safely presume that they exhibited typical coelurosaurian range of motion at the shoulder. As a result of having ventrally facing glenoids, such birds were incapable of humeral elevation higher than the level of the glenoid, and therefore incapable of flapping flight (Fig. 5). Previous hypotheses that basal birds engaged in flapping flight (Feduccia and Tordoff 1979; Olson and Feduccia 1979; Ruben 1991; Feduccia 1993; Bruggers and Chiappe 1999; Rayner 2001) were based on reasonable biological arguments, but were made with the assumption that the glenoids of basal birds faced laterally. Given that the glenoids faced ventrally in these animals, the hypothesis that they engaged in flapping flight is no longer tenable. This glenoid orientation in basal birds and their theropod precursors also precludes the use of wing-assisted incline running (WAIR), which requires wing flapping with significant elevation of the humerus above the dorsum (Dial 2003). Flapping flight and WAIR both originated at or crownward of the base of the clade Ornithothoraces, in which the shoulder joint is oriented as in extant birds.

However, a ventrally facing glenoid in basal birds does not preclude the use of laterally spread wings in gliding. The hypothesis that basal birds and their theropod precursors engaged in at least some aerial locomotion, e.g., gliding or parachuting (Xu et al. 2003; Chatterjee et al. 2004), is therefore plausible.

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References

- Achenbach, J. 2003. A new generation of scientists brings dinosaurs back to life. *National Geographic* 203 (3): 2–33.

- Bakker, R.T. and Galton, P.M. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature* 248: 168–172.
- Bodies to Bones. 2002. <http://btbones.co.uk/PreparedBirds.html>
- Brugers, P. and Chiappe, L.M. 1999. The wing of *Archaeopteryx* as a primary thrust generator. *Nature* 154: 587–588.
- Carpenter, K. 2002. Forelimb biomechanics of nonavian theropod dinosaurs in predation. *Senckenbergiana Lethaea* 82: 59–76.
- Carpenter, K., Miles, C., and Cloward, K. 2005. New small theropod from the Upper Jurassic Morrison Formation of Wyoming. In K. Carpenter (ed.), *The Carnivorous Dinosaurs*, 23–48. Indiana University Press, Bloomington.
- Chatterjee, S.C. and Templin, R.J. 2004. Feathered coelurosaurs from China: new light on the arboreal origin of avian flight. In: P.J. Currie, E. Koppelhaus, M.A. Shugar, M.A., and J.L. Wright (eds.), *Feathered Dragons. Studies on the Transition from Dinosaurs to Birds*, 251–281. Indiana University Press, Bloomington.
- Chiappe, L.M., Ji, S., Ji, Q., and Norell, M.A. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of northeastern China. *Bulletin of the American Museum of Natural History* 242: 1–89.
- Chure, D.J. and Madsen, J.H. 1996. On the presence of furculae in some non-maniraptoran theropods. *Journal of Vertebrate Paleontology* 16: 573–577.
- Clark, J.A., Norell, M.A., and Chiappe, L.M. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *American Museum Novitates* 3265: 1–36.
- Clark, J.A., Norell, M.A., and Makovicky, P.J. 2002. Cladistic approaches to the relationships of birds to other theropod dinosaurs. In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds, Above the Heads of the Dinosaurs*, 31–61. University of California Press, Berkeley.
- Currie, P.J. and Chen, P. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences* 38: 1705–1727.
- Czerkas, S.A., Zhang, D., Li, J., and Li, Y. 2002. Flying dromaeosaurs. In: S. J. Czerkas (ed.), *Feathered Dinosaurs and the Origin of Flight*, 97–126. The Dinosaur Museum, Blanding, Utah.
- Czerkas, S.A. and Xu, X. 2002. A new toothed bird from China. In: S. J. Czerkas (ed.), *Feathered Dinosaurs and the Origin of Flight*, 43–61. The Dinosaur Museum, Blanding, Utah.
- Dal Sasso, C. and Signore, M. 1998. Exceptional soft-tissue preservation in a theropod dinosaur from Italy. *Nature* 392: 383–387.
- Dames, W. 1884. Über *Archaeopteryx*. *Paläontologische Abhandlungen* 2: 119–196.
- Davis, P.G. and Briggs, D.E.G. 1998. The impact of decay and disarticulation on the preservation of fossil birds. *Palaio* 13: 3–13.
- Dial, K.D. 2003. Wing-assisted incline running and the evolution of flight. *Science* 299: 402–404.
- Elzanowski, A. 1981. Embryonic bird skeletons from the Late Cretaceous of Mongolia. *Palaentologia Polonica* 42: 147–176.
- Elzanowski, A. 2001. A new genus and species for the largest specimen of *Archaeopteryx*. *Acta Palaentologica Polonica* 46: 519–532.
- Feduccia, A. 1993. Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. *Science* 259: 790–793.
- Feduccia, A. 1999. *The Origin and Evolution of Birds, Second Edition*. 466 pp. Yale University Press, New Haven.
- Feduccia, A. and Tordoff, H.B. 1979. Feathers of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function. *Science* 203: 1021–1022.
- Galton, P.M. 1983. The cranial anatomy of *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North American and east Africa, with a review of hypsilophodontids from the Upper Jurassic of North America. *Geologica et Palaentologica* 17: 207–243.
- Gilmore, C.W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument. *Memoirs of the Carnegie Museum* 12: 347–384.
- Gishlick, A.D. 2001. The function of the manus and forelimb of *Deinonychus antirrhopus*, and its importance for the origin of avian flight. In: J. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds*, 301–318. New Haven, Yale Peabody Museum.
- Hou, L., Martin, L.D., Zhou, Z., and Feduccia, A. 1996. Early adaptive radiation of birds: evidence from fossils from northeastern China. *Science* 274: 1164–1167.
- Hwang, S.H., Norell, M.A., Ji, Q., and Gao, K. 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *American Museum Novitates* 3381: 1–44.
- Hwang, S.H., Norell, M.A., Ji, Q., and Gao, K. 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Palaentology* 2: 13–30.
- Jenkins, F.A. Jr. 1993. The evolution of the avian shoulder joint. *American Journal of Science* 293A: 253–267.
- Ji, Q., Chiappe, L.M., and Ji, S. 1999. A new late Mesozoic confuciusornithid bird from China. *Journal of Vertebrate Paleontology* 19: 1–7.
- Kobayashi, Y., Lu, J., Dong, Z., Barsbold, R., Azuma, Y., and Tomida, Y. 1999. Herbivorous diet in an ornithomimid dinosaur. *Nature* 402: 480–481.
- Lacasa-Ruiz, A. 1989. An Early Cretaceous bird from Montsec Mountain (Leida, Spain). *Terra Nova* 1 (1): 45–46.
- Larson, P. and Rigby, J.K., Jr. 2005. Furcula of *Tyrannosaurus rex*. In K. Carpenter (ed.), *The Carnivorous Dinosaurs*, 247–255. Indiana University Press, Bloomington.
- Lü, J. 2003. A new oviraptorosaurid (Theropoda: Oviraptorosauria) from the Late Cretaceous of southern China. *Journal of Vertebrate Paleontology* 22: 871–875.
- Lull, R.S. 1933. A revision of the Ceratopsia or horned dinosaurs. *Memoirs of the Peabody Museum of Natural History* 3: 1–175.
- Makovicky, P.J. and Currie, P.J. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. *Journal of Vertebrate Paleontology* 18: 143–149.
- Martin, L.M. 1983. The origin of birds and of avian flight. *Current Ornithology* 1: 105–129.
- Norell, M.A. and Clarke, J.A. 2001. Fossil that fills a critical gap in avian evolution. *Nature* 409: 181–184.
- Norell, M.A. and Makovicky, P.J. 1999. Important features of the dromaeosaurid skeleton II: data from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates* 3282: 1–45.
- Novas, F. and Puerta, P.F. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* 387: 390–392.
- Oliver, J.S. and Graham, R.W. 1994. A catastrophic kill of ice-trapped coots: time-averaged versus scavenger-specific disarticulation patterns. *Paleobiology* 20: 229–244.
- Olson, S.L. and Feduccia, A. 1979. Flight capability and the pectoral girdle of *Archaeopteryx*. *Nature* 278: 247–248.
- Osborn, H.F. 1916. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *Bulletin of the American Museum of Natural History* 35: 733–464.
- Ostrom, J.H. 1976. Some hypothetical anatomical stages in the evolution of avian flight. *Smithsonian Contributions to Paleobiology* 27: 1–21.
- Ostrom, J.H. 1978. The osteology of *Compsognathus longipes*. *Zitteliana* 4: 73–118.
- Ostrom, J.H., Poore, S.O., and Goslow, G.E. Jr. 1999. Humeral rotation and wrist supination: important functional complex for the evolution of powered flight in birds? *Smithsonian Contributions to Paleobiology* 89: 301–309.
- Parks, W.A. 1922. *Parasaurolophus walkeri*, a new genus and species of crested trachodont dinosaur. *University of Toronto Studies, Geological Series* 13: 1–32.
- Parks, W.A. 1928. *Struthiomimus samueli*, a new species of Ornithomimidae from the Belly River Formation of Alberta. *University of Toronto Studies (Geological Series)* 26: 1–24.
- Paul, G.S. 1988. *Predatory Dinosaurs of the World*. 464 pp. Simon & Schuster, New York.
- Peters, S. 1992. Messel birds: a land-based assemblage. In: S. Schaal and W. Ziegler (eds.), *Messel. An Insight in the History of Life and of the Earth*, 137–151. Clarendon Press, Oxford.

- Peters, D.S. 1996. Das Exponat des Monats: ein nahezu vollständiges Skelett eines urtümlichen Vogels aus China. *Natur und Museum* 126: 298–302.
- Poore, S.O., Sánchez-Halman, A. and Goslow, G.E. Jr. 1997. Wing upstroke and the evolution of flapping flight. *Nature* 387: 799–802.
- Rayner, J.M.V. 2001. On the origin and evolution of flapping flight aerodynamics in birds. In: J. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds*, 363–381. Yale Peabody Museum, New Haven.
- Ruben, J. 1991. Reptilian physiology and the flight capacity of *Archaeopteryx*. *Evolution* 45: 1–17.
- Sanz, J. and Bonaparte, J.F. 1992. A new order of bird (Class Aves) from the Early Cretaceous of Spain. In: K. E. Campbell (ed.), *Papers in Avian Paleontology Honoring Pierce Brodkorb*, 39–49. Natural History Museum of Los Angeles County, Los Angeles.
- Sanz, J., Pérez-Moreno, B.P., Chiappe, L.M., and Buscalioni, A.D. 2004. The birds from the Lower Cretaceous of Las Hoyas (province of Cuenca, Spain). In: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of the Dinosaurs*, 209–229. University of California Press, Berkeley.
- Sender, P., Barsbold, R., Britt, B.B., and Burnham, D.A. 2004. Systematics and evolution of Dromaeosauridae. *Bulletin of Gunma Museum of Natural History* 8: 1–20.
- Sender, P. and Robins, J.H. 2003. Taxonomic status of the specimens of *Archaeopteryx*. *Journal of Vertebrate Paleontology* 23: 961–965.
- Sender, P. and Robins, J.H. 2005. Range of motion in the forelimb of the theropod dinosaur *Acrocanthosaurus atokensis*, and implications for predatory behaviour. *Journal of Zoology* 266: 1–12.
- Sereno, P.C. and Rao, C. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science* 255: 845–848.
- Speakman, J.R. 1993. Flight capabilities in *Archaeopteryx*. *Evolution* 47: 336–340.
- Speakman, J.R. and Thomson, S.C. 1993. Flight capabilities of *Archaeopteryx*. *Nature* 370: 514.
- Sternberg, C. H. 1933 A new *Ornithomimus* with complete abdominal cuirass. *Canadian Field-Naturalist* 47: 79–83.
- Tarsitano, S. and Hecht, M.K. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zoological Journal of the Linnean Society of London* 64: 149–182.
- Tibor, B. 2004. <http://birdskeleton.fw.hu/>
- Vasquez, R.J. 1992. Functional osteology of the avian wrist and the evolution of flapping flight. *Journal of Morphology* 211: 259–268.
- Wageningen University Research Centre and Experimental Zoology Group. 2004. <http://www.skullsite.com>
- Wellnhofer, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica Abteilung A* 147: 169–216.
- Wellnhofer, P. 1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofen Schichten. *Archaeopteryx* 11: 1–47.
- Xu, X. and Norell, M.A. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* 431: 838–841.
- Xu, X., Wang, X., and Wu, X. 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401: 262–266.
- Xu, X., Zhou, Z., Wang, X., Kuang, X., Zhang, F., and Du, X. 2003. Four-winged dinosaurs from China. *Nature* 421: 335–340.
- Zhang, F., Ericson, P.G.P., and Zhou, Z. 2004. Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China. *Canadian Journal of Earth Sciences* 41:1097–1107.
- Zhang, F. and Zhou, Z. 2000. A primitive enantiornithine bird and the origin of feathers. *Science* 290: 1955–1999.
- Zhang, F., Zhou, Z., Hou, L., and Gu, G. 2001: Early diversification of birds: evidence from a new opposite bird. *Chinese Science Bulletin* 46: 945–950.
- Zhou, Z. 1995. The discovery of Early Cretaceous birds in China. *Courier Forschungsinstitut Senckenberg* 18: 9–22.
- Zhou, Z., Wang, X., Zhang, F., and Xu, X. 2000. Important features of *Caudipteryx*—evidence from two nearly complete new specimens. *Vertebrata Palasiatica* 38: 241–254.
- Zhou, Z. and Zhang, F. 2003. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of China. *Canadian Journal of Earth Sciences* 40: 731–747.