

The Morphological Basis of Hallucal Orientation in Extant Birds

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ABSTRACT The perching foot of living birds is commonly characterized by a reversed or opposable digit I (hallux). Primitively, the hallux of nonavian theropod dinosaurs was unreversed and lay parallel to digits II–IV. Among basal birds, a unique digital innovation evolved in which the hallux opposes digits II–IV. This digital configuration is critical for grasping and perching. I studied skeletons of modern birds with a range of hallucal designs, from unreversed (anteromedially directed) to fully reversed (posteriorly directed). Two primary correlates of hallucal orientation were revealed. First, the fossa into which metatarsal I articulates is oriented slightly more posteriorly on the tarsometatarsus, rotating the digit as a

unit. Second, metatarsal I exhibits a distinctive torsion of its distal shaft relative to its proximal articulation with the tarsometatarsus, reorienting the distal condyles and phalanges of digit I. Herein, I present a method that facilitates the re-evaluation of hallucal orientation in fossil avians based on morphology alone. This method also avoids potential misinterpretations of hallucal orientation in fossil birds that could result from preserved appearance alone. *J. Morphol.* 250:51–60, 2001. © 2001 Wiley-Liss, Inc.

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Theropod dinosaurs, which include such widely recognizable animals as *Tyrannosaurus*, *Allosaurus*, and *Velociraptor*, have a 225 million-year evolutionary history. Birds, a lineage of derived theropods that evolved flight, are known from the last two-thirds of that history, beginning with the earliest bird, *Archaeopteryx* (Ostrom, 1976). Most work on the functional morphology of Mesozoic birds has focused on the origin of feathered wings and flight (e.g., contributions in Hecht et al., 1985). Recently, however, more interest has been directed to other areas of the body, such as the tail (Gatesy and Dial, 1996a,b), hind limbs (Gatesy and Middleton, 1997), and respiratory system (Ruben et al., 1997).

One aspect of theropod evolution that has not been considered is the foot. Unlike nonavian theropods, most birds have an opposable or “reversed” first digit (hallux) (Fig. 1A,B). The reversed hallux of birds is a significant feature because it allows perching on a branch or grasping a prey item. Several examples underscore the importance of a reversed hallux to birds. Consider the difficulty that a songbird would have landing and balancing on a wire if it were not able to grip. Or consider a Harpy Eagle pulling a monkey or sloth from the treetops while in flight. Were it not for its reversed hallux, this type of predatory behavior would be virtually impossible.

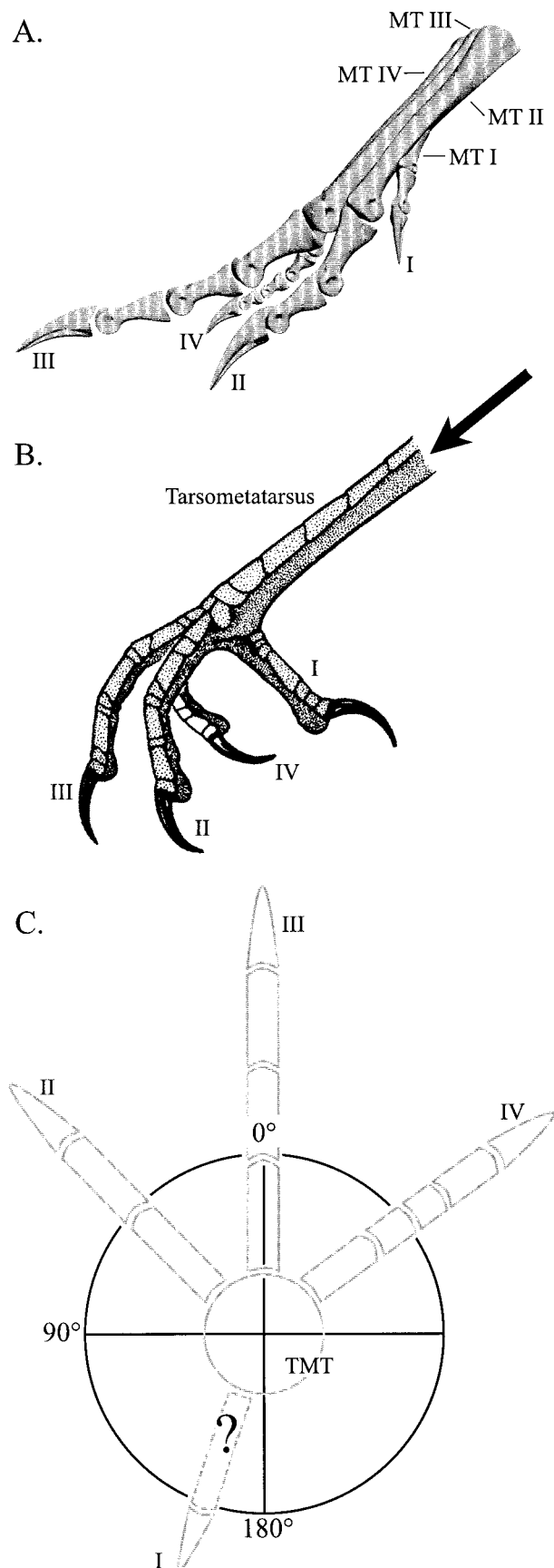
Primitively, the theropod foot had five metatarsals and a phalangeal formula of 2-3-4-5-0 (Fig. 1A). Birds retain a very similar pedal morphology, but with a few modifications. For example, extant birds have lost the phalanges of digit V as well as metatarsal V. Only four metatarsals (I–IV) remain. Dur-

ing ontogeny, three of the remaining metatarsals (II–IV) fuse with one another and the distal tarsals to form the tarsometatarsus (Fig. 1B). The articulation between the tarsometatarsus and metatarsal I is usually marked by a distinct fossa (*fossa metatarsi I*).

The hallux of theropods primitively lay alongside the other three digits of the foot, oriented “at a slight angle to the long axis of the metatarsus” (Norell and Makovicky, 1997, p 9; Tarsitano and Hecht, 1980; Tarsitano, 1981; Gatesy et al., 1999; Fig. 1A). The majority of extant birds possess an anisodactyl foot morphology, in which a “reversed” digit I opposes digits II, III, and IV (Raikow, 1985). In this study, the hallux is considered “reversed” if it is oriented at an angle greater than 90° to the long axis of digit III (Fig. 1C). Other terms that have been used to designate this condition include retroverted, reflexed, reflected, and reverted.

I will address two central questions. What characters contribute to hallucal orientation in extant birds? And, what changes are associated with the transition from the unreversed morphology of nonavian theropods to the anisodactyl, reversed design seen in extant birds? The hallux has a relatively limited number of potential mechanisms for hallucal reversion because it consists of only one metatarsal and two phalanges. The interaction of these bones

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must account for hallual reversion through changes in bone shape and/or articular conformation.

Herein I describe the osteological basis of hallual orientation among extant birds and present a standardized methodology that facilitates the determination of hallual orientation based on skeletal morphology. This new method eliminates the reliance on preserved position alone and permits interpretation of disarticulated or partially complete specimens.

MATERIALS AND METHODS

Skeletons of more than 50 specimens of birds representing a diverse taxonomic assemblage were examined for correlates between hallual orientation and osteology at the Museum of Comparative Zoology (Cambridge, MA) and the American Museum of Natural History (New York, NY). Morphological variables of 25 individuals (23 species and 16 families) were quantified. Comparisons were made only among anisodactyl feet; other pedal conformations such as digit IV reversion (heterodactyl) and digital reductions (i.e., ostriches, with only two digits) were not studied. The goal of this study was to assess variation in hallual orientation among birds, and species were chosen in order to maximize variation. Thus, certain families (Phalacrocoracidae, Sulidae) are overrepresented in comparison to their actual taxonomic distribution, while others (Passeriformes) are severely underrepresented. No attempt was made to correct for the phylogenetic relationships between species (Felsenstein, 1985; Garland et al., 1992; Garland and Janis, 1993). Furthermore, because of the nature of the measurements described below, small birds could not be included in the study, restricting the Passeriformes to one representative. Informal anatomical names are used to improve readability; however, ICAAN terminology of Baumel and Raikow (1993) and Baumel and Witmer (1993) are noted in italics with the first usage of each term. Common names for birds follow Monroe and Sibley (1993).

Tarsometatarsal and phalangeal measurements were made from either articulated or disarticulated

Fig. 1. Theropod foot morphology and data collection methodology. **A:** The generalized nonavian theropod foot morphology is represented by *Coelophysis bauri*. A right foot is shown in antero-medial view. Digit I is unreversed and is slightly abducted; metatarsal V is obscured by metatarsal IV. Roman numerals (I–IV) designate digit numbers, and metatarsals are denoted by MT I–IV. **B:** The foot of a blue jay (*Cyanocitta cristata*) shows the anisodactyl foot configuration common to most birds. Note the greater size of the hallux relative to the other digits compared to *Coelophysis*. The large arrow denotes the view that will be used throughout to diagrammatically represent avian foot design. **C:** With the leg in proximodistal view, the cross-section of the tarsometatarsus (TMT) is represented by a circle. Digits I–IV are shown in their approximate orientations as they project radially out from the center. The long axis of digit III is aligned with 0°, and all measurements are made relative to this axis. Blue jay foot from Proctor and Lynch (1993). (Reproduced with permission from Proctor and Lynch [1993] and Yale University Press; *Manual of Ornithology: Avian Structure and Function*. 340 p. 1993).

skeletal specimens. For disarticulated material, metatarsal I and the first hallucal phalanx were reattached to the tarsometatarsus approximately in life orientation (determined by comparisons with skeletons of conspecific or closely related species). Because the second hallucal phalanx (ungual) could not be easily distinguished from those of digits II–IV, the interphalangeal joint of digit I was studied only in articulated specimens.

To standardize measurements, each foot was mounted in a small clamp with the tarsometatarsus positioned vertically. The base of the tarsometatarsus was located at the center of a circle with the long axis of digit III at 0° (Fig. 1C). When viewed proximodistally, the digits projected radially from the tarsometatarsus. With the foot in this position, two angles were measured.

First, the orientation of digit I was defined as the angle between the long axis of digit III (0°) and the long axis of the hallux (Fig. 2A). Second, the orientation of the metatarsal I fossa was recorded. This angle was found by placing, in the fossa, a marker that projected perpendicular to the surface of the bone (Fig. 2B). Fossa orientation angle was measured from the medial surface of the tarsometatarsus because metatarsal I was situated ancestrally on the medial surface of metatarsal II (i.e., at 90° from the rotational axis of the phalanges of digit III). All measurements were rounded to the nearest 5°. Statistical analyses were not appropriate for this study because the data sample was small, nonrandom, and consisted of phylogenetically related species.

RESULTS

The range of hallucal orientations among the birds quantified was 100°, from a low of 80° in the northern gannet (*Morus bassanus*) to 180° in both the rhinoceros hornbill (*Buceros rhinoceros*) and the maleo (*Macrocephalon maleo*) (Fig. 3, Table 1). With a hallux oriented at less than 90°, the northern gannet is the only species of bird studied that does not have a reversed hallux. Increasing hallucal orientation angles are found in such species as the white-tailed tropicbird (*Phaethon lepturus*) and the Peruvian booby (*Sula variegata*), which have hallucal orientation angles of 110° and 120°, respectively (Fig. 3). Many of the birds with low hallucal orientation angles are thought to be closely related (e.g., boobies, pelicans, tropicbirds, gannets, and cormorants); all were formerly classified in the order Pelecaniformes and share the characteristic of interdigital webbing. In birds with higher hallucal orientation angles (greater than ≈165°), including the rhinoceros hornbill and maleo, the hallux was almost directly opposed to digit III. These species include both raptorial and perching birds (great horned owl, harpy eagle, Swainson's hawk, and common raven), as well as primarily ground-dwelling birds (maleo, a curassow, and the secretarybird) (Table 1).

The cutoff utilized here between unreversed and reversed halluces at 90° is arbitrary. Variation in

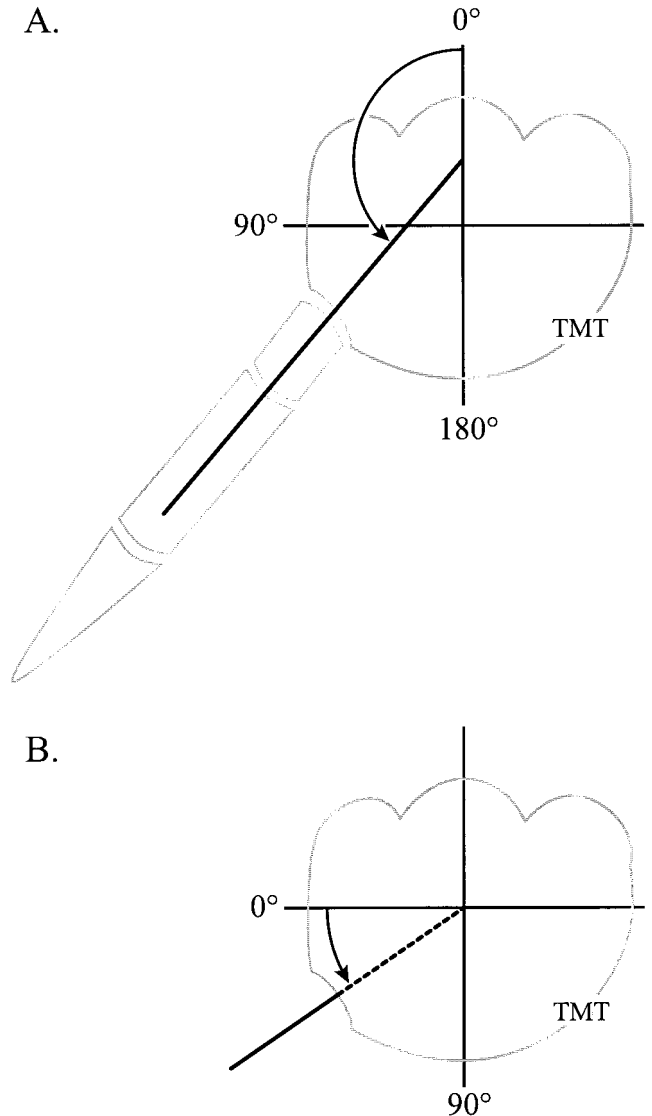


Fig. 2. Measurement of digit I orientation and metatarsal I fossa orientation. **A:** The tarsometatarsus is centered perpendicularly over a pair of axes, as in Figure 1C, with the long axis of digit III at 0°. The orientation of the hallux is the angle formed between 0° and a line passing through the long axis of digit I. **B:** To determine the orientation of the metatarsal I fossa, a marker (solid line) is placed in the fossa, perpendicular to the surface of the bone. This line is extended to the vertical axis. Metatarsal I fossa orientation is measured with 0° perpendicular to the axis of rotation of digit III. Note that the lines do not necessarily have to pass through the center of the circle.

hallucal orientation is more realistically regarded as a continuum from unreversed (anteromedially oriented halluces) through intermediate (posteromedially oriented halluces) to fully reversed (halluces directed at up to 180°). Using this continuum as a guide, the morphological correlates of variation can be assessed.

The tarsometatarsus affects digit I orientation through variation in the angle of the metatarsal I fossa. Changes in the angle of this fossa cause reorientation of the entire hallux, including metatarsal I

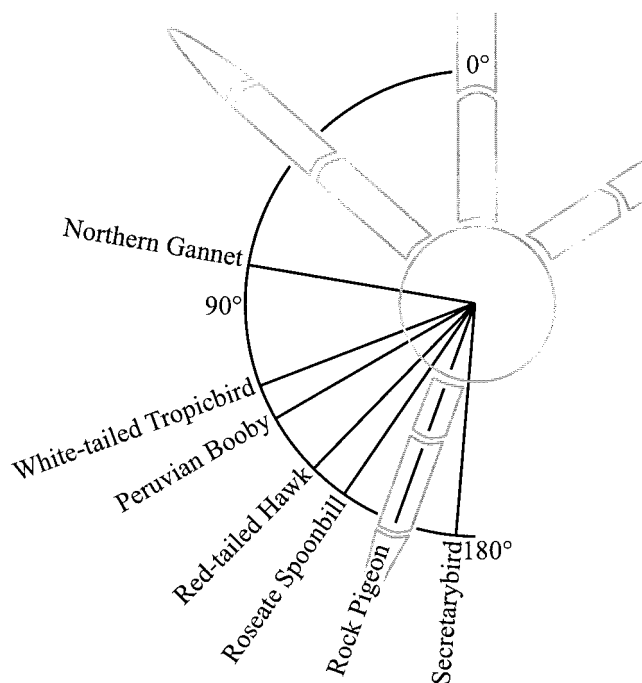


Fig. 3. Range of measured avian hallucal orientations. Plotting the hallucal orientation of a subset of the species studied shows that hallucal orientation varies from unreversed (less than 90°) to fully reversed (greater than 90°). Orientation of digit I is shown for the rock pigeon (*Columba livia*) and is represented by a line for all other species. The foot is diagrammed as in Figure 1C.

and the digit I phalanges. This angle varies from 10° in the northern gannet (*M. bassanus*) to 70° in a species of night heron (*Nycticorax* sp.) (Fig. 4, Table 1). Thus, in the gannet the articulation area for metatarsal I is directed more medially than posteriorly, as in the night heron. These species represent the extremes of fossa orientation; the fossae of most species examined fall between 30° and 50°. Some phylogenetic patterns appear to be present as well. The pelecaniform birds, which also have the lowest hallucal orientation angles, consistently have low fossa orientation angles ($\approx 10^\circ$). Conversely, long-legged wading birds (e.g., night heron and great blue heron) have more posteriorly oriented fossae (ca. 60–70°).

Because fossa orientation (10–70°) is much lower than digit I orientation (80–180°), other digital elements must also contribute to hallucal position. Potential sources of variation that were explored were mobility at the tarsometatarsal-metatarsal I joint (*syndesmosis intermetatarsalis hallucis*) and morphology of both metatarsal I and hallucal phalanx 1. Mobility of the tarsometatarsal-metatarsal I joint was assessed in eight fresh and alcohol-preserved specimens. Mobility varied from around 0° (*Falco* and *Accipiter*) to around 30° (*Numida*), with most birds having 10–15° of mobility at this joint. These data suggest that movement at this joint, which has been characterized as “slightly moveable” (Baumel

and Raikow, 1993, p 172), is insufficient for hallucal reversion, even when coupled with metatarsal I fossa orientation.

Hallucal phalanx 1 shows some morphological features that are associated with, but do not contribute to, hallucal reversion. In some birds (*Ardea*, *Buceros*, and *Nycticorax*), the proximal end of the first phalanx has slightly offset condyles (phalanx proximalis basis phalangis cotyla articularis), which force slight adduction and abduction with flexion and extension. This morphology would not, however, result in hallucal reversion. Furthermore, in some genera of birds (*Ardea*, *Corvus*, *Nycticorax*, and *Pandion*), the proximal end of phalanx 1 bears a large posterolateral extension. Expansion of the articular surface appears to allow for increased hyperextension of the hallux in these birds but does not increase hallucal orientation angle.

A distinctive metatarsal I morphology is present among birds with reversed halluces. This morphology is characterized by a marked torsion of the bone's shaft, which rotates the distal condyles relative to the proximal articulation on metatarsal II (Fig. 5). Torsion of metatarsal I was quantified by subtracting metatarsal I fossa orientation from digit I orientation (Fig. 4, Table 1). Metatarsal I torsion ranged from 65° in the northern gannet (*M. bassanus*) and the Peruvian booby (*S. variegata*) to 145° in the rhinoceros hornbill (*B. rhinoceros*) and the secretarybird (*Sagittarius serpentarius*). Metatarsal torsion increased with digit I orientation. In general, higher hallucal angles were associated with higher degrees of torsion (Fig. 4).

DISCUSSION

The evolution of hallucal reversion in birds exemplifies a relatively common phenomenon in biology, the differential elaboration of a structural “copy.” Shubin et al. (1997, p 639) describe this process as “adaptive modification of serially homologous organs.” Redundancy thus allows the organism to explore a new functional or behavioral realm with one or more structures while maintaining primitive function with the remaining structures. Morphological examples include changing functions of synergistic muscles (Lauder and Liem, 1989), the elongate fourth digit of pterosaurs (Wellnhofer, 1991), and the opposable hominid thumb (Marzke, 1997; Moyà-Solà et al., 1999). More disparate examples are duplication and differentiation of HOX clusters (Tabin, 1992; Shubin et al., 1997) and of protein coding regions of DNA (Ohno, 1970; Markert et al., 1975).

Metatarsal Morphology and Hallucal Orientation

Despite the presence of several potential morphological areas that could have contributed to hallucal reversion, the orientation of the hallux in living birds results primarily from the interaction of only

TABLE 1. Hallucal orientation, metatarsal I fossa orientation, and metatarsal I torsion angles measured in extant birds

Family	Species	Common name	Specimen number	Digit I orientation	Metatarsal I fossa orientation	Metatarsal I torsion
Accipitridae	<i>Buteo jamaciensis</i>	Red-tailed hawk	MCZ 1278	135°	40°	95°
	<i>Buteo swainsoni</i>	Swainson's hawk	MCZ 1450	165°	50°	115°
	<i>Harpia harpyja</i>	Harpy eagle	MCZ 333	165°	30°	135°
	<i>Pandion haliaetus</i>	Osprey	MCZ 1462	160°	55°	105°
Ardeidae	<i>Nycticorax sp.</i>	Night heron	MCZ 7000	145°	70°	75°
	<i>Ardea herodias</i>	Great blue heron	MCZ 3447	150°	60°	90°
Bucerotidae	<i>Buceros bicornis</i>	Great hornbill	MCZ 3179	165°	50°	115°
	<i>Buceros rhinoceros</i>	Rhinoceros hornbill	MCZ 1446	180°	35°	145°
Ciconiidae	<i>Sarcorhamphus papa</i>	King vulture	MCZ 210	140°	50°	90°
Corvidae	<i>Corvus corax</i>	Common raven	MCZ 7798	165°	45°	120°
Cracidae	<i>Crax nigra</i>	Currasow	MCZ 2084	165°	50°	115°
Megapodiidae	<i>Macrocephalon maleo</i>	Maleo	MCZ 355	180°	45°	135°
Phaethontidae	<i>Phaethon lepturus</i>	White-tailed tropicbird	MCZ 2073	110°	30°	80°
Phalacrocoracidae	<i>Phalacrocrax auritus</i>	Double-crested cormorant	MCZ 6549	135°	25°	110°
	<i>Phalacrocrax auritus</i>	Double-crested cormorant	MCZ 7537	120°	15°	105°
	<i>Phalacrocorax urile</i>	Red-faced cormorant	MCZ 722	120°	30°	90°
Phasianidae	<i>Tetrao urogallus</i>	Western capercaillie	MCZ 315	160°	55°	105°
Pelecanidae	<i>Pelecanus occidentalis</i>	Brown pelican	MCZ 1956	125°	45°	80°
Sagittariidae	<i>Sagittarius serpentarius</i>	Secretarybird	MCZ 1925	175°	30°	145°
Steatornithidae	<i>Steatornis caripensis</i>	Oilbird	MCZ 1404	125°	45°	80°
Strigidae	<i>Bubo virginianus</i>	Great horned owl	MCZ 1275	170°	35°	135°
Sulidae	<i>Morus bassanus</i>	Northern gannet	MCZ 3443	80°	15°	65°
	<i>Morus bassanus</i>	Northern gannet	MCZ 7043	80°	10°	70°
	<i>Sula variegata</i>	Peruvian booby	MCZ 6834	120°	55°	65°
Threskiornithidae	<i>Ajaia ajaja</i>	Roseate spoonbill	MCZ 6534	145°	50°	95°

two areas—fossa orientation and metatarsal I torsion. Examination of their relationship to hallucal orientation revealed two general patterns. First, over a 100° range of hallucal orientation, fossa angle varies 60° and does not appear to correlate substantially with increasing hallucal orientation. Second, metatarsal I torsion increases in conjunction with hallucal angle (Fig. 4). In all species studied, metatarsal I torsion contributes more to hallucal angle than does fossa orientation. This difference is larger in birds with higher hallucal orientation angles (e.g., rhinoceros hornbill and secretarybird).

The significance of these two patterns can be better appreciated in the context of the evolutionary history of the theropod hallux. Primitively, theropod digits lay approximately parallel to one another, with digit I unreversed (Fig. 1). The foot was used primarily for terrestrial locomotion, and all of the digits likely experienced similar functional demands. With the exception of the enlarged predatory digit II claw in dromaeosaurs

and troodontids, no single digit was specialized for other functions (e.g., grasping). The flexor musculature of the digits (m. flexor digitorum longus and m. flexor hallucis longus) probably functioned synergistically and were coactive during the step cycle. The evolution of hallucal reversion entailed a significant morphological change of one digit. With the hallux directed posteriorly, a novel digital conformation is present, in which the plantar (i.e., flexor) surface of digit I opposes those of digits II–IV. Thus, during flexion, the digits close toward one another.

Reorientation of the hallux could have affected the flexor tendons, which pass along the posterior surface of the metatarsus. If metatarsal I were to articulate on the posterior surface of the tarsometatarsus (fossa orientation angle near 90°), passage of the flexor tendons along the posterior surface of the tarsometatarsus would be compromised. This possibility suggests a functional explanation for the reliance on metatarsal torsion for hallucal reversion;

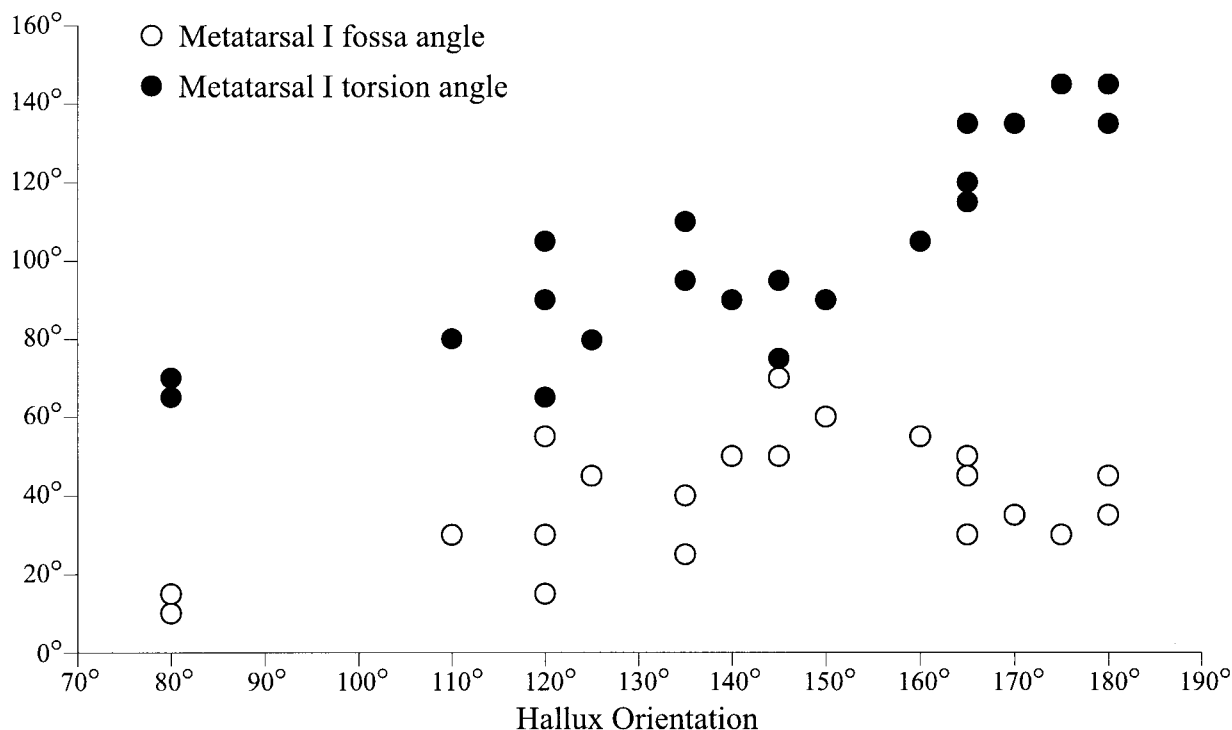


Fig. 4. Contributions of metatarsal I fossa and torsion angles to hallux orientation. Along the x-axis, hallux orientation angle increases from 80 to 180°. Open circles represent the metatarsal I fossa angle. No clear trend is present relating fossa angle to hallux orientation. Closed circles represent metatarsal I torsion angle. Increased metatarsal I torsion is associated with higher digit I orientation angles.

the metatarsal I articulation could not rotate far enough posteriorly on the tarsometatarsus to permit full hallux reversion. Two species illustrate this point. Both the white-tailed tropicbird (*P. lepturus*) and the secretarybird (*S. serpentarius*) have equal metatarsal I fossa orientations (30°). Yet the difference in hallux orientation between these two genera is 75° (70 and 145°, respectively), all of which results from differential torsion of metatarsal I.

Some variation is present, however, in the relationship between fossa orientation and metatarsal torsion (Fig. 4). The tarsometatarsi of raptorial birds are concave posteriorly, resembling a trough or U. The metatarsal I fossa is typically located on the medial edge of this trough, which can result in unusually low fossa orientations (ca. 30–35° for the harpy eagle and great horned owl). In some cases, curvature of the tarsometatarsus is so extreme that the proximal end of the first phalanx of digit I almost touches digit IV (e.g., osprey). However, higher metatarsal torsion in these birds compensates for low fossa orientation.

Long-legged wading birds fall at the opposite end of the spectrum, with a metatarsal I fossa directed most posteriorly of all species quantified. In the great blue heron (*A. herodias*) and a species of night heron (*Nycticorax* sp.), fossa orientations are 60° and 70°, respectively, and torsion values are relatively low for these two genera (≈80°). These birds seem to have circumvented the potential difficulties

associated with the metatarsal I fossa articulating on the posterior surface of the tarsometatarsus, which poses interesting questions about foot design and function in long-legged birds.

For a century, nonavian theropods have been reconstructed with reversed halluces (Osborn, 1899, 1906; Ostrom, 1969, 1978; and the majority of mounted museum specimens). Metatarsal I was thought to articulate on the posterior surface of metatarsal II. This interpretation was questioned on the grounds that the rugose area where metatarsal I was thought to attach was, in fact, a muscle scar for the m. gastrocnemius (Tarsitano and Hecht, 1980; Tarsitano, 1981). However, it was not considered that the flexor tendons must also pass through this region in nonavian theropods. If the first metatarsal of nonavian theropods had attached to the posterior surface of metatarsal II, passage of the flexor tendons could have been disrupted.

Bone Surface Homologies and Nomenclature

Because digit I of theropods was primitively unreversed (Norell and Makovicky, 1997; Gatesy et al., 1999), the distal condyles (tubercula) of metatarsal I were in approximately the same orientation as those of metatarsals II–IV (Fig. 1A), directed anteromedially. On metatarsals II–IV, the medial and lateral tubercula can be unambiguously distinguished from

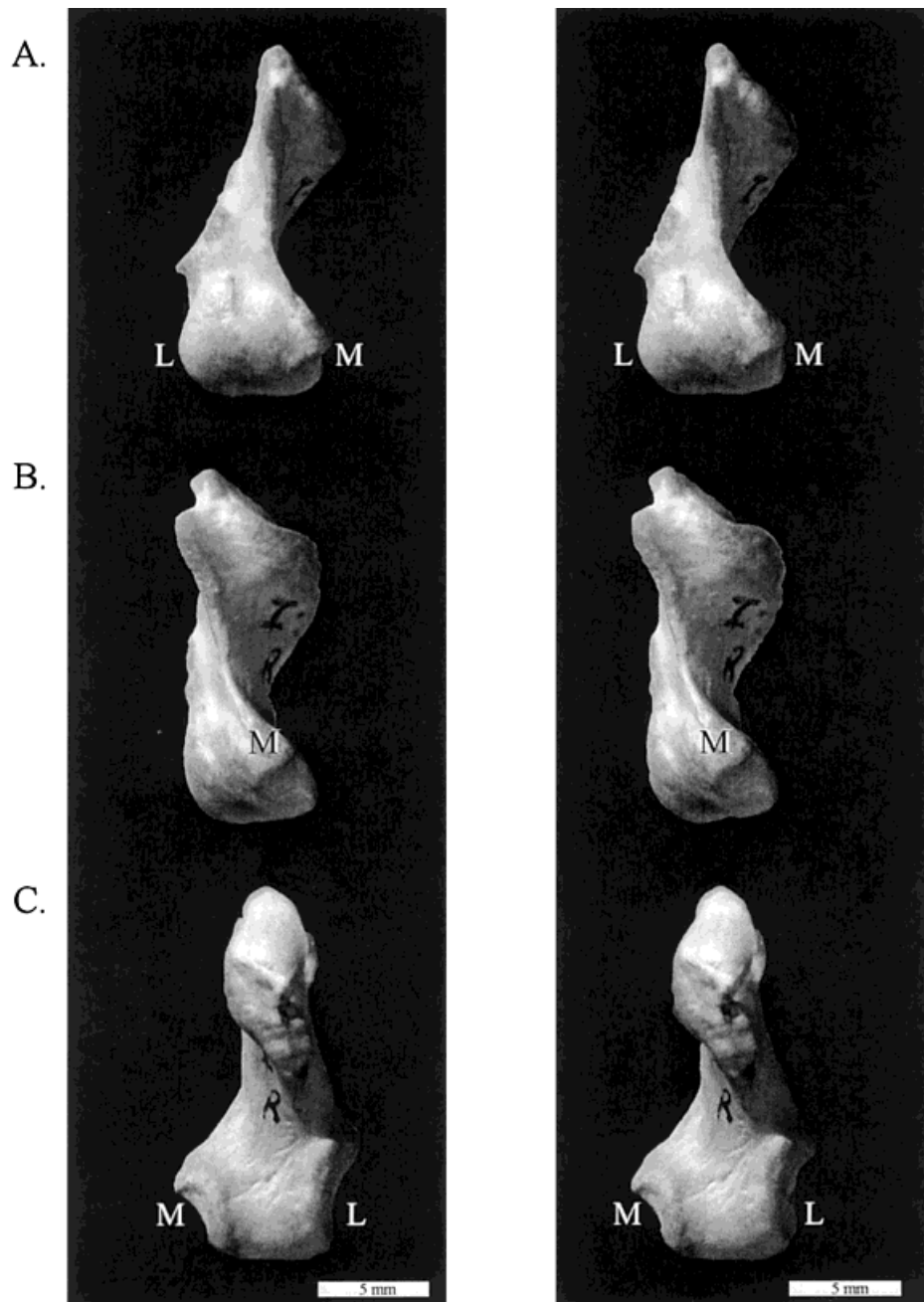


Fig. 5. Metatarsal I of *Gallus gallus*. Stereo pairs of three views of a right metatarsal I are shown: (A) posterior, (B) posteromedial, (C) anterior. The proximal end of the metatarsal is up, and the tubercula, which articulate with the first phalanx of digit I, are down. The posterior view (A) shows the extensor surface of the metatarsal, while the anterior view (C) shows the flexor surface. The medial (M) and lateral (L) tubercula (condyles) of the metatarsal are marked.

one another because their orientations relative to one another have changed little during theropod evolution.

However, the anatomical designations medial and lateral are not straightforward in the reversed avian hallux. A result of metatarsal I torsion is that the ancestral *tuberculum mediale*, that which was originally nearer to the median plane, is situated more laterally than the ancestral *tuberculum laterale* (Fig. 5). An example of the confusion that can result

is the naming of the *os metatarsale I: Tuberculum laterale* (Baumel and Witmer, 1993; = *os metatarsale I: Tuberositas lateralis* in figure 5.9 of Baumel and Raikow, 1993). While anatomically oriented on the lateral aspect of the foot, evolutionarily it is the *tuberculum mediale*. Thus, naming this structure according to its appearance does not take into consideration its evolutionary history. One solution to this problem is to name the tubercula or condyles strictly according to their evolutionary history. Such

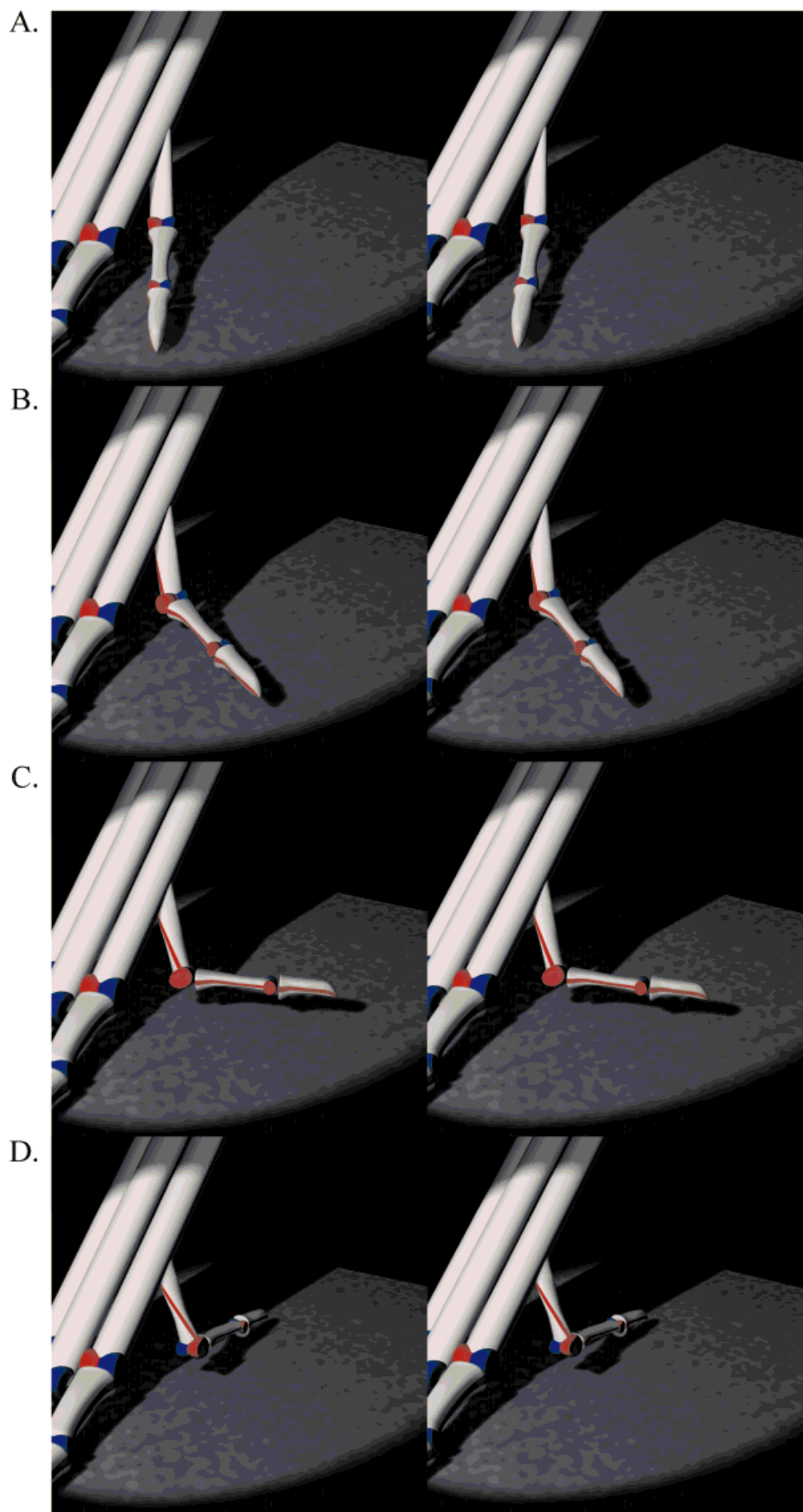


Figure 6

nomenclature may help to avoid potential confusion when describing, for example, digital orientation or anatomical characters among birds that have unreversed or intermediate hallucal orientations.

Identification of Reversed Halluces in Fossil Birds

Despite recent advances in Mesozoic avian paleontology (for review see Padian and Chiappe, 1998), the life orientation of the hallux in fossil birds has remained an unexplored question. Difficulties can arise when trying to interpret three-dimensional anatomy based on skeletons that are preserved in only two dimensions. Nonetheless, preserved appearance has been used for assessment of hallucal orientation in *Archaeopteryx* (Wellnhofer, 1974, 1992, 1993; Martin, 1991), *Boluochia* (Zhou, 1995), *Changchengornis* (Chiappe et al., 1999), *Concornis* (Sanz et al., 1995), *Confuciusornis* (Hou et al., 1995, 1996, 1999; Chiappe et al., 1999), *Iberomesornis* (Sanz and Bonaparte, 1992), *Rahonavis* (Forster et al., 1998), and *Sinornis* (Serenio and Rao, 1992). An understanding of the morphology associated with hallucal reversion could be used to determine the hallucal orientation of any avian skeleton. Because most skeletons are found at least partially disarticulated, the morphological method presented here has potential applications in avian paleontology.

Avian fossils now can be studied with a better understanding of metatarsal design to avoid misinterpreting potentially misleading preservational appearance. Two features will be of interest: the orientation of the metatarsal I fossa, and the amount of torsion in metatarsal I. Because birds with reversed halluces exhibit metatarsal I torsion that correlates with hallucal orientation, recognition of torsion alone should be sufficient to determine whether the hallux was reversed in life. This may be particularly important in the absence of a well-defined metatarsal I fossa in most nonavian theropods (personal observations). The method presented here avoids the presently unknown effects of two-dimensional

preservation of three-dimensional structures such as the avian foot.

CONCLUSIONS

Studying osteological morphology of the reversed hallux is the first step in understanding the function and evolution of this complex morphology. Two main questions remain. What is the evolutionary history of the reversed hallux? I present here one possible model for the evolution of the avian reversed hallux (Fig. 6). This model is based on a computer reconstruction of the ancestral nonavian theropod foot. The evolution of hallucal reversion is hypothesized as a 25° increase in fossa orientation angle and a 150° increase in metatarsal torsion. However, this model requires testing. Does the variation in hallucal orientation present among living birds accurately reflect the evolutionary transition to hallucal reversion? What functional pressures led to the evolution of this feature? It has been suggested that the reversed hallux could have evolved only as an adaptation for perching (Reichenow, 1871; Bock and Miller, 1959; Bock, 1986). Analysis of the foot morphology of Mesozoic birds will provide important details of this evolutionary change (Fig. 6). When and how did the nonsynovial joint between metatarsals I and II originate? Is there a single evolution of the reversed hallux? Is the presence of a reversed hallux plesiomorphic for all living birds? If so, what evolutionary pressure leads to the secondary loss of reversion?

The other main question is: What functional changes are associated with hallucal reversion? What effect does the presence of a large reversed hallux have on foot function? What is the function of the hallux during nonperching locomotor movements such as terrestrial walking or vertical climbing? Does a functional trade-off exist between a better grasping foot and terrestrial locomotor ability, as suggested by Feduccia (1996)? More questions than answers may appear to be present, but a better understanding of foot design, diversity, and function in living birds can help reveal patterns of foot evolution in the earliest birds.

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Fig. 6. Hypothetical stages in the evolution of the avian reversed hallux. A diagrammatic theropod right foot is shown in anterioromedial view. The medial edge of the metatarsals, as well as the medial tubercula, are colored blue. The corresponding lateral sides are red. The ancestral, nonavian theropod configuration (A) is digit I unreversed and directed anteromedially. Two intermediate stages are shown. First, the hallux is unreversed (B), comparable to the morphology of the northern gannet. Second, the hallux is reversed, but is still medially oriented (C), comparable to the hallucal orientation in the Peruvian booby. Finally, the fully reversed hallux is shown (D). As hallucal orientation increases, two changes occur: the angle of metatarsal I fossa increases approximately 25°, and metatarsal I undergoes approximately 150° of torsion. Because of this torsion, the lateral surface of the metatarsal, marked by the red stripe, curves toward the medial aspect of the foot, and the lateral (red) condyle is located on the medial aspect of the foot, in contrast to the primitive condition (A).

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