



# Theropod forelimb design and evolution

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We examined the relationship between forelimb design and function across the 230-million-year history of theropod evolution. Forelimb disparity was assessed by plotting the relative contributions of the three main limb elements on a ternary diagram. Theropods were divided into five functional groups: predatory, reduced, flying, wing-propelled diving, and flightless. Forelimbs which maintained their primitive function, predation, are similarly proportioned, but non-avian theropods with highly reduced forelimbs have relatively longer humeri. Despite the dramatically different forces imparted by the evolution of flight, forelimb proportions of basal birds are only slightly different from those of their non-avian relatives. An increase in disparity accompanied the subsequent radiation of birds. Each transition to flightlessness has been accompanied by an increase in relative humeral length, which results from relatively short distal limb elements. We introduce theoretical predictions based on five biomechanical and developmental factors that may have influenced the evolution of theropod limb proportions.

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**ADDITIONAL KEY WORDS:**—Aves – bipedalism – Dinosauria – disparity – flight – limb morphology – locomotion – morphospace – Theropoda – wing.

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## INTRODUCTION

One of the fundamental features of any limb's design is the relative proportions of its skeletal components. These proportions are often expressed as the ratio of two bone lengths, such as the femorotibial and humeroradial indices (Howell, 1965). Such ratios are thought to have functional significance for limb use because they reflect the basic layout of an appendage's compound lever system. Most frequently, proportions have been employed to identify and categorize mammalian limbs specialized for running, weight support, or digging (Gregory, 1912; Osborn, 1929; Smith & Savage, 1956; Garland & Janis, 1993; Gebo & Rose, 1993; Carrano, 1997). Proportions have also been invoked as indicators of cursoriality in dinosaurs (e.g. Osborn, 1916; Ostrom, 1976a; Coombs, 1978; Colbert, 1989; Holtz, 1995a; Sereno *et al.*, 1996). The majority of work to date has focused on limbs used for terrestrial locomotion. Such limbs bear loads by transmitting muscular, gravitational, and inertial forces to the substrate, and thus lend themselves to hypotheses based on lever mechanisms.

Comparatively little is known about limbs that are not loaded in this manner. Forelimbs used during flight, prey capture, or food manipulation likely experience mechanical forces quite different from those used exclusively during terrestrial locomotion but with a few exceptions (Mattison & Giffin, 1989; Mattison, 1993; Christiansen, 1997), remain relatively unexplored. Theoretical predictions are few, and many questions remain unanswered. For example, how well does the relative size of skeletal elements reflect limb function? How should a predatory forelimb be constructed, and how might this arrangement differ from that of a wing? Are limb proportions informative about the evolutionary origin of flight and secondary loss of volant function? Do the demands of flight impose strong constraints on wing design?

Theropod dinosaurs are an ideal group in which to examine these questions. Theropods were primitively bipedal (Gauthier, 1986; Sereno, 1997) and remained so throughout their 230-million-year history, thereby freeing the forelimb from a significant role in terrestrial locomotion. This liberation was accompanied by the evolution of a wide diversity of forelimb morphologies. From a primitive predatory morphology, at least two lineages evolved highly reduced forelimbs. A third lineage transformed the forelimb into a feathered wing for generating aerodynamic forces during flight (Ostrom, 1976b; Gauthier, 1986; Chiappe, 1995; Chiappe, Norell & Clark, 1996; Padian & Chiappe, 1998). Although over 98% of extant birds use their

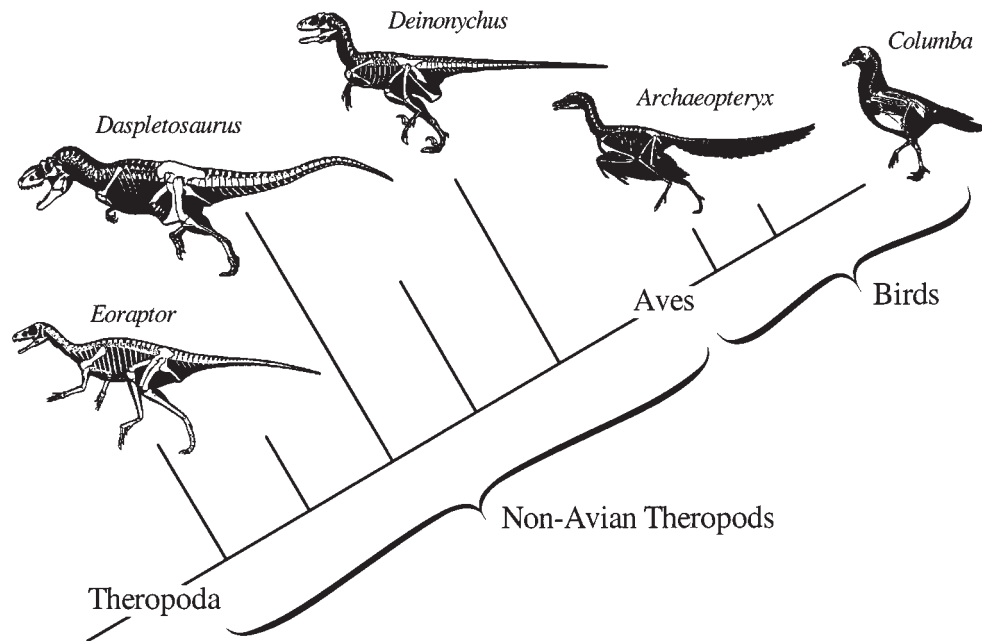


Figure 1. Simplified cladogram of Theropoda (after Sereno, 1997). *Eoraptor* from Sereno *et al.* (1993); *Daspletosaurus* from Paul (1988); *Deinonychus*, *Archaeopteryx*, and *Columba* from Chatterjee (1997).

wings exclusively for aerial flight, several groups also fly underwater, and many other lineages have become flightless (for a comprehensive review, see Livezey, 1995). Herein, we examine forelimb disparity in the morphologically and functionally diverse clade Theropoda.

## MATERIAL AND METHODS

### *Systematics and terminology*

Throughout this paper, we employ the phylogenetic hypotheses of Gauthier (1986), supplemented by the work of Holtz (1994a) and Sereno (1997) for subsequently described fossil taxa. We follow the cladistic analyses proposed by Chiappe *et al.* (1996) for basal birds and by Sibley & Ahlquist (1990) for extant birds. All members of the clade Aves are included in Theropoda. Thus, theropods include the most recent common ancestor of *Archaeopteryx* and all modern birds, as well as all of its descendants (Fig. 1). We will use the term theropod to refer to any member of this clade, both avian and non-avian, unless further restricted. For example, non-avian theropods will be denoted as such, and bird or avian will be used to refer to members of Aves (Fig. 1).

As in our previous study of theropod hind limbs (Gatesy & Middleton, 1997), we again distinguish taxonomic diversity (number of species) from functional diversity (scope of limb use) and disparity ('range of anatomical design' or morphological diversity; Gould, 1991: 412; Foote, 1989, 1993, 1997; Wagner, 1995).

*Data collection*

Lengths of the humerus, radius, and metacarpal II were measured for this study. Although a wealth of non-avian theropods is presently known, the paucity of specimens with sufficiently complete forelimbs restricted our data set. From the literature, we collected data for 23 individuals of 20 species (Appendix 1). The length of the carpometacarpus was used as the third limb element for birds; lengths of individual carpal elements were excluded from non-bird measurements. For ease of use, we will refer to the three elements as humerus, radius, and carpometacarpus in both birds and non-avian theropods. Bird forelimbs (Appendix 2) were measured on specimens housed at the Museum of Comparative Zoology, Cambridge, MA (MCZ) and the Yale Peabody Museum, New Haven, CT (YPM). Wing element measurements were made with either digital calipers or ruler of 543 individuals from 324 species of 260 genera in 82 families. Nineteen of the 23 modern avian orders are represented. Additionally, measurements of fossil (32 forelimbs from 28 species) and extant birds (78 forelimbs from 46 species) were taken from the literature (Appendix 3). Inclusion of mean lengths allowed the use of additional data from published specimens, which often come from fossil deposits in which bones cannot be associated positively with a single individual.

*Analysis: ternary diagrams*

The lengths of the humerus, radius, and carpometacarpus were added together to obtain total forelimb length. Each of the three elements was then divided by limb length to calculate its percentage of the total. Traditionally, bivariate plots have been used to study theropod limb morphology and function (Coombs, 1978; Gatesy, 1991; Holtz, 1995a). However, interpreting all three variables in such graphs proves cumbersome (Gatesy & Middleton, 1997). Ternary diagrams were used to determine the range of morphological diversity present in theropod forelimb proportions. Such diagrams depict the relative contributions of three variables to a whole and have common applications in geology and genetics. They have been used less frequently for morphological variables (Kershaw & Riding, 1978; Fortey, 1983; Mattison & Giffin, 1989; Alexander, 1991; Mattison, 1993; Gatesy & Middleton, 1997; Carrano, 1998; Clark *et al.*, 1998). A ternary diagram consists of three axes oriented at 120° to one another, each running from zero to 100% (Fig. 2). A limb proportion ternary represents a size-free morphospace composed of all the possible combinations of three limb element percentages.

*Disparity index*

To facilitate comparison between two limbs and to quantify maximal group ranges, we calculated the linear distance between pairs of points. This distance, divided by the maximum possible distance between two points (from one vertex to another) yields a disparity index (DI). Two points at opposite vertices of a ternary diagram have a disparity index of 100, while two points at the same location have a disparity index of 0. We define the disparity index as a unitless value rather than a percentage to avoid confusion with individual limb element proportions. For the

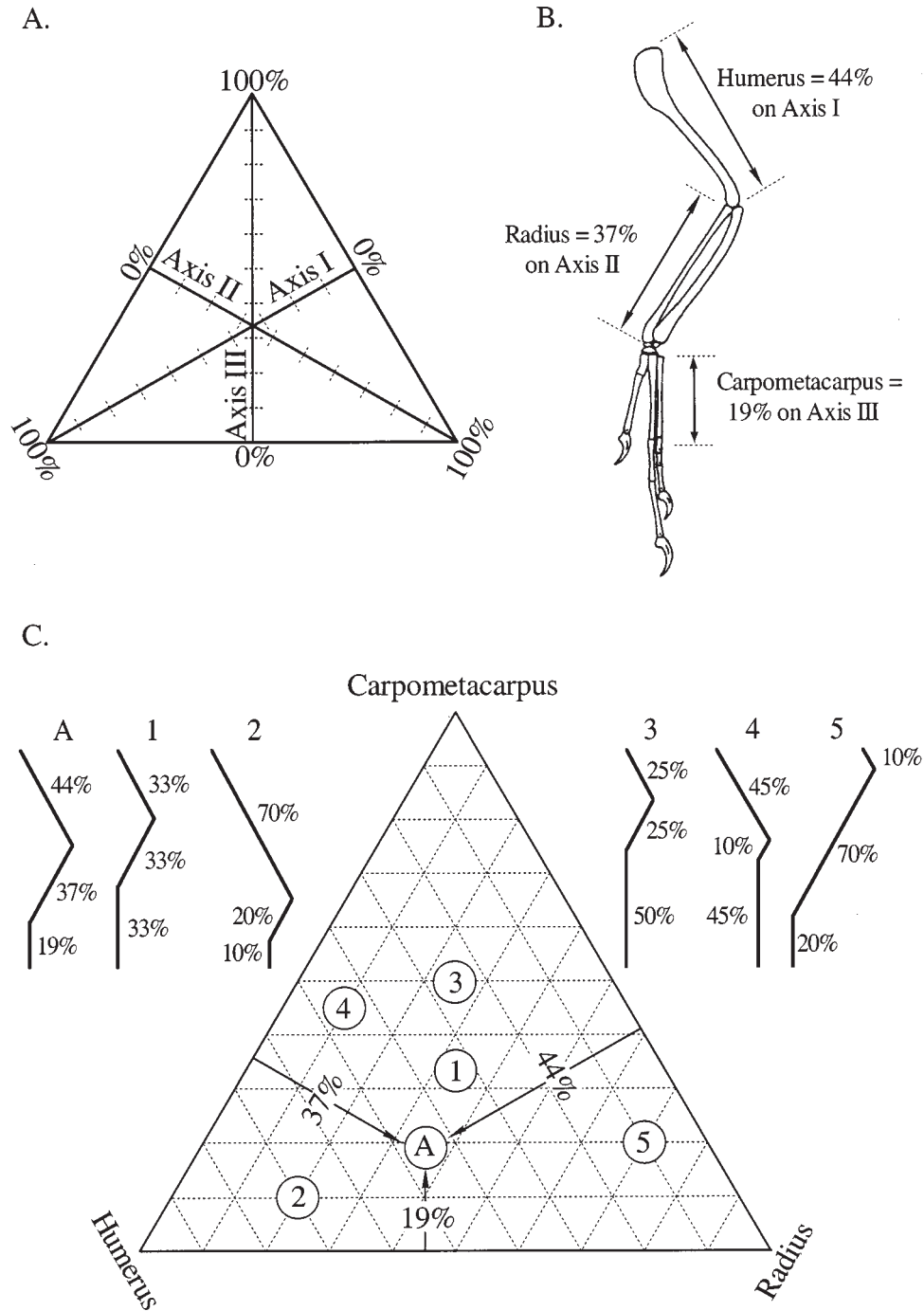


Figure 2. Methodology for ternary morphospace visualization. A, a ternary diagram consists of three axes (I, II, and III), each oriented at  $120^\circ$  to one another. B, a tripartite limb, in this case of *Archaeopteryx*, showing the fractional contributions of its three main segments. C, a forelimb proportion morphospace showing the position of *Archaeopteryx* (A). Hypothetical limbs (1–5) are shown with their respective positions in morphospace. *Archaeopteryx* skeleton modified from Ostrom (1976b). All limb segment orientations are arbitrary and used for comparison only.

purposes of this study, we considered each data point independent and did not try to correct for phylogenetic relationships between taxa (Felsenstein, 1985; Garland, Harvey & Ives, 1992; Garland & Janis, 1993).

### *Functional groups*

Because our goal was to explore the relationship between proportions and function, we separated all taxa into five functional groups based on forelimb use: (1) predatory, (2) reduced, (3) flying, (4) wing-propelled diving, and (5) flightless. Membership was determined either by direct observation or inference; no functional group is monophyletic. Note that the ‘flightless’ functional group includes only secondarily flightless avians and not primitively flightless non-avian theropods. Our analysis will focus primarily on the disparity within and transitions between these five functional groups.

## RESULTS

### *All theropods*

Theropod forelimb proportions are not evenly distributed in ternary morphospace (Figs 3A, 4); instead, large empty areas exist, particularly at radius over 50% and carpometacarpus greater than *c.* 45%. Birds overlap non-avian theropod proportions such that just a single non-bird lies outside the range of birds (Figs 3B, 4). However, birds occupy large areas of proportion morphospace unexploited by non-birds. Among all theropods, the humeral contribution varies the greatest (25–70%). The radius spans 30% (20–50%), while the carpometacarpus spans 35%. The disparity index for the most distant taxa was 43 (*Carnotaurus* to swifts), indicating that the descendants of the ancestor of theropods radiated to cover a range encompassing almost half of the maximum potential morphological difference.

Non-avian theropods occupy a subset of this range. The humerus spans 25%, the radius 21%, and the carpometacarpus just 11%. The disparity index is 25 between *Carnotaurus* and *Herrerasaurus*, the most proportionally different non-avian theropods. In contrast, bird humeri have a 40% range (24–64%), while the radius covers almost 30% (19–48%), and the carpometacarpus 35% (8–43%). This final range is deceptively high because of a small group with relatively long carpometacarpi; most fall between 8% and 30%. The disparity index among avian theropods is 36 (ostriches to swifts).

### *Predatory*

Proportions of non-avians retaining predatory limbs are clustered with a humerus between 45% and 55%, a radius of 29% to 40%, and a carpometacarpus from 12% to 20% (Fig. 5, Table 1). The disparity index is only 7.8. Members of this functional group have functionally tridactyl, grasping or raking limbs.

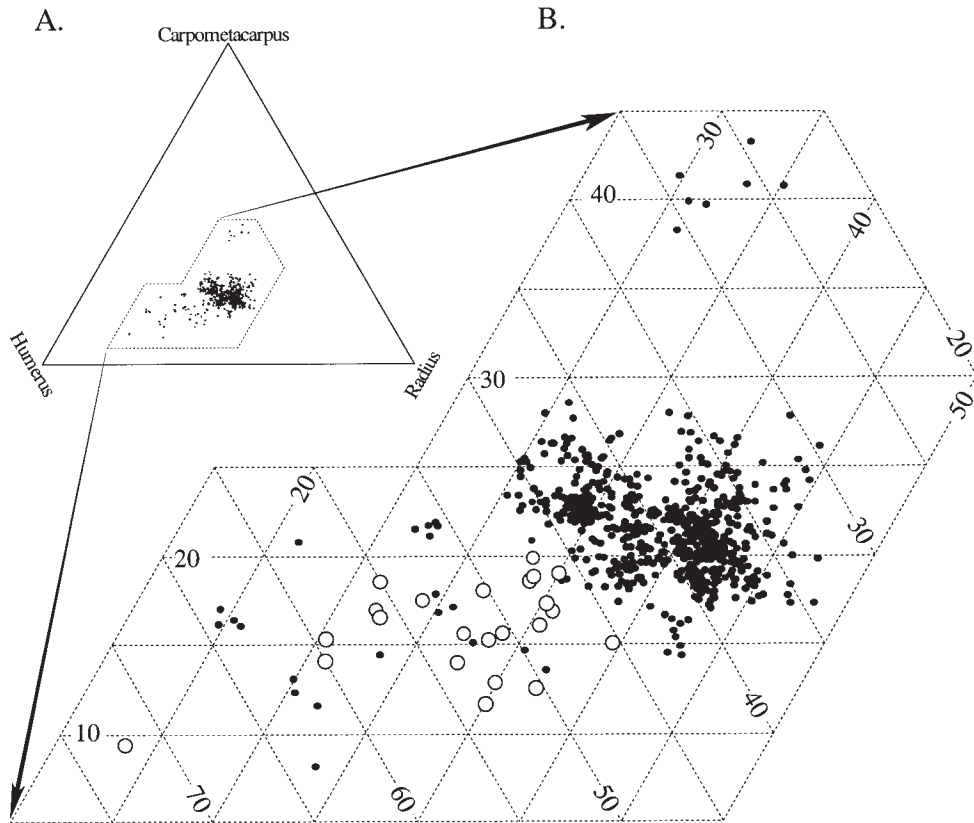


Figure 3. Forelimb proportion distribution for all theropods plotted in ternary morphospace. A, theropods are found in a small subset of the overall potential morphospace. B, when expanded, this distribution reveals that the range of avian theropods (●) almost completely overlaps the area occupied by non-avian theropods (○). Only one non-bird (*Carnotaurus*) has proportions that fall outside the range of birds.

### *Reduced*

Forelimb length is significantly reduced relative to hind limb length (Table 2) in tyrannosaurids (*Tarbosaurus*, *Daspletosaurus*, and *Albertosaurus*) as well as in *Carnotaurus*, a Late Cretaceous abelisaurid (Fig. 5). This functional group is characterized by proportionally longer humeri than non-avian theropods which retain predatory forelimbs. In both of these independent lineages, the humerus is elongate relative to the other forelimb elements (greater than 55%). *Carnotaurus* represents the most extreme condition of all theropods that retain three limb elements. Its humerus composes 72% of the forelimb, the radius 19%, and the carpometacarpus just 9%.

### *Flying*

Non-avian theropods that retain predatory forelimbs, including those considered most closely related to birds, such as *Ingenia*, *Sinornithoides*, and *Deinonychus* (Sereno,

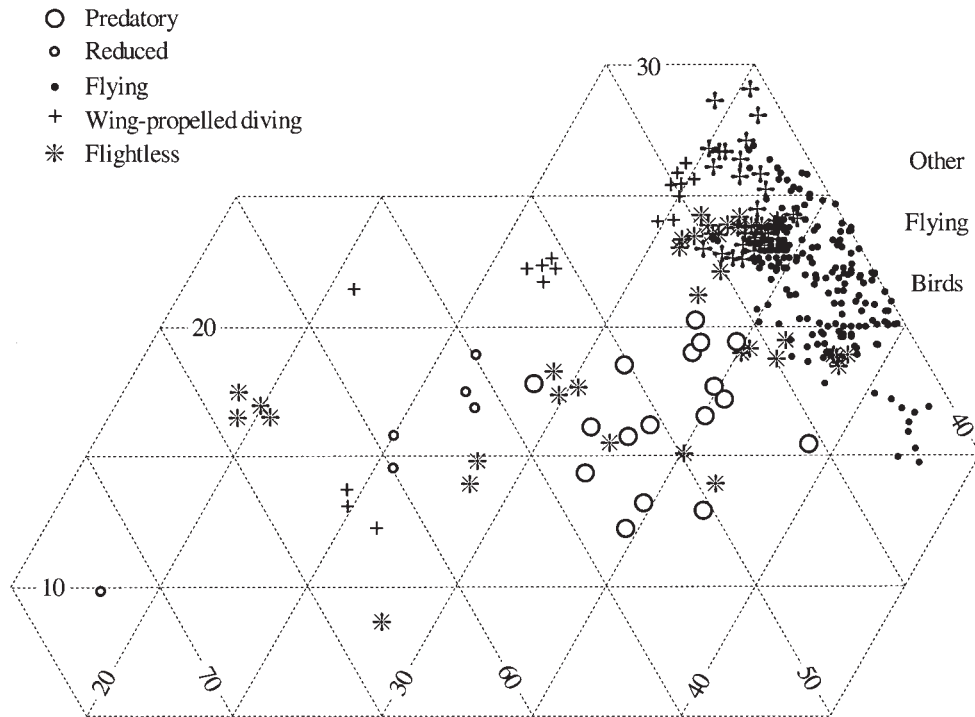


Figure 4. Forelimb proportions for all theropods categorized by functional group. Non-birds are restricted to humeral percentages less than 45%; all flying birds have humeral values greater than or equal to 45%. Note the high degree of overlap among other functional groups.

1997), share similar, but not identical, proportions with early birds such as *Archaeopteryx* and *Concornis*. *Deinonychus* and *Archaeopteryx* are nearly co-proportional, with a disparity index of only 2.5.

Several general patterns can be recognized within the flying bird cloud (Fig. 6A). First, birds that fly in air have a humerus that makes up no more than about 45% of the forelimb. Humeral contribution spans 20% (DI=21) between swifts and murres, which have the lowest and highest humeral values, respectively. Second, hummingbirds (Trochiliformes) and swifts (Apodiformes) lie outside the main group of flying birds, due to their elongate carpometacarpus, which approaches half of the wing length. Almost 10% of the maximum possible morphological difference separates hummingbirds from lories, which have the highest carpometacarpal values in the main group of flying birds (Fig. 6A). Finally, humeral percentage appears to correlate with aerial maneuverability (Fig. 6B). The most maneuverable fliers (passerines, hummingbirds, and swifts) have the relatively shortest humeri, whereas the least maneuverable fliers (albatrosses, alcids, cuckoos, grebes, and loons) have the relatively longest.

#### *Wing-propelled diving*

We sampled birds from three (alcids, penguins, diving petrels) evolutionary transitions to wing-propelled diving (Figs 4, 6). All have proportionately longer



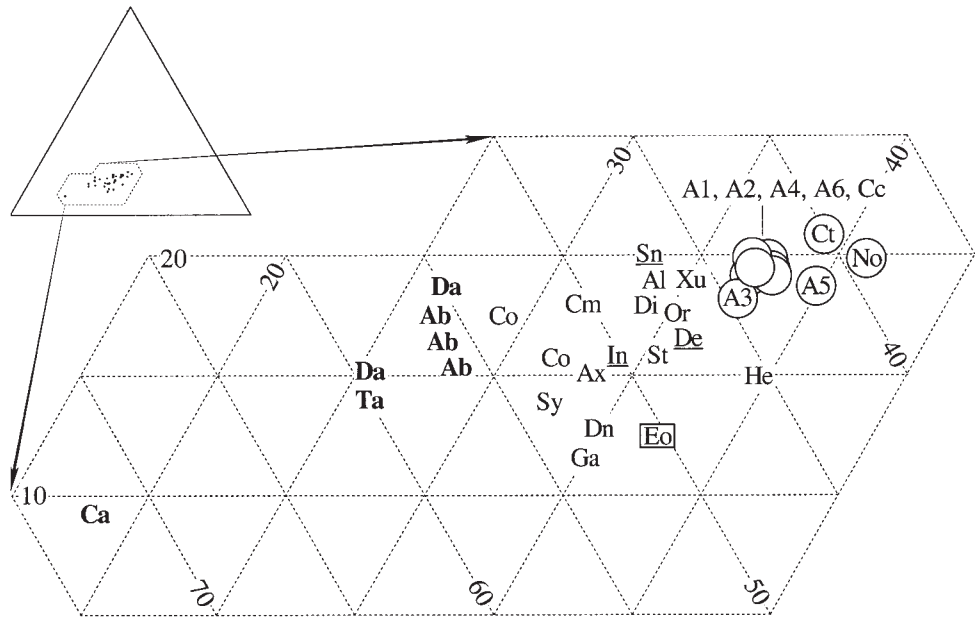


Figure 5. Forelimb proportions of non-avian theropods and early birds. Most non-birds are clustered between 45% and 55% humerus, near the basal theropod, *Eoraptor* (boxed), which may represent primitive theropod proportions. Tyrannosaurids and *Camotaurus* have highly reduced forelimbs relative to their hind limbs (bold). Note the close proximity of early birds (circled) to their most closely related non-bird taxa (underlined). Non-avian symbols: **Ab**, *Albertosaurus*; Al, *Allosaurus*; Ax, *Alxasaurus*; **Ca**, *Camotaurus*; Cm, *Compsognathus*; Co, *Coelophysis*; **Da**, *Daspletosaurus*; De, *Deinonychus*; Di, *Dilophosaurus*; Dn, *Deinocheirus*; Eo, *Eoraptor*; Ga, *Gallimimus*; He, *Herrerasaurus*; In, *Ingenia*; Or, *Ornithomimus*; Sn, *Sinornithoides*; St, *Struthiomimus*; Sy, *Syntarsus*; **Ta**, *Tarbosaurus*; Xu, *Xuanhanosaurus*. Avian symbols: A1, *Archaeopteryx* (London); A2, *Archaeopteryx* (Berlin); A3, *Archaeopteryx* (Solnhofen); A4, *Archaeopteryx* (Eichstätt); A5, *Archaeopteryx* (SAV); A6, *Archaeopteryx* (Maxberg); Cc, *Concornis*; Ct, *Cathayornis*; No, *Noguerornis*.

TABLE 1. Percentage ranges for each of the three main forelimb elements for each functional group

	Humerus	Radius	Carpometacarpus
Predatory	45–54%	29–40%	12–20%
Reduced	55–72%	19–27%	9–19%
Flying	24–45%	30–48%	15–43%
Flightless	40–64%	19–39%	8–24%
Wing-propelled diving	41–62%	25–38%	12–29%

humeri than the vast majority of birds. Alcids that fly in both water and air have the highest humeral proportions of any aerial fliers (45% in the common murre, *Uria aalge*). Extinct alcids with relatively longer humeri (*c.* 50% in the great auk, *Plautus impennes*, and *c.* 60% in mancalline auks) lost the ability to fly in air. The disparity index between wing-propelled diving birds and volant birds is 0 because these two functional groups overlap.

TABLE 2. Hind limb length (mm), forelimb length (mm), and forelimb/hind limb ratios for selected theropods. Note that limb lengths are the sum of the lengths of the three main segments, excluding phalanges. See Appendices 1 and 3 for sources

Taxon	Hind limb	Forelimb	Fore/hind
<i>Albertosaurus libratus</i> (AMNH 5664)	1928	365	0.19
<i>Albertosaurus libratus</i> (NCM 2120)	2634	578	0.22
<i>Syntarsus rhodesiensis</i> (QG 1)	563	187	0.33
<i>Allosaurus fragilis</i> (USNM 4734)	1867	655	0.35
<i>Compsognathus longipes</i> (BSP AS I 536)	211	78	0.37
<i>Dilophosaurus wetherilli</i> (UCMP 38302)	1437	567	0.39
<i>Sinornithoides youngi</i> (IVPP V.9612)	449	177	0.39
<i>Coelophysis bauri</i> (AMNH 7223)	559	224	0.40
<i>Ingenia yanshini</i> (GI 100/30)	633	268	0.42
<i>Eoraptor lunensis</i> (PVSJ 512)	390	169	0.43
<i>Struthiomimus altus</i> (AMNH 5339)	1380	641	0.46
<i>Herrerasaurus ischigualastensis</i> (PVSJ 373)	825	386	0.47
<i>Coelophysis bauri</i> (AMNH 7224)	544	256	0.47
<i>Ornithomimus edmontonicus</i> (ROM 851)	1220	582	0.48
<i>Gallimimus bullatus</i> (GI 100/11)	1915	995	0.52
<i>Deinonychus antirrhopus</i> (MCZ 4371)	882	536	0.61
<i>Archaeopteryx lithographica</i> (Eichstätt)	120	94	0.79
<i>Archaeopteryx bavarica</i> (SAV)	160	133	0.83
<i>Archaeopteryx lithographica</i> (Solnhofen)	204	186	0.91
<i>Archaeopteryx lithographica</i> (Berlin)	158	146	0.92
<i>Archaeopteryx lithographica</i> (London)	182	174	0.96
<i>Cathayornis yandica</i> (IVPP V.9769A/B)	69	67	0.97

### Flightless

Flight has been lost independently numerous times in at least 34 families of birds, including both extant and extinct forms (Livezey, 1995). We sampled 22 species of flightless birds from 12 of these families. Reduction of the distal wing elements relative to total forelimb length, resulting in a higher humeral proportion, is seen in all flightless birds (Fig. 6). This reduction causes these birds to overlap non-avian theropods in some proportions. Ratites consistently have, proportionally, among the longest humeri (e.g. short distal elements) of all birds. Flightless birds with volant relatives also exhibit a shift toward increased humeral percentage. For example, flightless members of the grebes, cormorants, ducks, parrots, and pigeons all have higher humeral proportions than do flighted members of their orders. The disparity index among flightless birds is 29, from ostriches (*Struthio*) to a flightless goose (*Cnemiornis*). The humerus is the most variable in contribution, spanning 30% in these two taxa. These figures underestimate the actual disparity. Hesperornithiformes may not have ossified the forelimb distal to the humerus or lost these segments. If the latter were true, hesperornithiformes would be located at 100% humerus. Moas appear to have lost the entire wing, and thus cannot even be plotted.

### DISCUSSION

Data from this study created intriguing distribution patterns when plotted in a ternary morphospace. Groups that we treated as functionally homogenous often proved to be more disparate than expected (Fig. 4). Theropod forelimb proportions are functionally diagnostic in some cases, but are frequently less informative due to conservation or homoplasy; similarly proportioned limbs can have vastly different

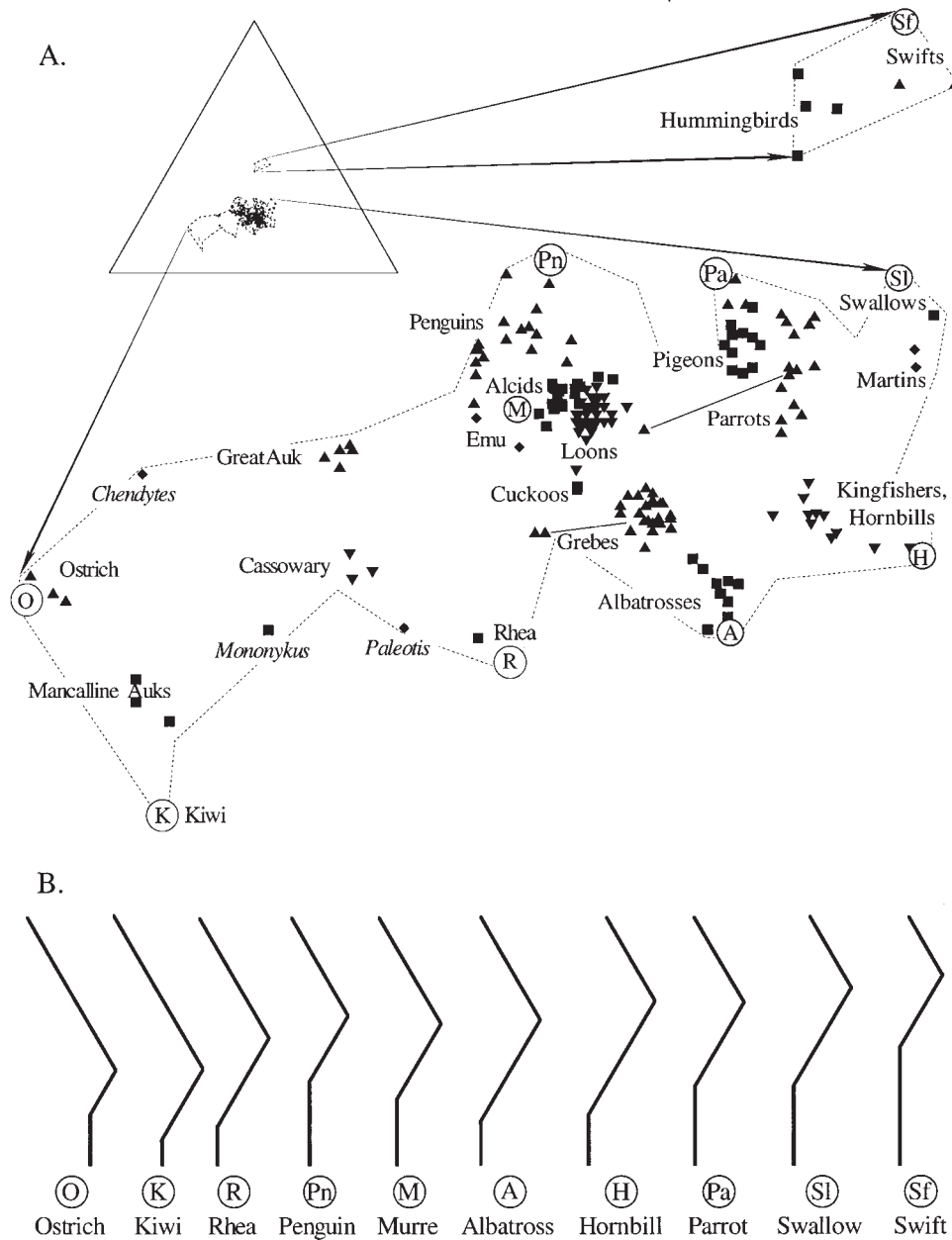


Figure 6. Forelimb proportions for selected groups of birds. A, maneuverable birds like swallows, martins, swifts, and hummingbirds have the lowest humeral contributions. As humeral contribution increases, maneuverability decreases. Loons, grebes, cuckoos, and alcids are among the least maneuverable and have high humeral percentages. B, diagrammatic forelimbs of ten birds. The first four on the left are flightless. Note the variation in proportions with flight style in the remaining six.

functions. Our discussion will focus on two central themes, within-group disparity and between-group transitions, followed by an attempt to address theropod forelimb proportions from a more biomechanical perspective.

### *Predatory*

We hypothesized that theropods retaining this function would have highly disparate forelimbs, reflecting the potential for diverse non-locomotor designs. However, proportional variation among predatory forelimbs was very low ( $DI = 7.8$ ). Such low disparity was particularly unexpected in light of the broad taxonomic sampling, tremendous size variation, and purported functional specializations of taxa in our data set. Although representatives from all major clades of non-birds are present, phylogenetic patterns are not evident in their morphospace distribution. For example, data from three ornithomimids (*Ornithomimus*, *Struthiomimus*, *Gallimimus*) are spread across the entire point cluster (Fig. 5). Predatory proportions are also unaffected by absolute limb size; forelimbs spanned more than an order of magnitude in overall length. Although *Deinocheirus* (1798 mm) has a forelimb 23 times longer than that of *Compsognathus* (77 mm), these two taxa are separated by less than five disparity units (Fig. 5).

We grouped forelimbs together as predatory, but within this category more specific functional hypotheses have been proposed. For *Struthiomimus* alone, suggestions have included: clamping and hooking (Nicholls & Russell, 1985), climbing (Gregory in Osborn, 1916), and insectivory (Beebe in Osborn, 1916). Digging has been suggested for *Gallimimus* (Osmólska, Roniewicz & Barsbold, 1972), uncovering food items for all ornithomimids (Russell, 1972), and grasping or raking for *Herrerasaurus* (Sereno, 1993). Osmólska & Roniewicz (1969: 15) concluded that the forelimbs of *Deinocheirus* were ill-suited for prehension, but more likely used for “tearing dead or weakly agile prey asunder”. Therizinosaurids such as *Alxasaurus* have been interpreted as herbivores, which used their extremely long forelimbs for grasping foliage (Russell & Russell, 1993; Russell, 1997). Chatterjee (1997) concluded that the long hands and swivel wrists of dromaeosaurids were used for climbing up vertical tree trunks. The ambiguity surrounding such ecologically relevant behaviours points out how little is known about this area of theropod biology. If non-avian theropods exhibited such functional diversity, evidence cannot be found in intramembral proportions alone. Specializations are likely more obvious in other aspects of skeletal morphology, such as the phalanges (Holtz, 1994b, 1995b; Gatesy & Middleton, 1997).

### *Reduced*

Although predatory limb morphology was retained by the majority of non-birds, two lineages, tyrannosaurids (e.g. *Tyrannosaurus*, *Albertosaurus*, *Daspletosaurus*, *Tarbosaurus*) and abelisaurids (*Carnotaurus*) independently evolved highly reduced forelimbs relative to their hind limbs (Table 1, Fig. 7). The forelimb is approximately 20% of hind limb length in *Albertosaurus* and only about 14% in *Carnotaurus*. Non-birds with reduced forelimbs cover a broad range of humeral proportions, from 55% to 72%. The lower end of this humeral range approaches predatory proportions.

The function, if any, of tyrannosaur forelimbs has a long history of debate. Hypotheses range from ‘apparently useless’ (Bakker, 1986: 272) to an active role in clutching prey to the chest (Smith & Carpenter, 1990; Carpenter & Smith, 1995), assisting the hind limbs when rising from the ground (Newman, 1970), and clasping during mating (Osborn, 1906). Proportion data do not support or falsify any of these hypotheses, but reveal only that tyrannosaur forelimbs are displaced from

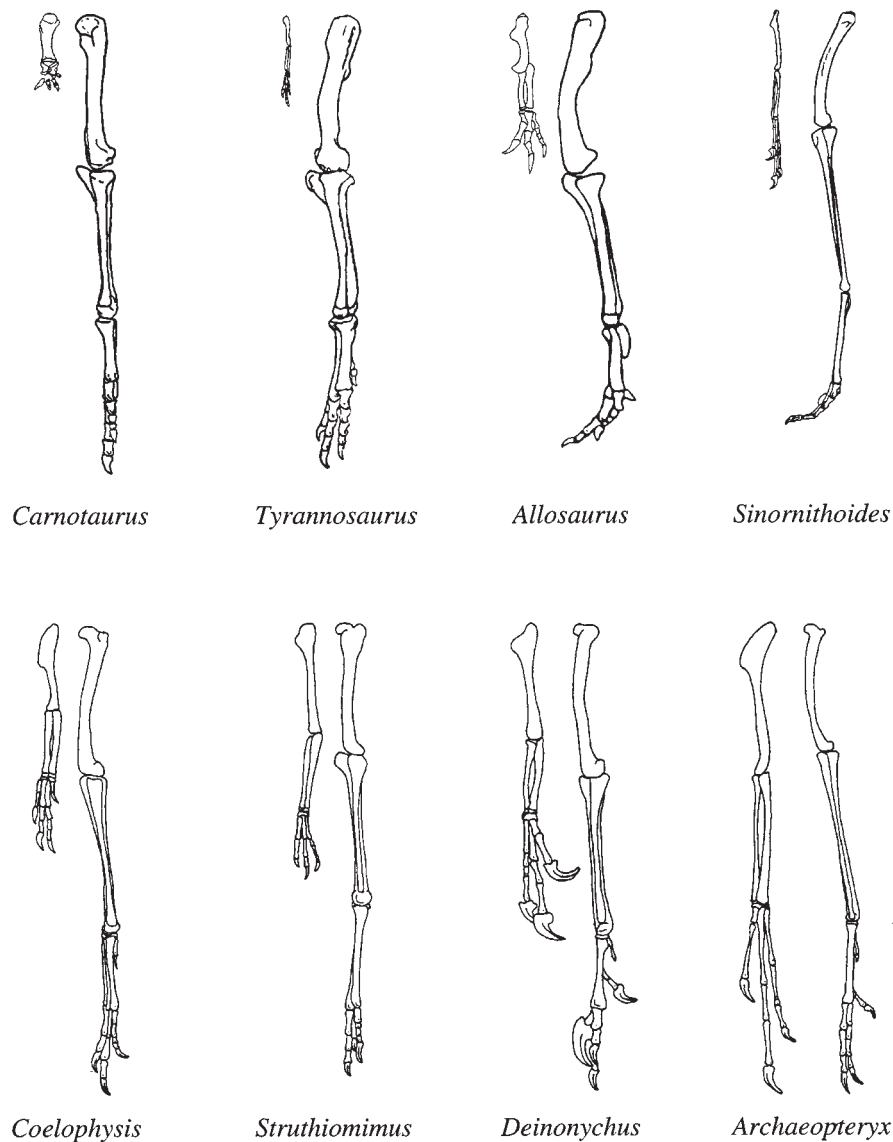


Figure 7. Relative proportions of forelimb and hind limb in various theropods. Note the extremely reduced forelimbs of *Carnotaurus* and *Tyrannosaurus*, in which forelimb length is less than 20% of the hind limb length. Forelimb/hind limb ratio is 46% in *Struthiomimus*, 61% in *Deinonychus*, and 96% in *Archaeopteryx*. This pattern is even more pronounced when phalanges and unguals are included. *Carnotaurus* modified from Bonaparte, Novas & Coria (1990); *Tyrannosaurus* modified from Heilmann (1927); *Allosaurus* after Paul (1987); *Sinornithoides* modified from Russell & Dong (1993a); *Coelophysis*, *Struthiomimus*, *Deinonychus*, and *Archaeopteryx* modified from Padian & Chiappe (1997).

other presumed predatory non-avian theropods. Although this derived position in morphospace may indicate specialization for a new role, the direction of this shift from primitive proportions is similar to that seen in birds with reduced function.

*Origin of flight*

The forelimb proportions of *Archaeopteryx* and other early birds do not deviate substantially from those of non-birds that retain the primitive function of predation (Fig. 4). The disparity index is only 2.5 between *Deinonychus* and *Archaeopteryx*, no larger than intraspecific disparity among specimens of *Archaeopteryx*, *Coelophysis*, or *Daspletosaurus*. This similarity suggests that the evolution of flight did not necessarily involve large-scale repositioning of forelimb elements. However, proportional homogeneity among non-avian theropods masks many important differences important to the origin of flight. One example is the ratio of forelimb to hind limb length (excluding phalanges), which is highly variable (Table 2). Non-avian theropods most closely related to birds have proportionately longer forelimbs than do more basal theropods (Fig. 7; Heilmann, 1927; Padian & Chiappe, 1997). *Deinonychus*, a dromaeosaur closely allied to birds, has a forelimb that is 61% of hind limb length, whereas values of 30–50% are most common in theropods further from avian ancestry. Wings of the five specimens of *Archaeopteryx* for which hind limbs are known range from 79% to 96% of hind limb length.

*Flying birds*

Given the extreme biomechanical demands of flight, the disparity among volant avian forelimbs was not anticipated. Flying may be less restrictive of limb proportions than previously thought. However, we interpret wing disparity as evidence of skeletal adaptation to different types of flight. If wings are specialized, their proportions should vary according to flight style (Norberg & Rayner, 1987; Rayner, 1988). One such pattern may be relative humerus length, which appears to correlate inversely with aerial maneuverability. As humeral contribution decreases, maneuverability increases. For instance, swallows, martins, and other Passeriformes have the shortest relative humerus length of all birds except swifts and hummingbirds. Qualitatively, these birds are considered very maneuverable fliers. Conversely, birds that are widely regarded as poorly maneuvering fliers (including loons, grebes, cuckoos, and alcids) have the highest relative humeral percentages of all flying birds, approaching the percentage (*c.* 45%) beyond which flying birds are absent (Fig. 6).

Another example is hummingbirds (Trochiliformes) and swifts (Apodiformes), which share extremely proportioned wings that are 9.7 disparity units outside the main cloud of flying birds (Fig. 6). These similar skeletal morphologies have been attributed to convergence (Cohn, 1968), but molecular evidence (Sibley & Ahlquist, 1990) suggests their unusual wing design was likely present in their most recent common ancestor. Despite superficially different flight behaviors (hovering and backward flight in hummingbirds, high-speed aerial foraging in swifts) these clades share the ability to produce thrust during the upstroke (Savile, 1950). Increased area for attachment of the stiff primary feathers relative to the secondaries may account for their exploitation of novel ternary morphospace (Savile, 1950; Cohn, 1968).

*Wing-propelled diving*

Wing-propelled diving birds may be considered in two categories, those that are also aerial fliers and those that are flightless. The alcids and diving petrels, which

are the only wing-propelled diving birds that also fly in air, share proportion morphospace with birds that are not wing-propelled divers (Fig. 6). The wings of these birds are likely constrained by the conflicting requirements of aerial and aquatic flight. Flightless wing-propelled divers, including penguins, some alcid, and *Chendytes*, span a range along the humeral axis from those of volant birds (40–45% humerus) to near ostriches (>60% humerus). Such disparity and overlap make it difficult to distinguish adaptation for wing-propelled diving from changes due to the relaxation of aerial flight demands.

### *Flightless*

Proportional differences between flightless birds and their volant relatives suggest that when flight is abandoned, the constraints that formerly shaped the wing are relaxed. Flightlessness is invariably associated with decreased distal element contribution relative to humeral percentage (Fig. 6). The shift of flightless birds toward the lower left on the ternary is not only found in birds with vestigial limbs, such as kiwis. Flightless birds that use their wings for display (ostriches) or aquatic locomotion (Great Auk, *Chendytes*, *Mancalla*, *Praemancalla*) have relatively longer humeri than their volant relatives.

The contentious Late Cretaceous theropod *Mononykus* has been described as a flightless bird (Perle *et al.*, 1993, 1994) and the sister taxon to all birds other than *Archaeopteryx*. However, the avian status of *Mononykus* has been repeatedly questioned (Ostrom, 1994; Wellnhofer, 1994; Zhou, 1995; Feduccia, 1996; Chatterjee, 1997) in part due to its unusual forelimb morphology. Wellnhofer (1994: 306), for example, stated that “it would be very difficult to imagine how a primitive bird wing, such as that of *Archaeopteryx*, could have evolved into a forelimb like that of *Mononykus*”. Similarly, Ostrom (1994: 172) concluded that *Mononykus* “never flew and never had a volant ancestry” (but see Chiappe, Norell & Clark, 1997; Padian & Chiappe, 1998). The short, stout, forelimb of *Mononykus* precludes flight, but does its design give clues to the limb function of its ancestors? Forelimb proportions of *Mononykus* (58%:28%:14%) place it within the region occupied by both flightless birds and non-avian theropods (Fig. 7). If *Mononykus* is not a bird, its proportions appear to be those of a non-avian theropod with reduced forelimbs, having undergone a shift in proportion similar to tyrannosaurs and *Carnotaurus*. On the other hand, if *Mononykus* had volant ancestors, they likely had humeral percentages less than 45%, which increased after the loss of flight. Thus, the ternary location confirms that *Mononykus* could not fly, but is unable to discriminate between primary and secondary flightlessness.

### *Limb proportion theory*

As obligate bipeds, theropods possessed forelimbs free from locomotor constraints that were present in quadrupedal archosaurs. Those archosaurs which used their forelimbs during terrestrial locomotion consistently had forelimbs with relatively longer humeri and radii as well as short metacarpals. Theropod forelimbs are localized to an area of less than 20% of the total proportion morphospace (Fig. 3). We hoped that by visualizing this pattern and the distribution of theropods within



it, we might gain insight into the factors influencing limb design in this clade. Herein we offer initial hypotheses for non-terrestrial forelimb design from a more theoretical and biomechanical perspective. We address five potential factors: limb folding, limb inertia, spatial access, minimum proportions, and developmental pathways.

#### *Limb folding*

During bipedal locomotion, interference between limbs could be reduced by tucking the forelimbs up against the body. Limb folding is likely most important in theropods with relatively long forelimbs and those that must protect flight feathers from damage. A limb's proportions will affect how compactly it can fold. Predicted proportions for optimal limb folding depend on the degree of flexibility at the shoulder, elbow, wrist, metacarpophalangeal (MP), and interphalangeal (IP) joints. Primitively, the wrist in theropods appears to have been less mobile than the other joints. Compact limb folding with a stiff wrist could have been achieved by bringing the humerus against the body and flexing the elbow, MP, and IP joints. A limb's folded length would be minimized if the humerus were 50% of limb length (Fig. 8A). The radius and carpometacarpus would sum to 50%, forming a V-configuration limb in which the MP joint was nearest the shoulder. Predatory non-birds have humeri approximately 50% of the forelimb (Fig. 3); this would be predicted if the wrist was more restricted than the elbow, such that the forearm and palm effectively constituted a single segment during folding.

In contrast, the wrist of most birds can undergo substantial ulnar deviation, enabling them to fold the wings up in a Z-configuration (Fig. 8B). This flexibility first evolved in non-avian theropods and is present, at least to some degree, in forms such as *Deinonychus* (Ostrom, 1969; Gauthier & Padian, 1985). The ideal proportions for Z-folding would be for the humerus, radius, and hand (carpometacarpus + phalanges) to be of equal length. Having the humerus and radius of comparable length positions the wrist near the shoulder when the limb is fully folded. The wings of many flying birds lie on or near the midline of the ternary diagram, indicating that they have humeri and radii of similar length (Fig. 3). We did not measure phalanges, but if their length were added to the carpometacarpus it would raise the proportions of many wings closer to the center of the ternary (33%:33%:33%). Flightless birds are likely freed from folding constraints because their wings are either relatively small (e.g. ratites) or have less mobile joints for aquatic use (Raikow, Bicanovsky & Bledsoe, 1988).

#### *Limb inertia*

Wings that flap would benefit from minimizing limb inertia. Although feathers make up the distal portion, skeletal elements and soft tissues form the framework of the wing. If elements were proportioned to reduce total limb inertia, the proximal segments should be shortened because they bear the most muscle. In contrast to folding, high frequency flapping would favour a humerus shorter than the radius; such limbs are found on the right half of the ternary (Fig. 8B). The radius is up to 50% longer than the humerus in some birds, including the most maneuverable fliers, which might benefit from inertial reduction.

#### *Spatial access*

During predation, theropod forelimbs access regions around the shoulder to grasp and clutch prey. When the fully extended limb is rotated about the shoulder joint,



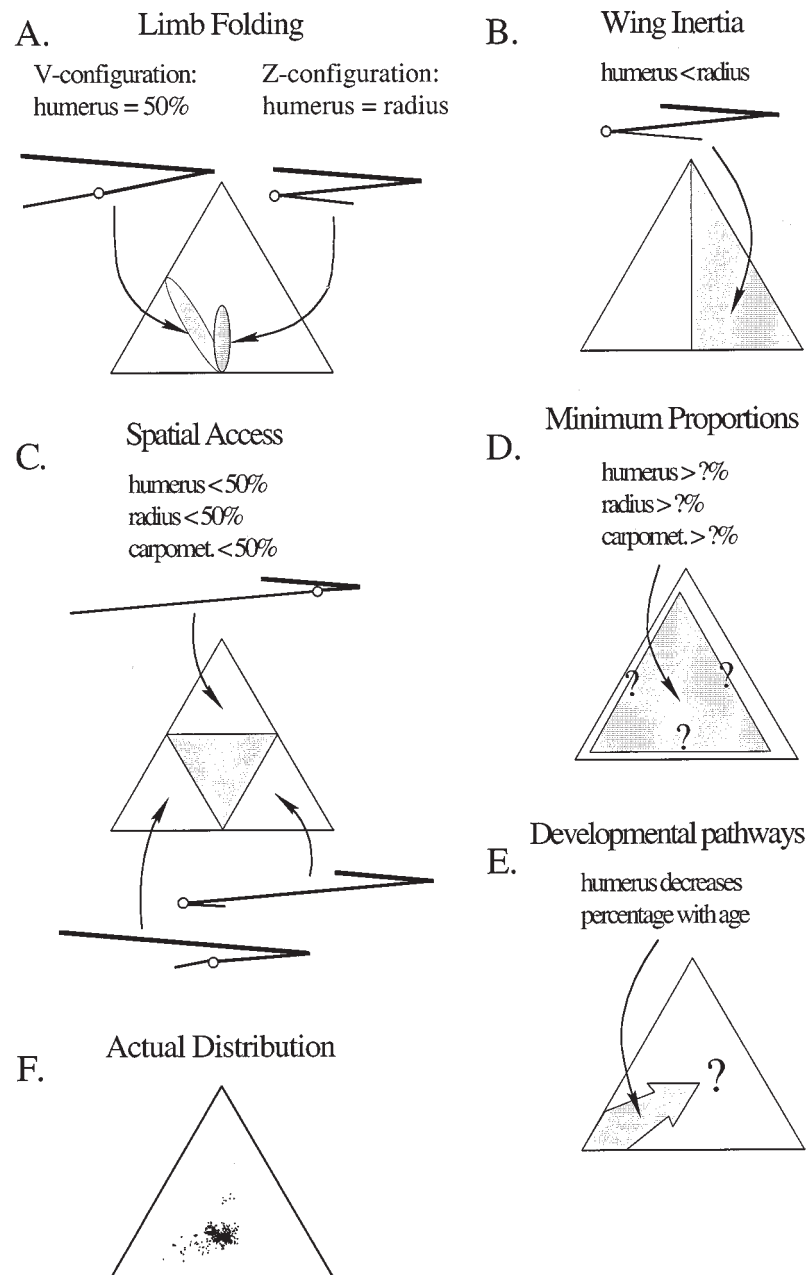


Figure 8. Factors potentially influencing limb design. Proportions favored for each factor are shown as shaded regions of ternary morphospace. Simplified limb models consist of humerus (thick line), radius (medium line), wrist joint (circle) and carpometacarpus (thin line). See text for details.

its distal tip delineates a spherical volume of space in which the limb operates. Proportions affect a limb's ability to reach the space within its maximum span. Only a subset of possible limb proportions allow access to the entire volume of the sphere.

To permit full accessibility, limbs should be restricted to a triangular subset of morphospace in which no element is more than 50% of the limb (Fig. 8C). If one element were more than half the limb length, the other two segments would not be long enough to reach the innermost volume around the shoulder. Despite the simplicity of this model, which does not include phalanges or restrict joint movement, theropod distribution within the morphospace conforms remarkably well to these predictions. Most theropods are found within a central region of the ternary, with radii up to *c.* 48% and carpometacarpi up to *c.* 43%. Predatory non-birds have humeri approximately 50% of the limb. However, the humerus is up to 70% of limb length in a few theropods, those whose limbs are reduced with questionable functionality.

#### *Minimum proportions*

Regions near the edges of ternary morphospace may be off limits due to the constructional demands of joints and muscles (Fig. 8D). First, the absolute lengths of the humerus, radius and carpometacarpus may be restricted by the amount of bone needed to form complete joints on each end. Even if the diaphysis (shaft) were eliminated, the two articular ends would have a finite length. This restriction may have a proximo-distal gradient. The humerus, as a single element at the base of the limb, has a larger diameter and more expansive joint surface than the paired bones of the forearm or the multiple elements of the hand. Second, the functional demands of muscle may set minimum bone lengths. Because bone and muscle lengths are correlated, a very short bone will carry very short muscles, with few sarcomeres in series. Such a muscle will have a limited operational range, and may not be capable of the length changes required for proper joint excursion. For example, a very short humerus would bear a very short humerotriceps muscle, which could limit elbow mobility. Again, proximal elements may be influenced more than distal ones. Phalanges and carpals, for example, lack long, fleshy muscle attachments and can therefore be both absolutely and relatively short. However, we do not know what these minima might be. *Carnotaurus* provides evidence that they are as low as 20% for the radius and 10% for the carpometacarpus. However, even a minimum proportion of 5% for each element would reduce the area of viable ternary morphospace by one fourth.

#### *Developmental pathways*

A final factor that likely biases the distribution of theropod limb proportions is embryonic development and growth. Paedomorphosis is one of the primary mechanisms that have been proposed for the evolution of flightlessness (Livezey, 1995). A ternary diagram may be a convenient way to visualize limb proportion ontogeny in extant birds. Changes in wing proportions from embryonic limb formation through adulthood should form a trajectory through proportion morphospace. Preliminary analysis of wing growth in *Larus californicus* reveals such a shift. The humerus progressively decreases in relative length from *c.* 43% in hatchlings to *c.* 38% in adults of this gull (data courtesy of D. Carrier). If other species grow along a similar trajectory (towards relatively shorter humeri, Fig. 8E), the presence of theropods in the lower left of the ternary could be described by heterochrony. Changes in developmental timing could lead to adult flightless birds with proportions resembling a juvenile stage of their flying ancestor.

## CONCLUSIONS AND PROSPECTS

Despite many recent advances in theropod palaeobiology, the evolution of limb design remains poorly understood. The paucity of functional studies may result from an inability to compare limbs of vastly different size, shape, and function. In this study we present the distribution of theropod forelimb elements in a morphospace. Such a visualization of disparity is a foundation for functional study, because it reveals patterns which require explanation. We selected five factors that we think may play a role in the evolution of theropod forelimb design. Clearly, our predictions do not completely explain the distribution of theropods in proportion morphospace, but they are a first step towards understanding theropod disparity. More realistic models incorporating joint mobility data and phalanges may help answer questions raised by our data. One that we find particularly intriguing is the absence of flying birds with humeri greater than 45% of the limb. Is this a true biomechanical limit imposed by flight, a side effect of other factors such as limb folding, or just a product of chance?

In a larger sense, our study highlights a conspicuous lack of vertebrate disparity studies in light of invertebrate analyses [ammonoids (Saunders & Swan, 1984; Swan & Saunders, 1987), arthropods (Briggs & Fortey, 1989; Foote, 1989; Gould, 1991, 1993; Briggs, Fortey & Wills, 1992a,b; Ridley, 1993; Lee, 1992; Foote & Gould, 1993; Wills, Briggs & Fortey, 1994), crinoids (Foote, 1994a,b, 1995a,b, 1996), gastropods (Wagner, 1995), rostroconch molluscs (Wagner, 1997), blastozoan echinoderms (Foote, 1992), and priapulids (Wills, 1998)]. We echo Gould's (1991: 420) plea "to define a full range of the abstract (and richly multivariate) space into which all organisms may fit (the morphospace)". As with invertebrates, studies of vertebrate morphological disparity possess tremendous potential for insights into major patterns of evolution.

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## APPENDIX 1

Non-avian theropod limb segment lengths (in mm; H, humerus; R, radius; MC, metacarpal II; †, ulna)

Species	Number	H	R	MC	Source
<i>Albertosaurus libratus</i>	NCM 2120	324	156	98	Russell (1970)
<i>Albertosaurus libratus</i>	AMNH 5664	205	100	60	Russell (1970)
<i>Allosaurus fragilis</i>	USNM 4734	310	222	123	Gilmore (1920)
<i>Alxasaurus elesitaiensis</i>	IVPP 88402	375	245	111	Russell & Dong (1993a)
<i>Carnotaurus sastrei</i>	MACN-CH 894	285	73	37	Bonaparte, Novas & Coria (1990)
<i>Coelophysis bauri</i>	AMNH 7223	120	65	39	Colbert (1989)
<i>Coelophysis bauri</i>	AMNH 7224	134	82	40	Colbert (1989)
<i>Compsognathus longipes</i>	BSP AS I 536	~39	24	14	Ostrom (1978)
<i>Daspletosaurus torosus</i>	NMC 8506	357	171	120	Russell (1970)
<i>Daspletosaurus torosus</i>	NMC 11315	225	96	58	Russell (1970)
<i>Deinocerurus mirificus</i>	ZPAL MgD-I/6	938	630	230	Osmólska & Roniewicz (1969)
<i>Deinonychus antirrhopus</i>	MCZ 4371	254	192	>90	Ostrom (1976a)
<i>Dilophosaurus wetherilli</i>	UCMP 37302	270	192	105	Welles (1984)
<i>Eoraptor lunensis</i>	PVSJ 512	85	63	21	Sereno (pers. comm.)
<i>Gallimimus bullatus</i>	GI 100/11	530	350	115	Osmólska, Roniewicz & Barsbold (1972)
<i>Herrerasaurus ischigualastensis</i>	PVSJ 373	~175	153	58	Sereno (1993)
<i>Ingenia yanshini</i>	GI 100/30	~135	~91	~42	Barsbold <i>et al.</i> (1990)
<i>Ornithomimus edmontonicus</i> †	ROM 851	276	206	100	Russell (1972)
<i>Sinornithoides youngi</i>	IVPP V9612	~83	59.1	~35	Russell & Dong (1993b)
<i>Struthiomimus altus</i>	AMNH 5339	310	228	103	Osborn (1916)
<i>Syntarsus rhodesiensis</i>	QG 1	100	61	26	Raath (1969)
<i>Tarbosaurus efremovi</i>	PIN 552-1	255	110	60	Maleev (1974)
<i>Xuanhanosaurus qilixiaensis</i>	IVPP V6729	265	202	109	Dong (1984)



## APPENDIX 2

Avian limb segment lengths (in mm; H, humerus; R, radius; CM, carpometacarpus)

Species	H	R	CM	Specimen Number
STRUTHIONIFORMES				
Struthionidae				
<i>Struthio camelus</i>	395.0	120.0	100.0	MCZ 2686
<i>Struthio camelus</i>	377.0	120.0	98.0	MCZ 2686
<i>Struthio camelus</i>	268.0	81.0	72.0	MCZ 1628
<i>Struthio camelus</i>	294.0	96.3	75.2	YPM 4347
Rheidae				
<i>Rhea americana</i>	260.0	184.0	77.0	MCZ 2083
<i>Rhea americana</i>	281.0	210.0	78.0	YPM 11524
Casuariidae				
<i>Casuaris bennetti</i>	69.0	39.0	22.0	MCZ display
<i>Casuaris</i> sp.	72.3	42.4	23.8	YPM 4351
<i>Casuaris</i> sp.	62.9	35.1	21.4	YPM 2123
<i>Dromecius novaehollandiae</i>	89.0	65.0	43.0	MCZ 198
<i>Dromecius novaehollandiae</i>	92.0	62.0	45.0	MCZ 1627
Apterygidae				
<i>Apteryx oweni</i>	39.2	17.5	5.1	MCZ 308
TINAMIFORMES				
Tinamidae				
<i>Crypturellus boucardi</i>	49.0	48.5	28.7	MCZ 2750
<i>Crypturellus noctivagus</i>	58.2	54.9	32.5	MCZ 276
<i>Nothura maculosa</i>	43.3	41.3	24.7	MCZ 1653
<i>Tinamus major</i>	75.0	72.2	42.6	MCZ 2774
<i>Tinamus tao</i>	80.0	80.9	45.8	MCZ 3705
CRACIFORMES				
Cracidae				
<i>Crax alberti</i>	109.0	105.0	53.0	MCZ 209
<i>Crax mitu</i>	110.0	107.0	55.0	MCZ 3575
<i>Crax pauxi</i>	110.0	111.0	56.0	MCZ 2121
<i>Ortalis vetula</i>	60.0	50.0	27.5	MCZ 3099
<i>Penelope purpurascens</i>	92.0	87.0	46.0	MCZ 293
<i>Penelopina nigra</i>	118.0	113.0	54.0	MCZ 2084
Megapodiidae				
<i>Macrocephalon maleo</i>	85.0	86.0	45.8	MCZ 355
GALLIFORMES				
Phasianidae				
<i>Agriocharis ocellata</i>	131.0	116.7	64.1	MCZ 2878
<i>Agriocharis ocellata</i>	119.0	108.0	61.0	MCZ 3049
<i>Agriocharis ocellata</i>	125.0	113.0	64.0	MCZ 3046
<i>Bonasa umbellus</i>	49.1	41.9	28.1	MCZ 7935
<i>Bonasa umbellus</i>	51.9	43.3	27.4	MCZ 7371
<i>Bonasa umbellus</i>	49.5	42.3	27.0	MCZ 6061
<i>Bonasa umbellus</i>	50.8	42.3	27.7	MCZ 7666
<i>Centrocercus urophasianus</i>	95.1	80.3	43.7	MCZ 110
<i>Centrocercus urophasianus</i>	87.7	85.0	46.6	MCZ 1441
<i>Coturnix coturnix</i>	33.6	26.7	18.8	MCZ 3164
<i>Coturnix coturnix</i>	33.8	27.1	18.7	MCZ 3298
<i>Coturnix delegorguei</i>	31.4	25.3	17.1	MCZ 3037
<i>Excalfactoria chinensis</i>	25.9	20.3	13.8	MCZ 7497
<i>Gallus gallus</i>	99.5	86.5	51.0	SMG pers. coll.
<i>Lagopus mutus</i>	63.4	54.1	33.5	MCZ 1469
<i>Lophortyx gambelli</i>	33.1	26.9	17.5	MCZ 7254
<i>Meleagris gallopavo</i>	144.0	129.0	73.0	MCZ 7157
<i>Meleagris gallopavo</i>	129.0	119.0	65.0	MCZ 819
<i>Meleagris gallopavo</i>	156.0	138.0	78.0	MCZ 1494
<i>Pavo cristatus</i>	131.0	108.0	63.0	MCZ 311

continued

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
GALLIFORMES				
Phasianidae				
<i>Pavo cristatus</i>	126.0	103.0	61.0	MCZ 2651
<i>Tetrao urogallus</i>	98.9	90.0	51.8	MCZ 315
<i>Tetrao urogallus</i>	131.1	119.7	67.6	MCZ 314
<i>Tympanuchus cupido</i>	65.6	55.4	34.9	MCZ 2193
Numididae				
<i>Guttera pucherani</i>	74.0	64.0	38.0	MCZ 2098
<i>Numida meleagris</i>	79.0	66.0	38.0	MCZ 1648
Odontophoridae				
<i>Callipepla squamata</i>	33.9	29.2	17.4	MCZ 1254
<i>Colinus nigrogularis</i>	32.5	26.6	17.3	MCZ 5029
<i>Colinus virginianus</i>	35.6	28.5	17.9	MCZ 7347
<i>Colinus virginianus</i>	36.1	29.1	18.9	MCZ 7337
<i>Dactylortyx thoracicus</i>	37.4	33.4	18.9	MCZ 2786
<i>Odontophorus guttatus</i>	43.8	39.3	23.0	MCZ 2727
<i>Odontophorus guttatus</i>	42.5	38.3	20.9	MCZ 2770
ANSERIFORMES				
Anhimidae				
<i>Anhima cornuta</i>	213.0	238.0	106.0	MCZ 1387
<i>Anhima cornuta</i>	183.0	181.0	90.0	MCZ 6993
<i>Chauna chavaria</i>	175.0	192.0	94.0	MCZ 307
Dendrocygnidae				
<i>Dendrocygna autumnalis</i>	92.0	93.0	52.0	MCZ 273
<i>Dendrocygna bicolor</i>	95.0	93.0	49.0	MCZ 7071
Anatidae				
<i>Aix sponsa</i>	67.0	51.0	43.0	MCZ 7372
<i>Alopochen aegyptiacus</i>	138.0	126.0	83.0	MCZ 260
<i>Anas clypeata</i>	73.0	58.0	44.5	MCZ 7105
<i>Anas platyrhynchos</i>	89.0	67.0	56.0	MCZ 1898
<i>Anas platyrhynchos</i>	74.0	56.0	45.0	MCZ 1914
<i>Anas rubripes</i>	89.0	70.0	56.0	MCZ 2850
<i>Anas specularoides</i>	95.0	78.0	58.0	MCZ 3053
<i>Anser caerulescens</i>	138.0	129.0	75.0	MCZ 1883
<i>Anser erythropus</i>	181.0	164.0	104.0	MCZ 330
<i>Anser fabalis</i>	147.0	131.0	83.0	MCZ 262
<i>Aythya marila</i>	79.0	64.0	43.0	MCZ 1471
<i>Biziura lobata</i>	104.0	88.0	60.0	MCZ 2067
<i>Branta canadensis</i>	185.0	164.0	104.0	MCZ 6738
<i>Branta canadensis</i>	170.0	153.0	95.0	MCZ 7645
<i>Branta leucopsis</i>	142.0	127.0	80.0	MCZ 6931
<i>Bucephala albeola</i>	64.0	52.0	37.0	MCZ 1915
<i>Cairina moschata</i>	110.0	88.0	68.0	MCZ 1901
<i>Callonetta leucophrys</i>	60.0	50.0	38.0	MCZ 7445
<i>Cereopsis novaehollandiae</i>	168.0	157.0	90.0	MCZ 7095
<i>Chloephaga picta</i>	162.0	147.0	89.0	MCZ 3031
<i>Clangula hyemalis</i>	70.0	58.0	44.0	MCZ 6497
<i>Cygnus atratus</i>	163.0	149.0	95.0	MCZ 6936
<i>Cygnus cygnus</i>	269.0	260.0	132.0	MCZ 335
<i>Cygnus columbianus?</i>	310.0	275.0	145.0	MCZ 3544
<i>Histrionicus histrionicus</i>	69.0	55.0	43.0	MCZ 2957
<i>Melanitta fusca</i>	96.0	83.0	58.0	MCZ 6956
<i>Merganetta armata</i>	53.0	40.0	27.0	MCZ 5094
<i>Mergus castor</i>	86.0	62.0	44.0	MCZ 1436
<i>Mergus merganser</i>	85.0	60.5	43.7	MCZ 1436
<i>Mergus merganser</i>	102.1	78.6	61.8	MCZ 318
<i>Mergus serrator</i>	90.0	70.0	52.0	MCZ 2835
<i>Netta peposaca</i>	94.0	75.0	53.0	MCZ 2988
<i>Oxyura australis</i>	78.0	62.0	36.0	MCZ 1437

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Anatidae				
<i>Plecopterus gambensis</i>	178.0	158.0	94.5	MCZ 196
<i>Somateria mollissima</i>	110.0	89.0	67.0	MCZ 7453
<i>Tachyeres brachypterus</i>	114.0	85.0	62.0	MCZ 2204
<i>Tadorna tadorna</i>	113.0	101.0	69.0	MCZ 7538
PICIFORMES				
Ramphastidae				
<i>Pteroglossus aracari</i>	70.0	81.0	34.0	MCZ 1498
<i>Ramphastos toco</i>	70.0	81.0	34.0	MCZ 6051
Picidae				
<i>Colaptes cafer</i>	41.0	41.6	21.5	MCZ 3624
<i>Dryocopus pileatus</i>	54.5	57.7	30.5	MCZ 1396
<i>Melanerpes erythrocephalus</i>	38.5	39.6	19.5	MCZ 1397
<i>Picus viridis</i>	40.8	43.7	21.5	MCZ 346
GABULIFORMES				
Bucconidae				
<i>Monasa morphoeus</i>	30.7	40.4	15.4	MCZ 6107
BUCEROTIFORMES				
Bucerotidae				
<i>Buceros bicornis</i>	137.0	181.0	66.8	MCZ 7859
<i>Buceros rhinoceros</i>	133.0	186.0	67.0	MCZ 1446
TROGONIFORMES				
Trogonidae				
<i>Trogon massena</i>	42.8	44.7	23.0	MCZ 2769
CORACIIFORMES				
Momotidae				
<i>Momotus mexicanus</i>	37.7	42.1	18.3	MCZ 3065
Alcedinidae				
<i>Alcedo atthis</i>	25.0	29.5	12.9	MCZ 2721
<i>Alcedo atthis</i>	19.9	23.7	9.7	MCZ 84
Halcyonidae				
<i>Dacelo novaeguineae</i>	64.0	76.6	32.4	MCZ 2079
<i>Halcyon chloris</i>	35.8	43.1	17.9	MCZ 1777
<i>Halcyon chloris</i>	34.9	42.9	16.8	MCZ 7002
<i>Halcyon chloris</i>	37.3	46.3	18.2	MCZ 6907
<i>Halcyon sancta</i>	30.5	36.7	15.2	MCZ 1802
<i>Halcyon sancta</i>	29.5	36.1	15.0	MCZ 6768
Cerylidae				
<i>Megaceryle alcyon</i>	46.4	55.2	25.1	MCZ 7285
CUCULIFORMES				
Opisthocomidae				
<i>Opisthocomus hoatzin</i>	69.0	63.1	40.3	MCZ 3617
<i>Opisthocomus hoatzin</i>	69.3	64.6	36.4	MCZ 5084
<i>Opisthocomus hoatzin</i>	71.0	65.0	38.0	YPM 2437
Neomorphidae				
<i>Geococcyx californianus</i>	47.0	38.0	21.0	MCZ 1495
PSITTACIFORMES				
Psittacidae				
<i>Amazona farinosa</i>	65.3	74.7	46.2	MCZ 3384
<i>Amazona farinosa</i>	66.7	77.3	47.5	MCZ 3062
<i>Amazona farinosa</i>	64.8	72.1	42.9	MCZ 2869
<i>Ara macao</i>	87.4	104.1	69.8	MCZ 3704
<i>Ara macao</i>	78.6	92.7	61.3	MCZ 6930
<i>Ara macao</i>	82.2	97.4	59.0	MCZ 2241
<i>Calyptorhynchus magnificus</i>	78.8	91.0	59.2	MCZ 359
<i>Cacatua galerita</i>	87.5	97.0	53.0	MCZ 1392
<i>Cacatua galerita</i>	86.2	96.7	54.0	MCZ 1974

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
PSITTACIFORMES				
Psittacidae				
<i>Kakatoe leadbeateri</i>	66.8	75.7	46.3	MCZ 1991
<i>Nestor meridionalis</i>	65.0	68.3	49.3	MCZ 1490
<i>Pionus senilis</i>	42.9	48.0	33.3	MCZ 2899
<i>Pionus senilis</i>	42.1	47.8	32.5	MCZ 2886
<i>Probosciger aterionus</i>	86.8	99.7	55.8	MCZ 1491
<i>Probosciger aterionus</i>	76.8	89.6	49.5	MCZ 1369
<i>Strigops habroptilus</i>	78.9	71.8	43.6	MCZ 309
<i>Trichoglossus ornatus</i>	27.9	28.5	20.9	MCZ 1926
<i>Trichoglossus ornatus</i>	26.0	25.8	20.3	MCZ 1929
<i>Trichoglossus ornatus</i>	26.4	27.5	20.9	MCZ 1997
APODIFORMES				
Apodidae				
<i>Apus apus</i>	12.2	17.7	20.7	MCZ 2077
<i>Apus apus</i>	12.9	16.5	20.4	MCZ 349
<i>Chaetura pelagica</i>	9.2	12.1	16.3	MCZ 3118
TROCHILIFORMES				
Trochilidae				
<i>Archilochus colubris</i>	3.8	4.0	5.2	MCZ 7644
<i>Archilochus colubris</i>	3.9	4.0	5.6	MCZ 7397
<i>Glaucis hirsuta</i>	6.6	6.7	8.3	MCZ 6140
<i>Patagona gigas</i>	10.2	11.4	14.3	MCZ 246
STRIGIFORMES				
Tytonidae				
<i>Tyto alba</i>	83.0	91.0	43.0	MCZ 352
<i>Tyto alba</i>	84.0	90.0	43.0	MCZ 656
Strigidae				
<i>Aegolius acadica</i>	40.0	44.3	19.7	MCZ 3772
<i>Aegolius funereus</i>	43.4	48.8	22.0	MCZ 2828
<i>Asio flammeus</i>	78.1	85.5	40.9	MCZ 6053
<i>Asio otus</i>	78.2	84.9	41.0	MCZ 7534
<i>Bubo africanus</i>	102.0	113.0	50.0	MCZ 255
<i>Bubo virginianus</i>	130.0	143.0	65.0	MCZ 2174
<i>Bubo virginianus</i>	130.0	146.0	66.0	MCZ 7017
<i>Ciccaba virgata</i>	77.0	85.0	37.5	MCZ 3007
<i>Nyctea scandiaca</i>	156.0	169.0	84.0	MCZ 6933
<i>Otus asio</i>	54.5	58.0	28.5	MCZ 3763
<i>Otus asio</i>	57.5	61.0	30.0	MCZ 6009
<i>Pulsatrix perspicata</i>	109.0	116.0	50.0	MCZ 3702
<i>Speotyto cunicularia</i>	61.0	73.0	35.0	MCZ 270
<i>Strix varia</i>	114.0	120.0	56.0	MCZ 1414
<i>Strix varia</i>	98.0	102.0	48.0	MCZ 2934
Steatornithidae				
<i>Steatornis caripensis</i>	73.6	105.0	44.3	MCZ 1404
Aegothelidae				
<i>Podargus ocellatus</i>	87.7	97.0	40.7	MCZ 1400
Caprimulgidae				
<i>Caprimulgus ridgwayi</i>	31.3	36.4	20.2	MCZ 2974
<i>Caprimulgus vociferus</i>	32.0	39.5	21.5	MCZ 1402
<i>Caprimulgus vociferus</i>	31.5	37.0	19.0	MCZ 2416
<i>Chordeiles minor</i>	43.0	49.0	28.0	MCZ 7266
<i>Chordeiles minor</i>	40.0	47.0	25.5	MCZ 3783
<i>Chordeiles minor</i>	41.2	47.0	26.1	MCZ 1480
<i>Nyctidromus albigollis</i>	35.0	40.6	22.2	MCZ 3422
COLUMBIFORMES				
Columbidae				
<i>Caloenas nicobarica</i>	58.5	63.0	39.2	MCZ 6958

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
COLUMBIFORMES				
Columbidae				
<i>Columba aquatrix</i>	50.6	52.8	35.6	MCZ 6798
<i>Columba cayennensis</i>	39.6	42.6	28.2	MCZ 5012
<i>Columba livia</i>	44.1	47.2	33.0	MCZ 1250
<i>Columba speciosa</i>	42.8	43.6	29.0	MCZ 4062
<i>Columbina talpacoti</i>	21.2	22.2	14.0	MCZ 3514
<i>Ducula aenea</i>	55.9	57.8	36.3	MCZ 7543
<i>Ectopistes migratorius</i>	42.4	44.2	30.5	MCZ 2355
<i>Geotrygon montana</i>	34.5	37.8	24.3	MCZ 2759
<i>Leptoptila verreauxi</i>	34.2	35.4	22.9	MCZ 3591
<i>Ocyphaps lophotes</i>	37.6	35.3	23.6	MCZ 279
<i>Zenaidura macroura</i>	31.0	32.4	21.8	MCZ 2109
GRUIFORMES				
Otididae				
<i>Ardeotus australis</i>	220.0	239.0	101.0	MCZ 2856
<i>Ardeotus kori</i>	246.0	262.0	118.0	MCZ 2192
<i>Chlamydotis undulata</i>	135.0	144.0	70.0	MCZ 194
<i>Chlamydotis undulata</i>	109.0	112.0	58.0	MCZ 297
Gruidae				
<i>Balearica pavonina</i>	201.0	213.0	92.0	MCZ 3601
<i>Balearica pavonina</i>	198.0	206.0	94.0	MCZ 2952
<i>Balearica pavonina</i>	188.0	190.0	88.0	MCZ 200
<i>Grus antigone</i>	277.0	306.0	125.0	MCZ 6600
<i>Grus canadensis</i>	214.0	237.0	108.0	MCZ 2483
<i>Grus canadensis</i>	235.0	255.0	121.0	MCZ 7482
<i>Grus canadensis</i>	208.0	223.0	97.0	MCZ 1336
<i>Grus leucogeranus</i>	266.0	287.0	123.0	MCZ 339
<i>Grus paradisea</i>	214.0	231.0	106.0	MCZ 7481
<i>Grus virgo</i>	171.0	194.0	93.0	MCZ 3036
<i>Grus virgo</i>	215.0	229.0	104.0	MCZ 7569
<i>Grus virgo</i>	178.0	194.0	95.0	MCZ 208
Heliornithidae				
<i>Aramus guarauna</i>	103.0	106.0	58.0	MCZ 3576
<i>Aramus guarauna</i>	110.0	111.0	62.0	MCZ 1383
Cariamidae				
<i>Cariama cristata</i>	107.0	97.0	50.0	MCZ 1011
<i>Cariama cristata</i>	103.0	96.0	55.0	MCZ 207
Rallidae				
<i>Gallirallus australis</i>	53.5	37.3	28.4	YPM 13391
<i>Gallirallus australis</i>	55.2	39.0	29.0	YPM 13475
<i>Gallirallus australis</i>	50.5	35.1	25.7	YPM 13420
<i>Gallirallus australis</i>	56.2	38.1	28.0	YPM 13421
<i>Gallirallus australis</i>	59.0	38.3	29.9	YPM 556
<i>Porphyrio porphyrio</i>	75.5	64.4	42.6	MCZ 321
CICONIIFORMES				
Scolopacidae				
<i>Bartramia longicauda</i>	49.8	54.0	30.1	MCZ 1246
<i>Bartramia longicauda</i>	49.7	53.6	31.1	MCZ 2107
<i>Limosa fedoa</i>	76.4	80.9	44.8	MCZ 1384
<i>Numenius americanus</i>	100.7	108.7	55.0	MCZ 454
<i>Numenius arquata</i>	94.4	100.9	53.5	MCZ 2108
<i>Numenius arquata</i>	95.6	99.1	53.5	MCZ 1385
<i>Phalaropus lobatus</i>	28.2	28.3	18.1	MCZ 2702
<i>Phalaropus fulicarius</i>	33.6	33.0	20.1	MCZ 7369
<i>Tringa flavipes</i>	42.7	44.1	25.5	MCZ 2693
<i>Tringa flavipes</i>	40.7	42.5	25.8	MCZ 2657

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APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Jacaniidae				
<i>Actophilornis albinucha</i>	48.4	52.4	34.1	MCZ 284
<i>Jacana spinosa</i>	39.8	40.4	22.6	MCZ 7013
<i>Jacana spinosa</i>	40.4	42.1	23.2	MCZ 6943
<i>Jacana spinosa</i>	37.4	40.5	22.6	MCZ 7060
Burhinidae				
<i>Burhinus capensis</i>	71.9	76.2	36.7	MCZ 6978
<i>Burhinus capensis</i>	82.4	88.7	43.4	MCZ 5077
<i>Burhinus magnirostris</i>	99.9	104.8	46.9	MCZ 285
Charadriidae				
<i>Himantopus himantopus</i>	51.9	54.3	31.8	MCZ 191
<i>Himantopus himantopus</i>	56.3	59.7	35.2	YPM 2192
<i>Himantopus himantopus</i>	59.8	62.3	36.8	YPM 5950
<i>Himantopus leucocephalus</i>	50.4	51.1	28.7	YPM 13424
<i>Himantopus mexicanus</i>	56.4	60.0	32.6	YPM 6108
<i>Recurvirostra americana</i>	69.5	68.8	39.8	MCZ 33
<i>Recurvirostra americana</i>	70.4	70.7	41.0	MCZ 31
<i>Recurvirostra americana</i>	65.7	66.1	39.0	MCZ 29
<i>Recurvirostra americana</i>	70.4	73.9	43.5	MCZ 3300
<i>Recurvirostra americana</i>	68.9	69.3	39.9	MCZ 2760
<i>Recurvirostra americana</i>	71.7	71.8	40.7	MCZ 32
<i>Vanellus chilensis</i>	69.7	77.2	41.1	MCZ 6928
<i>Vanellus chilensis</i>	73.3	79.5	42.9	MCZ 7010
Glareolidae				
<i>Dromas ardeola</i>	70.2	72.2	36.6	MCZ 2991
Laridae				
<i>Alca torda</i>	77.2	60.1	41.6	MCZ 3688
<i>Alca torda</i>	78.0	61.7	41.9	MCZ 2956
<i>Alca torda</i>	77.9	60.9	40.4	MCZ 2867
<i>Catharacta skua</i>	140.3	137.0	70.5	MCZ 358
<i>Cepphus grylle</i>	60.2	49.7	34.6	MCZ 2995
<i>Cepphus grylle</i>	59.2	49.1	33.8	MCZ 4097
<i>Cerorhinca monocerata</i>	68.5	54.6	37.5	MCZ 7676
<i>Cerorhinca monocerata</i>	69.9	55.2	38.0	MCZ 7697
<i>Cerorhinca monocerata</i>	68.9	53.1	36.1	MCZ 7696
<i>Fratercula arctica</i>	64.4	49.0	33.5	MCZ 2994
<i>Fratercula arctica</i>	64.1	49.0	34.2	MCZ 6006
<i>Fratercula arctica</i>	58.9	44.6	31.4	MCZ 1434
<i>Larus argentatus</i>	139.9	148.5	78.3	MCZ 2712
<i>Larus atricilla</i>	91.7	100.0	52.5	MCZ 7271
<i>Larus glaucescens</i>	144.0	155.0	80.0	MCZ 723
<i>Larus leucopterus</i>	118.0	125.0	67.0	MCZ 2843
<i>Larus merinus</i>	150.8	165.0	85.1	MCZ 1617
<i>Larus pipixcan</i>	79.3	87.8	48.4	MCZ 6832
<i>Plautus alle</i>	43.2	33.0	22.8	MCZ 3425
<i>Plautus alle</i>	43.9	33.0	23.5	MCZ 1865
<i>Plautus alle</i>	43.2	34.4	23.0	MCZ 1871
<i>Plautus impennes</i>	104.2	56.2	45.1	MCZ
<i>Plautus impennes</i>	104.2	55.3	44.3	MCZ 18220
<i>Plautus impennes</i>	106.7	54.6	44.3	MCZ
<i>Plautus impennes</i>	101.3	55.0	43.4	MCZ
<i>Plautus impennes</i>	105.0	56.1	43.3	MCZ
<i>Rissa tridactyla</i>	83.0	88.0	48.0	MCZ 1502
<i>Rynchops nigra</i>	75.0	91.0	46.0	MCZ 1426
<i>Stercorarius parasiticus</i>	96.1	97.2	49.4	MCZ 183
<i>Sterna fuscata</i>	63.0	73.0	38.0	MCZ 3375
<i>Sterna hirundo</i>	54.0	62.0	33.0	MCZ 2147
<i>Sterna maxima</i>	88.0	106.0	53.0	MCZ 1427
<i>Sterna striata</i>	58.0	67.0	35.0	MCZ 5015

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Laridae				
<i>Uria aalge</i>	86.9	61.1	43.4	MCZ 6991
<i>Uria aalge</i>	86.3	62.5	43.3	MCZ 2989
<i>Uria aalge</i>	92.0	69.1	45.5	MCZ 3690
<i>Uria lomvia</i>	87.7	66.8	45.4	MCZ 7029
<i>Uria lomvia</i>	87.6	65.3	43.9	MCZ 6925
<i>Uria lomvia</i>	92.1	69.8	46.9	MCZ 7018
Accipitridae				
<i>Accipiter gentilis</i>	95.0	100.0	56.0	MCZ 216
<i>Aquila chrysaetus</i>	181.0	201.0	102.0	MCZ 1419
<i>Buteo jamaicensis</i>	118.0	130.0	66.0	MCZ 7793
<i>Buteo magnirostris</i>	64.0	67.0	35.0	MCZ 2743
<i>Buteo rufinus</i>	114.0	118.0	61.0	MCZ 6912
<i>Circus cyaneus</i>	96.0	107.0	57.0	MCZ 1417
<i>Elanus leucurus</i>	80.0	90.0	44.0	MCZ 3430
<i>Geranospiza caerulescens</i>	77.0	80.0	40.0	MCZ 3032
<i>Gypaetus barbatus</i>	222.0	233.0	114.0	MCZ 329
<i>Gyps fulvus</i>	251.0	296.0	132.0	MCZ 1412
<i>Haliaeetus leucocephalus</i>	211.0	231.0	113.0	MCZ 3519
<i>Harpia harpyia</i>	182.0	202.0	88.0	MCZ 333
<i>Hieraetus fasciatus</i>	150.0	168.0	83.0	MCZ 211
<i>Melierax metabates?</i>	95.0	95.0	50.0	MCZ 7127
<i>Milvus migrans</i>	109.0	120.0	60.0	MCZ 241
<i>Neophron percnopterus</i>	142.0	156.0	75.0	MCZ 213
<i>Pandion haliaetus</i>	146.0	178.0	88.0	MCZ 7607
<i>Pernis apivorus</i>	118.0	125.0	63.0	MCZ 253
<i>Spizaetus ornatus</i>	115.0	129.0	60.0	MCZ 2839
Sagittariidae				
<i>Sagittarius serpentarius</i>	183.0	178.0	89.0	MCZ 1925
<i>Sagittarius serpentarius</i>	179.0	175.0	86.0	YPM 14510
Falconidae				
<i>Falco jugger</i>	88.0	97.0	59.0	MCZ 294
<i>Falco sparverius</i>	45.0	46.0	26.0	MCZ 7402
<i>Herpetotheres cachinnans</i>	85.0	88.0	44.0	MCZ 2931
<i>Phalacroboenus australis</i>	116.0	107.0	65.0	MCZ 252
<i>Polyborus plancus</i>	104.0	104.0	55.0	MCZ 1496
<i>Polyborus plancus</i>	103.0	102.0	58.0	MCZ 2845
Podicipedidae				
<i>Aechmophorus occidentalis</i>	113.2	98.3	50.7	MCZ 2951
<i>Podiceps auritus</i>	77.8	68.3	34.3	MCZ 6429
<i>Podiceps auritus</i>	74.4	64.2	32.4	MCZ 7099
<i>Podiceps auritus</i>	75.3	66.0	31.7	MCZ 7163
<i>Podiceps auritus</i>	77.2	67.3	35.2	MCZ 6044
<i>Podiceps auritus</i>	79.7	70.3	34.3	MCZ 2726
<i>Podiceps caspicus</i>	69.6	63.4	31.9	MCZ 6070
<i>Podiceps caspicus</i>	69.2	61.1	29.8	MCZ 4076
<i>Podiceps caspicus</i>	69.4	62.0	31.3	MCZ 4080
<i>Podiceps grisegena</i>	117.2	102.9	46.6	MCZ 1015
<i>Podilymbus podiceps</i>	79.3	71.8	36.2	MCZ 1466
<i>Podilymbus podiceps</i>	67.6	60.9	30.7	MCZ 7647
<i>Podilymbus podiceps</i>	68.1	61.1	31.5	MCZ 7648
Phaethontidae				
<i>Phaethon lepturus</i>	81.8	83.3	42.3	MCZ 2073
<i>Phaethon lepturus</i>	85.1	86.7	43.5	MCZ 1798
<i>Phaethon lepturus</i>	83.8	85.0	42.5	MCZ 1765
Sulidae				
<i>Morus bassanus</i>	218.0	185.0	90.2	MCZ 3443
<i>Sula</i> sp.	173.0	182.0	79.7	MCZ 455
<i>Sula variegata</i>	153.0	156.0	71.0	MCZ 6959

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Anhingidae				
<i>Anhinga anhinga</i>	108.0	103.1	60.5	MCZ 1483
<i>Anhinga anhinga</i>	130.5	111.8	65.2	MCZ 3615
Phalacrocoracidae				
<i>Phalacrocorax auritus</i>	141.5	144.3	67.9	MCZ 7537
<i>Phalacrocorax bougainvilli</i>	153.5	163.0	67.6	MCZ 6953
<i>Phalacrocorax carbo</i>	160.0	166.0	76.1	MCZ 1447
<i>Phalacrocorax urile</i>	139.5	146.0	65.7	MCZ 722
Ardeidae				
<i>Ardea cocoi</i>	164.0	174.0	82.8	MCZ 3706
<i>Ardea goliath</i>	201.0	235.0	107.0	MCZ 1452
<i>Ardea goliath</i>	197.0	211.0	96.0	MCZ 202
<i>Ardea herodias</i>	195.0	221.0	102.0	MCZ 7038
<i>Ardea herodias</i>	190.0	207.0	100.0	MCZ 1970
<i>Ardea herodias</i>	188.0	217.0	101.0	MCZ 2473
<i>Ardeola ralloides</i>	75.7	83.4	43.2	MCZ 7237
<i>Botaurus lentiginosus</i>	114.0	119.0	67.0	MCZ 1759
<i>Botaurus lentiginosus</i>	113.0	120.0	65.0	MCZ 1499
<i>Botaurus lentiginosus</i>	105.0	112.0	68.0	MCZ 1279
<i>Botaurus stellaris</i>	138.0	144.0	77.0	MCZ 2064
<i>Butorides striata</i>	65.9	67.4	34.5	MCZ 3573
<i>Butorides striata</i>	62.1	65.9	34.8	MCZ 5014
<i>Butorides virescens</i>	72.4	78.2	42.0	MCZ 1860
<i>Cochlearius cochlearius</i>	99.0	110.0	52.0	MCZ 3517
<i>Cochlearius cochlearius</i>	93.0	101.0	48.0	MCZ 2201
<i>Egretta alba</i>	144.0	166.0	76.0	MCZ 6731
<i>Egretta alba</i>	155.0	178.0	84.0	MCZ 6954
<i>Egretta caerulea</i>	92.4	104.8	52.8	MCZ 6977
<i>Egretta gularis</i>	100.3	108.7	56.6	MCZ 226
<i>Egretta thula</i>	100.6	114.4	54.6	MCZ 7301
<i>Egretta thula</i>	94.1	108.5	53.4	MCZ 7616
<i>Egretta thula</i>	85.9	100.5	47.9	MCZ 3821
<i>Nycticorax</i> sp.	105.7	118.4	58.6	MCZ 7000
<i>Pilherodias pileatus</i>	66.9	70.2	36.3	MCZ 3830
<i>Tigrisoma lineatum</i>	98.1	107.6	52.5	MCZ 3831
Phoenicopteridae				
<i>Phoenicopiterus antiquarum</i>	206.0	218.0	97.0	MCZ 1445
<i>Phoenicopiterus antiquarum</i>	193.0	202.0	92.0	MCZ 289
<i>Phoenicopiterus ruber</i>	188.0	197.0	88.0	MCZ 7731
<i>Phoenicopiterus ruber</i>	212.0	221.0	105.0	MCZ 7572
<i>Phoenicopiterus ruber</i>	182.0	191.0	87.0	MCZ 7053
<i>Phoenicopiterus ruber</i>	204.0	215.0	97.0	MCZ 6736
<i>Phoenicopiterus ruber</i>	180.0	191.0	87.0	MCZ 1939
<i>Phoenicopiterus ruber</i>	191.0	198.0	93.0	MCZ 2950
<i>Phoenicopiterus ruber</i>	196.0	208.0	94.0	MCZ 2884
Threskiornithidae				
<i>Ajaia ajaja</i>	134.0	151.0	74.0	MCZ 6534
<i>Ajaia ajaja</i>	129.0	143.0	69.0	MCZ 6533
<i>Eudocimus ruber</i>	92.0	101.0	54.0	MCZ 7528
<i>Eudocimus ruber</i>	89.0	96.0	52.0	MCZ 7446
<i>Eudocimus ruber</i>	92.0	100.0	55.0	MCZ 6741
<i>Eudocimus ruber</i>	90.0	97.0	51.0	MCZ 6987
<i>Guara rubra</i>	90.0	100.0	51.0	MCZ 3450
<i>Guara rubra</i>	91.0	94.0	50.0	MCZ 1378
<i>Guara rubra</i>	92.0	93.0	53.0	MCZ 326
<i>Platalea leucoroidia</i>	145.0	161.0	80.0	MCZ 1468
<i>Plegadis falcinellus</i>	92.0	99.0	54.0	MCZ 6983
<i>Plegadis</i> sp.	90.0	97.0	52.0	MCZ 6955

*continued*



APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Threskiornithidae				
<i>Plegadis falcinellus?</i>	95.0	99.0	55.0	MCZ 7288
<i>Theristicus melanopis</i>	115.0	122.0	65.0	MCZ 206
<i>Theristicus melanopis</i>	121.0	132.0	66.0	MCZ 295
Pelecanidae				
<i>Pelecanus erythrorhynchos</i>	315.0	347.0	143.0	MCZ 7480
<i>Pelecanus erythrorhynchos</i>	317.0	344.0	150.0	MCZ 2914
<i>Pelecanus occidentalis</i>	271.0	315.0	126.0	MCZ 1448
<i>Pelecanus occidentalis</i>	268.0	323.0	125.0	MCZ 1956
Ciconiidae				
<i>Cathartes aura</i>	133.0	149.0	72.0	MCZ 1372
<i>Ciconia maguari</i>	223.0	246.0	106.0	MCZ 7483
<i>Ciconia nigra</i>	206.0	222.0	113.0	MCZ 6997
<i>Ciconia nigra</i>	202.0	224.0	112.0	MCZ 6747
<i>Ciconia nigra</i>	180.0	205.0	97.0	MCZ 290
<i>Coragyps atratus</i>	124.0	132.0	69.0	MCZ 3577
<i>Jabiru mycteria</i>	237.0	262.0	119.0	MCZ 1377
<i>Leptoptilus crumeniferus</i>	238.0	299.0	125.0	MCZ 338
<i>Leptoptilus dubius</i>	278.0	373.0	163.0	MCZ 337
<i>Mycteria americana</i>	163.0	195.0	92.0	MCZ 3442
<i>Mycteria ibis</i>	158.0	178.0	84.0	MCZ 288
<i>Mycteria ibis</i>	176.0	204.0	96.0	MCZ 6740
<i>Mycteria</i> sp.	199.0	220.0	97.0	MCZ 1745
<i>Sarcorhamphus papa</i>	166.0	199.0	88.0	MCZ 6960
<i>Vultur gryphus</i>	260.0	299.0	131.0	MCZ 342
<i>Xenorhynchus asiaticus</i>	216.0	245.0	107.0	MCZ 261
Fregatidae				
<i>Fregata aquila</i>	186.0	238.0	114.0	MCZ 1354
<i>Fregata</i> sp.	150.0	190.0	92.0	MCZ 7744
Spheniscidae				
<i>Aptenodytes patagonica</i>	110.0	82.2	68.0	MCZ 7208
<i>Aptenodytes patagonica</i>	115.0	83.5	71.2	MCZ 7478
<i>Aptenodytes patagonica</i>	116.0	92.0	72.0	YPM 2351
<i>Eudyptes chrysolophus</i>	59.4	44.2	35.3	MCZ 6022
<i>Eudyptes cristatus</i>	59.4	44.4	37.9	MCZ 6428
<i>Eudyptula minor</i>	46.7	31.3	25.3	MCZ 6025
<i>Eudyptula minor</i>	45.0	30.0	25.5	MCZ 1451
<i>Eudyptula minor</i>	49.7	33.3	25.5	YPM 13356
<i>Megadyptes antipodes</i>	73.7	57.7	43.7	YPM 13392
<i>Spheniscus demersus</i>	67.1	47.6	39.9	YPM 15882
<i>Spheniscus humboldti</i>	69.2	46.5	39.7	MCZ 7040
<i>Spheniscus humboldti</i>	70.8	47.9	40.3	MCZ 6957
<i>Spheniscus humboldti</i>	76.1	50.8	42.1	MCZ 7571
<i>Spheniscus mendiculus</i>	54.2	37.1	30.5	MCZ 3638
<i>Spheniscus</i> sp.	67.0	47.0	44.7	MCZ 142(5)
Gaviidae				
<i>Gavia immer</i>	198.0	158.0	100.1	MCZ 1432
<i>Gavia immer</i>	200.0	160.0	106.0	MCZ 1658
<i>Gavia immer</i>	192.0	158.0	101.0	MCZ 1661
<i>Gavia immer</i>	177.0	144.0	90.5	MCZ 2148
<i>Gavia immer</i>	194.0	151.0	88.0	MCZ 2593
<i>Gavia immer</i>	196.0	155.0	102.5	MCZ 3030
<i>Gavia immer</i>	180.0	139.0	91.9	MCZ 7019
<i>Gavia immer</i>	187.0	150.0	96.0	MCZ 7103
<i>Gavia immer</i>	170.0	138.0	90.1	MCZ 7893
<i>Gavia immer</i>	198.0	159.0	104.0	MCZ 7894
<i>Gavia immer</i>	195.0	157.0	108.0	MCZ 7895
<i>Gavia immer</i>	207.0	167.0	113.0	MCZ 7896
<i>Gavia immer</i>	167.0	132.0	86.4	MCZ 7903

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Gaviidae				
<i>Gavia immer</i>	199.0	156.0	100.8	MCZ 7904
<i>Gavia immer</i>	196.0	153.0	99.9	MCZ 7905
<i>Gavia immer</i>	192.0	155.0	102.0	MCZ 7912
<i>Gavia immer</i>	177.0	141.0	95.2	MCZ 7913
<i>Gavia immer</i>	195.0	153.0	99.7	MCZ 7914
<i>Gavia immer</i>	185.0	153.0	96.7	MCZ 7915
<i>Gavia immer</i>	200.0	160.0	105.4	MCZ 7916
<i>Gavia immer</i>	191.0	151.0	99.6	MCZ 7917
<i>Gavia immer</i>	194.0	154.0	102.1	MCZ 7918
<i>Gavia immer</i>	190.0	151.0	100.4	MCZ 7919
<i>Gavia immer</i>	204.0	163.0	105.0	MCZ 7920
<i>Gavia immer</i>	193.0	155.0	99.2	MCZ 7921
<i>Gavia immer</i>	180.0	145.0	93.3	MCZ 7939
<i>Gavia immer</i>	180.0	145.0	96.0	MCZ 7940
<i>Gavia immer</i>	181.0	154.0	99.0	MCZ 7941
<i>Gavia immer</i>	194.0	157.0	98.9	MCZ 7942
<i>Gavia immer</i>	211.0	167.0	111.0	MCZ 7943
<i>Gavia immer</i>	185.0	145.0	93.4	MCZ 7944
<i>Gavia immer</i>	210.0	165.0	108.8	MCZ 7945
<i>Gavia immer</i>	208.0	167.0	110.0	MCZ 7946
<i>Gavia immer</i>	211.0	164.0	108.5	MCZ 7947
<i>Gavia immer</i>	205.0	158.0	104.1	MCZ 7948
<i>Gavia immer</i>	184.0	148.0	95.9	MCZ 7950
<i>Gavia immer</i>	192.0	153.0	100.5	MCZ 7951
<i>Gavia immer</i>	176.0	139.0	91.4	MCZ 7952
<i>Gavia immer</i>	173.0	136.4	90.7	MCZ 7956
<i>Gavia immer</i>	208.0	171.0	109.0	MCZ 7957
<i>Gavia</i> sp.	182.0	142.0	91.0	MCZ 417
<i>Gavia</i> sp.	176.0	138.0	91.0	MCZ 899
<i>Gavia stellata</i>	140.5	111.4	76.7	MCZ 7009
<i>Gavia stellata</i>	138.3	107.8	73.1	MCZ 6996
<i>Gavia stellata</i>	136.6	108.6	67.0	MCZ 6531
<i>Gavia stellata</i>	128.5	104.5	70.7	MCZ 6913
Procellariidae				
<i>Daption capense</i>	97.5	80.7	42.4	MCZ 3873
<i>Daption capense</i>	89.1	83.4	42.3	MCZ 6056
<i>Daption capense</i>	84.0	78.8	42.0	MCZ 6496
<i>Daption capense</i>	88.0	79.0	40.0	MCZ 6970
<i>Daption capense</i>	89.0	82.0	44.0	MCZ 2955
<i>Diomedea chrysostoma</i>	264.0	263.0	104.0	MCZ 5006
<i>Diomedea exulans</i>	438.0	447.0	150.0	MCZ 408
<i>Diomedea exulans</i>	394.0	397.0	145.0	MCZ 2481
<i>Diomedea exulans</i>	398.0	405.0	142.0	MCZ 6191
<i>Diomedea immutabilis</i>	247.0	256.0	99.0	MCZ 3050
<i>Diomedea immutabilis</i>	257.0	252.0	102.0	MCZ 2959
<i>Diomedea nigripes</i>	287.0	287.0	108.0	MCZ 2999
<i>Fregatta grallaria</i>	25.5	21.5	17.0	MCZ 6756
<i>Fregatta grallaria</i>	25.5	21.5	17.0	MCZ 6752
<i>Fulmarus glacialis</i>	97.2	90.3	47.5	MCZ 4079
<i>Fulmarus glacialis</i>	106.0	98.0	50.0	MCZ 4078
<i>Fulmarus glacialis</i>	102.0	96.0	49.0	MCZ 4090
<i>Fulmarus glacialis</i>	107.0	102.0	51.0	MCZ 5011
<i>Oceanites oceanicus</i>	22.5	19.5	15.5	MCZ 2984
<i>Oceanites oceanicus</i>	23.0	19.5	15.5	MCZ 6722
<i>Oceanodroma leucorhoa</i>	37.0	35.0	21.0	MCZ 7883
<i>Oceanodroma leucorhoa</i>	37.5	35.5	21.0	MCZ 6058
<i>Pelecanoides urinatrix</i>	56.9	52.3	29.7	MCZ 1430

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Procellariidae				
<i>Pelecanoides urinatrix</i>	44.7	34.6	25.2	MCZ 6141
<i>Phoebastria fusca</i>	242.0	230.0	98.0	MCZ 2949
<i>Phoebastria palpebrata</i>	235.0	239.0	92.0	MCZ 2953
PASSERIFORMES				
Eurylaimidae				
<i>Calyptomina viridis</i>	27.3	32.2	17.0	MCZ 7349
<i>Eurylaimus ochromalus</i>	20.1	22.6	12.8	MCZ 2982
Passeridae				
<i>Anthus correndera</i>	19.9	21.2	11.2	MCZ 3138
<i>Budytes flavus</i>	17.1	20.3	11.5	MCZ 3091
<i>Motacilla alba</i>	19.6	23.7	13.0	MCZ 6945
Bombycillidae				
<i>Bombycilla cedrorum</i>	20.7	24.6	13.6	MCZ 2713
Tyrannidae				
<i>Campostoma obsoletum</i>	12.1	14.4	8.1	MCZ 6285
<i>Empidonax flaviventris</i>	14.4	18.6	9.7	MCZ 7877
<i>Muscigralla brevicauda</i>	17.9	19.4	10.2	MCZ 6304
<i>Muscisaxicola plauinucha</i>	22.3	28.3	17.1	MCZ 7213
<i>Myiobius barbatus</i>	14.4	17.7	8.6	MCZ 3509
<i>Pitangus sulfuratus</i>	30.1	39.6	18.2	MCZ 3358
<i>Platyrhynchus mystaceus</i>	14.7	16.9	8.6	MCZ 3451
<i>Pyrocephalus rubinus</i>	17.2	20.4	11.8	MCZ 6500
<i>Rupicola rupicola</i>	45.3	57.5	29.0	MCZ 3699
<i>Tyrannus tyrannus</i>	24.0	32.2	17.5	MCZ 2557
<i>Tyrannus tyrannus</i>	25.3	32.8	18.1	MCZ 1404
<i>Tyrannus verticalis</i>	26.1	34.8	19.3	MCZ 7600
Certhiidae				
<i>Certhia familiaris</i>	13.0	16.5	8.3	MCZ 1487
Furnariidae				
<i>Dendrocolaptes certhia</i>	27.2	31.9	17.9	MCZ 3842
<i>Furnarius rufus</i>	26.0	26.0	15.3	MCZ 6030
Thamnophilidae				
<i>Taraba major</i>	25.5	25.2	12.5	MCZ 4083
Rhynocryptidae				
<i>Conopophaga castaneiceps</i>	18.8	19.0	8.9	MCZ 6014
<i>Scelorchilus albicollis</i>	22.2	20.0	11.6	MCZ 224
Pittidae				
<i>Pitta erythrogaster</i>	30.1	32.8	17.3	MCZ 6581
Menuridae				
<i>Menura novaehollandiae</i>	60.4	59.0	33.8	MCZ 313
Alaudidae				
<i>Eremophila alpestris</i>	23.2	26.0	14.6	MCZ 7440
<i>Eremophila alpestris</i>	23.0	25.8	14.1	MCZ 7439
<i>Melanocorypha yeltoniensis</i>	29.4	31.1	18.8	MCZ 188
<i>Mirafa javanica</i>	22.1	22.9	12.6	MCZ 7290
Hirundinidae				
<i>Delichon urbica</i>	15.0	21.3	12.0	MCZ 1479
<i>Hirundo rustica</i>	14.5	21.5	12.8	MCZ 2697
<i>Hirundo rustica</i>	14.3	19.7	13.2	MCZ 4004
<i>Progne subis</i>	21.8	31.2	17.0	MCZ 1481
Corvidae				
<i>Coracina caeruleogrisea</i>	40.6	43.8	23.5	MCZ 6475
<i>Corcorax melanorhamphus</i>	54.7	55.7	32.0	MCZ 291
<i>Dicrurus macroceros</i>	28.4	39.1	19.9	MCZ 3288
<i>Pityriasis gymnocephala</i>	37.0	38.4	21.3	MCZ 230
<i>Strepera graculina</i>	53.6	63.5	35.5	MCZ 277

*continued*

APPENDIX 2—*continued*

Species	H	R	CM	Specimen Number
Sittidae				
<i>Sitta carolinensis</i>	18.3	21.4	12.8	MCZ 2526
Cinclidae				
<i>Cinclus cinclus</i>	20.5	23.0	14.2	MCZ 361
Sylviidae				
<i>Garrulax striatus</i>	31.5	31.5	18.2	MCZ 286
Muscicapidae				
<i>Myiophoneus caeruleus</i>	41.5	46.6	25.3	MCZ 6059
<i>Turdus migratorius</i>	27.2	30.0	18.2	MCZ 2701
Sturnidae				
<i>Gracula religiosa</i>	40.3	46.4	29.1	MCZ 7027
<i>Toxostoma rufum</i>	27.3	27.2	14.9	MCZ 1801
Vireonidae				
<i>Gymnorhina tibicen</i>	56.0	61.3	37.2	MCZ 1405
Fringillidae				
<i>Habia rubica</i>	21.7	23.2	12.0	MCZ 2455
Callaeatidae				
<i>Heteralocha acutirostris</i>	42.1	41.8	24.0	MCZ 350

## APPENDIX 3

Avian limb segment lengths taken from the literature (in mm; H, humerus; R, radius; CM, carpometacarpus; \*, mean; †, ulna; ‡, MCII; m, male; f, female)

Species	H	R	CM	Source
STRUTHIONIFORMES				
Struthionidae				
<i>Palaeotis weigelti</i>	~117	72.0	34.0	Houde & Haubold (1987)
GALLIFORMES				
Paraortigidae				
<i>Palaeortyx gallica</i> *†	41.0	42.1	20.6	Mourer-Chauviré (1992)
<i>Paraortyx lorteti</i> *†	40.0	36.8	21.1	Mourer-Chauviré (1992)
ANSERIFORMES				
Anatidae				
<i>Chendytes lawi</i> *†	68.1	24.9	24.5	Livezey (1993)
<i>Cnemiornis calcitrans</i>	158.0	115.9	63.2	Worthy <i>et al.</i> (1997)
<i>Lophodytes cucullatus</i> (m)*†	67.8	55.5	40.8	Livezey (1989a)
<i>Lophodytes cucullatus</i> (f)*†	64.9	53.1	39.2	Livezey (1989a)
<i>Melanitta fusca</i> (m)*†	104.7	93.2	60.0	Livezey (1993)
<i>Melanitta fusca</i> (f)*†	98.3	88.5	57.3	Livezey (1993)
<i>Mergus australis</i> (m)†	72.1	57.7	40.7	Livezey (1989a)
<i>Mergus australis</i> (f)*†	68.3	54.8	38.7	Livezey (1989a)
<i>Mergus merganser</i> (m)*†	96.4	81.4	58.7	Livezey (1989a)
<i>Mergus merganser</i> (f)*†	88.2	74.2	53.1	Livezey (1989a)
<i>Mergus serrator</i> (m)*†	88.2	72.8	51.4	Livezey (1989a)
<i>Mergus serrator</i> (f)*†	81.6	68.1	47.9	Livezey (1989a)
<i>Somateria mollissima</i> (m)*†	118.5	104.7	72.0	Livezey (1993)
<i>Somateria mollissima</i> (f)*†	110.0	100.3	68.7	Livezey (1993)
<i>Tachyeres brachypterus</i> (m)*	124.1	91.7	66.0	Livezey & Humphrey (1986)
<i>Tachyeres brachypterus</i> (f)*	117.1	87.7	62.4	Livezey & Humphrey (1986)

*continued*

APPENDIX 3—*continued*

Species	H	R	CM	Source
<i>Tachyeres leucocephalus</i> (m)*	122.5	94.4	66.3	Livezey & Humphrey (1986)
<i>Tachyeres leucocephalus</i> (f)*	115.8	90.2	62.4	Livezey & Humphrey (1986)
<i>Tachyeres patachonicus</i> (m)*	124.1	96.2	67.2	Livezey & Humphrey (1986)
<i>Tachyeres patachonicus</i> (f)*	118.0	91.7	63.5	Livezey & Humphrey (1986)
<i>Tachyeres pteneres</i> (m)*	132.6	95.5	68.9	Livezey & Humphrey (1986)
<i>Tachyeres pteneres</i> (f)*	125.1	90.2	64.6	Livezey & Humphrey (1986)
CUCULIFORMES				
Coccyzidae				
<i>Coccyzus americanus</i> *	29.6	26.7	15.6	Berger (1952)
<i>Coccyzus erythrophthalmus</i> *	27.9	24.7	14.6	Berger (1952)
Cuculidae				
<i>Crotophaga sulcirostris</i> *	33.5	25.9	16.8	Berger (1952)
Neomorphidae				
<i>Geococcyx californianus</i> *	45.1	35.4	20.0	Berger (1952)
Foratidae				
<i>Foro panarium</i>	52.5	44.5	26.7	Olson (1992)
STRIGIFORMES				
Palaeoglaucidae				
<i>Palaeoglaux artophoron</i>	~ 40	~ 49	~ 24	Peters (1992)
GRUIFORMES				
Gruidae				
<i>Balearica exigua</i> *	149.5	169.8	82.2	Feduccia & Voorhies (1992)
Rallidae				
<i>Atlantisia rogersi</i>	20.0	14.0	9.0	Lowe (1928)
Messelornithidae				
<i>Messelornis neartica</i>	35.5	33.5	19.0	Hesse (1992)
CICONIIFORMES				
Laridae				
<i>Mancalla cedrosensis</i>	73.5	29.3	15.6	Howard (1976)
<i>Mancalla diegense</i>	76.5	30.9	15.3	Howard (1976)
<i>Praemancalla wetmorei</i>	82.7	35.8	15.7	Howard (1976)
Accipitridae				
<i>Accipiter cooperii</i>	71.2	69.6	39.9	Fisher (1946)
<i>Aquila chrysaetos</i> *	189.8	209.9	102.9	Fisher (1946)
<i>Astur atricapillus</i>	96.0	98.0	51.1	Fisher (1946)
<i>Buteo jamaicensis</i>	113.7	128.8	64.1	Fisher (1946)
Podicipedidae				
<i>Podiceps occipitalis</i> (m)*†	66.2	60.8	29.4	Livezey (1989b)
<i>Podiceps occipitalis</i> (f)*†	65.6	61.1	28.8	Livezey (1989b)
<i>Podiceps taczanowskii</i> (m)*†	71.5	64.1	30.6	Livezey (1989b)
<i>Podiceps taczanowskii</i> (f)*†	67.1	61.0	29.1	Livezey (1989b)
<i>Podilymbus gigas</i> (m)*†	85.8	76.6	36.9	Livezey (1989b)
<i>Podilymbus gigas</i> (f)*†	79.7	71.8	33.7	Livezey (1989b)
<i>Podilymbus podiceps</i> (f)*†	69.6	62.7	33.2	Storer (1976)
<i>Podilymbus podiceps</i> (m)*†	75.8	70.0	33.9	Livezey (1989b)
<i>Podilymbus podiceps</i> (f)*†	71.7	66.4	31.8	Livezey (1989b)
<i>Rollandia microptera</i> (m)*†	71.6	54.6	29.0	Livezey (1989b)
<i>Rollandia microptera</i> (f)*†	67.4	52.0	27.6	Livezey (1989b)
<i>Rollandia rolland</i> (m)*†	57.2	51.0	26.3	Livezey (1989b)
<i>Rollandia rolland</i> (f)*†	55.7	49.9	25.3	Livezey (1989b)

*continued*

APPENDIX 3—*continued*

Species	H	R	CM	Source
Phalacrocoracidae				
<i>Compsohalieu harrisi</i> (m)*	101.6	82.9	41.4	Livezey (1992)
<i>Compsohalieu harrisi</i> (f)*	92.0	75.7	39.6	Livezey (1992)
<i>Compsohalieu penicillatus</i> (m)*	147.6	156.6	65.0	Livezey (1992)
<i>Compsohalieu penicillatus</i> (f)*	137.7	145.3	60.9	Livezey (1992)
<i>Compsohalieu perspicillatus</i>	172.8	189.2	76.9	Livezey (1992)
<i>Hypoleucus auritus</i> (m)*	152.1	160.8	72.6	Livezey (1992)
<i>Hypoleucus auritus</i> (f)*	143.6	152.2	70.0	Livezey (1992)
<i>Leucocarbo bougainvilli</i> (m)*	156.7	170.6	68.3	Livezey (1992)
<i>Leucocarbo bougainvilli</i> (f)*	154.3	168.6	66.7	Livezey (1992)
<i>Microcarbo melanoleucos</i> (m)*	107.3	111.3	54.6	Livezey (1992)
<i>Microcarbo melanoleucos</i> (f)*	102.9	107.3	52.3	Livezey (1992)
<i>Notocarbo atriceps</i> (m)*	142.6	152.6	64.4	Livezey (1992)
<i>Notocarbo atriceps</i> (f)*	138.0	147.2	62.8	Livezey (1992)
<i>Phalacrocorax carbo</i> (m)*	169.3	178.9	80.8	Livezey (1992)
<i>Phalacrocorax carbo</i> (f)*	155.6	165.8	75.5	Livezey (1992)
<i>Stictocarbo magellanicus</i> (m)*	116.6	124.2	55.7	Livezey (1992)
<i>Stictocarbo magellanicus</i> (f)*	114.1	119.7	55.3	Livezey (1992)
<i>Stictocarbo urile</i> (m)*	137.8	147.8	65.7	Livezey (1992)
<i>Stictocarbo urile</i> (f)*	125.6	134.1	60.7	Livezey (1992)
Ciconiidae				
<i>Cathartes aura</i> *	150.0	169.5	82.8	Fisher (1946)
<i>Cathartes aura</i> †	143.3	171.8	81.2	Campbell & Tonni (1983)
<i>Coragyps atratus</i> *	134.0	146.0	75.0	Fisher (1946)
<i>Coragyps atratus</i> †	134.0	155.4	75.6	Campbell & Tonni (1983)
<i>Gymnogyps californianus</i> *	266.0	293.0	132.0	Fisher (1946)
<i>Gymnogyps californianus</i> †	273.0	315.5	140.0	Campbell & Tonni (1983)
<i>Gymnogyps californianus</i> †	266.0	308.0	132.0	Campbell & Tonni (1983)
<i>Sarcorhamphus papa</i> *	169.0	197.0	89.0	Fisher (1946)
<i>Sarcorhamphus papa</i> †	167.4	205.3	88.2	Campbell & Tonni (1983)
<i>Teratomis merriami</i> †	317.0	421.0	167.0	Campbell & Tonni (1983)
<i>Vultur gryphus</i> †	280.7	341.0	144.2	Campbell & Tonni (1983)
<i>Vultur gryphus</i> †	280.0	340.6	139.5	Campbell & Tonni (1983)
<i>Vultur gryphus</i> *	280.0	326.0	139.5	Fisher (1946)
Spheniscidae				
<i>Aptenodytes patagonica</i> *	117.4	84.7	72.5	Simpson (1946)
<i>Palaeospheniscus patagonicus</i> *	75.2	57.3	51.2	Simpson (1946)
<i>Palaeospheniscus robustus</i> *	83.7	62.7	58.9	Simpson (1946)
Procellariidae				
<i>Diomedea exulans</i> †	405.9	400.5	138.3	Campbell & Tonni (1983)
PASSERIFORMES				
Certhiidae				
<i>Certhia familiaris</i> *†	12.7	15.7	9.0	Norberg (1979)
Regulidae				
<i>Regulus regulus</i> *	9.6	12.9	7.2	Norberg (1979)
Paridae				
<i>Parus ater</i> *†	12.7	15.1	8.7	Norberg (1979)
<i>Parus cristatus</i> *†	13.9	16.3	9.1	Norberg (1979)
<i>Parus montanus</i> *†	13.6	16.3	9.0	Norberg (1979)
SANDCOLEIFORMES				
Sandcoleidae				
<i>Sandcoleus copiosus</i>	46.3	41.2	25.9	Houde & Olson (1992)
<i>Anneavis anneae</i>	41.7	37.0	21.6	Houde & Olson (1992)
<i>Chascacocolius oscitans</i>	26.5	23.8	15.9	Houde & Olson (1992)
MESOZOIC BIRDS				
<i>Archaeopteryx bavarica</i>	~55	53.0	25.0	Wellnhofer (1993)
<i>Archaeopteryx lithographica</i>	83.0	~69	34.3+	Wellnhofer (1988)

*continued*

APPENDIX 3—*continued*

Species	H	R	CM	Source
MESOZOIC BIRDS				
<i>Archaeopteryx lithographica</i>	75.0	65.0	34.4	Wellnhofer (1974)
<i>Archaeopteryx lithographica</i>	72.0	63.0	~ 33	Wellnhofer (1974)
<i>Archaeopteryx lithographica</i>	63.5	54.4	28.0	Wellnhofer (1974)
<i>Archaeopteryx lithographica</i> †	41.5	35.0	17.8	Wellnhofer (1974)
<i>Cathayornis yandica</i>	27.0	26.0	14.0	Zhou, Jin & Zhang (1992)
<i>Concomis lacustris</i>	31.1	27.4	14.1	Sanz, Chiappe & Buscalioni (1995)
<i>Mononykus olecranus</i>	36.6	18.1	8.6	Perle <i>et al.</i> (1994)
<i>Noguerornis gonzalezi</i>	22.0	23.3	11.3	Lacasa Ruiz (1989)
Unnamed Enantiornithine	31.0	41.0	~ 18.5	Dong (1993)