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Source: *Journal of Vertebrate Paleontology*, Jun. 19, 1997, Vol. 17, No. 2 (Jun. 19, 1997), pp. 308-329

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BIPEDALISM, FLIGHT, AND THE EVOLUTION OF THEROPOD LOCOMOTOR DIVERSITY

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ABSTRACT—The evolution of theropod flight has been characterized as a shift from one to three locomotor modules. Basal theropods, which were terrestrial bipeds, had a single locomotor module composed of the hind limb and tail. In birds, aerial locomotion was acquired with the origination of the wing module and a decoupling of the hind limb and tail into separate pelvic and caudal modules. This increase in modularity is thought to have granted birds more locomotor “options” than non-avian theropods. More specifically, an aerial locomotor system could have eased constraints on the hind limb and allowed specialization for habitats and lifestyles unavailable to non-birds. If so, bird hind limbs should be more disparate than those of non-avian theropods. We addressed this hypothesis by visualizing one aspect of limb design, the proportions of the three main segments, using ternary diagrams. Our results show that avian hind limb proportions are much more disparate than those of non-avian theropods. This broad range of limb design correlates with a radiation in locomotor diversity founded on three locomotor modules. We propose that birds have reached regions of proportion morphospace that are off limits to bipeds with only one locomotor module. In comparison, the limbs of non-avian theropods are conservatively proportioned. Despite great variation in body size, theropods other than birds do not exhibit specializations for locomotion other than terrestrial bipedalism. Although other aspects of size and shape need to be analyzed, the relationship between modular flexibility and morphological disparity appears to play an important role in theropod locomotor evolution.

INTRODUCTION

Birds are now widely recognized as flying theropod dinosaurs (Ostrom, 1976a; Gauthier, 1986; Fig. 1). During its 230 million year history, the clade Theropoda has given rise to an array of organisms as divergent as hummingbirds and tyrannosaurs. This spectrum of body form and scale makes the group particularly appealing for studying the evolution of disparity—the “range of anatomical design” (Gould, 1991:412; Foote, 1989, 1993; Wagner, 1995). By analyzing the distribution of theropods within a morphospace, it may be possible to reveal constraints on shape, to discern general rules of musculoskeletal design, and to shed light on locomotor evolution.

Birds have been characterized as having three anatomical subregions of the musculoskeletal system that are highly integrated and act as functional units during locomotion (Fig. 1A; Gatesy and Dial, 1996). These so-called “locomotor modules” are the wings, hind limbs, and tail. In contrast, basal theropods are thought to have had only a single locomotor module composed of the hind limb and tail, which were morphologically and functionally coupled. The origin of avian flight required transformation of the primitively non-locomotor forelimb into an aerodynamic surface; accordingly, the inception of the pectoral module has been the focus of most work (e.g., contributions in Hecht et al., 1985). All theropods remained bipedal, but modifications of the hind limb and tail (Gatesy, 1990, 1994) eventually led to their decoupling into separate pelvic and caudal locomotor modules (Gatesy and Dial, 1996). It has been proposed that such an increase in modularity (from one to three modules) offered birds more locomotor “options” than were available to non-bird theropods (Gatesy and Dial, 1996). This reorganization permitted a radiation of avian limb designs and locomotor strategies through the differential elaboration of modules in various lineages.

In this study, we analyze how the multi-segmented hind limbs of theropods are distributed in a limb morphospace. Patterns of design space filling are used to test the prediction that the hind limbs of birds (which have three locomotor modules or ancestors that did) should be more disparate than those of non-avian theropods (which had only one module). Theropods were primitively terrestrial obligate bipeds, in which the hind

limbs were vital to the sole locomotor mechanism. In birds a second, aerial locomotor capability was added through the novel allegiance of the wing and tail modules. We hypothesize that flight eased constraints on theropod hind limb design. If so, bird hind limbs should have been freed to evolve novelties and pioneer areas of morphospace that were inaccessible to non-flying theropods.

Herein we concentrate on one aspect of limb shape, the proportions of the main limb elements, which are visualized using ternary diagrams. Limb proportions have been employed to discern adaptations for different locomotor styles in mammals (e.g., Gregory, 1912; Osborn, 1929; Smith and Savage, 1956; Garland and Janis, 1993) and dinosaurs (e.g. Coombs, 1978; Holtz, 1994a). We intentionally disregard other important aspects related to function in order to simplify the complexities of limb design. Factors such as body size, body form, relative limb size, muscular mechanisms of limb movement, and differences in the phalanges all influence limb function, but we hoped that limb proportions alone would reveal major patterns.

MATERIALS AND METHODS

Terminology and Systematics

We consider birds to be a subclade of theropod dinosaurs (Fig. 1B). As such, birds are theropods, and we will use the term theropod to mean all theropods, including birds, unless further specified. We will use the terms birds and avian to refer to the common ancestor of *Archaeopteryx* and modern birds plus all of its descendants. Theropods that are not birds will be called either non-avian theropods, non-birds, or be designated by a more specific name (e.g., ceratosaurs, tyrannosaurs, non-avian maniraptorans, etc.). Despite major advances, theropod phylogeny still has many uncertainties. We follow the general hypotheses of Gauthier (1986) and Chialpe (1995), but draw upon phylogenies of Holtz (1994b) and Sereno et al. (1996) for more recently described non-bird taxa. Traditional bird orders (Wetmore, 1960) are used to organize modern theropods, even though some are probably not monophyletic. We treat ratites (ostriches, rheas, emus, cassowaries, kiwis, moas, elephant-birds, dromornithids) as a single group. Throughout the paper

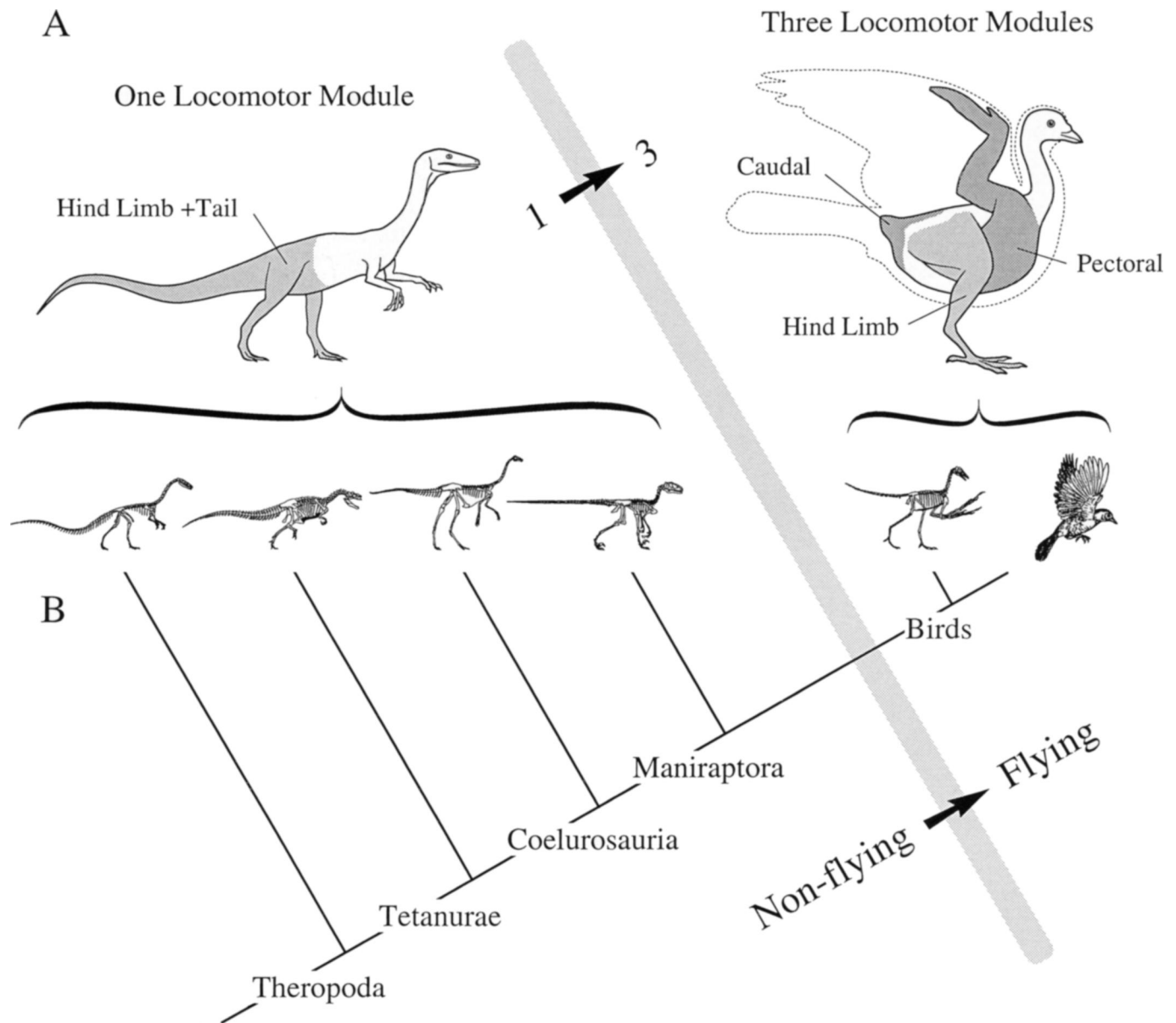


FIGURE 1. Locomotor modules and theropod phylogeny (Modified from Gatesy and Dial, 1996). **A**, Theropod locomotor modules. Non-avian theropods were terrestrial bipeds in which the hind limb and tail were anatomically and functionally linked in a single locomotor module. In birds this primitive module decoupled into separate pelvic and caudal modules. The wing and tail formed the aerial locomotor system. **B**, A simplified cladogram of Theropoda (after Gauthier, 1986).

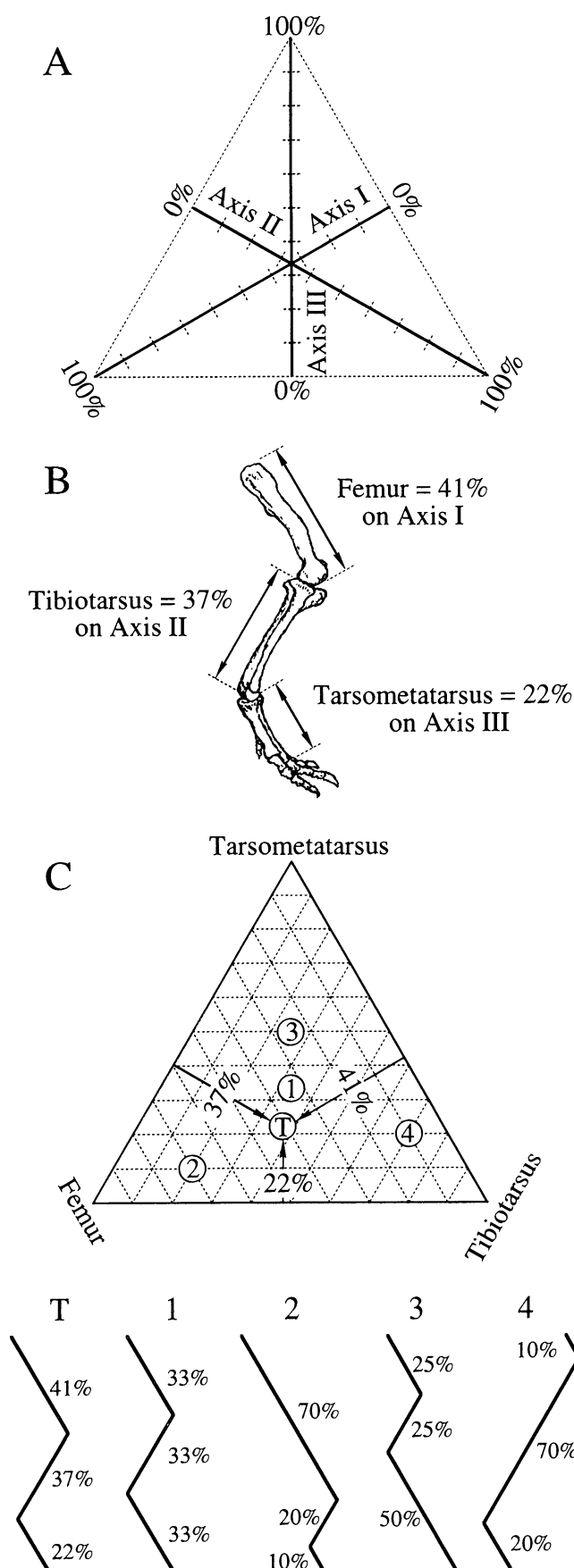
we make a distinction between disparity (range of anatomical design, Gould, 1991), taxonomic diversity (number of species), and locomotor diversity (range of locomotor ability and function). All potential anatomical designs constitute a morphospace.

Data Collection

We analyzed theropod hind limb shape by measuring the lengths of its three main segments: the femur, tibiotarsus, and tarsometatarsus (Fig. 2). The length of the femur is relatively straightforward, but tarsal elements make quantifying other segments more complicated. The length of the tibia is augmented by the proximal tarsals, which fuse in some theropods to form a tibiotarsus. We included the tarsal contribution to the tibia in all birds and in non-birds when available. Similarly, the distal

tarsals and metatarsals may fuse to form a tarsometatarsus. In theropods with unfused feet the length of metatarsal III was measured; the small distal tarsals were not included. For convenience, we will use the terms tibiotarsus and tarsometatarsus for all theropods, even those that lack fusion. Processes extending beyond the joint, such as the greater trochanter and cnemial crest, were excluded from measurement when possible to obtain interarticular segment lengths.

The vast majority of the data were restricted to complete limbs of individual specimens. For extinct theropods, segment lengths were taken from the literature. Fossil specimens with missing or incomplete elements were not included, although some bone lengths must be considered estimates due to distortion. Individual data on 91 hind limbs of 37 non-avian theropod genera were collected. Since complete limbs of extinct theropods are so rare, all are included in this study (Appendix 1).



Modern bird skeletons in the Museum of Comparative Zoology and the Peabody Museum were measured with a ruler and calipers. Birds were not randomly sampled. Instead, a preliminary survey was undertaken to estimate the area of morphospace birds might fill. We then deliberately sought out taxa at the periphery of this area to try to define the limits of bird limb design. At the same time, a more systematic survey of representatives of each order was done to insure adequate taxonomic coverage. As a result, the density of bird points does not reflect accurately the true distribution of modern bird diversity; taxa at the edges are heavily overrepresented and passerines are underrepresented. Our data set includes proportions of 649 hind limbs from 353 species of 262 genera in 104 families in 23 orders of living birds (Appendix 2). Fossil birds are represented by 86 hind limbs from 47 species (Appendix 3). The remaining bird data are published means of bone lengths from multiple individuals of 75 species (Appendix 3). These are plotted on the same graph as points for measured individuals. Mean lengths permit the inclusion of more published data, particularly from avian fossil deposits where individuals are not easily identified.

Analysis

Segment lengths were added to obtain total hind limb length. Percentages were calculated by dividing each segment's length by limb length and multiplying by 100. We visualized the potential limb morphospace using a ternary diagram, in which the percentage of each segment's contribution to the total is plotted on one of three axes oriented 120° apart (Fig. 2). Theoretically, a tripartite limb could be designed with any combination of segment lengths as long as none is zero. Any tripartite limb must fall somewhere within, but not on, the perimeter of the ternary triangle. In the following analysis we will refer to ternary diagram area as limb proportion morphospace. To estimate the area inhabited by each group, we split the ternary diagram into 5% divisions (400 triangles) and counted the number of occupied cells. We also calculated the range as the difference between highest and lowest percentages along each axis. No attempt was made to correct for the phylogenetic relatedness of data points (Felsenstein, 1985; Garland et al., 1992; Garland and Janis, 1993).

RESULTS

All Theropods

Theropods fill a small area of the overall range of proportions available to tripartite limbs, occupying only one ninth (45) of the 400 possible cells (Fig. 3A). Because the theropod area is contiguous (at 5% resolution), large regions of proportion mor-

FIGURE 2. Visualization of theropod limb proportion morphospace. **A**, A ternary diagram is constructed with three axes (I, II, and III) running from a side to the opposite vertex of an equilateral triangle. Each axis spans from 0–100% and represents the percentage of a limb segment's contribution to limb length. **B**, A tripartite limb, such as the hind limb of *Tyrannosaurus*, is divided into its three segmental proportions. Data are plotted on the ternary by making axis I the percent femur, axis II the percent tibiotarsus, and axis III the percent tarsometatarsus. **C**, A hind limb proportion ternary showing the position of *Tyrannosaurus* (T) in proportion morphospace. The positions of four hypothetical limbs (1–4) having different combinations of limb segment percentages are also shown. Limb 1 has equal elements and falls in the center of the ternary diagram. Any combination of three segments will fall within the boundaries of the morphospace triangle. *Tyrannosaurus* skeleton modified after Heilmann (1926). Limb segments have been arbitrarily oriented at 30° from the vertical.

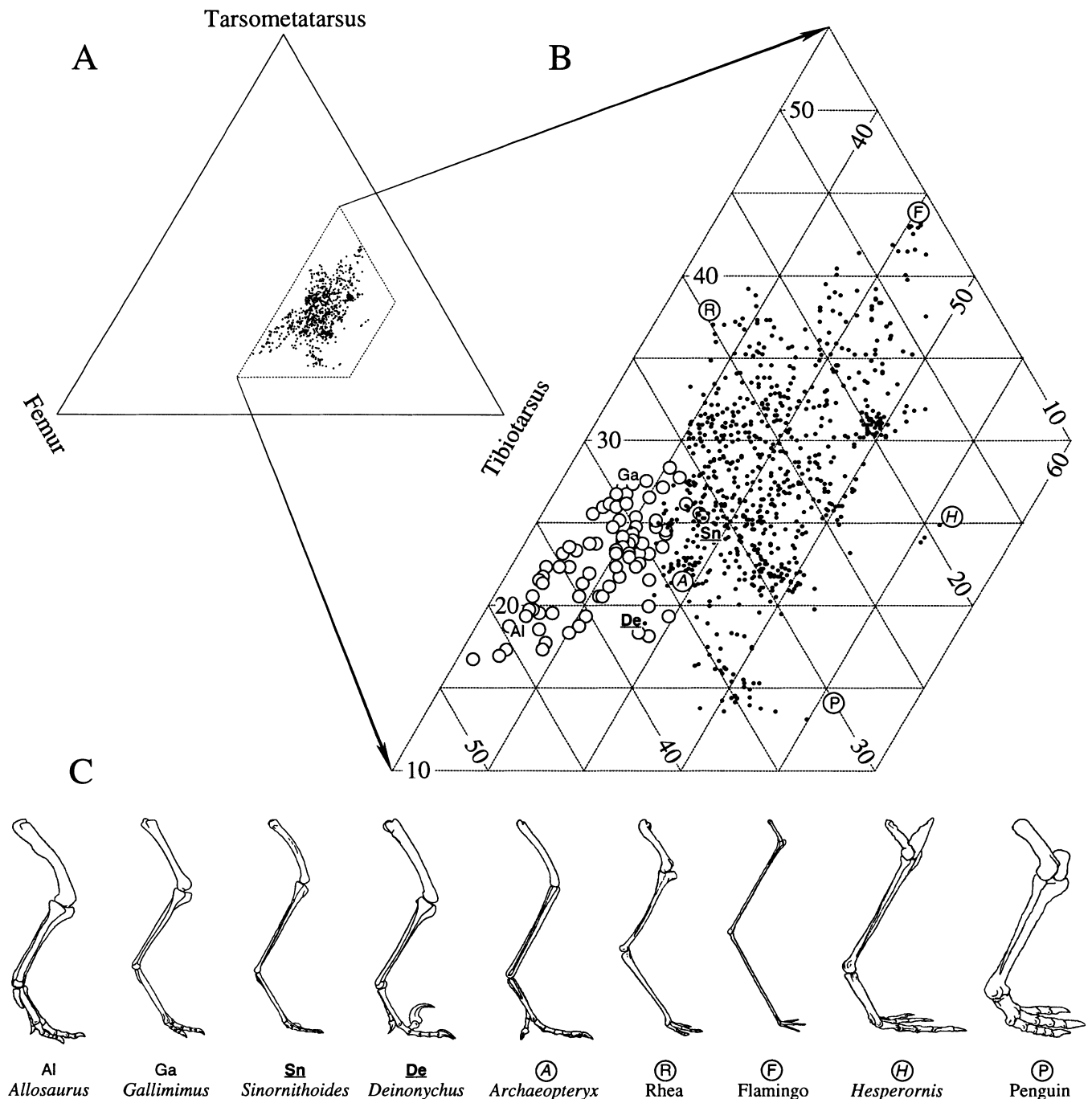


FIGURE 3. Theropod hind limb proportions in ternary morphospace. **A**, All theropods occupy only a small fraction of potential tripartite limb designs; most regions are empty. **B**, Within theropods, non-birds (open circles) form a subset that is much smaller than that of birds (dots). Avian and non-avian distributions overlap in five cells. **C**, Hind limb skeletons representing extreme proportions (symbols in **B**) within non-avian theropods and birds. The femur, tibiotarsus, and tarsometatarsus have all been arbitrarily oriented at 30° from the vertical to permit comparison of proportions. *Allosaurus* after Paul, 1987; *Gallimimus* after Osmolska et al., 1972; *Sinornithoides* after Russell and Dong, 1993b; *Deinonychus* after Ostrom, 1976b; *Archaeopteryx* after Ostrom, 1976a; rhea after Heilmann, 1926; flamingo after Howell, 1965; *Hesperornis* after Marsh, 1880; penguin after Feduccia, 1980.

phospace are vacant. No limbs were found with a femur less than 10% or more than 48% of total length. Tibiotarsi vary from 35% to 57% of the limb, whereas tarsometatarsi range from 13% to 45%. Thus the femur is most variable in its contribution (38% range), followed by the tarsometatarsus (32% range) and the tibiotarsus (22% range).

Non-Avian Theropods

Limb proportions of non-avian theropods are restricted to a subset of theropod morphospace (Figs. 3B, 4). Of the 45 triangles occupied by the entire clade, non-birds are present in only 11. This represents one quarter of the theropod region and

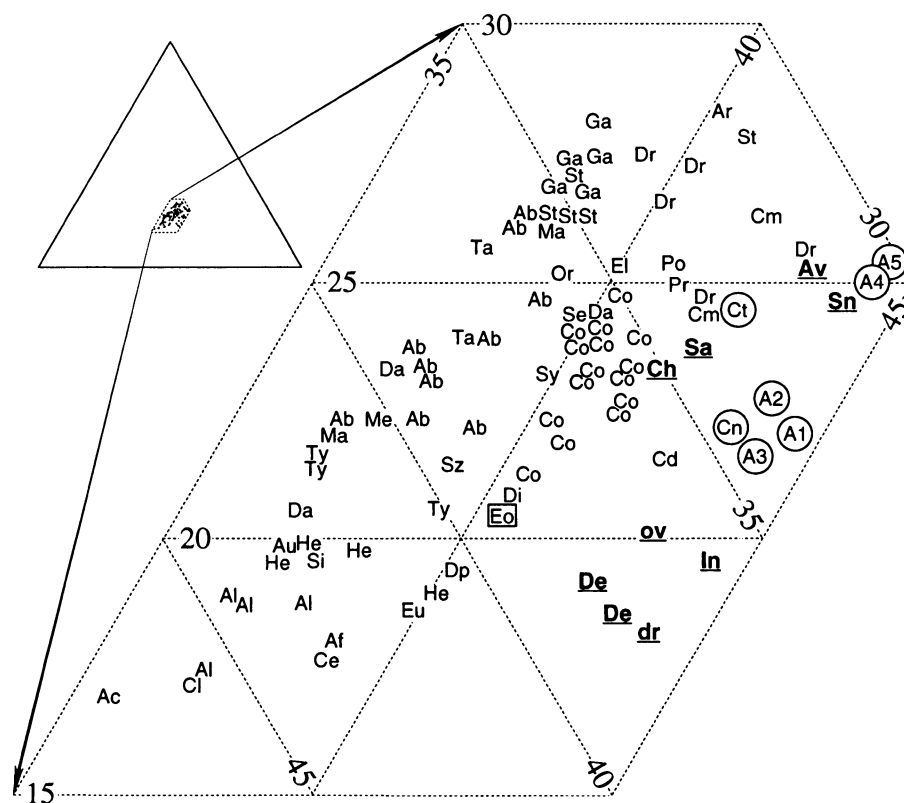


FIGURE 4. Non-avian theropod and early bird hind limb proportion morphospace. Each point represents data from a single specimen. Note that non-avian maniraptoran theropods (underlined and bold), are found adjacent to *Archaeopteryx* and other Mesozoic birds (circled). The basal theropod, *Eoraptor*, is boxed. Symbols: **A1**, London *Archaeopteryx*; **A2**, Berlin *Archaeopteryx*; **A3**, Solnhofen *Archaeopteryx*; **A4**, Eichstätt *Archaeopteryx*; **A5**, Munich *Archaeopteryx*; **Ab**, *Albertosaurus*; **Ac**, *Acrocanthosaurus*; **Af**, *Afrovenator*; **Al**, *Allosaurus*; **Ar**, *Archaeornithomimus*; **Au**, *Aublysodon*; **Av**, *Avimimus*; **Cd**, *Chuandongocoelurus*; **Ce**, *Ceratosaurus*; **Ch**, *Chirostenotes*; **Cl**, *Chilantaisaurus*; **Cm**, *Compsognathus*; **Cn**, *Confuciusornis*; **Co**, *Coelophysis*; **Ct**, *Cathayornis*; **Da**, *Daspletosaurus*; **De**, *Deinonychus*; **Di**, *Dilophosaurus*; **Dp**, *Dryptosaurus*; **Dr**, *Dromiceiomimus*; **dr**, undescribed dromaeosaur; **El**, *Elaphrosaurus*; **Eo**, *Eoraptor*; **Eu**, *Eustreptospondylus*; **Ga**, *Gallimimus*; **He**, *Herrerasaurus*; **In**, *Ingenia*; **Ma**, *Maleevosaurus*; **Me**, *Megalosaurus*; **Or**, *Ornithomimus*; **ov**, undescribed oviraptorid; **Po**, *Podokesaurus*; **Pr**, *Procompsognathus*; **Sa**, *Saurornithoides*; **Se**, *Segisaurus*; **Si**, *Sinraptor*; **Sn**, *Sinornithoides*; **St**, *Struthiomimus*; **Sy**, *Syntarsus*; **Sz**, *Szechuanosaurus*; **Ta**, *Tarbosaurus*; **Ty**, *Tyrannosaurus*.

a mere 2.8% of the potential limb morphospace. The homogeneity of non-birds is borne out in the low variation in proportions of each element (Fig. 4). The femur has a range of only 17%, the tibiotarsus 9%, and the tarsometatarsus 11% across all non-avian theropods. The lowest femur values (ca. 31% of the limb) are shared by *Sinornithoides*, *Avimimus*, and three ornithomimids (*Archaeornithomimus*, *Struthiomimus*, *Dromiceiomimus*). *Acrocanthosaurus* has the largest femoral percentage of 48%. The extreme tibiotarsal values are represented by several taxa near 36% (*Acrocanthosaurus*, *Tarbosaurus*) and 44% of the limb (*Ingenia*, *Sinornithoides*, undescribed dromaeosaur). *Acrocanthosaurus* also has the lowest tarsometatarsal percentage (17%), whereas the ornithomimids *Gallimimus* and *Archaeornithomimus* have the highest at near 28%.

Species are not randomly distributed; clusters of more closely related taxa can be identified within the theropod cloud (Fig. 4). *Tyrannosaurs* (*Tyrannosaurus*, *Tarbosaurus*, *Albertosaurus*, *Daspletosaurus*, *Aublysodon*, *Maleevosaurus*) form a cluster running diagonally along the upper left edge of the distribution. Ornithomimids (*Ornithomimus*, *Struthiomimus*, *Dromiceiomimus*, *Gallimimus*, *Archaeornithomimus*) occupy the top of the cloud. Ceratosaurs (*Ceratosaurus*, *Coelophysis*, *Syntarsus*, *Dilophosaurus*, *Procompsognathus*, *Podokesaurus*, *Elaphrosaurus*) are located in a cluster running parallel below these groups. Non-coelurosaur tetanurines (*Allosaurus*, *Acrocanthosaurus*,

Sinraptor, *Afrovenator*, *Chilantaisaurus*, *Eustreptospondylus*) occupy the lower left region of the distribution, along with the basal theropods *Eoraptor* and *Herrerasaurus*. Non-avian maniraptoran groups such as dromaeosaurs (*Deinonychus*, undescribed form), elmsaurids (*Chirostenotes*), troodontids (*Sinornithoides*, *Saurornithoides*), and oviraptorids (*Ingenia*, undescribed form) have hind limb proportions making up the right side of the cloud.

Avian Theropods

Birds show much more disparity of hind limb proportions than do other theropods (Fig. 3B). Of the 45 theropod cells, birds occupy 39, and cover one tenth of the 400 potential hind limb morphospace cells. Birds and other theropods share five cells, indicating an overlap of one ninth of the theropod distribution and one hundredth of all possible designs. The ranges of bird proportions are all larger than in non-birds: femur 27%, tibiotarsus 19%, and tarsometatarsus 32%. Femur length is just over 10% of the limb in the flamingo (*Ciconiiformes*), but is over 37% of limb length in the oilbird (*Caprimulgiformes*). The tibiotarsus remains most conservative, with a minimum of 37% in the rhea (*ratite*) and a maximum of 56% in *Hesperornis* (*Hesperornithiformes*) and penguins (*Sphenisciformes*). Varia-

tion is greatest in the tarsometatarsus, spanning from a low of 13% in penguins to almost 45% in flamingos.

Basal birds are located on the right side of the non-avian theropod cloud amidst non-bird maniraptorans (Fig. 4). This position lies in the left region of the avian cloud (Fig. 5). Hind limbs of five specimens of *Archaeopteryx* are present in two of the five cells that birds and non-birds share. Tibiotarsal values are similar in all specimens, but the Eichstätt and Munich specimens have lower femoral values and higher tarsometatarsal values than the London, Berlin and Maxberg specimens, which cluster with *Confuciusornis*. Two enantiornithine birds (*Sinornis*, *Cathayornis*) are located in this general area.

Insight into the distribution of birds within avian morphospace can be found by studying different regions of the bird cloud (Fig. 5). The upper right portion is composed of birds with a relatively low femoral and high tarsometatarsal percentages. Taxa from several orders are present. Many are ciconiiforms, such as herons, egrets, storks, ibises, and flamingos. Others are gruiforms: cranes, limpkins, bustards, and the seriema. Of similar proportions are some charadriiforms, including stilts, avocets, jacanas, godwits, crab plovers, stone curlews, and sandpipers. Finally, storm petrels (Procellariiformes) and a lone member of the Falconiformes, the secretarybird (*Sagittarius*), are found in this region.

Along the right side of the avian distribution (Fig. 5) are the loons (Gaviiformes), some grebes (Podicipediformes), alcids (Charadriiformes), and an extinct diving duck, *Chendytes* (Fig. 6). The extinct hesperornithiforms (*Hesperornis*, *Baptornis*) have a unique combination of high tibiotarsal values (patella not included) and intermediate femoral and tarsometatarsal proportions, placing them on the extreme right side of the avian cloud (Fig. 6). All but the alcids, which fly underwater, are foot propelled diving birds. Moas (Fig. 6), noted below, are also in this area. The lower regions of the bird cloud are also taxonomically mixed. Penguins (Sphenisciformes) dominate the lower edge (Fig. 6), forming a narrow band at tarsometatarsal values around 14%. Frigatebirds (Pelecaniformes) are present in this cluster. Parrots (Psittaciformes) and some kingfishers (Coraciiformes) also have limbs with relatively low tarsometatarsal percentages.

The left side of the avian distribution is dominated by the Galliformes, the chicken-like birds (Fig. 5). In this region bird and non-bird limb proportions overlap; quail, ptarmigan, grouse and capercaillie, in particular, have hind limb proportions indistinguishable from some non-avian theropods. Other taxa are also present, however. Some hawks, eagles, falcons, and kites (Falconiformes), boobies, gannets, and some pelicans (Pelecaniformes), woodpeckers (Piciformes), a trogon (Trogoniformes), and tinamous (Tinamiformes) have limbs that fall in this region. The upper left corner of bird morphospace is filled almost exclusively by ratites, such as ostriches, rheas, emus, and cassowaries (Fig. 6), although some passerines are present (Fig. 5). These birds have hind limbs with relatively short tibiotarsi, relatively large tarsometatarsi, and femora of intermediate proportion. Not all ratites inhabit this region, however. Moas, kiwis, and elephantbirds have smaller tarsometatarsal percentages and are thus located much lower in the distribution. These are subdivided into an upper cluster containing the extinct elephant-bird *Aepyornis*, the dromornithid *Genyornis*, and moas of the genus *Dinornis*, and a lower cluster containing kiwis and all other moas.

Between these edges and extremes lie birds with intermediate limb proportions (Fig. 5). As in other regions, the middle of the avian cloud is a mix of taxa from various orders that share similar combinations of limb segment length. Within this central area lie most passerines (Passeriformes), owls (Strigiformes), cuckoos and roadrunners (Cuculiformes), pigeons and doves (Columbiformes), ducks, geese, and screamers (Anseri-

formes), albatrosses, shearwaters, petrels, and fulmars (Procellariiformes), gulls and terns (Charadriiformes), nighthawks and goatsuckers (Caprimulgiformes), cormorants, anhingas, tropicbirds, and some pelicans (Pelecaniformes), vultures, condors, and ospreys (Falconiformes), rails and some bustards (Gruiformes), hornbills and most kingfishers (Coraciiformes), hummingbirds and swifts (Apodiformes), toucans (Piciformes), and the extinct sandcoleiforms.

Flying birds are found in three fourths (30) of the 39 bird cells. Flightless birds are also well distributed, occupying about one half (21) of the cells and sharing 12 cells with flying forms (Fig. 6). Major groups of flightless birds include the ratites (ostriches, rheas, emus, cassowaries, kiwis, moas, elephantbirds, *Genyornis*), the hesperornithiforms, and the penguins. Flight was also lost independently in members of otherwise flying orders, such as pigeons (*Raphus*), ducks (*Chendytes*, *Mergus*, *Tachyeres*), cormorants (*Compsahallius*), parrots (*Strigops*), rails (*Gallirallus*, *Aptornis*, *Atlantisia*), alcids (*Pinguinus*, *Mancalla*, *Praemancalla*), and grebes (*Rollandia*).

DISCUSSION

Theropods have a 230 million year history of bipedal locomotion. One lineage of theropods, birds, evolved aerial locomotion. In turn, multiple independent lineages of birds lost this ability and became secondarily flightless. Such a clade offers an interesting opportunity to study locomotor evolution. We predict that theropods with such different locomotor module histories should differ in their limb morphology. In the following sections we address how the distribution of limbs in proportion morphospace allows us to gain insight into the evolution of theropod hind limb design.

Limb Proportion Disparity and Flight

We predicted that birds, because of their greater modularity, would have more disparate hind limb morphologies than non-avian theropods. The distribution of hind limbs within proportion morphospace lends strong support to this prediction. Compared to birds, which fill about 10% of the potential morphospace, non-avian theropods have much more conservative limb proportions and occupy less than 3%. This is consistent with the idea that birds have dual locomotor systems (Ostrom, 1979, 1986; Pennycuik, 1986; Butler, 1991; Gatesy and Dial, 1996) and are thus less constrained in their hind limb morphology than other theropods. Flight eased barriers to hind limb novelty previously imposed by obligate bipedalism and thereby made unused regions of morphospace accessible.

We suggest that the hind limb of non-avian theropods could not undergo major modification without jeopardizing walking or running proficiency. The hind limbs of many birds seem maladaptive for a theropod that is unable to capture food and escape predators in some other way. For example, it is highly unlikely that the feeble hind limbs of hummingbirds, swifts, nighthawks, and other highly specialized aerial foragers would have evolved in exclusively terrestrial theropods. Similarly, freshwater and marine habitats must have been available to non-bird theropods, but may have been rendered relatively inaccessible by their reliance on a single locomotor module. Only after the acquisition of flight do theropods become aquatic and evolve more bizarre hind limb morphologies. In general, we conclude that the initial morphological steps toward locomotor specialization are more easily tolerated by theropods with functional wing modules, since selective forces repressing hind limb novelty would be relatively weaker than in theropods with only one module.

If the possession of three locomotor modules allowed birds to colonize new hind limb morphospace, what happened when flight was subsequently lost? Interestingly, loss of the pectoral

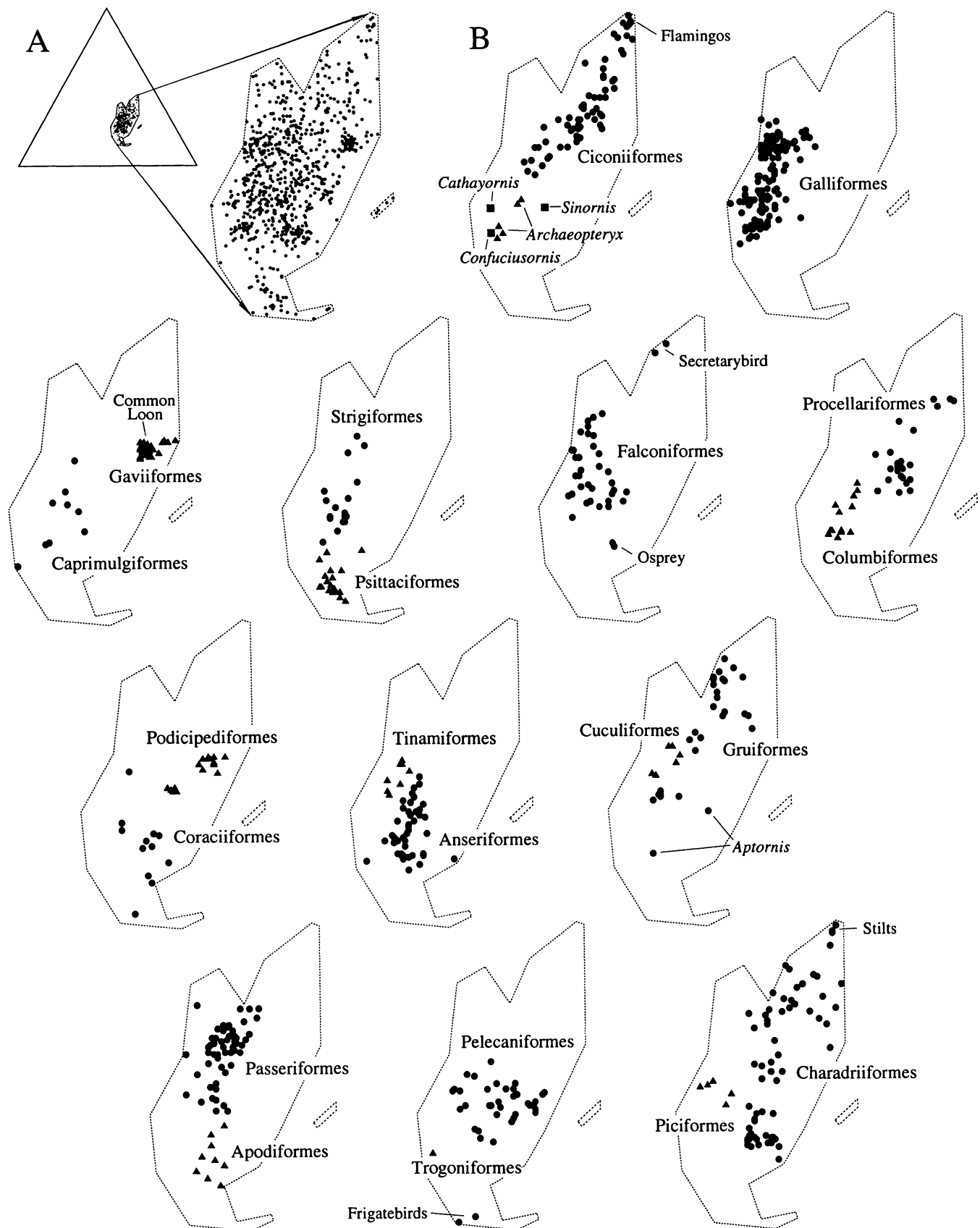


FIGURE 5. A, Avian hind limb proportions in ternary morphospace. B, Extant bird orders with flying members occupy distinct regions of the avian cloud. Four genera of Mesozoic birds are included. Note that the two polygons drawn around bird data are intended to facilitate comparison only, not to represent the known or presumed edges of the avian cloud.

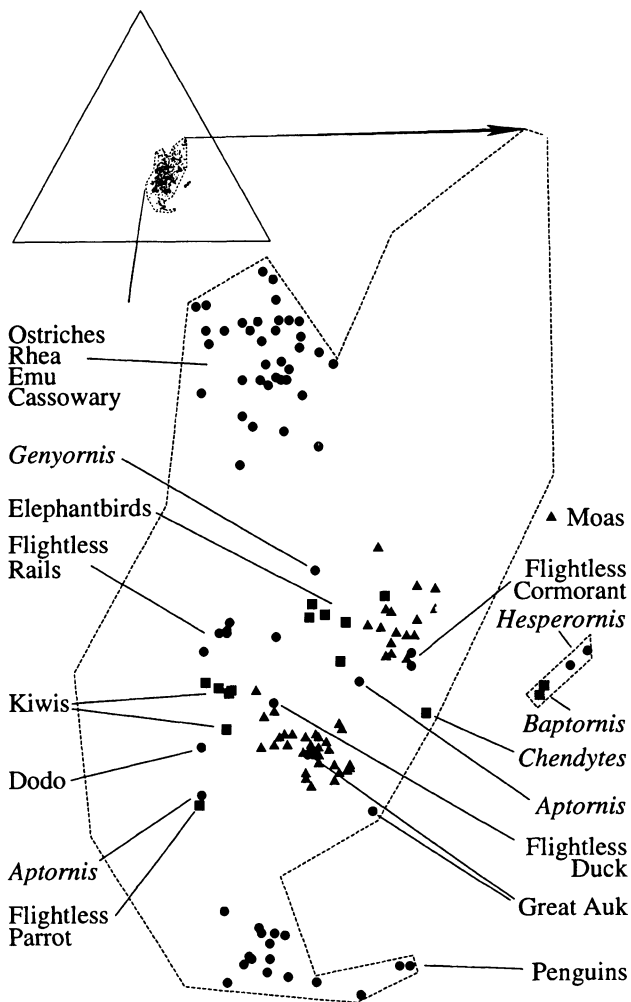


FIGURE 6. Ternary distribution of flightless bird hind limb proportions. Points are plotted within polygons drawn around data from all birds as in Figure 5. All moas are shown as triangles. Note the complete absence of flightless forms from the upper right region of the bird polygon.

module does not return birds to a more primitive, non-avian hind limb morphology. Rather, flightless birds occupy some of the extreme regions of the avian cloud (Fig. 6). Although there is not room here to fully discuss this issue (see Livezey, 1992, 1989, and Livezey and Humphrey, 1986 for more detail), such a distribution is not surprising when one considers the history of flightlessness. First, since flight was lost many times in birds, each lineage could have evolved from flying ancestors that already had disparate morphologies. For example, parrots (Psittaciformes) and cormorants (Pelecaniformes) occupy different regions of hind limb proportion morphospace (Fig. 5), and their relatively recent flightless members retain this distinction (Fig. 6). Second, the ecological conditions permissive to flightlessness (isolation, lack of predators, large body size) may themselves ease pressures hindering novelty. Although the importance of locomotor performance in their demise is not always clear, the relatively helpless Dodo, Great Auk, and other insular forms have fared poorly in the face of introduced predators. Third, many flightless birds (ducks, grebes, auks, cormorants, penguins, hesperornithiforms) are primarily aquatic. Penguins and some alcid are flightless, but still have three locomotor modules since the wings and tail function in water. Hesperor-

nithiform hind limbs were so modified for subaqueous propulsion as to be useless on land. Specializations in other swimming forms are not so dramatic, but in most cases convergence with exclusively terrestrial flightless forms would not be expected. Thus, birds that revert to flightlessness should not necessarily return to a primitive hind limb morphology. Each started from a different point in morphospace, and many have limbs adapted for lifestyles other than terrestrial bipedalism. In this way the limb proportions of flightless birds often reflect their descent from flying theropods with three locomotor modules. It is for this reason that we included them in our comparison of avian and non-avian hind limbs.

Benefits of the Ternary Diagram

Ternary diagrams are a useful way of studying the relative contribution of three elements simultaneously, such as the percentage of quartz, feldspar, and clay in sandstones, the frequencies of three alleles at a locus, or morphological variables (Mattison and Giffin, 1989; Mattison, 1993). Bivariate plots have been used to study theropod limb design (Coombs, 1978; Gatesy, 1991; Holtz, 1994a), but representing three elements simultaneously has proven awkward. Typically, pairs of elements are plotted separately, making it difficult to compare data between graphs for single individuals. More derived graphs of tibia to femur ratio (T/F) versus metatarsal to tibia ratio (M/T) contain the same information as our ternary diagrams (Coombs, 1978; Holtz, 1994a), but in a less accessible form. Because it has three linear axes, the contribution of each element to limb length can be read directly from the ternary diagram. Another alternative has been expressing segment proportions as histograms (e.g., Engels, 1938), but this format severely limits comparison among individuals or species. Patterns of variation would be impossible to assimilate if we had made over nine hundred histograms from our data set. The ternary diagram allows proportion differences to be assessed easily since data for all individuals of all species can be plotted on the same graph.

A ternary diagram also sheds light on intramembral ratios. Traditional indices such as tibia length to femur length (T/F ratio) have been used to judge the degree of cursoriality in mammals (Gregory, 1912; Osborn, 1929). A high T/F ratio is typically interpreted as an adaptation for running, whereas a low T/F ratio is indicative of mediportal or graviportal locomotion. These criteria have been applied to dinosaurs in general (Coombs, 1978), and a relationship between T/F ratio and cursoriality continues to be invoked in almost every theropod described (e.g., Osborn, 1916; Ostrom, 1976b; Colbert, 1989).

The scope of avian hind limb disparity revealed by our data makes the reliance on T/F ratio alone highly suspect. Ratites such as ostriches, which have T/F ratios of about 1.5–2.0, are often used to exemplify cursorial birds. Unfortunately, there is no simple relationship between cursoriality and T/F ratio across birds. The problem can be visualized by projecting lines of equivalent T/F ratio on the theropod hind limb ternary (Fig. 7A). Birds to the right of ostriches have increasingly higher T/F ratios (Fig. 7B). Flamingos have ratios as high as 4.1, but like other wading birds in this region they could not be considered more cursorial than ostriches. Clearly, T/F ratios increase in birds for reasons other than cursoriality (Howell, 1965), making any straightforward interpretation of locomotor function impossible. Assuming that lower T/F ratios relate directly to cursoriality is likely to be similarly flawed. Yet, theropods with identical T/F ratios can still differ in proportion; the tarsometatarsus is variable and must be included in any evaluation of basic limb design. This points out the need to consider all three of the major skeletal elements when assessing limb function. The ternary allows one component of the limb to be assessed while the ratio of the other two is held constant. For example,

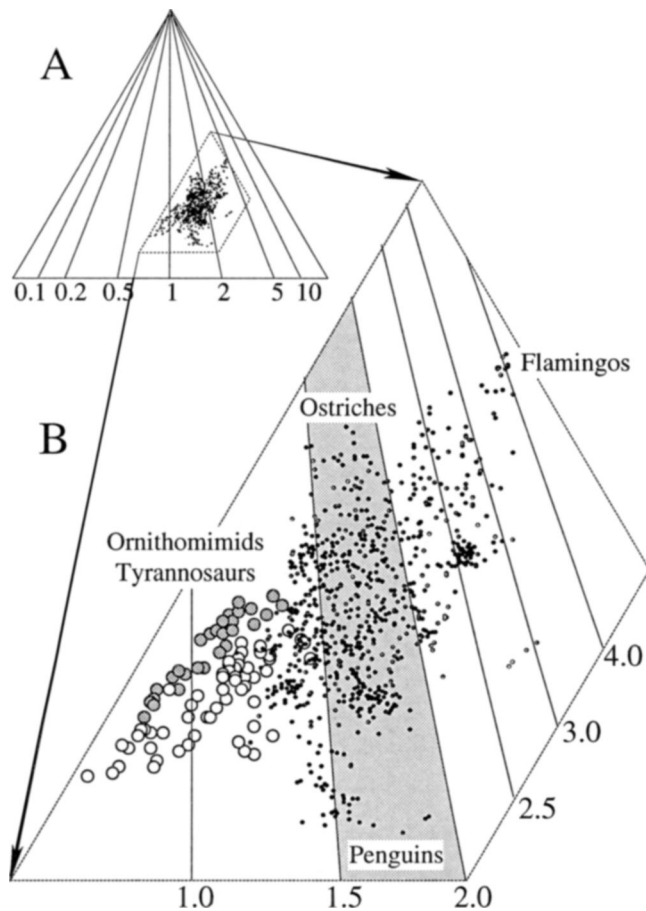


FIGURE 7. Intramembral ratios such as Tibia/Femur (T/F) can be visualized using ternary diagrams. A, Lines of equal ratio radiate from the top and allow hind limbs to be easily compared. B, Notice that ratites such as ostriches have the same T/F ratio as many non-cursorial birds, including penguins. Also note that birds with higher T/F ratios, such as flamingos, are not necessarily more terrestrial or adapted for running. However, at each T/F ratio species with the highest tarsometatarsal percentage may be more cursorial than those with relatively smaller tarsometatarsi. Ornithomimids and tyrannosaurs (shaded) are located along the top edge of the non-avian theropod cloud.

all birds within the shaded wedge (Fig. 7B) share similar T/F ratios. Hummingbirds, alcids, kingfishers, and penguins share T/F ratios with ostriches, but would never be considered cursors. This alone should warn of the absurdity of assessing running ability from just these two measures.

Running ratites, however, have the relatively longest tarsometatarsi among birds of similar T/F ratio. It is possible that for any given T/F ratio there is a gradient of cursoriality increasing with higher tarsometatarsal proportion. Within non-avian theropods the 0.75–1.4 range in T/F ratio is partially related to scale; larger taxa and more mature individuals tend to have lower T/F ratios (e.g., Gatesy, 1991; Holtz, 1994a). At any T/F ratio, however, tyrannosaurs and ornithomimids have higher tarsometatarsal values than other non-avian theropods (Fig. 7B). This pattern graphically distinguishes between the limbs of purported cursors (e.g., Holtz, 1994a) and other non-birds. Unfortunately, non-bird theropod tarsometatarsi have a very small range. Tyrannosaur tarsometatarsal values exceed those of *Sinraptor*, *Szechuanosaurus*, *Ceratosaurs*, *Afrovenator*, *Eustreptospondylus*, *Herrerasaurus*, *Dryptosaurus*, *Eoraptor*, *Coelophysis*, and *Dilophosaurus*, but only by 5% of limb length at most. This is within the range of variation among

ostriches, rheas, emus, and cassowaries. Therefore, the significance, if any, of such relatively minor differences for running ability or lifestyle (i.e., active predator, scavenger) is by no means clear.

Caveats

Several factors hamper the direct interpretation of our results. First, we are making a comparison between a paraphyletic group, non-avian theropods, and a monophyletic group, birds. Fortunately, the accepted time ranges for these groups are not too different. Non-birds survived for about 165 million years and birds at least 140 million, thus giving each group a similar amount of time to evolve limb disparity. A more rigorous comparison would be between birds and their sister taxon. However, this is difficult since the maniraptoran sister group of birds is still unclear and will have a very low diversity. Another concern is that the relationship we invoke between locomotor modules and limb disparity may be unique to theropods. Data from other clades will be required to advance our results toward more generalizable rules of limb evolution.

A more significant issue is sampling. This applies both to what was available as well as what was selected. Complete non-avian theropod limbs are relatively rare in paleontological collections. In contrast, bird limb skeletons are so abundant that thousands of individuals from thousands of extant species could have been measured. This led us to sample fossil and living theropods very differently; all complete non-bird limbs were used, whereas birds were selected non-randomly to try to define the edges of the avian cloud. Since our bird data set was nine times larger than that of non-birds, broader avian distributions could be due to sampling alone. By analyzing limb proportion disparity in terms of morphospace area or range, our conclusions are strongly influenced by sample size (Foote, 1993; Wagner, 1995). An alternative approach would have been to sample birds randomly to create equally sized data sets. However, we did our best to “push the envelope” and maximize morphospace filling with complete limbs. Even if this invalidates the testing of our hypothesis, we feel this is a more accurate representation of theropod morphospace as it is currently known. A random sampling from our bird data set or a calculation of average distance among points (e.g., Foote, 1993) would still be biased since we were so selective in our choice of taxa.

Biases against the preservation and recovery of small, thin-walled bones are probably skewing our knowledge about small extinct theropods, both bird and non-bird. The majority of theropod fossils of all size are incomplete; our exclusion of these specimens also affects our results. Notably missing from our hind limb data set are therizinosaurs (e.g., *Segnosaurus*, *Erlikosaurus*, *Therizinosaurus*, *Alxasaurus*), which have been reconstructed from partial material with a relatively long femur and a very short metatarsus (Russell and Russell, 1993; Russell and Dong, 1993a). If such restorations are correct, this clade of unusual theropods has deviated substantially from all other non-avian theropods. Another missing specimen is a juvenile *Saurornithoides* (Currie and Peng, 1993) with an incomplete tibia. Unlike any other non-avian theropod the tarsometatarsus is longer than the femur. The proportions of *Mononykus* are also of interest, but the metatarsals of the published specimen are incomplete (Perle, et al., 1994). Data from new theropod specimens and those that we were unable to obtain will undoubtedly expand the edges of the non-avian and avian clouds.

Measurement error will contribute to the displacement of proportions in morphospace. Excluding some tarsal elements will shift non-avian theropod points slightly, but not change our conclusions. Ontogenetic and intraspecific variation also has some impact. In birds we avoided immature specimens when possible. An assessment of individual variation was made by

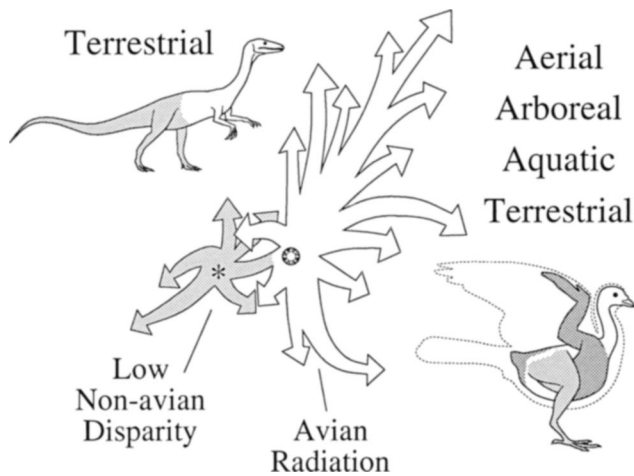


FIGURE 8. Non-avian theropods diverged little (shaded arrows) from basal proportions (asterisk) and were primarily terrestrial. Their single locomotor module may have constrained hind limb novelty, resulting in low proportion disparity. One lineage, birds, developed three locomotor modules and flight. This increase in modularity sparked a major radiation in limb design (white arrows) from basal bird proportions (circle). Hind limbs specialized for aerial, arboreal, aquatic, and terrestrial lifestyles evolved after the flight apparatus eased the primitive constraint.

measuring 39 specimens of the Common Loon (*Gavia immer*; Fig. 5). Proportion ranges in this population were only about 2% for each limb element, well below the resolution level of our interpretations. We also combined ratios from individual birds with ratios calculated from mean bone lengths on the same plot. This is inconsistent, but should not severely alter our results. Since we were dealing exclusively with proportions rather than absolute measures, size was less influential than in bivariate length plots. Additionally, a study of coot skeletons has shown limb segment lengths to be highly correlated, such that a ratio of mean lengths is almost identical to a mean of individual ratios (Engels, 1938).

Finally, our reliance on the proportions of the lengths of the three main skeletal elements is a gross oversimplification of the intricacies of limb morphology and function. In many cases, disparate limb proportions reflect known differences in limb morphology and function. In others, disparity is masked by similar limb proportions. In the middle of the avian hind limb cloud, for example, there are regions of overlap between ducks, tube-nosed sea birds, hornbills, owls, nighthawks, swifts, chicken-like birds, hawks, and kiwis. Clearly, the locomotor variation (based on body size, foot morphology, relative limb size, behavior, etc.) in this region of proportion morphospace is much higher than indicated by the ternary diagram. More detailed comparisons of all aspects of theropod organization, from scaling to muscle mechanics to phalangeal design, are needed before we have a more complete picture of locomotor evolution in this clade.

Theropod Locomotor Diversity

A striking result of this study is the relative homogeneity of non-avian theropod hind limb proportions in light of avian disparity (Fig. 3). This similarity supports the notion that non-birds were primarily adapted for terrestrial bipedalism (Fig. 8). We suggest that the body plan of theropods other than birds remained relatively conservative throughout the Mesozoic and was accompanied by low locomotor diversity. Unlike birds, and despite dramatic variation in body size, there is no evidence for

highly reduced hind limbs or those specialized for diving, paddling, wading, trunk climbing, or perching. Due in part to their modular locomotor system, birds evolved much more disparate limbs than non-birds. Therefore, we should not expect non-avian theropods to have had as broad a locomotor spectrum as seen in birds today.

This superficial homogeneity, however, masks structural variation with potential functional consequences. Significant transformations in tail size, hind limb retraction mechanism, scaling, and pelvic morphology resulted in modification of the basal theropod locomotor module in coelurosaurs closely related to birds (Gatesy, 1990, 1994; Gatesy and Dial, 1996). We believe that a change in hind limb mechanics occurred during theropod evolution, and that this is reflected in a shift of proportions into a new region of morphospace. Maniraptorans occupy the lower right side of the non-bird morphospace (Fig. 4), indicating that they have the highest tibiotarsal percentages of the group. Together with changes in the tail and femur, these data support the presence of an incipient hamstring-driven propulsion mechanism using knee flexion in maniraptorans, which was replacing the primitive caudofemoral retraction mechanism centered on hip extension (Gatesy 1990, 1994; Gatesy and Dial, 1996). Basal birds such as *Archaeopteryx* have limb proportions only a short step away from non-avian maniraptorans (Fig. 4). We view subsequent evolution of bird hind limb proportions from this ancestral design as evidence of an explosive radiation in locomotor diversity founded on three locomotor modules (Fig. 8).

Conclusions

As flying theropods with three locomotor modules, birds differ from their non-avian relatives, which only had a single locomotor module. We propose that non-birds were relatively conservative in design and were primarily terrestrial bipeds. However, a transformation of the primitive module occurred in theropods closely related to birds. This resulted in the eventual decoupling of the hind limb and tail into distinct locomotor modules in early birds, which had a flight apparatus formed by the novel allegiance of the pectoral and caudal modules (Gatesy and Dial, 1996). Aerial locomotion allowed birds access to previously unavailable habitats and food resources, but may not fully explain their success. We propose that flight increased modular flexibility, resulting in more disparity and locomotor diversity in birds than in non-avian theropods.

In the future, these conclusions need to be tested by addressing other aspects of limb morphology, since proportions alone do not adequately portray the true disparity among theropod limbs. However, proportions reveal patterns that are not yet fully understood. For example, is the shape of the theropod distribution real? Do theropods fill a relatively small or large portion of morphospace compared to other tetrapod clades? Are empty regions biomechanically off limits or simply vacant by chance? Further analysis of ontogenetic and phylogenetic trajectories within proportion morphospace may help answer these questions and reveal more general rules of theropod limb design.

ACKNOWLEDGMENTS

We thank R. Paynter of the Museum of Comparative Zoology and F. Sibley of the Peabody Museum for access to collections in their care. M. Norell and P. Sereno kindly provided data from their unpublished work. We appreciate the many helpful comments from two anonymous reviewers and from the Brown Morphology Group, particularly G. E. Goslow, Jr., D. Ritter, and K. Rafferty. K. Earls deserves special thanks for helpful insights and the use of her avian data set.

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Received 6 August 1996; accepted 30 September 1996.

APPENDIX 1. Limb segment lengths (in mm) of non-avian theropods (F, femur; T, tibiotarsus; M, tarsometatarsus).

Species	Specimen	F	T	M	Source
<i>Acrocanthosaurus atokensis</i>	MU 0-80-59	1153	865	416	Stovall and Langston (1950)
<i>Afrovenator abakensis</i>	UC OBA 1	760	687	321	Sereno et al. (1994)
<i>Albertosaurus libratus</i>	NCM 2120	1040	1000	594	Lambe (1917)
<i>Albertosaurus libratus</i>	AMNH 5458	1025	990	625	Holtz (1994a)
<i>Albertosaurus libratus</i>	AMNH 5218	954	850	515	Holtz (1994a)
<i>Albertosaurus libratus</i>	NMC 11593	940	900	580	Russell (1970)
<i>Albertosaurus libratus</i>	USNM 12814	880	850	535	Holtz (1994a)
<i>Albertosaurus libratus</i>	AMNH 5664	700	748	480	Holtz (1994a)
<i>Albertosaurus libratus</i>	ROM 1247	730	775	542	Holtz (1994a)
<i>Albertosaurus libratus</i>	AMNH 5423	600	630	440	Holtz (1994a)
<i>Albertosaurus sarcophagus</i>	ROM 807	1020	1030	590	Holtz (1994a)
<i>Albertosaurus sarcophagus</i>	TMP 81.10.1	950	970	610	Holtz (1994a)
<i>Allosaurus fragilis</i>	UVP 6000r	880	730	375	Holtz (1994a)
<i>Allosaurus fragilis</i>	UVP 60001	850	745	372	Holtz (1994a)
<i>Allosaurus fragilis</i>	USNM 4734	850	690	327	Gilmore (1920)
<i>Allosaurus</i> sp.	AMNH 290	985	810	423	Holtz (1994a)
<i>Archaeornithomimus asiaticus</i>	AMNH 6565	314	401	286	Holtz (1994a)
<i>Aublysodon</i> sp.	OMNH 10131	1033	891	483	Holtz (1994a)

APPENDIX 1. (Continued)

Species	Specimen	F	T	M	Source
<i>Avimimus portentosus</i>	PIN 3907/1	188	257	153	Holtz (1994a)
<i>Ceratosaurus nasicornis</i>	USNM 4735	620	555	254	Gilmore (1920)
<i>Chilantaisaurus tashuikouensis</i>	IVPP V.2884.7	1190	954	450	Holtz (1994a)
<i>Chirostenotes pergracilis</i>	TMP 79.30.1	310	367	208	Holtz (1994a)
<i>Chuandongocoelurus primitivus</i>		200	237	122	Holtz (1994a)
<i>Coelophysis bauri</i>	UCMP 129618	245	255	150	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7223	209	224	126	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7224	203	221	120	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7249	196	207	110	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7244	173	195	120	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7243	172	199	114	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7228	164	188	108	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7232	141	157	95	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7229	135	154	85	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7238	126	147	87	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7233	126	140	81	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7247	125	138	84	Holtz (1994a)
<i>Coelophysis bauri</i>	MNA V3318	123	136	82	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7246	122	136	79	Holtz (1994a)
<i>Coelophysis bauri</i>	AMNH 7234	118	135	84	Holtz (1994a)
<i>Compsognathus longipes</i>	MNHN CNJ 79	110	136	81	Bidar et al. (1972)
<i>Compsognathus longipes</i>	BSP AS I 536	67	88	56	Ostrom (1978)
<i>Daspletosaurus torosus</i>	AMNH 5438	1000	870	490	Holtz (1994a)
<i>Daspletosaurus torosus</i>	NMC 350	930	870	555	Holtz (1994a)
<i>Daspletosaurus torosus</i>	NMC 11315	655	736	448	Russell (1970)
<i>Deinonychus antirrhopus</i>	MCZ 4371	336	382	164	Ostrom (1976b)
<i>Deinonychus antirrhopus</i>	YPM	331	370	168	Holtz (1994a)
<i>Dilophosaurus wetherilli</i>	UCMP 37302	557	580	300	Welles (1984)
<i>Dromaeosaur—undescribed</i>		208	243	101	Norell (pers. comm.)
<i>Dromiceiomimus brevitertius</i>	NMC 12228	468	578	397	Holtz (1994a)
<i>Dromiceiomimus brevitertius</i>	NMC 12068	440	527	353	Holtz (1994a)
<i>Dromiceiomimus brevitertius</i>	ROM 852	440	520	370	Holtz (1994a)
<i>Dromiceiomimus brevitertius</i>	ROM 797	390	483	288	Holtz (1994a)
<i>Dromiceiomimus brevitertius</i>	NMC 12069	376	511	308	Holtz (1994a)
<i>Dryptosaurus aquilunguis</i>	ANSP 9995(10006)	787	781	380	Holtz (1994a)
<i>Elaphrosaurus bambergi</i>	HMN Gr.S 38-44	529	608	391	Holtz (1994a)
<i>Eoraptor lunensis</i>	PVSJ 512	152	157	81	Sereno (pers. comm.)
<i>Eustreptospondylus oxoniensis</i>	OUM J13558	520	500	235	Holtz (1994a)
<i>Gallimimus bullatus</i>	GI 100/11	665	740	530	Osmólska et al. (1972)
<i>Gallimimus bullatus</i>	ZPAL MgD-I/8	629	695	497	Holtz (1994a)
<i>Gallimimus bullatus</i>	ZPAL MgD-I/1	360	392	280	Holtz (1994a)
<i>Gallimimus bullatus</i>	ZPAL MgD-I/94	267	302	225	Holtz (1994a)
<i>Gallimimus bullatus</i>	GI 100/10	192	218	157	Osmólska et al. (1972)
<i>Herrerasaurus ischigualastensis</i>	PVL 2566	473	411	223	Holtz (1994a)
<i>Herrerasaurus ischigualastensis</i>	PVL 2054	385	327	176	Holtz (1994a)
<i>Herrerasaurus ischigualastensis</i>	PVSJ 373	345	315	165	Novas (1993)
<i>Herrerasaurus ischigualastensis</i>	MACN 1890	286	280	134	Holtz (1994a)
<i>Ingenia yanshini</i>	GI 100/30	228	281	125	Barsbold et al. (1990)
<i>Maleevosaurus novojlovi</i>	PIN 552-2	560	605	420	Maleev (1974)
<i>Maleevosaurus novojlovi</i>	PIN 551-2	970	880	540	Maleev (1974)
<i>Megalosaurus bucklandi</i>	BMNH 31806.9	700	650	393	Holtz (1994a)
<i>Ornithomimus edmontonicus</i>	ROM 851	435	475	310	Russell (1972)
<i>Oviraptorid—undescribed</i>		192	225	107	Norell (pers. comm.)
<i>Podokesaurus holyokensis</i>	Destroyed	86	104	65	Holtz (1994a)
<i>Procompsognathus triassicus</i>	SMNS 12591	93	113	69	Ostrom (1981)
<i>Saurornithoides mongoliensis</i>	AMNH 6516	198	243	139	Holtz (1994a)
<i>Segisaurus halli</i>	UCMP 32101	~145	160	99	Camp (1936)
<i>Sinornithoides youngi</i>	IVPP V9612	~140	198	111	Russell and Dong (1993b)
<i>Sinraptor dongi</i>	IVPP 10600	876	769	410	Currie and Zhao (1993)
<i>Struthiomimus altus</i>	AMNH 5257	513	560	385	Holtz (1994a)
<i>Struthiomimus altus</i>	UCMZ 1980.1	502	556	398	Holtz (1994a)
<i>Struthiomimus altus</i>	AMNH 5339	480	535	365	Russell (1972)
<i>Struthiomimus altus</i>	NMC 930	430	560	387	Holtz (1994a)
<i>Struthiomimus altus</i>	ROM 1790	397	430	297	Holtz (1994a)
<i>Syntarsus rhodesiensis</i>	QG 1	208	223	132	Raath (1969)
<i>Szechuanosaurus campi</i>	IVPP V.239	364	360	200	Holtz (1994a)
<i>Tarbosaurus bataar</i>	ZPAL MgD-I/3	700	700	445	Holtz (1994a)
<i>Tarbosaurus bataar</i>	ZPAL MgD-I/29	580	590	410	Holtz (1994a)
<i>Tyrannosaurus rex</i>	TMP 81.12.1	1340	1180	698	Holtz (1994a)
<i>Tyrannosaurus rex</i>	CM 9380	1300	1140	684	Holtz (1994a)
<i>Tyrannosaurus rex</i>	MOR 009	1143	1118	593	Holtz (1994a)

APPENDIX 2. Avian limb segment lengths (in mm; F, femur; T, tibio-tarsus; M, tarsometatarsus).

Species	F	T	M	Specimen number
Ratites				
Apterigidae				
<i>Apteryx australis</i>	86.7	128.1	68.7	YPM 4384
<i>Apteryx australis</i>	99.0	145.0	77.6	YPM 13486
<i>Apteryx oweni</i>	80.4	113.7	62.9	MCZ 308
<i>Apteryx oweni</i>	72.1	103.9	56.6	YPM 2118
Struthionidae				
<i>Struthio camelus</i>	230.0	410.0	398.0	MCZ 828
<i>Struthio camelus</i>	320.0	545.0	483.0	MCZ 2686
<i>Struthio camelus</i>	317.0	567.0	493.0	MCZ 2686
<i>Struthio camelus</i>	285.0	495.0	430.0	MCZ 3701
<i>Struthio camelus</i>	266.0	494.0	437.0	YPM 4347
Rheidae				
<i>Rhea americana</i>	210.0	318.0	325.0	MCZ 2083
<i>Rhea americana</i>	159.0	278.0	284.0	MCZ 689
<i>Rhea americana</i>	83.0	134.0	119.0	MCZ 6552
<i>Rhea americana</i>	215.0	325.0	320.0	MCZ 1631
<i>Rhea americana</i>	187.0	278.0	285.0	YPM 6503
<i>Rhea americana</i>	195.0	329.0	306.0	YPM 11524
<i>Rhea americana</i>	206.0	346.0	332.0	YPM 14047
Casuariidae				
<i>Casuarius bennetti</i>	203.0	320.0	250.0	MCZ
<i>Casuarius casuarius</i>	47.4	81.8	65.2	YPM 6208
<i>Casuarius sp.</i>	218.0	350.0	295.0	YPM 4351
<i>Casuarius sp.</i>	198.0	323.0	264.0	YPM 2123
Dromiceidae				
<i>Dromecius novaehollandiae</i>	227.0	415.0	385.0	MCZ 198
<i>Dromecius novaehollandiae</i>	225.0	400.0	375.0	MCZ 1627
Tinamiformes				
Tinamidae				
<i>Crypturellus boucardi</i>	50.7	75.9	52.0	MCZ 2750
<i>Crypturellus noctivagus</i>	58.0	86.4	59.5	MCZ 276
<i>Eudromia elegans</i>	56.0	77.1	46.6	MCZ 3064
<i>Nothura maculosa</i>	42.4	62.3	39.0	MCZ 1653
<i>Rhynchotus rufescens</i>	72.6	98.5	65.0	MCZ 1633
<i>Tinamus major</i>	65.0	98.2	69.0	MCZ 2774
<i>Tinamus tao</i>	70.0	108.0	70.8	MCZ 3705
Podicipediformes				
Podicipedidae				
<i>Aechmophorus occidentalis</i>	44.7	110.8	68.0	MCZ 2951
<i>Podiceps auritus</i>	33.6	77.0	46.9	MCZ 6429
<i>Podiceps auritus</i>	31.4	70.3	44.5	MCZ 7099
<i>Podiceps auritus</i>	30.8	70.7	43.3	MCZ 7163
<i>Podiceps auritus</i>	32.5	73.3	46.1	MCZ 6044
<i>Podiceps auritus</i>	33.2	77.1	48.4	MCZ 2726
<i>Podiceps caspicus</i>	31.7	66.6	41.7	MCZ 6070
<i>Podiceps caspicus</i>	30.3	64.3	38.9	MCZ 4076
<i>Podiceps caspicus</i>	29.8	63.9	40.8	MCZ 4080
<i>Podiceps grisegena</i>	46.0	107.5	61.9	MCZ 1015
<i>Podilymbus podiceps</i>	41.8	75.3	43.9	MCZ 1466
<i>Podilymbus podiceps</i>	36.2	63.2	36.9	MCZ 7647
<i>Podilymbus podiceps</i>	37.1	63.1	37.5	MCZ 7648
Gaviiformes				
Gaviidae				
<i>Gavia immer</i>	61.8	150.0	93.6	MCZ 1432
<i>Gavia immer</i>	60.3	150.4	94.2	MCZ 1658
<i>Gavia immer</i>	56.4	143.3	90.2	MCZ 1661
<i>Gavia immer</i>	51.1	134.0	85.3	MCZ 2148
<i>Gavia immer</i>	58.0	141.1	87.8	MCZ 2593
<i>Gavia immer</i>	60.0	146.0	91.7	MCZ 3030
<i>Gavia immer</i>	55.9	135.0	86.3	MCZ 7019
<i>Gavia immer</i>	57.7	140.0	87.1	MCZ 7103
<i>Gavia immer</i>	49.8	134.0	81.6	MCZ 7893
<i>Gavia immer</i>	60.5	155.0	97.0	MCZ 7894
<i>Gavia immer</i>	57.6	145.0	95.0	MCZ 7895
<i>Gavia immer</i>	65.9	160.0	101.0	MCZ 7896
<i>Gavia immer</i>	49.5	127.0	82.2	MCZ 7903
<i>Gavia immer</i>	57.3	146.0	92.5	MCZ 7904

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
<i>Gavia immer</i>	59.8	151.0	95.0	MCZ 7905
<i>Gavia immer</i>	62.1	150.0	93.2	MCZ 7912
<i>Gavia immer</i>	54.1	140.0	85.0	MCZ 7913
<i>Gavia immer</i>	59.1	144.0	91.8	MCZ 7914
<i>Gavia immer</i>	57.6	147.0	91.3	MCZ 7915
<i>Gavia immer</i>	57.8	149.0	93.6	MCZ 7916
<i>Gavia immer</i>	56.5	146.0	88.3	MCZ 7917
<i>Gavia immer</i>	56.5	145.0	92.4	MCZ 7918
<i>Gavia immer</i>	56.9	140.0	91.0	MCZ 7919
<i>Gavia immer</i>	61.3	154.0	95.1	MCZ 7920
<i>Gavia immer</i>	55.5	146.0	91.1	MCZ 7921
<i>Gavia immer</i>	52.8	135.0	84.3	MCZ 7939
<i>Gavia immer</i>	54.1	138.0	88.6	MCZ 7940
<i>Gavia immer</i>	55.9	138.0	88.5	MCZ 7941
<i>Gavia immer</i>	55.9	140.0	89.2	MCZ 7942
<i>Gavia immer</i>	63.5	154.0	101.8	MCZ 7943
<i>Gavia immer</i>	57.3	138.0	89.1	MCZ 7944
<i>Gavia immer</i>	62.3	153.0	100.1	MCZ 7945
<i>Gavia immer</i>	62.9	160.0	97.7	MCZ 7946
<i>Gavia immer</i>	65.8	155.0	96.1	MCZ 7947
<i>Gavia immer</i>	63.5	151.0	93.2	MCZ 7948
<i>Gavia immer</i>	55.3	140.0	88.6	MCZ 7950
<i>Gavia immer</i>	58.8	146.0	94.2	MCZ 7951
<i>Gavia immer</i>	53.1	131.0	82.9	MCZ 7952
<i>Gavia immer</i>	50.2	129.0	82.2	MCZ 7956
<i>Gavia immer</i>	64.2	159.0	98.0	MCZ 7957
<i>Gavia stellata</i>	36.7	113.6	70.9	MCZ 7009
<i>Gavia stellata</i>	38.6	113.9	71.6	MCZ 6996
<i>Gavia stellata</i>	40.3	114.4	72.4	MCZ 6531
<i>Gavia stellata</i>	38.3	110.7	70.9	MCZ 6913
<i>Gavia sp.</i>	51.1	131.3	83.3	MCZ 899
Sphenisciformes				
Spheniscidae				
<i>Aptenodytes patagonica</i>	92.9	170.0	43.2	MCZ 7208
<i>Aptenodytes patagonica</i>	115.0	176.0	46.7	MCZ 7478
<i>Eudyptes chrysolophus</i>	63.3	108.3	26.1	MCZ 6022
<i>Eudyptes crestatus</i>	66.5	105.6	27.2	MCZ 6428
<i>Eudyptula minor</i>	52.2	77.2	23.6	MCZ 6025
<i>Eudyptula minor</i>	48.9	73.9	22.4	MCZ 1451
<i>Eudyptula minor</i>	50.2	70.1	23.2	YPM 13356
<i>Megadyptes antipodes</i>	80.5	120.5	35.5	YPM 13392
<i>Spheniscus demersus</i>	70.4	101.1	28.5	YPM 15882
<i>Spheniscus humboldti</i>	75.9	113.2	32.1	MCZ 7040
<i>Spheniscus humboldti</i>	77.9	112.7	32.3	MCZ 6957
<i>Spheniscus humboldti</i>	83.2	119.7	34.7	MCZ 7571
<i>Spheniscus mendiculus</i>	56.3	83.7	22.9	MCZ 3638
<i>Spheniscus sp.</i>	70.5	104.0	32.3	MCZ 142(5)
Procellariiformes				
Diomedidae				
<i>Diomedea chrysostoma</i>	82.0	157.0	84.0	MCZ 5006
<i>Diomedea exulans</i>	109.0	224.0	126.0	MCZ 408
<i>Diomedea exulans</i>	98.0	197.0	109.0	MCZ 2481
<i>Diomedea exulans</i>	99.0	202.0	107.0	MCZ 6191
<i>Diomedea immutabilis</i>	78.0	154.0	89.0	MCZ 3050
<i>Diomedea immutabilis</i>	71.0	142.0	88.0	MCZ 2959
<i>Diomedea nigripes</i>	75.0	157.0	94.0	MCZ 2999
<i>Phoebastria fusca</i>	97.0	165.0	93.0	MCZ 2949
<i>Phoebastria palpebrata</i>	68.0	136.0	78.0	MCZ 2953
Procellariidae				
<i>Daption capense</i>	37.7	73.5	44.9	MCZ 3873
<i>Daption capense</i>	37.7	73.6	45.7	MCZ 6056
<i>Daption capense</i>	36.0	72.0	43.0	MCZ 6970
<i>Daption capense</i>	38.0	76.0	46.0	MCZ 2955
<i>Fulmarus glacialis</i>	41.8	76.4	44.6	MCZ 4079
<i>Fulmarus glacialis</i>	42.0	72.0	49.0	MCZ 4078
<i>Fulmarus glacialis</i>	41.0	77.0	47.0	MCZ 4090
<i>Fulmarus glacialis</i>	44.0	85.0	51.0	MCZ 5011
Hydrobatidae				
<i>Fregata grallaria</i>	17.5	47.5	36.0	MCZ 6756
<i>Fregata grallaria</i>	17.5	48.0	35.0	MCZ 6752

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
<i>Oceanites oceanicus</i>	15.0	47.0	34.0	MCZ 2984
<i>Oceanites oceanicus</i>	15.5	47.0	34.5	MCZ 6722
<i>Oceanodroma leucorhoa</i>	15.5	34.5	24.0	MCZ 7883
<i>Oceanodroma leucorhoa</i>	17.0	35.0	26.0	MCZ 6058
Pelecanoididae				
<i>Pelecanoides urinatrix</i>	24.8	47.0	31.0	MCZ 1430
Pelecaniformes				
Phaethontidae				
<i>Phaethon lepturus</i>	29.1	43.8	22.0	MCZ 2073
<i>Phaethon lepturus</i>	30.5	46.1	22.2	MCZ 1765
Pelecanidae				
<i>Pelecanus erythrorhynchos</i>	108.4	183.0	126.4	MCZ 7480
<i>Pelecanus erythrorhynchos</i>	119.0	181.0	121.0	MCZ 2914
<i>Pelecanus occidentalis</i>	88.1	119.8	78.5	MCZ 1448
<i>Pelecanus occidentalis</i>	90.8	122.1	80.2	MCZ 1956
Phalacrocoracidae				
<i>Phalacrocorax auritus</i>	60.9	98.5	60.6	MCZ 7537
<i>Phalacrocorax bougainvilli</i>	56.5	107.5	60.7	MCZ 6953
<i>Phalacrocorax carbo</i>	61.7	105.7	65.0	MCZ 1447
<i>Phalacrocorax urile</i>	64.2	107.4	57.0	MCZ 722
Anhingidae				
<i>Anhinga anhinga</i>	54.4	80.2	40.9	MCZ 1483
<i>Anhinga anhinga</i>	59.4	87.5	60.0	MCZ 3615
Sulidae				
<i>Morus bassanus</i>	71.8	99.5	58.2	MCZ 3443
<i>Sula variegata</i>	54.9	78.5	46.6	MCZ 6959
<i>Sula</i> sp.	56.4	79.3	51.1	MCZ 455
Fregatidae				
<i>Fregata aquila</i>	51.0	67.0	19.0	MCZ 1354
<i>Fregata</i> sp.	43.8	62.4	18.0	MCZ 7744
Ciconiiformes				
Ardeidae				
<i>Ardea cocoi</i>	92.0	228.0	152.0	MCZ 3706
<i>Ardea goliath</i>	103.0	277.0	208.0	MCZ 1452
<i>Ardea goliath</i>	116.0	220.0	167.0	MCZ 202
<i>Ardea herodias</i>	103.5	240.0	173.0	MCZ 7038
<i>Ardea herodias</i>	100.0	238.0	174.0	MCZ 1970
<i>Ardea herodias</i>	97.4	242.0	177.0	MCZ 2473
<i>Ardea sumatrana</i>	99.4	195.0	129.0	MCZ 204
<i>Botaurus stellaris</i>	101.0	155.0	99.0	MCZ 2064
<i>Botaurus lentiginosus</i>	81.0	135.0	94.0	MCZ 1759
<i>Botaurus lentiginosus</i>	83.0	135.0	95.0	MCZ 1499
<i>Botaurus lentiginosus</i>	75.0	130.0	92.0	MCZ 1279
<i>Butorides striata</i>	47.8	72.0	48.5	MCZ 3573
<i>Butorides striata</i>	46.8	74.4	46.0	MCZ 5014
<i>Butorides virescens</i>	51.4	85.0	54.4	MCZ 1860
<i>Egretta alba</i>	75.0	195.0	148.0	MCZ 6731
<i>Egretta alba</i>	83.0	206.0	158.0	MCZ 6954
<i>Egretta caerulea</i>	53.1	121.3	91.3	MCZ 6977
<i>Egretta gularis</i>	57.0	122.5	88.8	MCZ 226
<i>Egretta thula</i>	57.0	137.0	96.6	MCZ 7301
<i>Egretta thula</i>	53.6	133.2	90.4	MCZ 7616
<i>Egretta thula</i>	48.4	123.0	86.9	MCZ 3821
<i>Nycticorax</i> sp.	63.5	131.3	97.6	MCZ 7000
<i>Ptilerodias pileatus</i>	49.5	78.2	52.5	MCZ 3830
<i>Tigrisoma lineatum</i>	70.9	122.4	92.6	MCZ 3831
Cochleariidae				
<i>Cochlearius cochlearius</i>	68.0	119.0	78.0	MCZ 3517
<i>Cochlearius cochlearius</i>	65.0	112.0	73.0	MCZ 2201
Ciconiidae				
<i>Ciconia nigra</i>	90.0	267.0	212.0	MCZ 6997
<i>Ciconia nigra</i>	86.0	250.0	218.0	MCZ 6747
<i>Ciconia nigra</i>	79.0	218.0	178.0	MCZ 290
<i>Ibis ibis</i>	83.0	229.0	188.0	MCZ 288
<i>Ibis ibis</i>	89.0	250.0	211.0	MCZ 6740
<i>Ibis</i> sp.	106.0	263.0	236.0	MCZ 1745

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
<i>Jabiru mycteria</i>	109.0	370.0	322.0	MCZ 1377
<i>Leptoptilus crumeniferus</i>	105.0	289.0	224.0	MCZ 338
<i>Leptoptilus dubius</i>	122.0	356.0	282.0	MCZ 337
<i>Mycteria americana</i>	92.0	268.0	205.0	MCZ 2180
<i>Mycteria americana</i>	82.0	227.0	186.0	MCZ 3442
<i>Xenorhynchus asiaticus</i>	102.0	350.0	301.0	MCZ 261
Threskiornithidae				
<i>Ajaia ajaja</i>	73.0	156.0	109.0	MCZ 6534
<i>Ajaia ajaja</i>	69.0	148.0	99.0	MCZ 6533
<i>Eudocimus ruber</i>	59.0	127.0	89.0	MCZ 7528
<i>Eudocimus ruber</i>	56.0	115.0	81.0	MCZ 7446
<i>Eudocimus ruber</i>	57.0	124.0	90.0	MCZ 6741
<i>Eudocimus ruber</i>	55.0	115.0	78.0	MCZ 6987
<i>Guara rubra</i>	55.0	115.0	81.0	MCZ 3450
<i>Guara rubra</i>	58.0	120.0	80.0	MCZ 1378
<i>Guara rubra</i>	57.0	115.0	83.0	MCZ 326
<i>Plagadis</i> sp.	53.0	129.0	101.0	MCZ 6955
<i>Platalea leucoroidia</i>	85.0	195.0	149.0	MCZ 1468
<i>Plegadis falcinellus</i>	59.0	133.0	101.0	MCZ 6983
<i>Plegadis [falcinellus?]</i>	54.0	136.0	97.0	MCZ 7288
<i>Theristicus melanopis</i>	60.0	112.0	75.0	MCZ 206
<i>Theristicus melanopis</i>	65.0	140.0	99.0	MCZ 295
Phoenicopteridae				
<i>Phoenicopus antiquarum</i>	90.8	367.0	351.0	MCZ 1445
<i>Phoenicopus antiquarum</i>	85.5	286.0	269.0	MCZ 289
<i>Phoenicopus ruber</i>	85.6	344.0	327.0	MCZ 7731
<i>Phoenicopus ruber</i>	94.9	361.0	340.0	MCZ 7572
<i>Phoenicopus ruber</i>	83.0	284.0	262.0	MCZ 7053
<i>Phoenicopus ruber</i>	90.0	352.0	313.0	MCZ 6736
<i>Phoenicopus ruber</i>	78.0	290.0	264.0	MCZ 1939
<i>Phoenicopus ruber</i>	89.0	335.0	321.0	MCZ 2950
<i>Phoenicopus ruber</i>	88.0	347.0	329.0	MCZ 2884
Anseriformes				
Anhimidae				
<i>Anhima cornuta</i>	99.0	184.0	126.0	MCZ 1387
<i>Anhima cornuta</i>	92.0	166.0	113.0	MCZ 6993
<i>Chauna chavaria</i>	95.0	177.0	126.0	MCZ 307
Anatidae				
<i>Aix sponsa</i>	40.0	62.0	35.0	MCZ 7372
<i>Alopochen aegyptiacus</i>	75.0	140.0	87.0	MCZ 260
<i>Anas clypeata</i>	49.0	65.0	34.0	MCZ 7105
<i>Anas platyrhynchos</i>	48.0	78.0	43.0	MCZ 1898
<i>Anas platyrhynchos</i>	41.0	67.0	37.0	MCZ 1914
<i>Anas rubripes</i>	48.0	75.0	42.0	MCZ 2850
<i>Anas specularoides</i>	56.0	87.0	49.0	MCZ 3053
<i>Anser caerulescens</i>	69.0	124.0	74.0	MCZ 1883
<i>Anser erythropus</i>	87.0	148.0	85.0	MCZ 330
<i>Anser fabalis</i>	75.0	127.0	74.0	MCZ 262
<i>Aythya marila</i>	44.0	70.0	35.0	MCZ 1471
<i>Biziura lobata</i>	62.0	108.0	50.0	MCZ 2067
<i>Branta canadensis</i>	89.0	148.0	94.0	MCZ 6738
<i>Branta canadensis</i>	78.0	140.0	85.0	MCZ 7645
<i>Branta leucopsis</i>	71.0	123.0	74.0	MCZ 6931
<i>Bucephala albeola</i>	40.0	59.0	33.0	MCZ 1915
<i>Cairina moschata</i>	58.0	90.0	49.0	MCZ 1901
<i>Callonetta leucophrys</i>	33.0	53.0	32.0	MCZ 7445
<i>Cereopsis novaehollandiae</i>	81.0	146.0	95.0	MCZ 7095
<i>Chloephaga picta</i>	88.0	159.0	97.0	MCZ 3031
<i>Clangula hyemalis</i>	40.0	64.0	32.0	MCZ 6497
<i>Cygnus atratus</i>	84.0	141.0	93.0	MCZ 6936
<i>Cygnus cygnus</i>	107.0	188.0	110.0	MCZ 335
<i>Cygnus [columbianus?]</i>	114.0	212.0	113.0	MCZ 3544
<i>Dendrocygna autumnalis</i>	50.0	87.0	56.0	MCZ 273
<i>Dendrocygna bicolor</i>	49.0	84.0	52.0	MCZ 7071
<i>Histrionicus histrionicus</i>	44.0	70.0	38.0	MCZ 2957
<i>Melanitta fusca</i>	55.0	90.0	47.0	MCZ 6956
<i>Merganetta armata</i>	35.0	65.0	38.0	MCZ 5094
<i>Mergus merganser</i>	51.4	84.0	45.3	MCZ 1436
<i>Mergus merganser</i>	51.5	85.9	47.6	MCZ 318
<i>Mergus serrator</i>	49.0	83.0	47.0	MCZ 2835
<i>Netta peposaca</i>	51.0	82.0	40.0	MCZ 2988

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
<i>Oxyura australis</i>	46.0	73.0	37.0	MCZ 1437
<i>Plecopterus gambensis</i>	96.6	173.0	112.8	MCZ 196
<i>Somateria mollissima</i>	67.0	110.0	50.0	MCZ 7453
<i>Tachyeres brachypterus</i>	76.0	120.0	61.0	MCZ 2204
<i>Tadorna tadorna</i>	57.0	102.0	68.0	MCZ 7538
Falconiformes				
Cathartidae				
<i>Cathartes aura</i>	58.0	102.0	57.0	MCZ 1372
<i>Coragyps atratus</i>	78.0	128.0	73.0	MCZ 3577
<i>Sarcorhamphus papa</i>	97.0	161.0	93.0	MCZ 6960
<i>Vultur gryphus</i>	138.0	220.0	121.0	MCZ 342
Sagittariidae				
<i>Sagittarius serpentarius</i>	100.0	283.0	272.0	MCZ 1925
<i>Sagittarius serpentarius</i>	107.0	270.0	258.0	YPM 14510
Pandionidae				
<i>Pandion haliaetus</i>	77.0	122.0	53.0	MCZ 7607
Falconidae				
<i>Falco jugger</i>	70.0	90.0	56.0	MCZ 294
<i>Falco sparverius</i>	36.0	49.0	33.0	MCZ 7402
<i>Herpetotheres cachinnans</i>	61.0	99.0	63.0	MCZ 2931
<i>Microcaster semitorquatus</i>	69.0	103.0	87.0	MCZ 3379
<i>Phalacroboenus australis</i>	80.0	108.0	83.0	MCZ 252
<i>Polyborus plancus</i>	65.0	106.0	89.0	MCZ 1496
<i>Polyborus plancus</i>	67.0	104.0	88.0	MCZ 2845
Accipitridae				
<i>Accipiter gentilis</i>	79.0	109.0	80.0	MCZ 216
<i>Aquila chrysaetus</i>	122.0	170.0	107.0	MCZ 1419
<i>Buteo jamaicensis</i>	84.0	114.0	87.0	MCZ 7793
<i>Buteo magnirostris</i>	53.0	76.0	62.0	MCZ 2743
<i>Buteo rufinus</i>	71.0	111.0	74.0	MCZ 6912
<i>Circus cyaneus</i>	69.0	103.0	82.0	MCZ 1417
<i>Elanus leucurus</i>	49.0	64.0	35.0	MCZ 3430
<i>Geranospiza caerulescens</i>	71.0	108.0	80.0	MCZ 3032
<i>Gypaetus barbatus</i>	111.0	160.0	92.0	MCZ 329
<i>Gyps fulvus</i>	128.0	182.0	104.0	MCZ 1412
<i>Harpia harpyia</i>	116.0	168.0	105.0	MCZ 333
<i>Hieraetus fasciatus</i>	103.0	145.0	99.0	MCZ 211
<i>Leucopternis albigollis</i>	67.0	103.0	80.0	MCZ 3333
<i>Melierax [metabutes?]</i>	71.0	106.0	87.0	MCZ 7127
<i>Milvus migrans</i>	57.0	79.0	53.0	MCZ 241
<i>Neophron percnopterus</i>	72.0	113.0	80.0	MCZ 213
<i>Pernis apivorus</i>	61.0	90.0	55.0	MCZ 253
<i>Spizaeus ornatus</i>	88.0	124.0	90.0	MCZ 2839
Charadriiformes				
Jacaniidae				
<i>Actophilornis albinucha</i>	36.8	96.6	71.7	MCZ 284
<i>Jacana spinosa</i>	29.2	82.6	50.8	MCZ 7013
<i>Jacana spinosa</i>	28.5	81.2	55.5	MCZ 6943
<i>Jacana spinosa</i>	27.9	75.9	54.1	MCZ 7060
Charadriidae				
<i>Vanellus chilensis</i>	37.8	98.3	82.6	MCZ 6928
<i>Vanellus chilensis</i>	40.6	92.2	72.8	MCZ 7010
Scolopacidae				
<i>Bartramia longicauda</i>	36.7	65.8	51.3	MCZ 1246
<i>Bartramia longicauda</i>	36.3	63.6	53.2	MCZ 2107
<i>Limosa fedoa</i>	44.5	96.4	75.9	MCZ 1384
<i>Numenius americanus</i>	59.6	118.3	96.6	MCZ 454
<i>Numenius arquata</i>	54.9	106.1	85.4	MCZ 2108
<i>Numenius arquata</i>	54.6	105.0	80.8	MCZ 1385
<i>Tringa flavipes</i>	25.9	64.2	53.7	MCZ 3261
<i>Tringa flavipes</i>	27.7	64.6	52.1	MCZ 2693
<i>Tringa flavipes</i>	26.7	63.5	50.1	MCZ 2657
Recurvirostridae				
<i>Himantopus himantopus</i>	31.9	114.4	104.6	MCZ 191
<i>Himantopus himantopus</i>	33.8	135.0	132.0	YPM 2192
<i>Himantopus himantopus</i>	34.2	129.0	124.0	YPM 5950
<i>Himantopus leucocephalus</i>	28.7	101.0	78.5	YPM 13424

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
<i>Himantopus mexicanus</i>	32.4	124.0	119.0	YPM 6108
<i>Recurvirostra americana</i>	36.8	108.0	90.7	MCZ 33
<i>Recurvirostra americana</i>	38.3	120.3	86.7	MCZ 31
<i>Recurvirostra americana</i>	36.6	107.4	82.7	MCZ 29
<i>Recurvirostra americana</i>	40.1	115.1	97.9	MCZ 3300
<i>Recurvirostra americana</i>	37.2	106.6	91.1	MCZ 2760
<i>Recurvirostra americana</i>	38.5	111.7	94.2	MCZ 32
Phalaropodidae				
<i>Phalaropus fulicarius</i>	19.3	37.4	21.8	MCZ 7369
<i>Phalaropus lobatus</i>	19.7	38.3	29.8	MCZ 3534
<i>Phalaropus lobatus</i>	15.9	32.1	21.1	MCZ 2702
Dromadidae				
<i>Dromas ardeola</i>	41.8	98.7	92.2	MCZ 2991
Burhinidae				
<i>Burhinus capensis</i>	48.7	102.3	88.2	MCZ 6978
<i>Burhinus capensis</i>	52.2	115.1	95.1	MCZ 5077
<i>Burhinus magnirostris</i>	58.6	142.6	129.8	MCZ 285
Stercorariidae				
<i>Catharacta skua</i>	63.0	109.2	72.5	MCZ 358
<i>Stercorarius parasiticus</i>	36.4	66.3	42.7	MCZ 183
Laridae				
<i>Larus argentatus</i>	58.3	116.0	70.5	MCZ 2712
<i>Larus atricilla</i>	36.7	73.0	51.7	MCZ 7271
<i>Larus glaucescens</i>	67.0	126.0	78.0	MCZ 723
<i>Larus leucopterus</i>	55.0	99.0	60.0	MCZ 2843
<i>Larus merinus</i>	65.4	125.1	80.4	MCZ 1617
<i>Rissa tridactyla</i>	35.0	64.0	32.0	MCZ 1502
<i>Sterna fuscata</i>	27.0	44.0	24.0	MCZ 3375
<i>Sterna hirundo</i>	24.0	40.0	20.0	MCZ 2147
<i>Sterna striata</i>	27.0	43.0	20.0	MCZ 5015
<i>Thalasseus maximus</i>	38.0	64.0	33.0	MCZ 1427
Rhynchopidae				
<i>Rynchops nigra</i>	34.0	55.0	30.0	MCZ 1426
Alcidae				
<i>Alca torda</i>	45.6	71.0	32.4	MCZ 3688
<i>Alca torda</i>	42.5	73.7	33.2	MCZ 2956
<i>Alca torda</i>	42.9	71.4	35.9	MCZ 2867
<i>Cephus grylle</i>	36.0	62.9	32.5	MCZ 2995
<i>Cerorhinca monocerata</i>	40.8	66.8	30.4	MCZ 7676
<i>Cerorhinca monocerata</i>	41.2	66.1	30.9	MCZ 7697
<i>Cerorhinca monocerata</i>	40.3	62.6	28.0	MCZ 7696
<i>Fratercula arctica</i>	38.9	62.4	27.3	MCZ 2994
<i>Fratercula arctica</i>	38.8	61.9	27.1	MCZ 6006
<i>Fratercula arctica</i>	36.1	56.6	26.0	MCZ 1434
<i>Plautus alle</i>	27.8	46.2	20.1	MCZ 3425
<i>Plautus alle</i>	27.7	44.5	21.5	MCZ 1865
<i>Plautus alle</i>	28.8	45.9	20.9	MCZ 1871
<i>Plautus impennes</i>	71.2	130.3	50.0	MCZ
<i>Plautus impennes</i>	75.8	125.9	56.4	MCZ 18220
<i>Uria aalge</i>	47.4	87.5	36.1	MCZ 6991
<i>Uria aalge</i>	48.0	86.0	38.1	MCZ 2989
<i>Uria aalge</i>	49.0	86.9	37.2	MCZ 3690
<i>Uria lomvia</i>	46.6	82.6	36.6	MCZ 7029
<i>Uria lomvia</i>	47.8	82.9	36.0	MCZ 6925
<i>Uria lomvia</i>	48.0	86.8	37.9	MCZ 7018
Columbiformes				
Columbidae				
<i>Caloenas nicobarica</i>	47.6	71.5	41.5	MCZ 6958
<i>Columba aquatrix</i>	41.7	53.7	26.6	MCZ 6798
<i>Columba cayennensis</i>	34.3	47.7	23.5	MCZ 5012
<i>Columba livia</i>	38.3	56.8	31.3	MCZ 1250
<i>Columba speciosa</i>	36.2	49.2	23.3	MCZ 4062
<i>Columbina talpacoti</i>	20.3	28.3	14.0	MCZ 3514
<i>Ducula aenea</i>	43.7	56.9	28.8	MCZ 7543
<i>Ectopistes migratorius</i>	40.6	53.8	27.0	MCZ 2355
<i>Geotrygon montana</i>	32.6	50.2	29.6	MCZ 2759
<i>Leptoptila verreauxi</i>	32.2	49.7	30.7	MCZ 3591

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
<i>Ocyphaps lophotes</i>	35.3	48.0	27.7	MCZ 279
<i>Zenaidura macroura</i>	26.2	36.2	19.9	MCZ 2109
Psittaciformes				
Psittacidae				
<i>Amazona farinosa</i>	53.5	74.5	24.7	MCZ 3384
<i>Amazona farinosa</i>	54.8	77.3	25.8	MCZ 3062
<i>Amazona farinosa</i>	51.8	71.4	23.9	MCZ 2869
<i>Ara macao</i>	63.0	88.4	32.0	MCZ 3704
<i>Ara macao</i>	58.1	78.9	29.3	MCZ 6930
<i>Ara macao</i>	62.0	84.3	30.2	MCZ 2241
<i>Calyptorhynchus magnificus</i>	52.4	74.1	24.5	MCZ 359
<i>Cacatua galerita</i>	59.2	84.6	26.4	MCZ 1392
<i>Cacatua galerita</i>	58.3	83.8	26.9	MCZ 1974
<i>Kakatoe leadbeateri</i>	43.5	60.6	20.9	MCZ 1991
<i>Nestor meridionalis</i>	53.6	87.1	36.0	MCZ 1490
<i>Pionus senilis</i>	37.8	50.0	17.4	MCZ 2899
<i>Pionus senilis</i>	37.6	49.1	17.1	MCZ 2886
<i>Probosciger aterrimus</i>	62.0	91.4	27.4	MCZ 1491
<i>Probosciger aterrimus</i>	58.2	81.4	26.5	MCZ 1369
<i>Strigops habroptilus</i>	85.6	117.9	51.1	MCZ 309
<i>Trichoglossus ornatus</i>	27.4	40.3	15.2	MCZ 1926
<i>Trichoglossus ornatus</i>	28.1	37.4	15.8	MCZ 1929
<i>Trichoglossus ornatus</i>	28.5	39.7	15.3	MCZ 1997
Cuculiformes				
Cuculidae				
<i>Geococcyx californianus</i>	55.0	85.0	63.0	MCZ 1495
Galliformes				
Megapodiidae				
<i>Macrocephalus maleo</i>	85.4	127.0	91.1	MCZ 355
Cracidae				
<i>Crax alberti</i>	107.0	155.0	103.0	MCZ 209
<i>Crax mitu</i>	106.0	157.0	110.0	MCZ 3575
<i>Crax pauxi</i>	110.0	169.0	113.0	MCZ 2121
<i>Ortalis vetula</i>	65.5	95.0	62.0	MCZ 3099
<i>Penelope purpurascens</i>	95.0	137.0	83.0	MCZ 293
<i>Penelopina nigra</i>	108.0	163.0	107.0	MCZ 2084
Tetraonidae				
<i>Bonasa umbellus</i>	56.2	75.0	41.4	MCZ 3999
<i>Bonasa umbellus</i>	52.8	75.0	41.2	MCZ 7935
<i>Bonasa umbellus</i>	56.6	78.0	41.6	MCZ 7371
<i>Bonasa umbellus</i>	27.3	36.2	22.1	MCZ 3809
<i>Bonasa umbellus</i>	53.0	75.6	42.1	MCZ 6061
<i>Bonasa umbellus</i>	53.0	75.6	41.5	MCZ 7666
<i>Centrocercus urophasianus</i>	70.8	91.1	44.5	MCZ 110
<i>Centrocercus urophasianus</i>	71.4	90.9	49.2	MCZ 1441
<i>Lagopus mutus</i>	58.5	79.5	41.2	MCZ 1469
<i>Tetrao urogallus</i>	80.9	106.7	55.0	MCZ 315
<i>Tympanuchus cupido</i>	62.3	82.1	45.7	MCZ 2193
Odontophorinae				
<i>Callipepla squamata</i>	37.3	55.7	31.3	MCZ 1254
<i>Colinus nigrogularis</i>	36.7	50.2	29.9	MCZ 5029
<i>Colinus nigrogularis</i>	34.9	46.9	27.6	MCZ 5030
<i>Colinus virginianus</i>	37.8	52.3	30.7	MCZ 7347
<i>Colinus virginianus</i>	39.7	54.0	32.3	MCZ 7337
<i>Lophortyx gambelli</i>	37.9	55.4	32.5	MCZ 7254
<i>Odontophorus guttatus</i>	50.3	70.3	45.0	MCZ 2727
<i>Odontophorus guttatus</i>	47.1	67.0	42.7	MCZ 2770
Phasianidae				
<i>Coturnix coturnix</i>	34.5	42.1	25.7	MCZ 3164
<i>Coturnix coturnix</i>	34.4	44.2	26.6	MCZ 3298
<i>Coturnix delegorguei</i>	31.5	39.9	24.2	MCZ 3037
<i>Excalfactoria chinensis</i>	27.3	33.8	21.1	MCZ 7497
<i>Gallus gallus</i>	91.0	128.0	94.0	MCZ 1388
<i>Lophura sp?</i>	94.3	142.0	118.0	MCZ 3144
<i>Pavo cristatus</i>	109.0	202.0	137.0	MCZ 7161
<i>Pavo cristatus</i>	107.0	193.0	139.0	MCZ 311
<i>Pavo cristatus</i>	105.0	175.0	116.0	MCZ 2651

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
Numididae				
<i>Guttera edouardii</i>	78.0	112.0	77.0	MCZ 2098
<i>Numida meleagris</i>	79.0	113.0	74.0	MCZ 1648
Meleagrididae				
<i>Agriocharis ocellata</i>	110.0	193.0	144.5	MCZ 2878
<i>Agriocharis ocellata</i>	101.0	177.0	131.0	MCZ 3049
<i>Agriocharis ocellata</i>	107.0	185.0	138.0	MCZ 3046
<i>Meleagris gallopavo</i>	127.0	200.0	144.0	MCZ 7157
<i>Meleagris gallopavo</i>	119.0	193.0	141.0	MCZ 819
<i>Meleagris gallopavo</i>	139.0	230.0	168.0	MCZ 1494
Opisthocomidae				
<i>Opisthocomus hoatzin</i>	62.8	86.7	53.5	MCZ 3617
<i>Opisthocomus hoatzin</i>	64.6	89.1	54.9	MCZ 5084
<i>Opisthocomus hoatzin</i>	68.0	90.0	56.0	YPM 2437
Gruiformes				
Gruidae				
<i>Anthropoides paradisea</i>	111.0	270.0	232.0	MCZ 7481
<i>Anthropoides virgo</i>	85.0	202.0	176.0	MCZ 3036
<i>Anthropoides virgo</i>	112.0	251.0	217.0	MCZ 7569
<i>Anthropoides virgo</i>	87.0	199.0	166.0	MCZ 208
<i>Balearica pavonina</i>	101.0	268.0	194.0	MCZ 3601
<i>Balearica pavonina</i>	98.0	266.0	179.0	MCZ 2952
<i>Balearica pavonina</i>	92.0	251.0	179.0	MCZ 200
<i>Grus antigone</i>	140.0	374.0	332.0	MCZ 6600
<i>Grus canadensis</i>	118.0	266.0	236.0	MCZ 2483
<i>Grus canadensis</i>	126.0	286.0	255.0	MCZ 7482
<i>Grus canadensis</i>	113.0	268.0	242.0	MCZ 1336
<i>Grus leucogeranus</i>	128.0	357.0	299.0	MCZ 339
Aramidae				
<i>Aramus scolopaceus</i>	74.0	167.0	126.0	MCZ 3576
<i>Aramus scolopaceus</i>	79.0	182.0	139.0	MCZ 1383
Rallidae				
<i>Gallirallus australis</i>	72.5	102.0	60.2	YPM 13391
<i>Gallirallus australis</i>	74.1	110.2	66.9	YPM 13475
<i>Gallirallus australis</i>	67.1	99.0	58.7	YPM 13420
<i>Gallirallus australis</i>	77.8	113.7	68.2	YPM 13421
<i>Gallirallus australis</i>	76.0	112.0	67.0	YPM 556
<i>Porphyrio porphyrio</i>	72.9	134.4	91.8	MCZ 321
Cariamidae				
<i>Cariama cristata</i>	82.0	205.0	193.0	MCZ 207
Otidae				
<i>Chlamydotis undulata</i>	72.0	136.0	101.0	MCZ 194
<i>Chlamydotis undulata</i>	59.0	114.0	82.0	MCZ 297
<i>Choriotus australis</i>	107.0	242.0	197.0	MCZ 2856
Strigiformes				
Tytonidae				
<i>Tyto alba</i>	52.0	84.0	60.0	MCZ 352
<i>Tyto alba</i>	50.0	90.0	64.0	MCZ 656
Strigidae				
<i>Aegolius acadica</i>	30.3	42.9	23.0	MCZ 3772
<i>Aegolius funereus</i>	32.8	48.0	23.4	MCZ 2828
<i>Asio flammeus</i>	48.9	74.5	39.7	MCZ 6053
<i>Asio otus</i>	49.9	75.9	39.9	MCZ 7534
<i>Bubo africanus</i>	64.0	106.0	65.0	MCZ 255
<i>Bubo virginianus</i>	82.0	124.0	63.0	MCZ 2174
<i>Bubo virginianus</i>	83.0	125.0	64.0	MCZ 7017
<i>Ciccaba virgata</i>	49.0	77.0	44.0	MCZ 3007
<i>Nyctea scandiaca</i>	88.0	118.0	56.0	MCZ 6933
<i>Otus asio</i>	41.0	57.5	34.0	MCZ 3763
<i>Otus asio</i>	41.5	57.5	36.0	MCZ 6009
<i>Pulsatrix perspicata</i>	64.0	98.0	51.0	MCZ 3702
<i>Speotyto cunicularia</i>	40.0	69.0	52.0	MCZ 270
<i>Strix varia</i>	77.0	113.0	63.0	MCZ 1414
<i>Strix varia</i>	69.0	98.0	53.0	MCZ 2934

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
Caprimuliformes				
Steatornithidae				
<i>Steatornis caripensis</i>	39.0	45.3	19.8	MCZ 1401
Aegothelidae				
<i>Podargus ocellatus</i>	47.6	76.1	40.7	MCZ 1400
Caprimulgidae				
<i>Caprimulgus ridgwayi</i>	21.5	32.7	18.5	MCZ 2974
<i>Caprimulgus vociferus</i>	22.0	36.0	17.0	MCZ 1402
<i>Caprimulgus vociferus</i>	20.0	30.5	18.5	MCZ 2416
<i>Chordeiles minor</i>	27.0	36.0	17.0	MCZ 7266
<i>Chordeiles minor</i>	21.5	29.5	14.0	MCZ 3783
<i>Chordeiles minor</i>	22.9	32.2	19.0	MCZ 1480
<i>Nyctidromus albigollis</i>	22.6	36.9	25.5	MCZ 3422
Apodiformes				
Apodidae				
<i>Apus apus</i>	18.7	25.5	10.4	MCZ 2077
<i>Apus apus</i>	16.5	24.8	11.4	MCZ 349
<i>Chaetura pelagica</i>	15.4	23.1	11.4	MCZ 3118
Trochilidae				
<i>Archilochus colubris</i>	7.3	10.9	4.6	MCZ 7644
<i>Archilochus colubris</i>	6.5	10.2	4.1	MCZ 7397
<i>Glaucis hirsuta</i>	9.1	12.9	5.7	MCZ 6140
<i>Patagona gigas</i>	13.7	20.9	7.4	MCZ 246
Trogoniformes				
Trogonidae				
<i>Trogon massena</i>	27.5	36.0	16.2	MCZ 2769
Coraciiformes				
Alcedinidae				
<i>Alcedo atthis</i>	16.3	24.8	8.7	MCZ 2721
<i>Alcedo atthis</i>	13.6	20.4	7.6	MCZ 84
<i>Ceryle alcyon</i>	25.7	35.8	10.3	MCZ 7285
<i>Dacelo novaeguineae</i>	36.5	54.2	24.2	MCZ 2079
<i>Halcyon chloris</i>	21.0	32.0	14.7	MCZ 1777
<i>Halcyon chloris</i>	21.3	33.7	16.0	MCZ 7002
<i>Halcyon chloris</i>	20.8	34.6	13.5	MCZ 6907
<i>Halcyon sancta</i>	19.8	30.9	13.7	MCZ 1802
<i>Halcyon sancta</i>	17.7	28.6	13.3	MCZ 6768
Momotidae				
<i>Momotus mexicanus</i>	27.5	39.8	27.4	MCZ 3065
Bucerotidae				
<i>Buceros bicornis</i>	102.0	138.0	74.5	MCZ 7859
<i>Buceros rhinoceros</i>	97.0	132.0	68.3	MCZ 1446
Piciformes				
Bucconidae				
<i>Monasa morphoeus</i>	21.8	31.9	18.4	MCZ 6107
Ramphastidae				
<i>Pteroglossus aracari</i>	58.7	89.0	53.7	MCZ 1498
<i>Ramphastus toco</i>	58.7	89.0	53.7	MCZ 6051
Picidae				
<i>Colaptes cafer</i>	30.3	41.8	28.0	MCZ 3624
<i>Dryocopus pileatus</i>	41.9	53.5	36.0	MCZ 1396
<i>Melanerpes erythrocephalus</i>	30.5	40.7	27.0	MCZ 1397
Passeriformes				
Eurylaimidae				
<i>Calyptrina viridis</i>	24.0	35.2	21.0	MCZ 7349
<i>Eurylaimus ochromalus</i>	18.5	30.9	20.3	MCZ 2982
Dendrocolaptidae				
<i>Dendrocolaptes certhia</i>	24.6	33.5	26.2	MCZ 3842
Furnariidae				
<i>Furnarius rufus</i>	22.9	39.5	31.3	MCZ 6030
Formicariidae				
<i>Taraba major</i>	28.4	45.6	35.9	MCZ 4083

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
Conopophagidae				
<i>Conopophaga castaneiceps</i>	20.3	35.5	27.0	MCZ 6014
Rhynchocryptidae				
<i>Scelorchilus albicollis</i>	27.7	46.7	37.8	MCZ 224
Cotingidae				
<i>Rupicola rupicola</i>	36.8	56.4	35.5	MCZ 3699
Tyrannidae				
<i>Compostoma absoletum</i>	11.2	20.7	15.6	MCZ 6285
<i>Empidonax flaviventris</i>	12.5	22.7	16.1	MCZ 7877
<i>Muscigralla brevicauda</i>	15.5	32.2	26.5	MCZ 6304
<i>Muscisaxicola plauinucha</i>	19.4	41.2	32.2	MCZ 7213
<i>Myiobius barbatus</i>	13.6	21.3	16.3	MCZ 3509
<i>Pitangus sulfuratus</i>	24.1	39.7	26.9	MCZ 3358
<i>Pyrocephalus rubinus</i>	13.1	21.3	16.3	MCZ 6500
<i>Sayornis phoebe</i>	14.4	25.6	18.2	MCZ 7728
<i>Tyrannus verticalis</i>	18.3	29.0	17.9	MCZ 7600
Pittidae				
<i>Pitta erythrogaster</i>	30.3	52.2	42.4	MCZ 6581
Menuridae				
<i>Menura novaehollandiae</i>	67.7	132.0	111.2	MCZ 313
Alaudidae				
<i>Eremophila alpestris</i>	17.7	28.9	20.6	MCZ 7440
<i>Eremophila alpestris</i>	16.8	28.2	21.6	MCZ 7439
<i>Galerida theklae</i>	17.6	29.0	22.6	MCZ 2905
<i>Melanocorypha yeltoniensis</i>	23.4	36.2	25.6	MCZ 188
<i>Mirafa javanica</i>	19.3	30.7	23.4	MCZ 7290
Hirundinidae				
<i>Hirundo rustica</i>	12.6	20.5	11.5	MCZ 2697
<i>Hirundo rustica</i>	12.4	19.5	10.8	MCZ 4004
<i>Progne subis</i>	18.4	30.2	16.4	MCZ 1481
Campephagidae				
<i>Coracina caeruleogrisea</i>	34.0	45.6	29.3	MCZ 6475
Dicruridae				
<i>Dicrurus macroceros</i>	21.8	34.8	22.0	MCZ 3288
Callaeidae				
<i>Heteralocha? actutiostis</i>	47.7	93.6	74.4	MCZ 350
Grallinidae				
<i>Corcorax melanorhamphus</i>	44.4	79.8	63.9	MCZ 291
Cracticidae				
<i>Strepera graculina</i>	44.7	78.3	52.5	MCZ 277
Certhiidae				
<i>Certhia familiaris</i>	10.6	16.1	15.1	MCZ 1487
Sittidae				
<i>Sitta carolinensis</i>	15.7	24.5	18.3	MCZ 2526
Timaliidae				
<i>Garrulax striatus</i>	34.2	58.0	42.9	MCZ 286
Cinclidae				
<i>Cinclus cinclus</i>	20.0	36.8	27.0	MCZ 361
Mimidae				
<i>Toxostoma rufum</i>	27.9	47.6	34.4	MCZ 1801
Turdidae				
<i>Turdus migratorius</i>	25.5	42.0	30.4	MCZ 2701
<i>Myiophonus caeruleus</i>	37.3	68.4	53.1	MCZ 6059
Motacillidae				
<i>Anthus correndera</i>	16.2	29.3	22.4	MCZ 3138
<i>Anthus lutescens</i>	15.5	27.8	20.1	MCZ 4016
<i>Budytes flavus</i>	15.4	30.9	22.9	MCZ 3091
<i>Motacilla alba</i>	16.1	31.5	22.9	MCZ 6945

APPENDIX 2. (Continued)

Species	F	T	M	Specimen number
Bombycillidae				
<i>Bombycilla cedrorum</i>	19.5	30.6	18.0	MCZ 2713
Laniidae				
<i>Gymnorhina tibicen</i>	45.2	82.8	61.4	MCZ 1405
<i>Pitynasis gymnocephala</i>	33.0	48.0	33.1	MCZ 230
Sturnidae				
<i>Gracula religiosa</i>	36.4	56.3	33.4	MCZ 7027
Nectariniidae				
<i>Anthreptes collaris</i>	11.5	20.5	15.7	MCZ 6880
Thraupidae				
<i>Habia rubica</i>	19.8	31.9	23.2	MCZ 2455

APPENDIX 3. Avian limb segment dimensions (in mm) taken from the literature (F, femur; T, tibiotarsus; M, tarsometatarsus; *, mean values; %, percentages rather than absolute lengths; m, males, f, females).

Species	F	T	M	Source
Ratites				
Apterigidae				
<i>Apteryx australis*</i>	89.5	129.9	64.9	Cracraft (1976)
Struthionidae				
<i>Palaeotis weigelti</i>	145.0	268.0	200.0	Houde and Haubold (1987)
<i>Struthio camelus</i>	314.0	550.0	474.0	Holtz (1994a)
<i>Struthio camelus</i>	308.0	527.0	455.0	Holtz (1994a)
<i>Struthio camelus</i>	305.0	511.0	447.0	Holtz (1994a)
<i>Struthio camelus</i>	293.0	480.0	461.0	Holtz (1994a)
<i>Struthio camelus</i>	273.0	497.0	410.0	Holtz (1994a)
<i>Struthio camelus</i>	277.0	490.0	420.0	Holtz (1994a)
<i>Struthio camelus</i>	278.0	490.0	432.0	Holtz (1994a)
Dinornithidae				
<i>Anomalopteryx didiformis</i>	235.0	360.0	190.0	Holtz (1994a)
<i>Anomalopteryx didiformis*</i>	238.5	377.2	179.0	Cracraft (1976)
<i>Anomalopteryx didiformis</i>	275.0	427.0	212.0	Gatesy (1991)
<i>Anomalopteryx didiformis</i>	265.0	405.0	190.0	Gatesy (1991)
<i>Dinornis gazella*</i>	231.0	469.7	259.0	Cracraft (1976)
<i>Dinornis giganteus</i>	375.0	759.0	470.0	Holtz (1994a)
<i>Dinornis giganteus*</i>	390.9	875.2	486.1	Cracraft (1976)
<i>Dinornis hercules*</i>	353.0	779.8	420.3	Cracraft (1976)
<i>Dinornis ingens</i>	340.0	737.0	417.0	Holtz (1994a)
<i>Dinornis maxiumus*</i>	406.1	866.6	463.4	Cracraft (1976)
<i>Dinornis maxiumus</i>	470.0	990.0	518.0	Holtz (1994a)
<i>Dinornis novaezealandiae</i>	278.0	560.0	313.0	Holtz (1994a)
<i>Dinornis novaezealandiae</i>	280.0	540.0	296.0	Holtz (1994a)
<i>Dinornis novaezealandiae</i>	285.0	585.0	295.0	Holtz (1994a)
<i>Dinornis novaezealandiae*</i>	340.5	701.7	368.1	Cracraft (1976)
<i>Dinornis robustus*</i>	354.5	718.6	382.6	Cracraft (1976)
<i>Dinornis sp.</i>	225.0	390.0	168.0	Holtz (1994a)
<i>Dinornis struthoides*</i>	265.0	520.7	282.2	Cracraft (1976)
<i>Dinornis struthoides</i>	300.0	600.0	315.0	Holtz (1994a)
<i>Dinornis torosus*</i>	295.3	588.4	303.1	Cracraft (1976)
<i>Dinornis torosus</i>	330.0	650.0	334.0	Holtz (1994a)
<i>Emeus crassus</i>	245.0	435.0	200.0	Holtz (1994a)
<i>Emeus crassus</i>	255.0	422.0	190.0	Holtz (1994a)
<i>Emeus crassus</i>	260.0	460.0	215.0	Holtz (1994a)
<i>Emeus crassus</i>	260.0	450.0	188.0	Holtz (1994a)
<i>Emeus crassus</i>	272.8	464.2	213.6	Cracraft (1976)
<i>Emeus crassus</i>	285.0	450.0	225.0	Holtz (1994a)
<i>Emeus crassus</i>	287.0	493.0	220.0	Gatesy (1991)
<i>Emeus huttonii</i>	238.4	386.6	184.4	Holtz (1994a)
<i>Emeus huttonii</i>	244.0	397.0	187.0	Gatesy (1991)
<i>Euryapteryx curtus*</i>	167.6	268.8	124.7	Cracraft (1976)
<i>Euryapteryx curtus</i>	179.0	286.0	136.0	Gatesy (1991)
<i>Euryapteryx exilis*</i>	198.2	331.7	148.4	Cracraft (1976)
<i>Euryapteryx exilis</i>	205.0	347.0	152.0	Gatesy (1991)
<i>Euryapteryx geranoides*</i>	236.6	387.6	174.8	Cracraft (1976)

APPENDIX 3. (Continued)

Species	F	T	M	Source
<i>Euryapteryx geranoides</i>	268.0	455.0	205.0	Holtz (1994a)
<i>Euryapteryx geranoides</i>	280.0	472.0	210.0	Holtz (1994a)
<i>Euryapteryx geranoides</i>	231.0	411.0	175.0	Gatesy (1991)
<i>Euryapteryx gravis</i> *	280.2	475.2	209.6	Cracraft (1976)
<i>Euryapteryx gravis</i>	315.0	520.0	217.0	Gatesy (1991)
<i>Euryapteryx tane</i> *	190.7	328.0	149.0	Cracraft (1976)
<i>Megalapteryx didinus</i> *	245.7	385.3	179.4	Cracraft (1976)
<i>Megalapteryx didinus</i>	265.0	405.0	190.0	Holtz (1994a)
<i>Pachyornis elephantopus</i>	329.0	574.0	242.0	Gatesy (1991)
<i>Pachyornis elephantopus</i>	320.0	525.0	225.0	Holtz (1994a)
<i>Pachyornis elephantopus</i> *	308.9	542.9	230.6	Cracraft (1976)
<i>Pachyornis elephantopus</i>	295.0	485.0	210.0	Holtz (1994a)
<i>Pachyornis mappini</i> *	206.3	365.5	156.3	Cracraft (1976)
<i>Pachyornis mappini</i>	203.0	336.0	156.0	Gatesy (1991)
<i>Pachyornis oweni</i>	143.0	243.0	113.0	Gatesy (1991)
<i>Pachyornis septentrionalis</i> *	174.1	291.7	133.0	Cracraft (1976)
Dromornithids				
<i>Aepyornis hildebrandti</i>	320.0	580.0	303.0	Gatesy (1991)
<i>Aepyornis hildebrandti</i>	240.0	485.0	275.0	Gatesy (1991)
<i>Aepyornis maximus</i>	465.0	810.0	480.0	Gatesy (1991)
<i>Aepyornis maximus</i>	410.0	730.0	420.0	Gatesy (1991)
<i>Aepyornis medius</i>	368.0	680.0	380.0	Gatesy (1991)
<i>Aepyornis medius</i>	330.0	572.0	330.0	Gatesy (1991)
<i>Genyornis newtoni</i>	340.0	602.0	374.0	Gatesy (1991)
Rheidae				
<i>Rhea americana</i>	210.0	330.0	320.0	Holtz (1994a)
<i>Rhea americana</i>	110.0	163.0	147.0	Holtz (1994a)
Dromiceidae				
<i>Dromecius novaehollandiae</i>	243.0	465.0	404.0	Holtz (1994a)
<i>Dromecius novaehollandiae</i>	228.0	451.0	380.0	Holtz (1994a)
<i>Dromecius novaehollandiae</i>	241.0	451.0	407.0	Holtz (1994a)
<i>Dromecius novaehollandiae</i>	234.0	436.0	401.0	Holtz (1994a)
<i>Dromecius novaehollandiae</i>	228.0	403.0	375.0	Holtz (1994a)
<i>Dromecius novaehollandiae</i>	218.0	390.0	389.0	Holtz (1994a)
<i>Dromecius novaehollandiae</i>	225.0	374.0	354.0	Holtz (1994a)
Tinamiformes				
Tinamidae				
<i>Rhynchotus rufescens</i>	70.0	95.0	59.0	Holtz (1994a)
Podicipediformes				
Podicipedidae				
<i>Podilymbus podiceps</i> *	40.4	72.7	41.6	Storer (1976)
<i>Podilymbus podiceps</i> *	41.1	71.6	41.9	Storer (1976)
<i>Podilymbus podiceps</i> *	36.6	64.8	37.4	Storer (1976)
Sphenisciformes				
Spheniscidae				
<i>Aptenodytes patagonica</i> *	100.6	186.6	47.6	Simpson (1946)
<i>Paraptenodytes antarcticus</i> *	115.9	178.0	53.4	Simpson (1946)
Pelecaniformes				
Phalacrocoracidae				
<i>Compsohalieus harrisi</i> (m)*	71.2	146.5	72.5	Livezey (1992)
<i>Compsohalieus harrisi</i> (f)*	63.9	132.9	67.3	Livezey (1992)
<i>Compsohalieus penicillatus</i> (m)*	62.3	127.6	66.2	Livezey (1992)
<i>Compsohalieus penicillatus</i> (f)*	57.5	119.8	62.7	Livezey (1992)
<i>Compsohalieus perspicillatus</i>	74.6	136.9	70.1	Livezey (1992)
<i>Hypoleucus auritus</i> (m)*	59.1	110.4	64.3	Livezey (1992)
<i>Hypoleucus auritus</i> (f)*	55.4	104.8	62.6	Livezey (1992)
<i>Leucocarbo bougainvilli</i> (m)*	57.0	125.4	68.1	Livezey (1992)
<i>Leucocarbo bougainvilli</i> (f)*	56.2	123.2	66.4	Livezey (1992)
<i>Microcarbo melanoleucos</i> (m)*	43.6	70.6	39.7	Livezey (1992)
<i>Microcarbo melanoleucos</i> (f)*	41.2	67.4	37.8	Livezey (1992)
<i>Notocarbo atriceps</i> (m)*	59.6	119.6	62.6	Livezey (1992)
<i>Notocarbo atriceps</i> (f)*	58.0	116.0	61.0	Livezey (1992)
<i>Phalacrocorax auritus</i> *	56.9	101.3	60.1	Owre (1967)
<i>Phalacrocorax carbo</i> (m)*	66.7	123.2	69.1	Livezey (1992)
<i>Phalacrocorax carbo</i> (f)*	59.1	110.0	64.0	Livezey (1992)
<i>Stictocarbo magellanicus</i> (m)*	54.7	93.9	51.3	Livezey (1992)
<i>Stictocarbo magellanicus</i> (f)*	53.3	91.2	51.1	Livezey (1992)
<i>Stictocarbo urile</i> (m)*	63.7	114.5	56.9	Livezey (1992)
<i>Stictocarbo urile</i> (f)*	57.6	104.4	52.8	Livezey (1992)

APPENDIX 3. (Continued)

Species	F	T	M	Source
Anhingidae				
<i>Anhinga anhinga</i> *	55.6	89.2	41.2	Owre (1967)
Ciconiiformes				
Phoenicopteridae				
<i>Phoenicopiterus ruber</i> *%	0.11	0.45	0.44	Howell (1965)
Anseriformes				
Anatidae				
<i>Chendytes lawi</i> *	71.3	149.2	66.8	Livezey (1993)
<i>Melanitta fusca</i> (m)*	59.1	105.0	51.1	Livezey (1993)
<i>Melanitta fusca</i> (f)*	55.5	98.9	47.6	Livezey (1993)
<i>Somateria mollissima</i> (m)*	66.8	113.3	55.5	Livezey (1993)
<i>Somateria mollissima</i> (f)*	65.6	109.0	53.1	Livezey (1993)
Falconiformes				
Cathartidae				
<i>Cathartes aura</i> *	69.8	119.3	64.5	Fisher (1946)
<i>Coragyps atratus</i> *	85.8	141.5	82.0	Fisher (1946)
<i>Gymnogyps californianus</i> *	138.5	210.0	114.7	Fisher (1946)
<i>Sarcorhamphus papa</i> *	100.0	165.0	99.0	Fisher (1946)
<i>Vultur gryphus</i> *	153.1	243.0	130.1	Fisher (1946)
Pandionidae				
<i>Pandion haliaetus</i> *	79.6	126.6	54.0	Fisher (1946)
Accipitridae				
<i>Aquila chrysaetos</i> *	127.4	168.8	104.6	Fisher (1946)
Charadriiformes				
Alcidae				
<i>Mancalla diegenae</i> *	52.1	67.9	41.0	Miller and Howard (1949)
Cuculiformes				
Cuculidae				
<i>Coccygus americanus</i> *	28.0	39.8	26.2	Berger (1952)
<i>Coccygus erythrophthalmus</i> *	26.4	36.9	24.8	Berger (1952)
<i>Crotophaga sulcirostris</i> *	34.4	54.3	36.6	Berger (1952)
<i>Geococcyx californianus</i> *	53.9	85.0	62.7	Berger (1952)
Foratidae				
<i>Foro panarium</i>	54.1	88.4	61.3	Olson (1992)
Galliformes				
Tetraonidae				
<i>Falcapennis falcipennis</i> (m)%	0.340	0.434	0.226	Kuz'mina (1992)
<i>Falcapennis falcipennis</i> (f)*%	0.350	0.430	0.220	Kuz'mina (1992)
<i>Lagopus lagopus</i> (m)*%	0.344	0.433	0.223	Kuz'mina (1992)
<i>Lagopus lagopus</i> (f)*%	0.349	0.436	0.215	Kuz'mina (1992)
<i>Lagopus mutus</i> (m)%	0.362	0.431	0.207	Kuz'mina (1992)
<i>Lagopus mutus</i> (f)*%	0.352	0.435	0.213	Kuz'mina (1992)
<i>Lyrurus tetrax</i> (m)*%	0.345	0.431	0.224	Kuz'mina (1992)
<i>Lyrurus tetrax</i> (f)*%	0.345	0.432	0.223	Kuz'mina (1992)
<i>Tetrao urogalloides</i> (m)*%	0.339	0.433	0.228	Kuz'mina (1992)
<i>Tetrao urogalloides</i> (f)*%	0.335	0.435	0.230	Kuz'mina (1992)
<i>Tetrao urogallus</i> (m)%	0.348	0.428	0.224	Kuz'mina (1992)
<i>Tetrao urogallus</i> (f)*%	0.344	0.430	0.226	Kuz'mina (1992)
<i>Tetrastes bonasia</i> (m)*%	0.334	0.440	0.226	Kuz'mina (1992)
<i>Tetrastes bonasia</i> (f)*%	0.333	0.437	0.230	Kuz'mina (1992)
Phasianidae				
<i>Alectoris chukar</i> (m)*%	0.322	0.435	0.243	Kuz'mina (1992)
<i>Alectoris chukar</i> (f)*%	0.322	0.431	0.247	Kuz'mina (1992)
<i>Alectoris griseogularis</i> (m)*%	0.311	0.443	0.246	Kuz'mina (1992)
<i>Alectoris griseogularis</i> (f)*%	0.316	0.432	0.252	Kuz'mina (1992)
<i>Coturnix coturnix</i> (m)*%	0.336	0.420	0.249	Kuz'mina (1992)
<i>Coturnix coturnix</i> (f)*%	0.332	0.413	0.260	Kuz'mina (1992)
<i>Coturnix japonica</i> (m)%	0.345	0.416	0.239	Kuz'mina (1992)
<i>Excalfactoria chinensis</i>	27.0	30.5	19.0	Alexander (1983)
<i>Francolinus francolinus</i> (m)*%	0.313	0.416	0.271	Kuz'mina (1992)
<i>Francolinus francolinus</i> (f)*%	0.307	0.418	0.275	Kuz'mina (1992)
<i>Gallus gallus</i> *	84.6	120.6	81.8	Fisher (1946)
<i>Palaeortyx brevipes</i> *	35.6	56.8	28.0	Mourer-Chauviré (1992)
<i>Palaeortyx gallica</i> *	41.4	59.7	30.6	Mourer-Chauviré (1992)
<i>Paraortyx lorteti</i> *	41.9	52.0	33.5	Mourer-Chauviré (1992)
<i>Perdix dauurica</i> (m)*%	0.337	0.413	0.250	Kuz'mina (1992)

APPENDIX 3. (Continued)

Species	F	T	M	Source
<i>Perdix dauurica</i> (f)*%	0.333	0.417	0.250	Kuz'mina (1992)
<i>Perdix perdix</i> (m)*%	0.332	0.417	0.251	Kuz'mina (1992)
<i>Perdix perdix</i> (f)*%	0.331	0.417	0.250	Kuz'mina (1992)
<i>Phasianus colchicus</i> (m)*%	0.309	0.414	0.277	Kuz'mina (1992)
<i>Phasianus colchicus</i> (f)*%	0.311	0.413	0.276	Kuz'mina (1992)
<i>Tetraogallus altaicus</i> (m)*%	0.344	0.439	0.228	Kuz'mina (1992)
<i>Tetraogallus altaicus</i> (f)%	0.337	0.438	0.225	Kuz'mina (1992)
<i>Tetraogallus caucasicus</i> (m)%	0.336	0.441	0.223	Kuz'mina (1992)
<i>Tetraogallus himalayensis</i> (m)*%	0.331	0.442	0.227	Kuz'mina (1992)
<i>Tetraogallus himalayensis</i> (f) *%	0.332	0.443	0.225	Kuz'mina (1992)
Gruiformes				
Gruidae				
<i>Balearica exigu*</i>	80.2	~151	125.3	Feduccia and Voorhies (1992)
Rallidae				
<i>Aptornis defosson</i>	140.0	260.0	130.0	Holtz (1994a)
<i>Aptornis otidiformis</i>	165.0	227.0	100.0	Holtz (1994a)
<i>Atlantisia rogersi</i>	26.0	42.0	24.0	Lowe (1928)
Messelornithidae				
<i>Messelornis neartica</i>	35.0	63.0	46.0	Hesse (1992)
Apodiformes				
Apodidae				
<i>Chaetura pelagica*</i>	9.3	15.0	7.6	Cohn (1968)
Trochilidae				
<i>Eugenes fulgens</i>	10.9	15.8	6.0	Cohn (1968)
<i>Florisuga mellivora*</i>	10.4	15.0	5.7	Cohn (1968)
<i>Patagona gigas</i>	16.0	23.2	8.8	Cohn (1968)
Passeriformes				
Dendrocolaptidae				
<i>Certhis familiaris*</i>	10.8	19.0	15.3	Norberg (1979)
Paridae				
<i>Parus ater*</i>	11.8	22.2	16.0	Norberg (1979)
<i>Parus cristatus*</i>	12.8	23.9	17.9	Norberg (1979)
<i>Parus montanus*</i>	12.9	23.8	16.6	Norberg (1979)
Sylviidae				
<i>Regulus regulus*</i>	9.7	21.2	17.1	Norberg (1979)
Sandcoleiformes				
Sandcoleidae				
<i>Anneavis anneae</i>	27.7	43.3	23.7	Houde and Olson (1992)
<i>Sandcoleus copiosus</i>	36.5	50.9	28.1	Houde and Olson (1992)
Mesozoic Birds				
<i>Archaeopteryx lithographica</i>	~70	89.5	47.8	Wellnhofer (1988)
<i>Archaeopteryx lithographica</i>	61.0	81.0	40.0	Wellnhofer (1974)
<i>Archaeopteryx lithographica</i>	53.0	69.0	36.0	Wellnhofer (1974)
<i>Archaeopteryx lithographica</i>	48.0	71.0	40.5	Wellnhofer (1993)
<i>Archaeopteryx lithographica</i>	37.0	53.0	30.0	Wellnhofer (1974)
<i>Baptornis advenus</i>	71.0	191.0	84.0	Martin and Tate (1976)
<i>Baptornis advenus</i>	72.0	191.0	83.0	Martin and Tate (1976)
<i>Cathayornis yandica</i>	23.0	29.0	17.0	Zhou et al. (1992)
<i>Confuciusornis sanctus</i>	33.0	41.0	21.0	Hou et al. (1995)
<i>Hesperornis regalis</i>	99.0	298.0	136.0	Marsh (1880)
<i>Hesperornis regalis</i>	105.0	302.0	136.0	Marsh (1880)
<i>Sinornis santensis</i>	14.4	23.8	12.5	Sereno and Rao (1992)