

Chapter 16 Skeletal Adaptations for Flight

Stephen M. Gatesy and Kevin M. Middleton

VERTEBRATES AROSE IN an aquatic environment dominated by the dynamics of fluid flow. With the advent of terrestriality, tetrapods moved into a substrate-based domain in which gravity and inertia became most significant for locomotion. Among the amniotes, three lineages once again exploited fluid forces to conquer the aerial realm through powered flight. The ancestors of birds, bats, and pterosaurs lengthened and broadened their forelimbs into aerodynamically proficient appendages that we collectively call “wings.” Such convergence in overall shape and movement presumably stems from the presence of stringent constraints on the aerodynamic performance of flapping forelimbs. Wings are thus a classic example of vertebrate limbs evolving common solutions to a shared mechanical demand. Yet these volant forms would never be mistaken for one another; each clade arose from a different preflight condition and exhibits unique specializations in airfoil design.

Many authors have addressed vertebrate flight from the viewpoint of aerodynamics, scaling, ecology, and evolution (e.g., Pennycuik 1975; Rayner 1979, 1981, 1988; Norberg 1981, 1985, 1990). In this chapter we focus on wings from an osteological perspective. We begin by introducing the phylogeny of powered fliers (fig. 16.1). Because flapping flight originated in both Reptilia (pterosaurs, birds) and Synapsida (bats), the most recent common ancestor of these groups lies at the root of the clade Amniota (e.g., Gauthier et al. 1988b). Following Sumida (1997), we use closely related fossil taxa to reconstruct the forelimb skeleton and pectoral girdle in the hypothetical ancestral amniote. This allows us to character-

ize wing osteology in each group relative to a common reference point in their evolutionary history.

We then delineate the disparity of wing skeletal design by constructing two theoretical morphospaces, within which we plot select forelimb dimensions of birds, bats, pterosaurs, their close nonvolant relatives, and taxa near the base of Amniota. The distribution of these data reveals patterns of “the range of anatomical design” (Gould 1991, 412) and is used to explore very basic questions about wing evolution. For example, how disparate are the skeletal and segmental proportions of vertebrate wings? Are wings highly constrained by aerodynamic requirements compared to nonflying forelimbs? Have pterosaurs, birds, and bats converged on a single design, or does each clade show singular proportions commensurate with their unique solutions to supporting the flight surface? Are some flying clades more disparate than others, and if so, why? How might variation in wing proportions relate to body size, flight style, and the forelimb’s role in behaviors other than flight? Finally, how do wing skeletons in each group differ from the limb skeletons of their close, nonvolant relatives, and what might these differences reveal about the origin of flight? Our aim is to begin to discern which character states preceded, coincided with, and followed the three transitions from limb into wing.

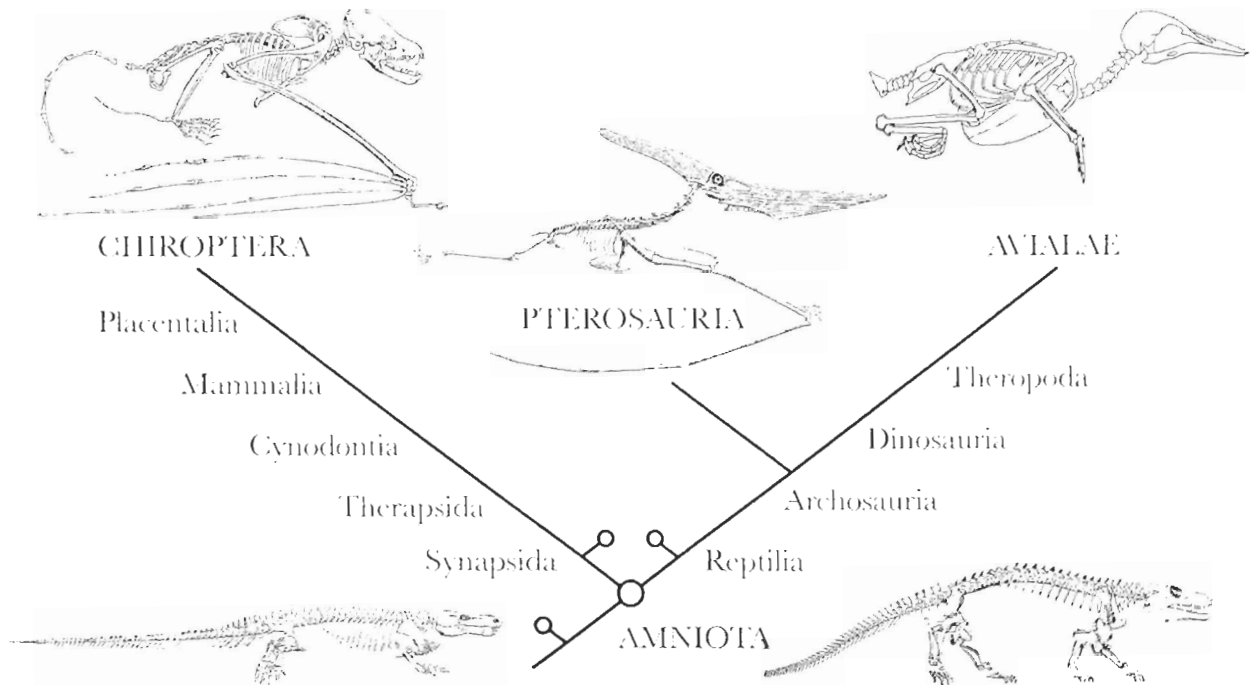


Figure 16-1 Simplified cladogram of amniote phylogeny showing three origins of powered flight. The highly derived wings of bats, pterosaurs, and birds evolved from the terrestrial forelimb of an ancestral amniote (large circle) that we reconstruct based on closely related taxa (small circles) such as *Limnoscelis* (lower left) and *Seymouria* (lower right). (Cladogram based on Laurin and Reisz 1995. Drawings modified from Eaton 1910, Williston 1911, T. E. White 1939, Jepsen 1970, R. L. Carroll 1987–1988, Jenkins et al. 1988.)

Overview and Wing Osteology

Ancestral Amniote

During flight the musculoskeletal elements of the forelimb support and deform the wing's aerodynamic surface—a membrane in pterosaurs and bats and feathers in birds (fig. 16.2). Such highly derived morphologies arose independently from the less specialized forelimb found in their most recent common ancestor at the base of the clade Amniota. Based on taxa near the origin of amniotes (e.g., *Limnoscelis*, *Seymouria* [Williston 1911; T. E. White 1939]; see Reisz 1997 and Sumida 1997 for further discussion), we briefly describe the forelimb skeleton of a hypothetical ancestral amniote so that it can serve as a reference for appreciating the modifications of its volant descendants.

Primitively, the amniote shoulder girdle (fig. 16.3A) consisted of paired scapulae, coracoids, clavicles, and splintlike cleithra, as well as an unpaired, median interclavicle (Sumida 1997). The scapula and coracoid both contributed to a “screw-shaped” glenoid fossa that formed the shoulder joint with the humeral head. The humerus had a tetrahedral organization (Romer 1956) with proximal and distal articular surfaces oriented approximately 90 degrees to one another and pronounced processes for muscle attachment. The radius

and ulna articulated with a distinct capitulum and trochlea on the distal humerus; pronation and supination were likely limited (Sumida 1997). Insufficient specimens with complete carpals make details of the wrist region unclear, but flexibility was likely spread across multiple joints rather than concentrated at a single articular axis (Holmes 1977; Sumida 1989). The manus was pentadactyl (fig. 16.3B), with digit IV longest (Sumida 1997).

This basal form can be reconstructed as an obligate quadruped (Sumida 1997) that lived in the Early Carboniferous approximately 340 million years ago (Paton et al. 1999). Its pectoral appendages were short relative to its trunk and bore comparatively homogeneous digits. Yet from such unspecialized forelimbs evolved three unique wing morphologies capable of powered flight.

Pterosaurs

Pterosaurs were the first amniotes to evolve flapping flight. Based on cranial morphology, pterosaurs have been reconstructed as piscivores, insectivores, filter feeders, and scavengers (Wellnhofer 1978, 1991), presumably filling many of the aerial niches now occupied by birds. The pterosaur fossil record extends back at least 210 million years to the Late Triassic (Wellnhofer 1978), and even the oldest and most primi-

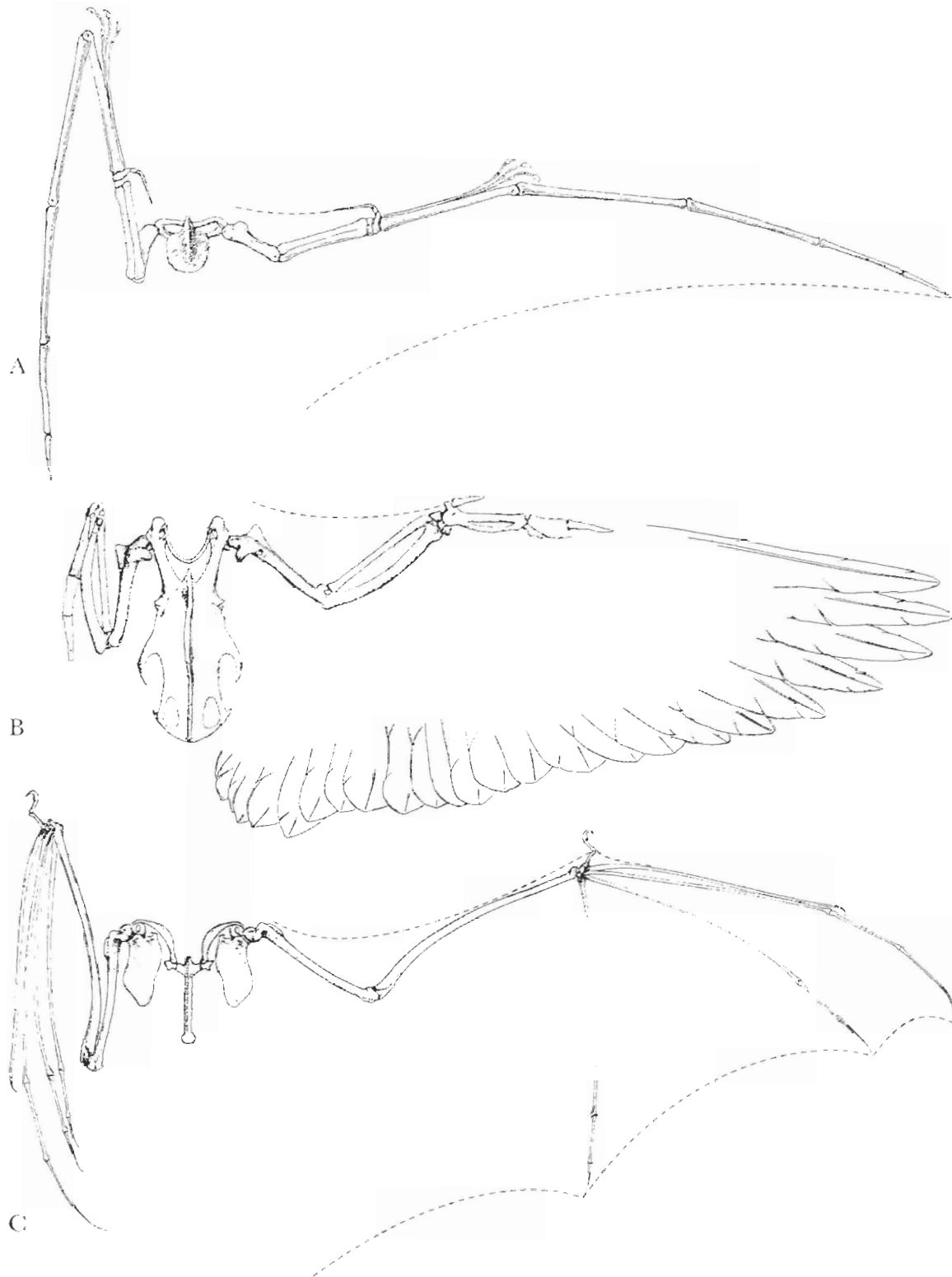


Figure 16-2 Wing osteology in vertebrate powered fliers, ventral view. (A) The pterosaur, *Pteranodon*. (modified from Eaton 1910). The main wing membrane is primarily supported by the hypertrophied fourth digit. Mobility was greatest at the shoulder, elbow, and fourth metacarpophalangeal joint. (B) An extant pigeon, *Columba* (modified from N. S. Proctor and Lynch 1993). Primary feathers extending from the manus significantly increase wingspan. Note the proximity of the wrist to the shoulder when folded. (C) An extant bat (modified from Hill and Smith 1984). Four elongated digits support the main wing membrane, which is also attached to the hindlimb.

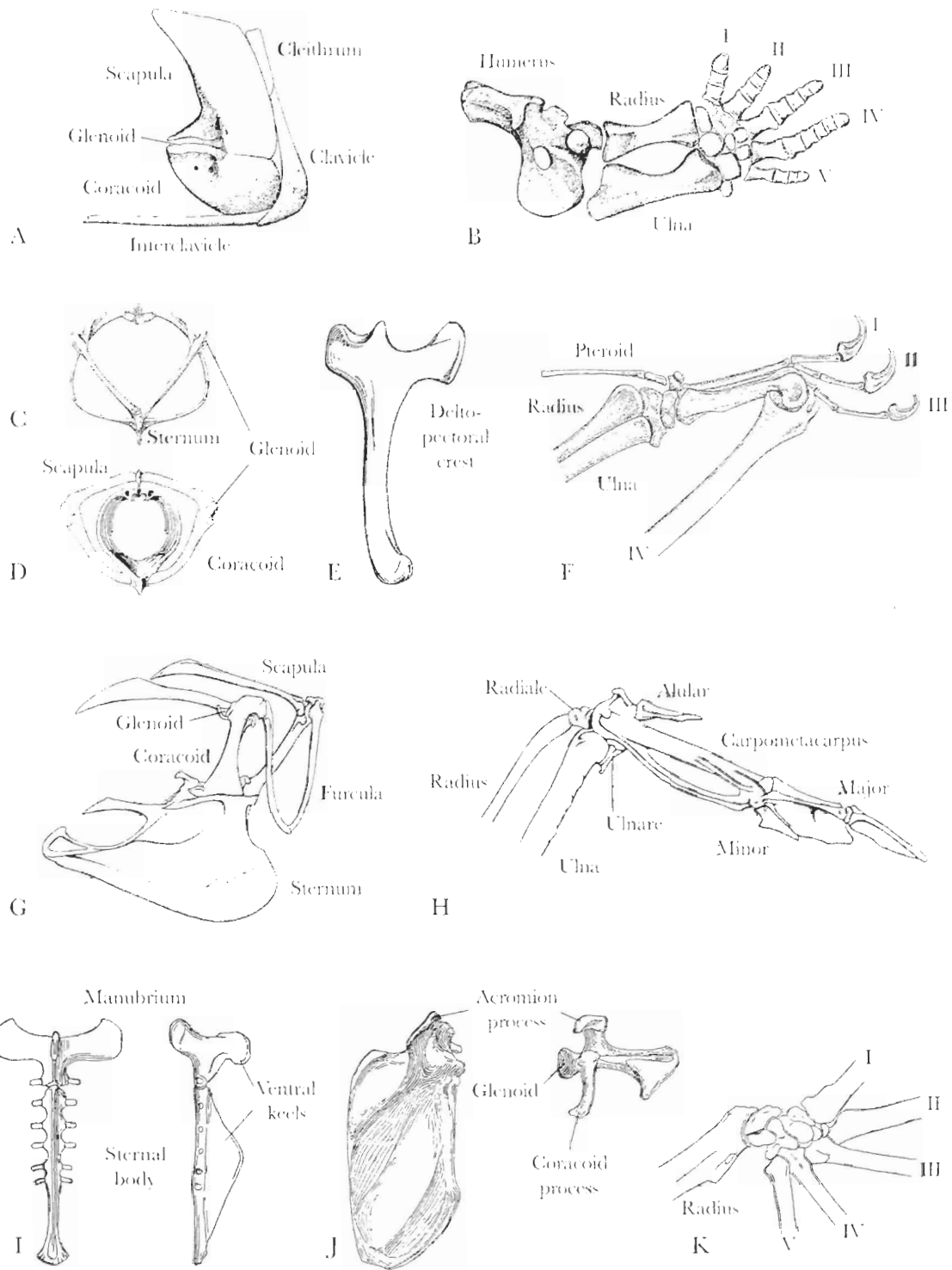


Figure 16-3 Osteology in taxa close to the origin of amniotes (A, B), pterosaurs (C–F), birds (G, H), and bats (I–K). (A) Right lateral view of the pectoral girdle of *Seymouria* (modified from Romer 1956 after T. E. White 1939). (B) Dorsal view of right forelimb of *Limnoscelus* (modified from R. L. Carroll 1987–1988 after Williston 1925), showing relatively short, stout elements and the full complement of digits. (C) Anterior view of thorax and pectoral girdle of a *Rhamphorhynchus* (modified from Wellnhofer 1991). (D) In pterodactyls such as *Pteranodon*, the scapulae articulate with fused vertebrae, which form a notarium (modified from Bramwell and Whitfield 1974). (E) Right humerus and (F) hand of *Rhamphorhynchus* in dorsal view (modified from Wellnhofer 1978, 1991). (G) Anterolateral view of the pectoral girdle of a pigeon, *Columba* (modified from N. S. Proctor and Lynch 1993). The sternum bears a prominent ventral keel, and the clavicles have fused into a furcula, or wishbone. (H) Wrist of *Columba* in dorsal view showing extensive fusion and reduction in element number (modified from Vasquez 1994). (I) A chiropteran sternum in ventral and right lateral view. (J) Dorsal and anterior views of a right scapula. (K) Right wrist in dorsal view showing the distal radius, complexly faceted carpals, and five proximal metacarpals (bat figures modified from Vaughn 1959).

tive pterosaurs are easily recognizable as volant organisms (Wild 1978, 1984a, 1984b; Jenkins et al. 2001). Despite the fragility of pterosaur bones, many are so distinctive (e.g., humeri, wing-finger phalanges) that even very fragmentary fossils can be confidently assigned to Pterosauria. General information on pterosaur anatomy and evolution has been reviewed by Eaton (1910), Romer (1956), Wellnhofer (1978, 1991), and R. L. Carroll (1987–1988).

Although no good transitional forms are known, pterosaurs are thought to be closely related to archosaurs near the base of Dinosauria (Sereno 1991; Sereno and Arcucci 1993, 1994; Benton 1999). Several phylogenetic analyses have found the small, bipedal archosaur, *Scleromochlus taylori*, from the Late Triassic of Scotland (Woodward 1907) to be the sister taxon of pterosaurs (Sereno 1991; S. C. Bennett 1996; Benton 1999). The monophyly of Pterosauria has never been questioned, and the clade has been traditionally divided into two groups, rhamphorhynchoids and pterodactyloids (Wellnhofer 1978). Rhamphorhynchoids, known from the Late Triassic to the Cretaceous, had relatively small heads, short necks, and long tails (Wellnhofer 1975a, 1975b, 1975c, 1991). The more derived pterodactyloids, known from the Jurassic through the end of the Cretaceous, were characterized by having relatively larger heads, longer necks, and shorter tails (Wellnhofer 1970; S. C. Bennett 2001a, 2001b). Pterodactyloids include the largest flying animals to have ever lived, reaching an estimated wingspan of 11–12 meters in *Quetzalcoatlus* (Lawson 1975). A recent cladistic study by Unwin (1995) supported pterodactyloid monophyly but revealed “rhamphorhynchoids” to be paraphyletic.

Pterosaur flight has received attention from a variety of researchers (Brower 1982; Padian 1985, 1991; Rayner 1988; Hazlehurst and Rayner 1992; Padian and Rayner 1993a, 1993b; Alexander 1994; Marden 1994; Unwin and Bakhurina 1994; S. C. Bennett 1997). Most modern workers concur that pterosaurs were capable of flapping flight, although the largest pterodactyloids are thought to have primarily harnessed winds and/or thermals for soaring (Bramwell and Whitfield 1974). A more contentious issue has been terrestrial locomotion. Padian (1983a, 1983b) and Padian and Olsen (1984a, 1984b) reconstructed pterosaurs as bipedal animals, whereas others have argued for quadrupedal progression (S. C. Bennett 1990; J. M. Clark et al. 1998; Unwin 1987, 1988a, 1988b, 1997, 1999; Unwin and Henderson 2002; Wellnhofer 1988). Recent analyses of footprints (e.g., Mazin et al. 1995; J. L. Wright et al. 1997) have convinced many workers that pterosaurs habitually used all four limbs when on the ground.

We characterize the pectoral girdle and wing of pterosaurs based largely on Wellnhofer (1978) and S. C. Bennett (2001a). The shoulder girdle is simplified relative to the ancestral amniote condition (figs. 16.3C, D). Dermal elements

are absent, leaving only an ossified sternum and paired scapulae and coracoids (Romer 1956). The fused sternal plates bear a large, anteroventrally projecting keel to accommodate enlarged flight musculature. Each scapula and coracoid is co-ossified into a V-shaped scapulocoracoid, which forms a saddle-shaped glenoid. In large pterodactyloids, such as *Azhdarcho*, *Dsungaripterus*, *Nyctosaurus*, *Pteranodon*, *Quetzalcoatlus*, and *Santanadactylus* (S. C. Bennett 2001a), the distal end of the scapula articulates with a series of three to eight fused thoracic vertebrae, which form a notarium (fig. 16.3D).

Many of the wing bones are pneumatic and thin-walled, and in large pterosaurs, even the distal phalanges are pneumatic (Bramwell and Whitfield 1974). The humerus's saddle-shaped proximal surface articulates with the glenoid to form a sellar joint. A large, linguiform deltopectoral crest projects forward for the insertion of the pectoral musculature (fig. 16.3E). The forearm is dominated by the ulna, and the elbow is a simple hinge joint (Bramwell and Whitfield 1974). The pterosaur wrist originally contained five carpal bones in two rows. The two proximal carpals fuse in all but the most primitive pterosaurs. In some derived forms the two distal carpals associated with metacarpal IV fuse as well. The remaining distal carpal articulates with a hollow spur of bone called the pteroid (fig. 16.3F), a structure unique to pterosaurs. The pteroid, which likely is bone rather than calcified tendon (Unwin et al. 1996), supports the edge of an anterior wing membrane spanning from neck to wrist (fig. 16.2A).

Digit IV dominates the hand of all pterosaurs. The fourth metacarpal is extremely robust but varies in length, being relatively short in rhamphorhynchoids (fig. 16.3F) and longer in pterodactyloids (figs. 16.1, 16.2A). The distal articular surface of metacarpal IV is a trochlea with offset condyles, allowing the wing finger to automatically supinate during upstroke (Padian 1983a; Jenkins et al. 2001) and to tuck alongside the body when on the ground (Bramwell and Whitfield 1974). Distally, the wing membrane is supported only by the four elongated phalanges of digit IV, and no ungual is present. Metacarpals I–III are slender and bear digits with a phalangeal formula of 2-3-4 (fig. 16.3F); the fifth metacarpal and digit are lost. Wellnhofer (1991) noted that the unguals of digits I–III show well-developed flexor tubercles and hypothesized that these digits had strong grasping ability.

Birds

The extant avifauna is globally distributed and includes over 9,000 species exhibiting a wide spectrum of body size, locomotor style, and diet. Birds are first found in the fossil record approximately 145 million years ago in the form of *Archaeopteryx lithographica* from the Late Jurassic Solnhofen

limestones of southern Germany (von Meyer 1861a, 1861b, 1862). During the last 20 years an influx of new fossil material, primarily from China, Spain, and South America, has substantially increased our understanding of Mesozoic bird diversity (for reviews see Chiappe and Witmer 2002 as well as Chiappe and Dyke 2003). In addition to ornithological texts (e.g., Proctor and Lynch 1993) there are several scientific volumes about avian anatomy and evolution (K. E. Campbell 1992; Baumel et al. 1993; Mindell 1997; Olson 1999; Gauthier and Gall 2001; Chiappe and Witmer 2002; Zhou and Zhang 2002c). General descriptions of avian osteology are relatively common (e.g., Fürbringer 1888; Fisher 1946; Owre 1967; Raikow 1985), with the *Handbook of Avian Anatomy: Nomenclatura Anatomica Avium* (Baumel et al. 1993) providing standardized nomenclature.

The evolutionary relationships of birds to other amniotes have been a persistent question for over 100 years (reviewed in Gauthier 1986; Sereno 1991; Witmer 1991, 2002). Workers using cladistic techniques have unanimously favored a theropod ancestry of birds (Cracraft 1986; Gauthier 1986; Norell et al. 2001; J. M. Clark et al. 2002), a conclusion reached by previous authors based on comparative anatomy (Huxley 1868, 1870a, 1870b; Ostrom 1973, 1974, 1975, 1976a, 1976b; Bakker and Galton 1974). In his phylogenetic analysis of Diapsida, Gauthier (1984, 1986) found strong support for birds being nested within maniraptoran coelurosaurs, with dromaeosaurs such as *Velociraptor* and *Deinonychus* as close sister taxa. More recent discoveries, in particular spectacular specimens preserving soft tissues from China (e.g., P.-J. Chen et al. 1998; Ji et al. 1998; Xu et al. 1999a, 1999b, 2000, 2001, 2003; Norell et al. 2002), have begun to blur the distinction between feathered theropods and primitive birds (Witmer 2002). Avian systematics has a rich and diverse history summarized by Sibley and Ahlquist (1990). Intraordinal relationships are being addressed using both morphological (Ericson 1997; Livezey and Zusi 2001; Cracraft and Clarke 2001; Dyke et al. 2003) and molecular approaches (contributions in Mindell 1997; Groth and Barrowclough 1999; van Tuinen et al. 2000; Ericson et al. 2001), but many nodes remain poorly resolved.

The mechanics of bird flight is addressed in an expansive and rapidly growing literature. Over the past 25 years, studies have elucidated flight from the perspectives of aerodynamics (e.g., Pennycuik 1975, 1986; Rayner 2001b; Hedrick et al. 2002, 2003; Spedding et al. 2003), kinematics (e.g., Jenkins et al. 1988; Tobalske and Dial 1996), and muscle activity/mechanics (e.g., Dial et al. 1987, 1988, 1991; Dial 1992a, 1992b; Biewener et al. 1992). Birds are the only group of powered fliers in which this ability has been secondarily lost. Flightlessness has evolved in at least 34 separate families

of birds, including auks, cormorants, dodos, ducks, grebes, and parrots (Livezey 1995).

The avian sternum (figs. 16.1, 16.2B, 16.3G) bears a ventrally expanded, midline keel to accommodate the hypertrophied flight musculature (supracoracoideus and pectoralis muscles). This keel is absent in the flightless ratites. Paired scapulae and coracoids articulate with the fused clavicles, which constitute the furcula or wishbone. Ventrally, the flared ends of the elongated coracoids fit into anterior sulci on the sternum. The coracoids meet the scapulae at an acute angle, together forming the saddle-shaped glenoid cavity (Jenkins 1993). An acrocoracoid process projects anteriorly, forming a pulley to deflect the tendon of the supracoracoideus muscle and allowing it to supinate and elevate the wing (Poore et al. 1997). The avian scapula has a very characteristic strap shape, thinning caudally as it lies along the ribcage roughly parallel to the vertebral column (fig. 16.3G).

The proximal humerus bears an ovoid articular head, a deltopectoral crest that is less prominent than that of pterosaurs, as well as dorsal and ventral tubercles (fig. 16.2B). The shaft is pneumatized in most species. Distally, the humerus bears articular condyles for the ulna and radius. The ulna is bowed caudally and bears quill knobs for the attachment of secondary flight feathers, whereas the radius is straighter and smaller in diameter. The ulna and radius articulate with a free pair of carpal bones, the ulnare and radiale (fig. 16.3H). These carpals articulate with the carpometacarpus, a complex co-ossification of three distal carpals and three metacarpals. The identity of the three digits has received a great deal of attention (Hinchliffe 1977; Hinchliffe and Hecht 1984; Burke and Feduccia 1997; G. P. Wagner and Gauthier 1999; Feduccia and Nowicki 2002; Wagner and Larsson, chap. 4 in this volume). Herein we follow Baumel and Witmer (1993) by referring to the digits as the alular, major, and minor rather than by number. Alular and minor digits typically have one phalanx, whereas the major digit has two (fig. 16.3H). Ungual phalanges are found on the alular and/or major digits in many birds (Fisher 1940).

Bats

With over 900 extant species, bats (Chiroptera) comprise approximately one-quarter of present mammalian diversity. Bats do not reach the size of the largest birds or pterosaurs; all bats retain the ability to fly. Diets include insects, vertebrates, fruit, pollen/nectar, and blood. Extant bats are found in most tropical and temperate regions except certain remote islands (Nowak 1991). Although tooth fragments from the Late Paleocene have been referred to Chiroptera (Gingerich 1987), the first definitive fossils are about 53 million years old

from Early Eocene deposits (Simmons and Geisler 1998). Fossil bats offer few clues to the order's phylogenetic position among mammals or the origin of chiropteran flight. Even the earliest known forms, such as *Icaronycteris*, have forelimbs modified into wings (Jepsen 1970) and ears specialized for echolocation (Novacek 1985).

Conventionally, bats have been divided into two suborders that form a monophyletic group closely allied with dermopterans ("flying lemurs"; Altringham 1996). Megachiropterans, or megabats, consist of a single family of Old World fruit bats, including the "flying foxes." Microbats, suborder Microchiroptera, encompass all other families. Over the past decade these viewpoints have been challenged on several fronts. First, Teeling et al. (2000, 188) found no molecular evidence for close relationship between Chiroptera and Dermoptera and remarked that any "presumed shared derived characters for flying lemurs and bats are convergent features that evolved in association with gliding and flight, respectively." Second, based on brain morphology, J. D. Pettigrew et al. (1989) suggested that megabats and microbats may have evolved separately from nonchiropteran ancestors. Later studies supported bats as a natural group (e.g., Bailey et al. 1992; Honeycutt and Adkins 1993). Finally, microchiropteran monophyly has also been questioned (Stanhope et al. 1998; Springer et al. 2001; Teeling et al. 2000, 2002). In these molecular phylogenies Megachiroptera remained monophyletic, but several microchiropteran families (Hipposideridae, Megadermatidae, Nycteridae, and Rhinolophidae) were found to be more closely related to Megachiroptera than to other microchiropterans. Some recent morphologic studies, however, have supported microbat monophyly (e.g., Novacek 1992; Shoshani and McKenna 1998; Simmons and Geisler 1998; K. E. Jones et al. 2002). This issue remains to be resolved.

Most bats flap continuously during flight, although some megachiropterans also soar (Norberg et al. 2000). Many species can hover and are extremely aerobic. The wing's aerodynamic surface is divided into regions between the digits, body wall, hindlimb, and tail. The axial skeleton of bats has been stiffened in association with flight. In some families, the final cervical vertebra fuses with the first and sometimes second thoracic vertebra. Functional studies of bat flight include descriptions of kinematics, muscle activity, bone stresses, and aerodynamic performance (e.g., Norberg 1972, 1976; Hermanson and Altenbach 1983; Rayner and Aldridge 1985; Rayner 1987; Swartz et al. 1992; Swartz 1998), as well as wing allometry (Norberg 1981; Swartz 1997) and ecomorphology (Norberg and Rayner 1987).

Our osteological description is largely based on the work of Vaughan (1959), Walton and Walton (1970), Strickler

(1978), Hill and Smith (1984), and Koopman (1984). The chiropteran sternum is T-shaped and composed of two segments (figs. 16.2C, 16.3I). Ventral keels project from the manubrium and sternal body in some forms (Cuvier 1805), but in others the enlarged pectoralis musculature meets at a midline tendon sheet (Altringham 1996). Large lateral processes of the manubrium articulate with the relatively massive clavicles. Each clavicle articulates with its scapula's acromion process, coracoid process, or both and likely functions as a spoke guiding scapular rotation during flight. The rectangular or oval scapular blades lie on the dorsal surface of the ribcage roughly parallel to the vertebral column. A scapular spine separates the small supraspinous fossa from the larger infraspinous fossa. As in other mammals, the coracoid is represented by the coracoid process but in bats is extremely large (up to half the length of the scapula), ventrally directed, and laterally curved (fig. 16.3J). The shallow glenoid socket faces laterally and in some bats is augmented by a dorsal facet that articulates with the greater tuberosity of the humerus.

Bats have non-pneumatized, marrow-filled longbones (Nowak 1991). Although not air-filled, the humerus and radius are relatively thin-walled (Swartz et al. 1992). The humerus has a straight or slightly sigmoid shaft and a head ranging "from nearly round to elliptical to roughly tear-shaped" (Strickler 1978, 43). A prominent pectoral crest similar to that in birds projects from the cranial border, merging with the greater tuberosity. In some species the greater tuberosity projects proximally beyond the humeral head far enough to articulate with the scapula, forming a "scapulo-humeral lock" (Vaughn 1959; Altenbach and Hermanson 1987). Distally, the olecranon fossa, which in other mammals accepts the olecranon process of the ulna, is rudimentary or absent. The radius is the dominant forearm element (figs. 16.1, 16.2C). The olecranon portion of the ulna is fused to the radius. Distally the ulna thins or becomes cartilaginous, and it may not reach the wrist. The carpal bones of bats are arranged in two rows, and the fusion pattern of some elements can be used to determine an animal's age. Grooves on the distal radius interlock with the proximal carpals to restrict wrist movement to flexion and extension (Grassé 1955a).

The hand is composed of five digits, with the metacarpals and phalanges of digits II–V supporting the wing membrane. When the wing is fully extended, the five metacarpals fan out almost 180 degrees with metacarpal V trailing chordwise behind the wrist (fig. 16.3K). Digit I is short and typically bears a strong claw for clinging (Nowak 1991). Other digits lack unguals in most bats, although some megabats retain an ungual on digit II. Compared with nonflying mammals, bat

hands have relatively long metacarpals, phalanges with tapering shafts, and a specialized proximo-distal gradient in cortical thickness and mineralization (Swartz 1997; Papadimitriou et al. 1996). Terminal phalanges can lack a marrow cavity and consist only of cartilage (Papadimitriou et al. 1996), a morphology thought to promote, rather than resist bending (Swartz 1997, 1998).

Wing Disparity

How Should Wing Skeletons Be Configured?

The skeletal elements of any wing must perform multiple tasks during flapping flight. Many of these functions are primitive, such as providing structural support against muscular, gravitational, and inertial forces, or articulating to allow changes in limb length and position. Other functions, however, are novel. For example, wing skeletons bear aerodynamic loads from the flight surface (feathers or wing membrane) far greater than their terrestrial ancestors ever encountered. The forelimb skeleton also dictates, to varying degrees, the overall size and shape of the airfoil. This is especially true in bats, where bones delineate the wing's length, chord (breadth), and tip shape. In pterosaurs, the forelimb skeleton determined wing length but not wing chord, which depended on the soft-tissue membrane and its attachment to the hindlimb (see Padian and Rayner 1993b; Unwin and Bakhurina 1994). A bird's wing is the least prescribed by bones because feathers contribute to both its length and its chord. As in the other two clades, however, the length and orientation of skeletal elements is critical for establishing the wing's internal points of mobility and the mechanics of these lever systems.

Wings, however, do not function exclusively for flight. Bats and pterosaurs (based on referred footprints) walk quadrupedally, demanding that their airworthy wings also operate as supportive limbs when on substrates. Birds, as obligate bipeds, are less hindered in this respect, but their wings are often used in nonflight behaviors such as display, brooding, defense, and predation. Bat wings can also have roles in feeding, either to trap flying insects or to manipulate fruit, and in thermoregulation. Finally, winged vertebrates must also manage their hypertrophied forelimbs when not in use. Compact folding may act as an additional constraint on skeletal proportions and joint mobility (Middleton and Gatesy 2000).

Given these basic demands, how should wing skeletons be configured? Most studies of vertebrate wing design use basic parameters of fixed wing aircraft, such as aspect ratio and wing loading (e.g., Pennycuik 1975; Norberg and

Rayner 1987). Such static representations of wing shape and size often correlate with flight performance and ecology but are insufficient for asking many basic morphological questions. How much of the wing should be supported by the arm, forearm, and hand skeleton? How should each of these elements be oriented within the wing? Where should the main joints be positioned for folding? How should the relative segment lengths vary in wings of different flight surface, size, and performance? In the absence of human-made flapping machines to use as paradigms for optimal design (e.g., Lauder 1996), it has been difficult to know how to interpret articulated biological wings from a mechanistic perspective. In the next section we carry out a simple analysis of skeletal proportions in pterosaurs, birds, and bats to begin to explore patterns of wing disparity (e.g., Gould 1991). These patterns may reveal some of the rules governing the construction of vertebrate wings.

How Are Wing Skeletons Proportioned?

The disparity of forelimb elements can be studied using a proportion morphospace (Gatesy and Middleton 1997; Middleton and Gatesy 2000). We visualize this morphospace as a ternary diagram (triangular graph) on which we plot the relative contribution of three variables to a whole. This is a theoretical morphospace, encompassing all possible combinations of three elements rather than an empirical morphospace created only from sampled data (McGhee 1999). Forelimbs with similar proportions will be restricted to one area of the ternary diagram, whereas more disparate limbs will be spread out into a larger point cloud. First, we calculated the relative length of bones representing the arm, forearm, and palm to create a skeletal proportion morphospace (fig. 16.4). For each specimen, the length of the humerus, radius, and metacarpal (IV in pterosaurs, carpometacarpus in birds, III in bats) was divided by the summed length of all three bones to yield percentages. These data are plotted on a ternary diagram in which the lower left, lower right, and upper vertices correspond to 100% humerus, 100% radius, and 100% metacarpal, respectively (fig. 16.4A). Our data set includes 113 specimens from 9 genera of pterosaurs, 554 specimens from 266 genera of volant birds, and 79 specimens from 45 genera of bats (see the appendix for references).

Our sample of vertebrate wings is neither widely nor evenly distributed in ternary morphospace (fig. 16.4A). Wings are restricted to the middle region, whereas the corners, representing limbs with one extremely long element, are entirely empty. The contribution of the humerus varies 24%, from 21% (pterosaur and bat) to 45% (bird). Radial variation is similar, spanning 26% between two pterosaurs at 28% and 54%. Metacarpal percentage is most variable

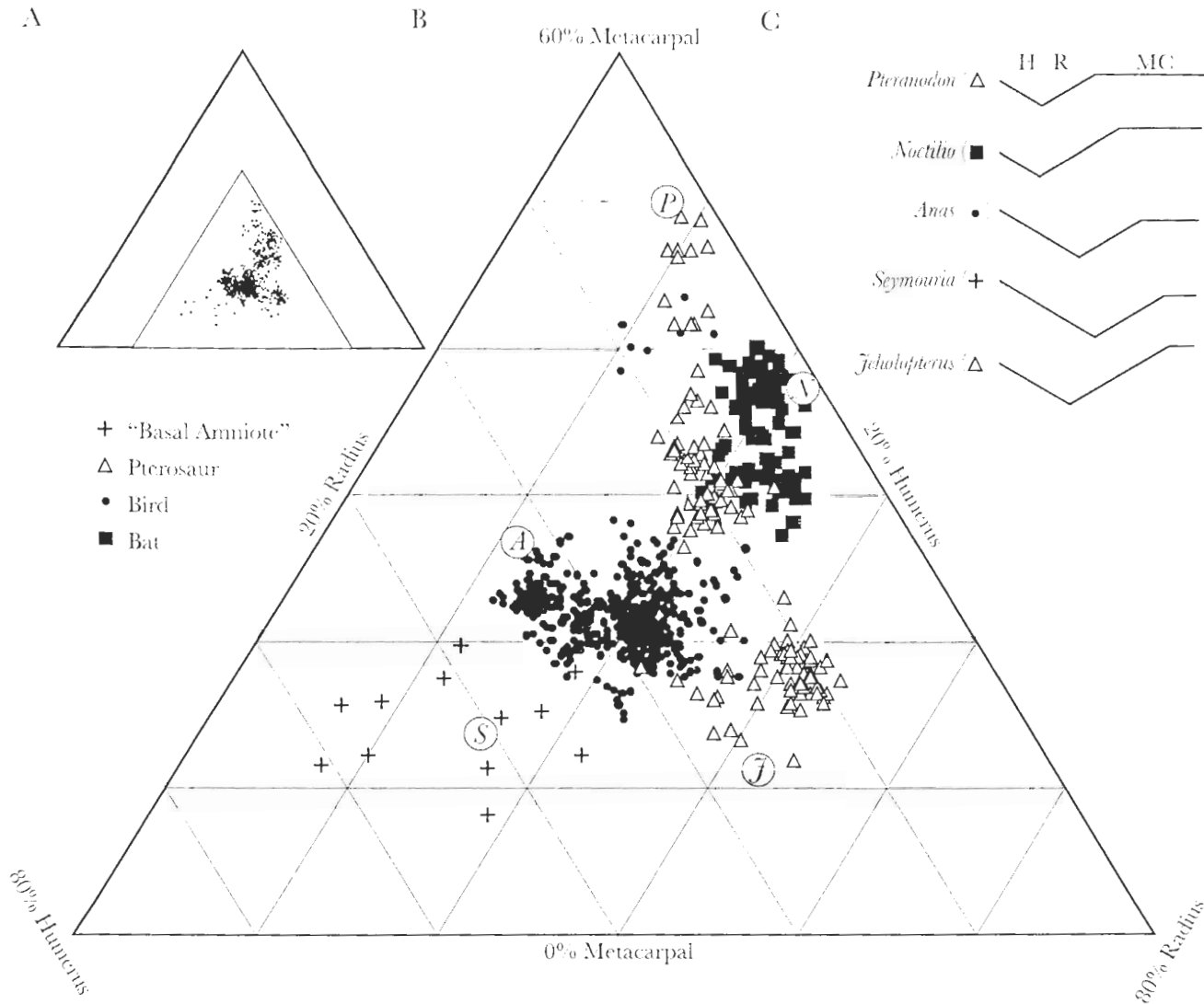


Figure 16-4 Forelimb skeletal proportions in ternary morphospace. (A) The relative lengths of the humerus, radius, and longest metacarpal are plotted for pterosaurs, birds, bats, and taxa near the origin of Amniota ("basal amniotes"). Wings are restricted to the middle of the morphospace. (B) A subset of ternary morphospace enlarged to show the distribution of each group. "Basal amniotes" fall to the lower left of birds, which cluster around the midline. Pterosaurs and bats have relatively shorter humeri than most birds, with the exception of hummingbirds and swifts, which have elongated carpometacarpi. (C) Diagrams of skeletal proportions drawn to identical total length to show the range of anatomical design. Figured specimens are shown in (B) with letters within open circles.

(38%), with pterosaurs again having both the lowest (12%) and highest (50%) values. Only a subset of birds crosses the midline by having the humerus longer than the radius. The radius is never the shortest element of the three, although all other combinations of rank order have evolved. Following Middleton and Gatesy (2000) we can use a disparity index (DI: 100 times the distance between points divided by the maximum possible distance) to quantify interpoint difference. The most disparate wings belong to two pterosaurs (figs. 16.4B, C). The lowermost (*Jeholopterus*) and uppermost (*Pteranodon*) have a DI of 34, representing a divergence in proportions of one-third the maximum theoretically pos-

sible. Flying birds have a disparity index of 25, while in bats it is 11.

Bird and bat wings occupy distinct regions of the morphospace, but pterosaurs fill this gap and overlap with both groups. Each clade is further divided into clusters, which we discuss in more detail later. The pterosaur point cloud is long and narrow compared to the more globular distributions of birds and bats. A simple way to estimate the area colonized is to subdivide the morphospace into 400 triangular cells (Gatesy and Middleton 1997). All vertebrate wings occupy 43 cells, of which birds are present in 24, pterosaurs in 21, and bats in just 10.

Basal amniotes and close nonamniote relatives (14 specimens of 12 genera) differ from most volant forms in their relative bone lengths, falling below and to the left of the main bird cloud. Although there is variation among these taxa, they can be characterized as having a humerus longer than the radius and relatively short fourth metacarpals of less than 20%.

How Are Functional Wing Segments Proportioned?

The proportions of the wing's three major longbones allow one aspect of anatomical disparity to be assessed, but func-

tional implications of these patterns are difficult to interpret. To help compare wing skeletons from different clades as articulating structures, we divided the entire wing into proximal, middle, and distal segments that move as units during flight. We plotted these data to create a segmental proportion morphospace (fig. 16.5). Bats primarily bend the wing skeleton at the elbow and wrist, so the three segments are the humerus, radius, and metacarpal + phalanges of digit III (79 specimens of 45 genera). For pterosaurs, most flexion/extension of the distal wing took place at the fourth metacarpophalangeal joint rather than at the relatively immobile wrist (Padian 1983a). Therefore, the three segments

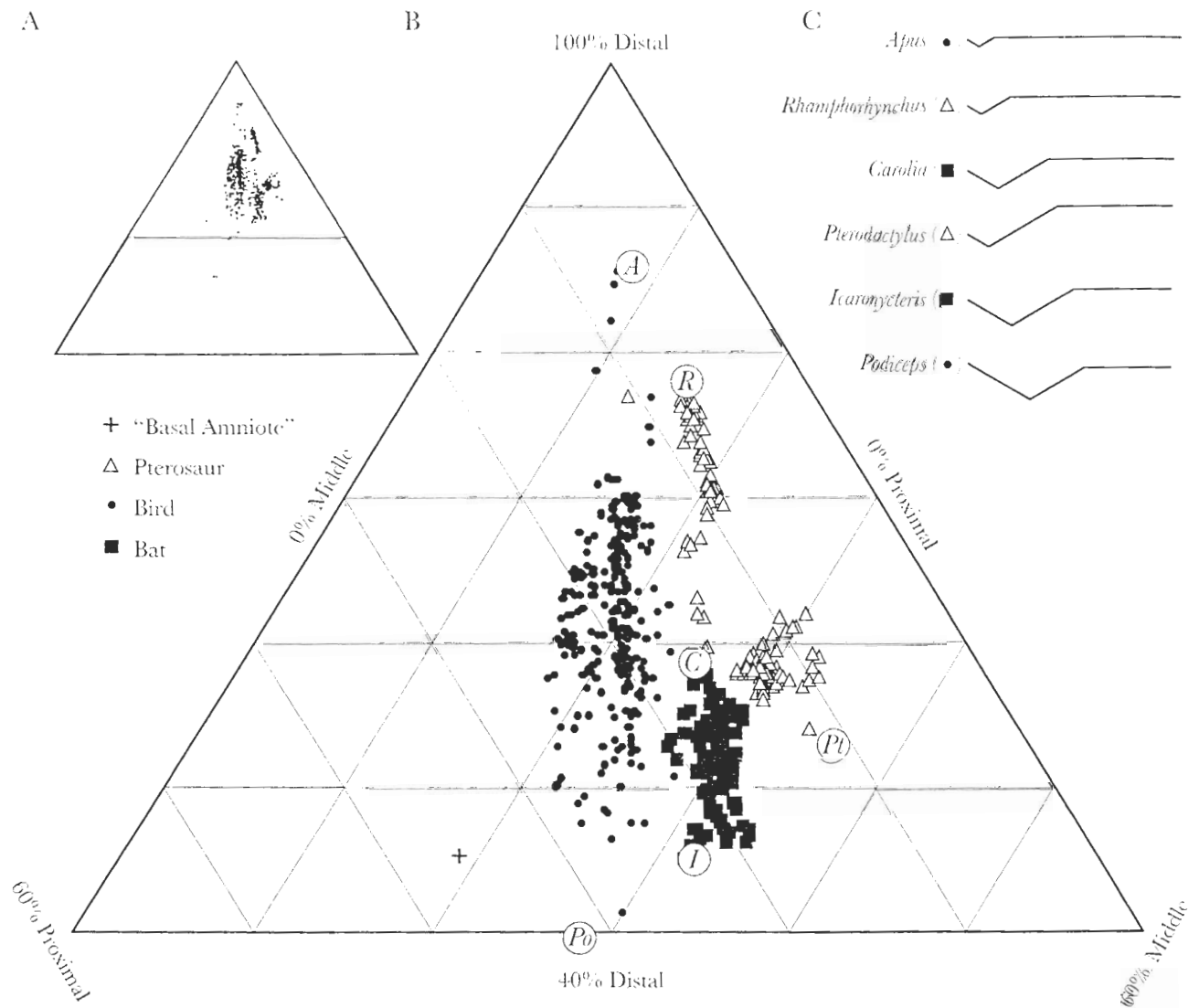


Figure 16-5 Forelimb segmental proportions in ternary morphospace. (A) The relative lengths of the proximal, middle, and distal wing segments are plotted for pterosaurs, birds, bats, and taxa near the origin of Amniota ("basal amniotes"). Wings are restricted to the upper portion of the morphospace because the distal segment is always longest. (B) A subset of ternary morphospace enlarged to show the distribution of each group. Birds, bats, and pterosaurs fill distinct regions with little overlap. (C) Diagrams of segmental proportions drawn to identical total length to show the range of anatomical design. Figured specimens are marked in (B) by circled letters.

in pterosaurs are the humerus, radius + metacarpal IV, and phalanges of digit IV (113 specimens from 9 genera). For birds, we measured the humerus and radius for the first two segments. Because the major digit of birds does not reach the wing tip, we used study skins to measure the length from the wrist to the tip of the longest primary feather (known as the "wing chord" in field ornithology) for the distal functional segment. Few museum preparations preserve measurable wing bones with primary feathers still attached. Consequently, we combined humeral and radial data with wing chord data from different specimens to make composite percentages for 268 specimens from 216 genera. The ternary diagram axes are organized such that the lower left, lower right, and upper vertices correspond to 100% proximal segment, 100% middle segment, and 100% distal segment, respectively.

Within this more functionally-based theoretical morphospace, wings are restricted to a narrow wedge near the top of the ternary (fig. 16.5A). The distal segment, representing the "handwing," is always the longest. Humeral contributions span 26% between two birds at 6% and 32%. The middle segment differs similarly (28%) from a bird (8%) to a pterosaur (36%). Variation is greatest (46%) in the distal segment's contribution, ranging from 40% to 86% of total wing length in two birds. This grebe and swift have the most disparate wings in our sample, with a DI of 38 (figs. 16.5B, C).

Each clade occupies a distinct region of morphospace (fig. 16.5B). Bats form a small, ovoid cluster nestled between the elongated bird and pterosaur clouds making up the left and right sides of the wedge, respectively. The most disparate pterosaurs have a DI of 24, whereas bats show a more conservative DI of only 12. Wings are present in 44 of the 400 possible cells (11%). Birds are present in 25 cells, whereas pterosaurs occupy 14 and bats only 6.

Our sample of taxa near the origin of amniotes is extremely limited by the small number of specimens with complete hands. One taxon, *Crassieria*, has an unusually long manus (Paton et al. 1999), but others fall lower with distal segments about one-third of limb length (fig. 16.5A).

Pterosaurs

The skeletal proportions of the two main groups of pterosaurs, pterodactyloids and rhamphorhynchoids, form loose upper and lower clouds, respectively (fig. 16.6A). These clusters correspond with the classic characterization of pterosaurs as having either short or long metacarpals. Basal pterosaurs cluster with the rhamphorhynchoids but tend to have relatively longer humeri. Members of the genus *Pteranodon*, a large, toothless, crested pterodactyloid from the Late Cretaceous, has the most extreme proportions with an elongated fourth metacarpal approaching the length of the

humerus and radius combined. Unfortunately, presumptive close relatives of pterosaurs such as *Scleromochlus* are too fragmentary to measure reliably.

The distribution of taxa changes significantly on the segmental ternary diagram (fig. 16.6D). Rhamphorhynchoids, which were lowest on the skeletal plot because of their relatively short metacarpals, are now highest with hypertrophied fourth digit phalanges making up 69–78% of the wing. In contrast, pterodactyloid wing fingers only contribute 53–61%; basal forms have distal segments of intermediate proportion. All pterosaurs have an exceptionally short humeral segment, which contributes only 6–15% to total length.

Birds

The majority of birds form a large, ovoid cloud near the bottom of the skeletal ternary diagram (fig. 16.6B). In contrast, swifts and hummingbirds are above the main cluster separated by a DI of 10. These are the only birds in which the carpometacarpus is longer than the humerus. As pointed out previously (Middleton and Gatesy 2000), birds with relatively short humeri (swifts, hummingbirds, swallows, martins) are regarded as highly maneuverable. Birds with the relatively longest humeri (alcids, loons, cuckoos, grebes, and albatrosses) are considered poorly maneuvering fliers. Six specimens of *Archaeopteryx*, the most primitive bird known, are located along this lower left edge of the distribution (43%:38%:19%) coproportional with grebes. Other Mesozoic birds (e.g., *Concornis*, *Confuciusornis*, *Jeholornis*, *Yanornis*) are scattered within the middle of the lower point cloud. Nonavian theropods considered closely related to birds have relatively longer humeri, but recently described forms with feathered forelimbs (*Caudipteryx*, *Microraptor*, *Sinornithosaurus*) are coproportional with many extant birds.

On the segmental ternary diagram (fig. 16.6E), birds form a tall cloud along the midline. The addition of phalanges and primary feathers to the carpometacarpus makes the distal segment the longest and again the most variable. As before, hummingbirds and swifts top the distribution, with wing chords as long as 86%. Below this, with handwings making up 74–79% are a storm petrel, a swallow, and two martins. A diversity of birds show a distal segment of ca. 70%, including pigeons, terns, caprimulgiforms (nighthawks and whip-poor-wills), parrots, and various passerines (songbirds). Most of these taxa are small and considered adept fliers; many are able to hover and/or feed on the wing. By contrast, birds with the relatively shortest wing chords (less than 50%; grebes, albatrosses, and pelicans) are larger and less maneuverable. All other birds in our sample have distal segment proportions of 50–70%, including *Archaeopteryx* (23%:20%:57%), *Confuciusornis* (16%:13%:71%), an Early Cretaceous bird from China, appears among relatively adept extant aerialists.

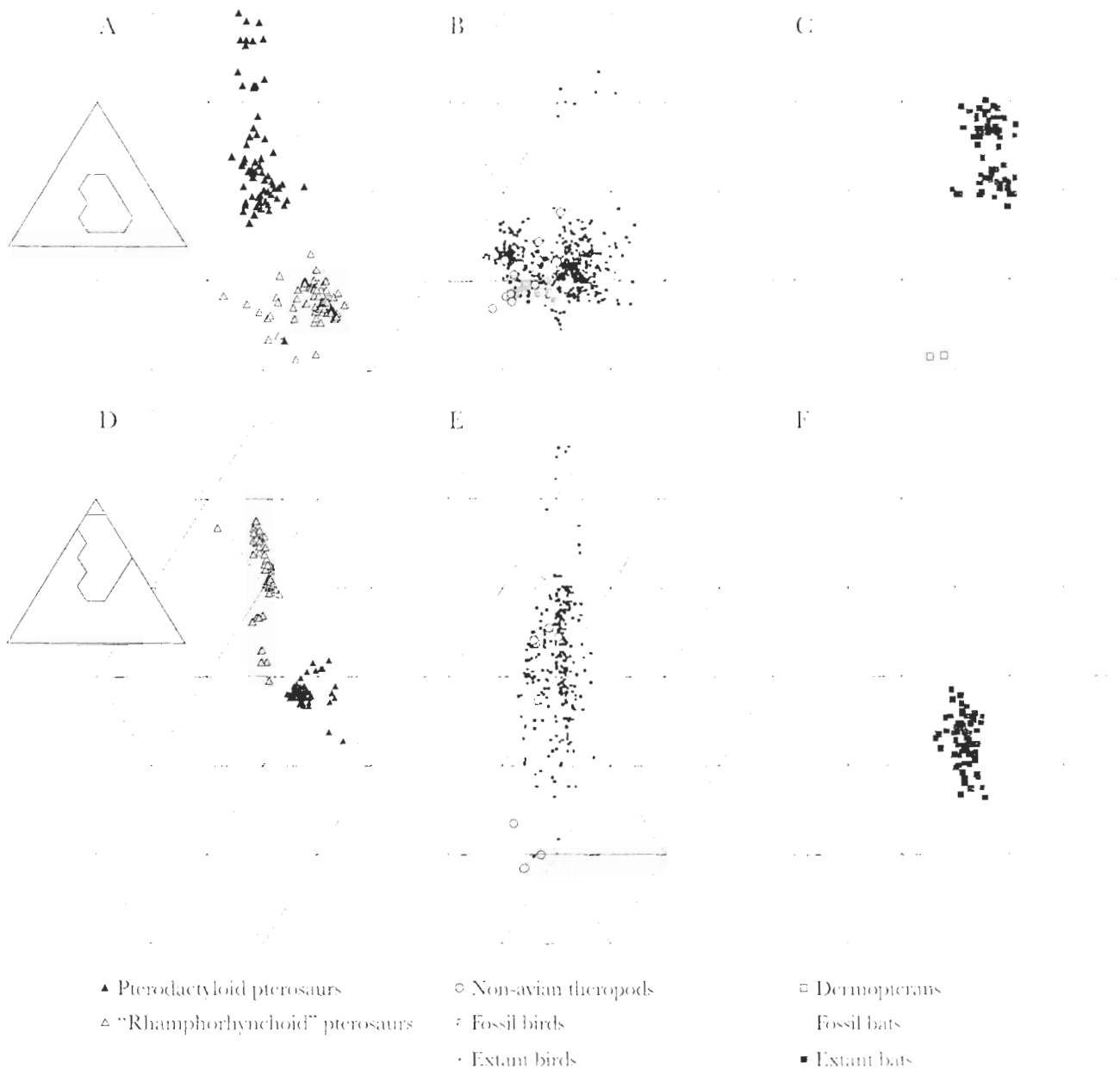


Figure 16-6 Within-group distribution of skeletal and segmental proportions (A–C) Skeletal proportions of pterosaurs, birds, and bats, respectively, are subdivided into phylogenetic groups (pterosaurs) and into extant and fossil taxa. Note the overlap between nonavian theropods and fossil and extant birds in (B). Dermopteran gliders, shown in (C), are widely separated from both fossil and extant bats. While no longer believed to be closely related to bats, dermopterans are still used as a proxy for the intermediate gliding morphology presumably present during chiropteran evolution. Similarly, (D–F) show segmental proportion in pterosaurs, birds, and bats. Note the distal elongation in "rhamphorhynchoid" pterosaurs, which reverses their position relative to pterodactyls (A). In (E), nonavian theropods are coproportional with extant birds.

Surprisingly, nonavian theropods with preserved feathers (two specimens each of *Caudipteryx* and *Microraptor*) have distal segment proportions of ca. 65%. Three genera of closely related nonavian theropods (*Bambiraptor*, *Deinonychus*, *Smornithosaurus*) are proportioned much like grebes despite lacking preserved hand feathers.

Bats

On the skeletal ternary graph (fig. 16.6C) bats form two closely spaced clusters with relatively low humeral percentages (20–30%) and average radial and metacarpal values compared with other fliers. The upper cloud contains mi-

crochiropterans having a third metacarpal relatively longer than the other bats in our sample. The lower cloud is primarily composed of megachiropterans, but also includes several microchiropterans. Interestingly, these genera are members of those microchiropteran families (Hipposideridae, Megadermatidae, Nycteridae, and Rhinolophidae) that Teeling and colleagues (2000, 2002) found to be more closely related to megabats in their phylogenetic analyses. Most fossil bats have proportions intermediate between these two clusters, although the extinct megabat, *Archaeopteropus*, is an exception with the lowest metacarpal percentage in the sample. Dermopteran gliders (genus *Cynocephalus*) exhibit some metacarpal elongation relative to arboreal rodents but fall short of chiropteran values.

The division among clusters is lost when the phalanges of digit III are added to the third metacarpal to yield a distal segment length (fig. 16.6F). Megabats and microbats form a single cloud with very little variation in segmental proportions. Bats with the longest distal segments (56–58%) are all phyllostomids (leaf-nosed bats). Fossil forms fall to the bottom of the distribution, with handwings of only 45–48%, although *Archaeopteropus* is slightly higher. Despite the relative homogeneity of bats in our segmental plot (fig. 16.6C), correlations between other aspects of wing morphology (wing loading, aspect ratio, tip shape) and flight style, feeding strategy, and ecology have been identified (see Norberg and Rayner 1987 and references therein).

Functional and Evolutionary Insights

Sampling Artifacts

How accurately do the skeletal and segmental ternary diagrams reflect disparity in wing proportions? One concern is sampling bias, which distorts the actual distribution of each clade to different degrees. Birds are best represented in terms of the number of specimens and genera, but we still only have data from a small fraction of the ca. 9,000 extant species. On the other hand, we specifically sought out unusual birds to try to delineate their distribution in morphospace as well as possible. We suspect that the large gap separating swifts and hummingbirds from other birds is not spanned by extant forms. Fossils could bridge these clusters, and extinct taxa could also expand the bird cloud in other directions. In contrast, few of the ca. 900 species of bats are in our plots, but it is unlikely that we have overlooked an extant form with wings grossly different than those sampled. Pterosaurs are a different case yet again. Our sample is surprisingly disparate given that the specimens are 210 to 65 million years old and extremely fragile. Therefore, it is quite possible that we

are missing a significant fraction of true pterosaur wing disparity.

Specializations

What factors might be responsible for differences in morphospace distribution among volant clades? One likely candidate is body size. Bats could be less disparate simply because of their smaller size range. Even the largest flying fox (1,400 g) is small compared to the largest extant flying bird (12,000 g) and minute compared to the largest pterosaur (Norberg 1981). What is striking, however, is the relative uniformity of bats compared to birds and pterosaurs of similar size.

Another obvious difference among vertebrate wings is the nature of the flight surface. One might predict that membranous wings would evolve to be more similar to each other than they are to feathered wings, but a tight clustering of bats and pterosaurs to the exclusion of birds is not obvious on either ternary graph. On the contrary, bats occupy relatively exclusive regions of skeletal morphospace, whereas some pterosaurs and birds converge on similar proportions. Segmental proportions are remarkably clade-specific, with little overlap among groups. Basal birds, bats, and pterosaurs had unique combinations of wing segment lengths. Flying descendants in each group pioneered new regions of segmental morphospace but without converging on common proportions (fig. 16.5). Why is there so little homoplasy in relative segment lengths among volant clades? Differences in handwing support may be partially responsible. The mechanical and aerodynamic properties of the flexible wing tips of bats might be different enough from the stiffer fourth digit of pterosaurs and primary feathers of birds to preclude similar proportions. Further quantitative analyses are warranted.

The forelimb's role in terrestrial locomotion is likely to be important as well. Although there has been controversy (e.g., Padian 1983a), pterosaurs appear to have been competent quadrupeds, contacting the substrate with digits I–III and the fourth metacarpophalangeal joint. Few bats are agile on the ground (but see Schutt et al. 1997), but movement on surfaces and through branches involves all four limbs. In contrast, birds walk, run, and hop exclusively on their hindlimbs. Could quadrupeds be restricted to distinct regions of morphospace because their forelimbs must function as both wings and legs? In pterosaurs the middle segment (radius + metacarpal IV) is always much longer than the proximal segment, ranging from 163 to 321% of humeral length. Unfortunately, we are unable to explain why walking would favor these proportions over those found in birds.

Alternatively, avian wings could be prohibited from colonizing pterosaur and bat segmental morphospace because of

bipedalism. When not in flight, birds compactly fold their wings by retracting the humerus against the body and flexing the elbow and wrist joints (fig. 16.2B). This Z-configuration allows the primary feathers to cross over the back, irrespective of their length. Folding is most effective when the proximal (humerus) and middle (radius) segments are of comparable length, so that upon elbow flexion the wrist lies adjacent to the shoulder (Middleton and Gatesy 2000). If the middle segment was exceedingly long, as in pterosaurs (figs. 16.1, 16.2A), the wrist would project forward beyond the contour of the thorax (up to two humeral lengths) and interfere with neck and head movement. Bird wings avoid this conflict by being centered along the midline of the segmental ternary (radius = humerus). Taxa in our sample have radii ranging from 72 to 148% of humeral length; more than half fall within $\pm 10\%$ of parity.

The relevance of folding for wing design in birds has been questioned. Workers consider the relative lengths of the proximal and middle wing segments to be dominated by selection for flapping flight (Dyke and Rayner 2001; Rayner and Dyke 2003; Nudds et al. 2004). These authors have found that the ratio of humeral length to radial or ulnar length, known as the brachial index (BI; Howell 1944), correlates with several measures of flight morphology (Rayner and Dyke 2003). In particular, bird wings with low BI tend to have low moments of inertia, which should reduce power requirements. But Rayner and Dyke (2003) were unable to conceive of selective pressures favoring aerial wings with high BI. To put avian BI values in perspective, intersegmental ratios can be superimposed on a ternary diagram. Two patterns are apparent. First, BI exhibits the least amount of variation of any such ratio among birds. BI only varies over a twofold range, whereas humerus/handwing and radius/handwing both vary by a factor of more than seven. Such dramatic differences in relative primary length likely have greater aerodynamic significance than do minor inequities in arm and forearm size. Second, birds have higher BI than all but a few bats and pterosaurs. Reducing BI likely benefits flight performance and cost, but for some reason birds have failed to realize the lower ratios achieved by other fliers. Folding is likely a contributing factor constraining birds to remain close to a BI of 1.

Additional support for this folding hypothesis may come from a correlation between feeding ecology and radio-humeral proportions. Birds that feed while their wings are folded should have radii short enough to prevent the wrist from obstructing the head. Indeed, taxa falling on the left side of the segmental ternary (radius < humerus) are almost entirely ground-dwelling galliforms (chickenlike birds) and various waterbirds (ducks, geese, swans, grebes, loons) that feed with their wings furled. Birds on the right side of the

ternary (radius > humerus) either catch their prey on the wing (swifts, swallows, flycatchers), are plunge-divers (kingfishers, pelicans), or have long necks (storks, vultures), thereby minimizing any reduction in cranial mobility. In bats the radius varies from 131 to 201% of humeral length, but the projecting wrist (figs. 16.1, 16.2C) remains clear of the head in aerial insectivores/nectivores or is used for climbing and manipulating in frugivores. Given their more extreme proportions, pterosaurs must have been even more prone to interference between the neck, head, and wing while not in flight.

Convergent Similarities

Based on our comparison of flying forms with their most recent common ancestor at the base of Amniota, several generalizations can be made about skeletal evolution. First, the origin of flight entailed not only hypertrophy of the pectoral appendage and girdle, but also a change in forelimb proportions. All clades have converged on elongated handwing segments, albeit by different solutions. Pterosaurs are the most dramatic in this respect; the four phalanges of digit IV account for up to 78% of total segment length. Most birds show the least derived skeletal proportions, presumably because feathers make up a significant portion of the handwing. Second, the number of independent components was reduced by loss and fusion. Bird wings are most derived, such that living taxa typically have only seven functional elements making up the wrist and hand skeleton compared to a primitive count of about two dozen. Other fliers are less reduced but still show digit loss and carpal fusion (pterosaurs) or radio-ulnar fusion (bats). Finally, each clade independently acquired humeral shapes to counter torsion. Bird and bat humeri experience high torsional and bending stresses during flight (Biewener et al. 1992; Swartz et al. 1992); pterosaurs are thought to have been similar. A structural solution to this type of loading, which can cause failure due to shear, is to increase bone diameter while keeping wall thickness low to minimize mass (Currey and Alexander 1985).

Comparisons to such a deep ancestor can be deceiving, however. Some of the differences between volant forms and the ancestral amniote condition are present in more closely related taxa that do not fly. For example, many features of extant birds traditionally interpreted as flight adaptations arose well before the origin of flight. Maniraptoran theropods possessed a tridactyl manus, feathers, fused clavicles, hollow bones, and carpal fusion before the origin of flight (although birds later fuse and reduce further). Unfortunately, the ancestry of bats and pterosaurs is more ambiguous, making the sequence of spectacular hypertrophic changes in their hand morphology less well clarified.

Appendix: Data Sources

Basal Tetrapods: Benton 1999; R. L. Carroll 1969a; Colbert and Kitching 1975; Heaton and Reisz 1980; Holmes 1984; Langston and Reisz 1981; Paton et al. 1999; Reisz et al. 1984; Sumida 1989; Watson 1957; T. E. White 1939.

Bats: Personal measurements (Museum of Comparative Zoology, Cambridge, MA); Habersetzer and Storch 1987; Jepsen 1970.

Birds: Personal measurements (Museum of Comparative Zoology, Cambridge, MA); Dong 1993; Lacasa Ruiz 1989; Middleton and Gatesy 2000; Perle et al. 1994; Sanz et al. 1995; Wellnhofer 1974a, 1988, 1993; Zhou 1992; Zhou and Zhang 2001, 2002a, 2002b.

Nonavian Theropods: Burnham et al. 2000; Hwang et al. 2002; Middleton and Gatesy 2000; Ostrom 1976c; Xu et al. 1999b, 2003; Zhou and Wang 2000; Zhou et al. 2000.

Pterosaurs: S. C. Bennett 2001a; Dalla Vecchia 1998; Jenkins et al. 2001; Unwin 1988b; X. Wang and Lü 2001; X. Wang et al. 2002; Wellnhofer 1970, 1974b, 1975a, 1991; Wild 1978, 1984a, 1984b.

All data are available from the authors.

Acknowledgments

We would like to thank Brian Hall for inviting us to write this chapter and for his patience while we completed it. For access to specimens in their care, we thank Douglas Causey and Judith Chupasko of the Museum of Comparative Zoology. This chapter benefited greatly from discussions with Sharon Swartz.