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An Introduction to Birds, the Geological Settings of Their Evolution, and the Avian Skeleton

What is a bird? Just by looking at the extant world, this question is easily answered: a bird is a bipedal, feathered animal without teeth, which, with very few exceptions, is capable of flight. These and numerous other avian characteristics were, however, sequentially acquired in the more than 160 million years of avian evolution. As a result, the distinction between birds and their closest relatives becomes more blurred the further one goes back in time.

With about 10,000 living species, birds are the second most species-rich group of extant vertebrates, outnumbered only by teleost fishes. Owing to the constraints of their aerial way of life, most extant birds have quite a uniform appearance. Whereas the morphological diversity of mammals spans extremes like bats and whales, all present-day birds have two wings, two legs, and an edentulous beak, with most major external differences concerning plumage traits, neck and limb proportions, as well as beak shapes. This alikeness of bird shapes notwithstanding, their skeletons show a high diversity of morphological details. In this chapter, the reader is introduced to some of the main features of the avian skeleton. In addition, general terms and the geological setting of avian evolution are briefly outlined to aid understanding of the subsequent accounts.

Birds are Evolutionarily Nested within Theropod Dinosaurs

An understanding of avian evolution hinges on a robust phylogenetic framework, with a knowledge of the interrelationships of the studied groups being central to many evolutionary and paleobiological questions arising from the fossil record. The most rigorous method of reconstructing evolutionary trees is called **phylogenetic systematics**, or cladistics, and aims at identification of **monophyletic** groups or **clades** (readers who are not acquainted with phylogenetic terminology are referred to Figure 1.1 and the glossary at the end of this book, which explains words highlighted in the text). Organisms can be remarkably different from their closest relatives and the results of phylogenetic reconstructions

are sometimes counterintuitive. Overall similarities may be misleading, because they are often based on the retention of primitive features (**plesiomorphies**) that were inherited from a common ancestor. Closely related organisms, on the other hand, can become profoundly different if they are on disparate evolutionary trajectories.

Birds are one of those animal groups that underwent particularly pronounced morphological transformations in their evolutionary history, and as a result their anatomy strongly departs from that of their closest living relatives. Even so, unanimous consensus exists that birds belong to the Archosauria. This clade also includes crocodylians and all non-avian dinosaurs and is characterized by a number of **derived characters (apomorphies)**, such as teeth sitting in sockets of the jaw bones, a skull with an opening (antorbital

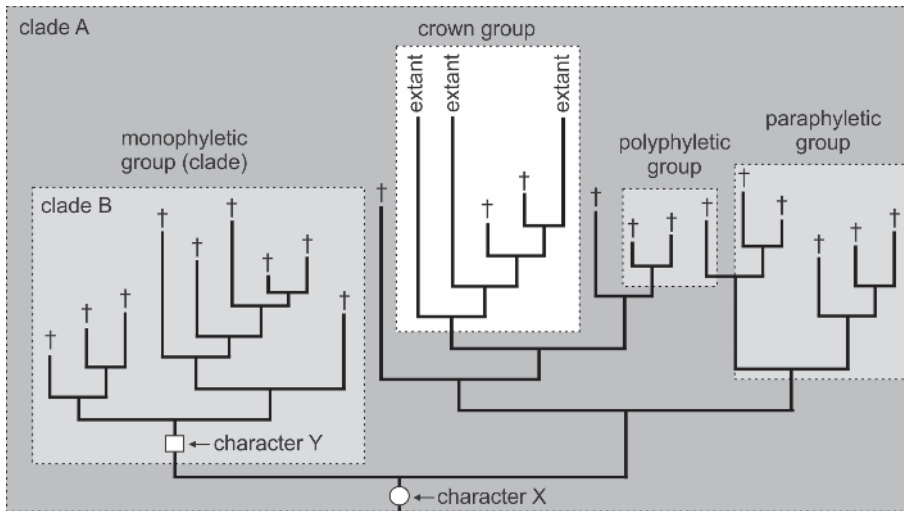


Figure 1.1 Illustration of some general phylogenetic terms used in this book. Phylogenetic systematics aims at identification of monophyletic groups (clades), which include an ancestral species and all of its descendants and are characterized by shared derived characters (apomorphies). Depicted is a hypothetical clade A with extant and extinct species, the latter being denoted by daggers. Character X is an apomorphy of this clade, whereas character Y represents an apomorphy of the subclade B. Groups are polyphyletic if they consist of only distantly related taxa, and paraphyletic if they do not include all of the taxa that descended from their last common ancestor. The white field marks the crown group of clade A, whereas all taxa in the dark and light gray areas are stem group representatives of this clade.

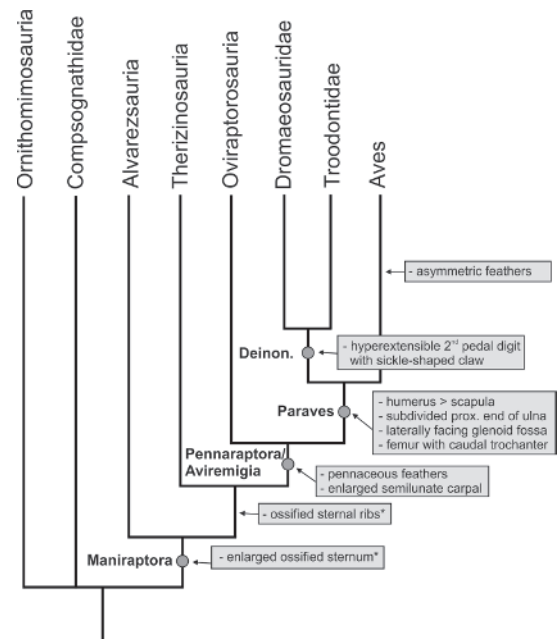
fenestra) between the orbits and the nostrils, and a four-chambered heart.

In the 19th century some scientists already assumed that the closest archosaurian relatives of birds are to be found among bipedal theropod dinosaurs. In its modern form, this hypothesis goes back to Ostrom (1976), who proposed an avian origin from one particular theropod clade, the Coelurosauria. At one time vigorously contested, a theropod ancestry for birds is now widely accepted. For space constraints and because an extensive literature already exists, these largely settled debates are not reviewed here (see, e.g., Prum 2002; Chiappe 2007; Makovicky and Zanno 2011; Xu et al. 2014).

Likewise, it is now generally appreciated that, within coelurosaurs, birds belong to the Maniraptora, which also include dromaeosaurs, troodontids, oviraptorosaurs, and a few other coelurosaurian theropods, such as ornithomimosaurs and therizinosaurs (Figure 1.2). Aside from features also present in some more distantly related dinosaurs (e.g., bipedal locomotion and a highly pneumatized skeleton), maniraptoran theropods are characterized by greatly elongated hands with only three fingers, a semilunate carpal bone, a bowed ulna, and thin radius, as well as an avian-like eggshell structure (Gauthier 1986; Makovicky and Zanno 2011). Most current phylogenetic analyses recognize oviraptorosaurs, dromaeosaurs, and troodontids as the closest avian relatives. Oviraptorosaurs are placed outside a clade formed by dromaeosaurs, troodontids, and birds for which the term Paraves was introduced (e.g., Makovicky and Zanno 2011; Turner et al. 2012).

A clade including oviraptorosaurs, dromaeosaurs, troodontids, and birds is robustly supported in most analyses, but, as will be detailed later, the jury may still be out on the exact interrelationships between these groups. Not only do various analyses show conflicting results, but some new

Figure 1.2 Phylogenetic interrelationships of birds and their closest theropod relatives, with some key apomorphies characterizing major groups (after Makovicky and Zanno 2011; Turner et al. 2012). The asterisked characters are absent in *Archaeopteryx* and the Troodontidae.



findings from the Early Cretaceous of China exhibit unexpected character mosaics, which challenge current phylogenetic hypotheses.

Aves, Avialae, or what constitutes a “bird”

Extant birds are classified in the **taxon** Aves, which is one of the traditional higher categories of vertebrates. If fossils are also considered, the content of Aves is a matter of considerable debate and depends on the underlying definition, which varies among current authors.

In phylogenetic discussions of groups, which include both fossil and extant species, it is important to distinguish between the **stem group** of a certain taxon and its **stem group** (Figure 1.1). At times when only a few Mesozoic birds were known, Aves was defined as the least inclusive clade comprising the

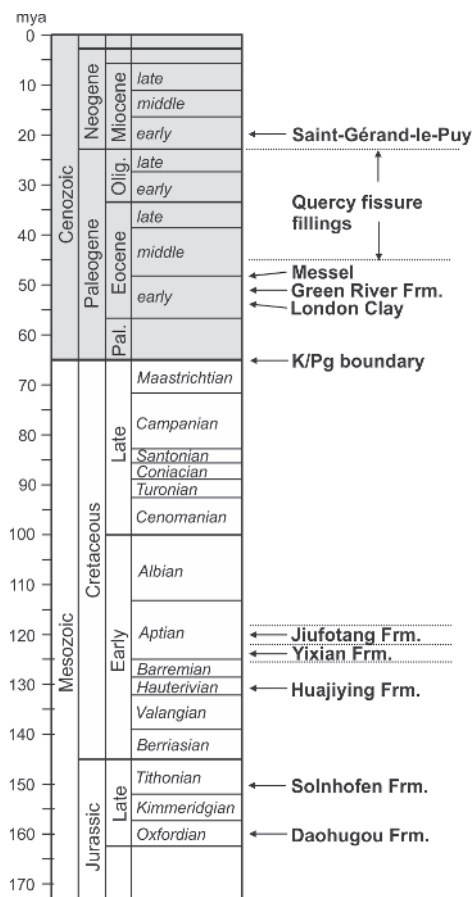
earliest known bird, *Archaeopteryx*, as well as all extant species (i.e., the crown group), which were designated Neornithes. This terminology is still used by many authors and is also employed here. Following Gauthier (1986), who restricted the use of Aves to the crown group, the clade including *Archaeopteryx* and crown group birds is nowadays often termed “Avialae.” This renders the well-established term Neornithes redundant and conflicts with common practice in paleontology, where crown group taxa are expanded to encompass fossil stem group representatives (e.g., in the case of Equidae, the clade including fossil and extant horses, or *Homo*, the taxonomic category for archaic and modern humans).

Restriction of the term Aves to the crown group would furthermore lead to the awkward classification of all Mesozoic birds outside the crown group as “non-avian avialans,” no matter how similar to modern birds these may be, and would result in a discrepancy between the contents of the terms “avian” and “bird-like.” As this is more counterintuitive than recognizing the avian affinities of aberrant fossil stem group taxa, Aves is used for the clade including *Archaeopteryx* and extant birds throughout this book.

The Geological Settings of Avian Evolution in a Nutshell

The known history of birds spans more than 160 million years, from the Late Jurassic until now. Avian evolution therefore extended over two geological eras, the Mesozoic and the Cenozoic, which showed profound differences in their paleogeographic, paleoenvironmental, and climatic regimes. Most readers of this book will probably have a basic acquaintance with these facts, so only some of the major geological settings are briefly summarized in the following (Figure 1.3).

Figure 1.3 Time chart showing geological periods relevant for avian evolution and the stratigraphic position of some important fossil localities.



Geological eras are subdivided into periods, epochs, and stages. The **Mesozoic** era includes three periods, of which only the last two, the Jurassic and the Cretaceous, yielded avian fossils, with controversial reports of a Triassic “*Protoavis*” (Chatterjee 2015) being dismissed by most current researchers. All of the few Jurassic avian or avian-like fossils stem from the latest epoch of this period; that is, the Late Jurassic. Until recently, Jurassic birds were solely represented by the *Archaeopteryx* specimens from the Solnhofen limestone in southern Germany, which was deposited in the Tithonian

stage, 150 million years ago (mya). In the past decade, however, a diverse array of somewhat earlier avian-like theropods was described from the Tiaojishan Formation of the Daohugou Biota in northeastern China, which stems from the Oxfordian stage of the Late Jurassic and has an estimated age of 160 million years (Liu et al. 2012; Sullivan et al. 2014).

Virtually all other early avians, however, are from Cretaceous deposits. The Cretaceous period lasted from 145–66 mya and includes two epochs, the Early and Late Cretaceous, each of which is further divided into several stages (Figure 1.3). It is beyond the scope of this brief account to review all localities that yielded Cretaceous avian fossils. The exceptionally fossil-rich Jehol Biota in northeastern China, however, is of particular relevance for avian evolution, and has a quite complex stratigraphy that is briefly outlined to aid understanding of the geological context of the finds discussed later.

The fossiliferous strata of the Early Cretaceous, lacustrine sediments of the Jehol Biota cover a large area in Inner Mongolia, Hebei, and Liaoning provinces. They can be divided into three stratigraphic units, which altogether span some 10 million years (Pan et al. 2013; Zhou 2014). The earliest of these is represented by the Huajiying (“Dabeigou”) Formation (130.7 mya), which is mainly exposed in Hebei Province. Most fossils of the Jehol Biota, however, stem from the Barremian to early Aptian (125–122 mya) Yixian Formation and from the Aptian (120 mya) Jiufotang Formation. The Jehol Biota not only yielded great numbers of early avian taxa, but also numerous well-preserved fossils of small non-avian maniraptorans, which shed further light on the dinosaurian ancestry of birds.

The end of the Mesozoic is characterized by large-scale extinction events at the Cretaceous/Paleogene (K/Pg) boundary,

which involved both marine and terrestrial organisms and ushered in the **Cenozoic**. This era falls into two major periods (Figure 1.3), the **Paleogene**, which includes the Paleocene, Eocene, and Oligocene epochs, and the **Neogene**, with the Miocene and Pliocene epochs. The latest Cenozoic period is the Quaternary, which encompasses the Pleistocene and Holocene epochs.

Numerous Cenozoic fossil sites yielded avian fossils, but some localities stand out with regard to the number of bird fossils found, the quality of their preservation, and the insights into avian evolution that can be gained from these specimens. Of particular significance are several Eocene sites, which yielded many of the fossils mentioned in this book. Among the most important of these are the marine deposits of the early Eocene (53 mya) London Clay in England, as well as the lacustrine sediments of the early Eocene (51 mya) Green River Formation in North America, and the slightly younger early Eocene (48 mya) Messel oil shale in Germany (until recently, this latter site was considered to be of middle Eocene age, but see Lenz et al. 2015). Many Paleogene bird fossils were also retrieved from karstic fissure fillings in the Quercy region in France, which cover a long temporal range, from the middle Eocene to the late Oligocene, and yielded thousands of avian bones. As early as the 19th century, numerous early Miocene avian fossils were furthermore described from lacustrine deposits of the Saint-Gérard-le-Puy area in France, one of the classical localities for Neogene birds.

Avian evolution was accompanied by the final break-up of the southern supercontinent Gondwana, which involved three major paleogeographic events. The earliest of these was the split of South America and Africa in the Early Cretaceous, which led to the opening of the South Atlantic. Australia and South America separated from Antarctica in the latest Cretaceous and late

Eocene, respectively. In the early Cenozoic, finally, the North Atlantic opened between Europe and North America. All of these geographic events seem to have had impacts on marine and atmospheric circulation systems, which in turn affected the prevailing climatic regimes (e.g., Smith et al. 1994; Haug and Tiedemann 1998; Scher and Martin 2006).

The global average temperatures in the Mesozoic were much higher than today. Although they decreased towards the Cenozoic, global temperatures in the earliest Cenozoic were still high, and subtropical vegetation flourished even in northern latitudes. After the Thermal Maximum at the Paleocene–Eocene boundary, global climatic cooling commenced in the Oligocene, but was interrupted by a warm period during the middle Miocene Climatic Optimum, some 15–17 mya (e.g., Zachos et al. 2001; Jenkyns 2003).

As will be detailed in later chapters, major biotic events that may have influenced avian evolution include the Cretaceous radiation of angiosperm (flowering) plants (e.g., Friis et al. 2011), as well as the rise of placental mammals, with the emergence and initial diversification of mammalian crown group taxa showing a broad temporal coincidence with avian evolution. For various avian groups, broad-scale Cenozoic habitat changes were also of great significance, which is especially true for the spread of open grasslands towards the mid-Cenozoic (e.g., Jacobs et al. 1999).

Characteristics of the Avian Skeleton

Avian evolution was characterized by the formation of compound bones through the fusion of individual skeletal elements, mainly in the skull and **distal** limb bones. Co-ossification of the limb elements probably

went in parallel with another avian trait, the reduction of the distal limb muscles. Unlike in other tetrapods, the movements of the hand and foot of extant birds are largely due to the action of tendons of muscles that are situated near the body center, and in the course of avian evolution the muscle masses therefore came close to the center of gravity of these flying animals.

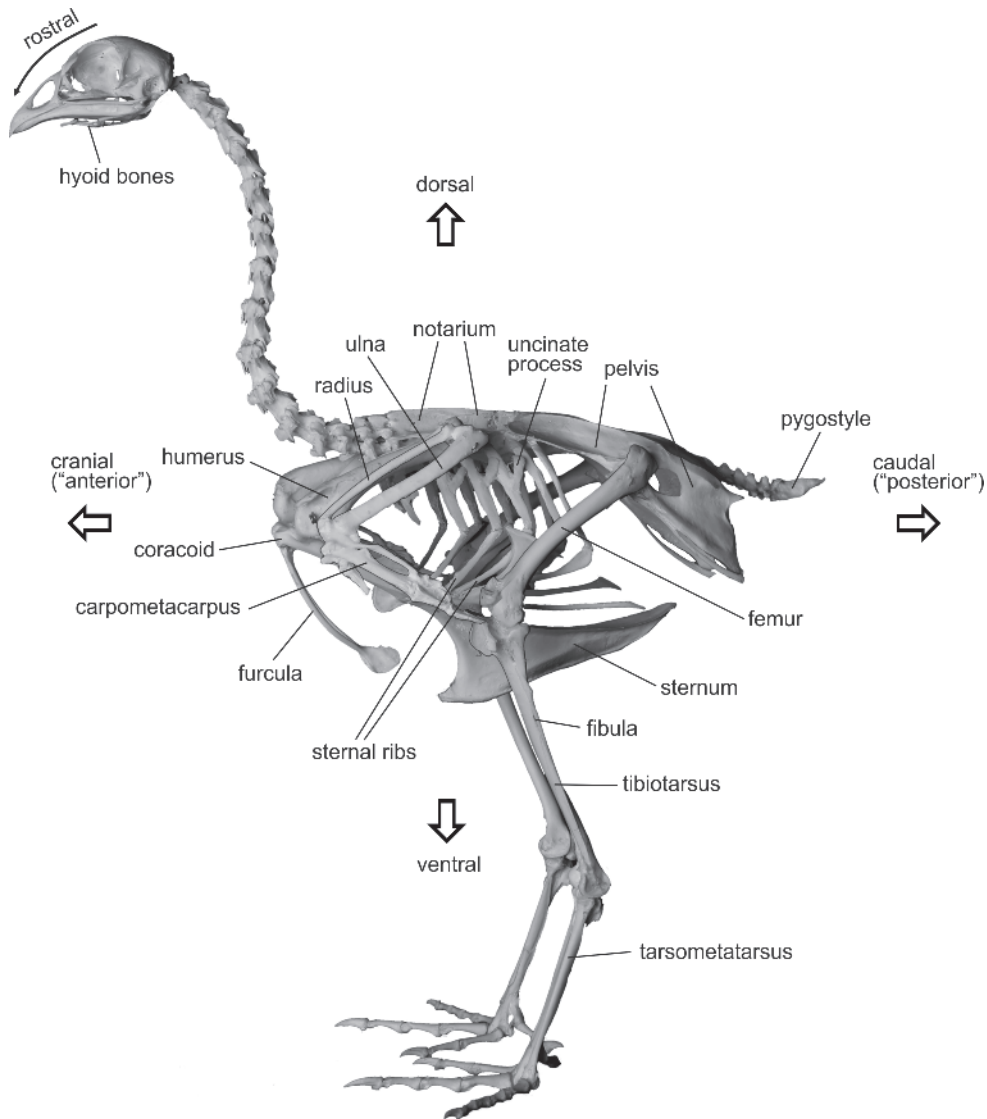
The aerodynamic demands of flight led to numerous other changes in the skeleton of birds, which set these animals apart from other vertebrates. In the following account of avian osteology, a focus was put on the characteristics of the skeleton of modern (neornithine) birds (Figure 1.4). The morphological diversity seen in their Mesozoic ancestors, as well as some of the key transformations that took place in the avian skeleton, are outlined in later sections, after the various fossil groups are introduced.

The avian skull

The skull of birds can be broadly divided into three units: the snout, the neurocranium, and the lower jaws (mandibles). The snout is formed by the paired nasal, maxillary, and praemaxillary bones. It is edentulous in neornithine birds and the bones are covered with a horny rhamphotheca. Upper and lower jaws therefore form a beak, which shows a great diversity of shapes within and across different neornithine taxa.

Neornithine birds have a kinetic skull, in which the beak is movable against the neurocranium. This movability is enabled by a flexible, sheet-like connection with the neurocranium, the nasofrontal hinge. A critical role in avian skull kinetics is fulfilled by the quadrate, which articulates with the jugal bar and the pterygoid and pushes these elements rostrally (i.e., towards the bill tip), so that the upper beak is uplifted. There are two different kinds of kinesis in Neornithes: In the prokinetic skull the beak does not change its shape, whereas

Figure 1.4 Skeleton of a domestic fowl (*Gallus*). Major bones and anatomical directions are labeled.

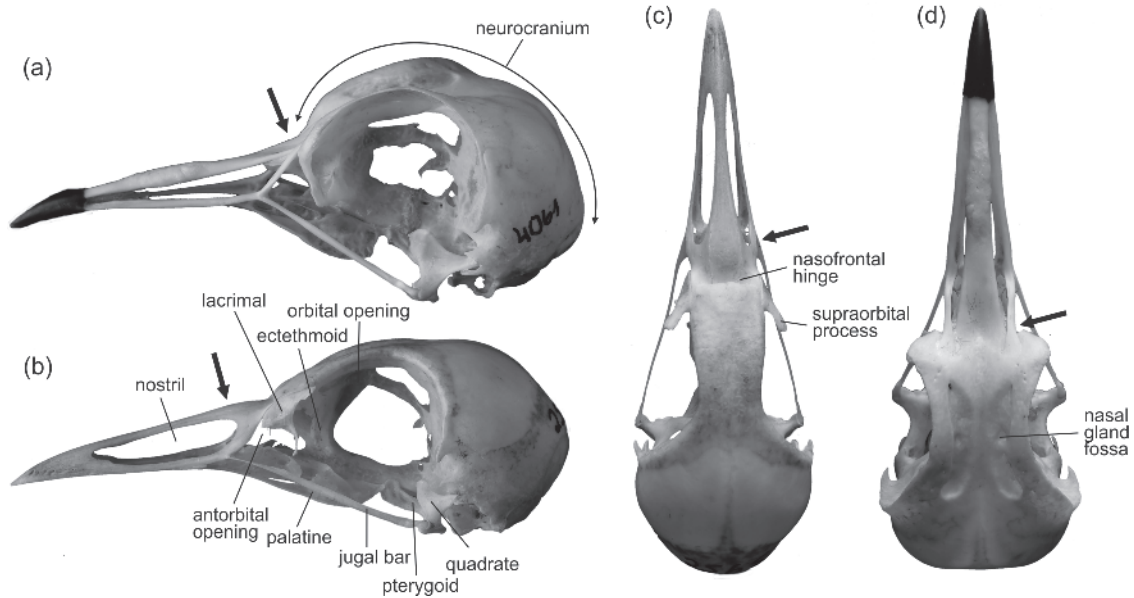


the rynchokinetic skull exhibits additional bending zones within the upper beak.

Two basic types of nostril shapes can be distinguished in neornithine birds. The most widespread and presumably primitive condition is characteristic for the holorrhinal beak, where the nostrils are ovate openings. In the schizorrhinal beak, by contrast, the

nostrils are elongated and have slit-like caudal ends, which reach beyond the nasofrontal hinge, the transition zone between beak and neurocranium (Figure 1.5). The schizorrhinal condition increases the flexibility of the tip of the upper beak and is often found in particularly long-beaked species, which probe substrate for food.

Figure 1.5 Skulls of (a, d) a lapwing (*Vanellus*, Charadriidae) and (b, c) a moorhen (*Gallinula*, Rallidae) in lateral (left) and dorsal (right) views, with some major anatomical features. The arrows identify the caudal ends of the nostrils of the holorhinal moorhen and the schizorhinal lapwing. Not to scale.



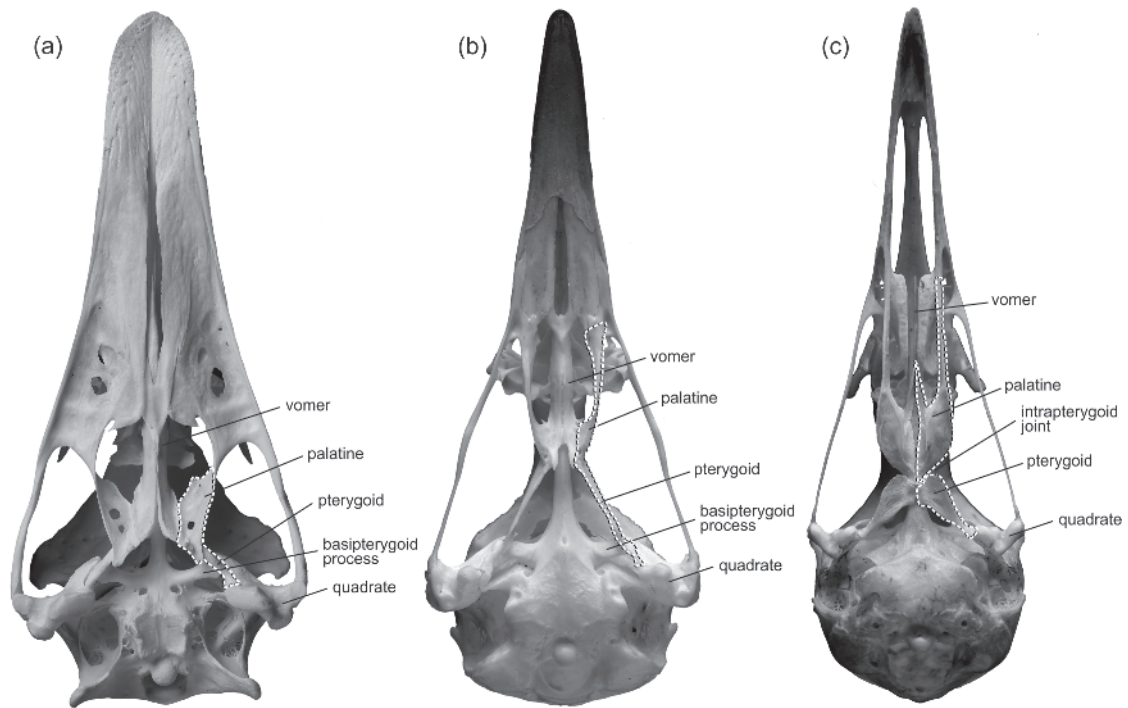
Besides the praemaxillary and maxillary bones, the osseous palate of birds is mainly formed by five bones: the vomer and the paired pterygoids and palatines (Figure 1.6). Anatomists of the 19th century noted that Neornithes can be divided into two major groups based on the structure of their palatal bones, which were termed Palaeognathae (“old jaws”) and Neognathae (“new jaws”). Apart from differences in the proportions and relative positions of the involved bones, one of the major characteristics of the palaeognathous palate is a fusion of the pterygoids and palatines, which form a rigid unit and articulate with the braincase via well-developed basiptyergoid processes. The neognathous palate, by contrast, exhibits a movable joint between pterygoid and palatine, which allows a greater mobility of the upper beak; basiptyergoid processes are often reduced in neognathous birds (Figure 1.6).

The avian lower jaws, or mandibles, are composed of several bones, of which the dentaries bear teeth in many Mesozoic non-neornithine birds. In all Neornithes, the tips of the mandibles are fused and form an ossified mandibular symphysis.

Pectoral girdle and sternum

The avian pectoral girdle consists of six bones, the paired coracoids and scapulae, as well as the furcula and the sternum. These bones anchor the wing to the trunk, provide attachment sites of the flight muscles, and act as pulleys for the tendons of some of them. The coracoids articulate with the sternum, whereas the blade-like scapulae are situated laterodorsal of the ribcage. Where both bones meet, they form the glenoid fossa (see Figure 1.10), with which the **proximal** end of the humerus articulates. As will be detailed in Chapter 3, the position and orientation of this fossa changed in the course of

Figure 1.6 Palates of (a) a palaeognathous nandu (*Rhea*, Rheiformes), (b) a palaeognathous tinamou (*Rhynchotus*, Tinamiformes), and (c) a neognathous lapwing (*Vanellus*, Charadriiformes). In each image the left palate is highlighted by dotted lines. In palaeognathous birds palatine and pterygoid are fused, whereas both bones are separated by an intrapterygoid joint in neognathous birds. Not to scale.

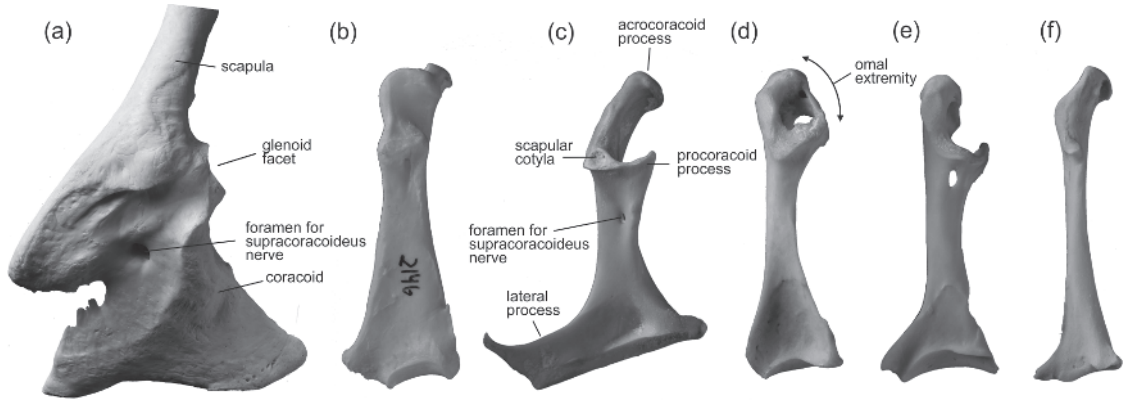


avian evolution, during the transition from gliding to flapping flight.

Initially, the coracoid of birds was a squarish bone, which closely resembled the coracoid of non-avian theropods. In the evolution towards the crown group, the bone became elongated and strut-like, although it regained a squarish shape in some palaeognathous birds (Figure 1.7). The coracoid has a broad sternal end, which articulates with the sternum. The opposite (upper) end of the bone is formed by the acrocoracoid process. Unlike in more basal avians, this upper end of the neornithine coracoid exhibits a well-developed procoracoid process, which projects medially from the shaft (Figure 1.7). Together with the cranial end of the scapula and the dorsal end of the

furcula, the procoracoid process contributes to the formation of the “triosseal canal,” through which passes the tendon of the supracoracoideus muscle, the main elevator of the wing. In the neornithine **stem species**, the articulation facet of the coracoid for the scapula was cup-like, thereby forming a so-called scapular cotyla (Figure 1.7). In many extant taxa, however, it is only a shallow facet. This loss of a cup-like articulation facet occurred multiple times independently and is well documented in, for example, galliform, procellariiform, and psittaciform birds (Mourer-Chauviré 1992a; Mayr et al. 2010; Mayr and Smith 2012a). The functional significance of this character variability has not yet been studied. However, there appears to be a correlation with the shape

Figure 1.7 Coracoids of selected neornithine birds, to illustrate different morphologies of this bone and some major anatomical features. (a) Cassowary (*Casuarius*, Casuariiformes), (b) tinamou (*Tinamus*, Tinamiformes), (c) petrel (*Pterodroma*, Procellariiformes), (d) seriema (*Cariama*, Cariamiformes), (e) owl (*Strix*, Strigiformes), (f) woodpecker (*Dryocopus*, Piciformes). In (a) scapula and coracoid are co-ossified and form a scapulocoracoid. Not to scale.



of the furcula, and taxa with a cup-like articulation facet usually feature a robust furcula. Bird groups with a shallow scapular articulation facet, by contrast, tend to have a furcula with narrow arms. The coracoid of many birds is pierced by a foramen for the supratoracoideus nerve. This foramen is primitively present in Neornithes, but it is lost in a large number of taxa, especially those with slender and strut-like coracoids. In flightless birds, especially species of the Palaeognathae, coracoid and scapula sometimes fuse to form a single bone, the scapulocoracoid.

The furcula is formed by the fused clavicles and primitively was a boomerang-shaped and robust bone, which may have contributed to the attachment of some pectoral muscles in early avians without an ossified sternum. In more advanced birds, the bone primarily acts as a spring and stores kinetic energy of the flight strokes. The sternal end often bears a ventral process, the furcular apophysis, which articulates with the tip of the sternal keel in some long-winged taxa. In a few birds,

the sternal end of the furcula is reduced, so that its arms are no longer connected.

The sternum of most neornithine birds bears a deep midline keel, which increases the attachment area of the greatly enlarged pectoral muscles, and which is one of the prerequisites of powered flapping flight. A keeled sternum distinguishes extant birds from all other living vertebrates. Paired ossified sternal plates can, however, already be traced back to non-avian theropods, in some of which they are even fused to form a single sternal plate. The sternal keel is lost or greatly reduced in a number of flightless taxa, in particular among palaeognathous birds. The proportions of the neornithine sternum vary greatly, and a long sternum is, for example, found in diving birds, such as loons or auks, whereas it tends to be short in soaring birds, such as frigatebirds. The caudal margin of the bone can be entire and straight, but usually it bears one or two pairs of incisions of varying depth, which may be closed to form fenestrae. These incisions are particularly marked in taxa that are capable

of powerful burst take-offs, such as tinamous (Tinamiformes) and landfowl (Galliformes), whereas they are shallow in soaring birds.

The forelimb skeleton and the identity of the avian wing digits

The wing skeleton of birds is composed of three sections: a proximal one formed by the humerus, a midsection consisting of ulna and radius, and a distal hand section with the three digits, which are fused and – except for the central one – greatly reduced in neornithine birds.

The neornithine humerus shows a considerable variation in shape and proportions, being very long in soaring birds and greatly shortened in the stiff-winged swifts (Apodiformes; Figure 1.8). The tendons of various major wing muscles insert on the bone, and differences in the position and development of the tubercles, processes, and fossae at their attachment areas provide characters of phylogenetic relevance. The proximal humerus end bears the deltopectoral crest, on which the pectoral muscles insert. The

humerus of most Neornithes is pneumatized and exhibits openings for the entrance of air sacs into the hollow bone lumen. These foramina are situated on the bottom of a “pneumotricipital” fossa (Figure 1.8), which derives its name from the circumstance that it does not only receive air sac diverticula that are part of the complex avian lung system (e.g., Proctor and Lynch 1993), but also serves as an attachment site for the tendons of so-called tricipital pectoral muscles. On the distal end of the humerus, there are two condyles for the articulation of the bone with ulna (ventral condyle) and radius (dorsal condyle).

The ulna of birds primitively does not exceed the humerus in length, but the relative lengths of these bones are highly variable in Neornithes, with the ulna being much longer than the humerus in many long-winged birds and greatly shortened in, for example, some wing-propelled divers. The ulna serves for the attachment of the **secondary feathers**, and in some taxa the shaft of the bone forms distinctly raised

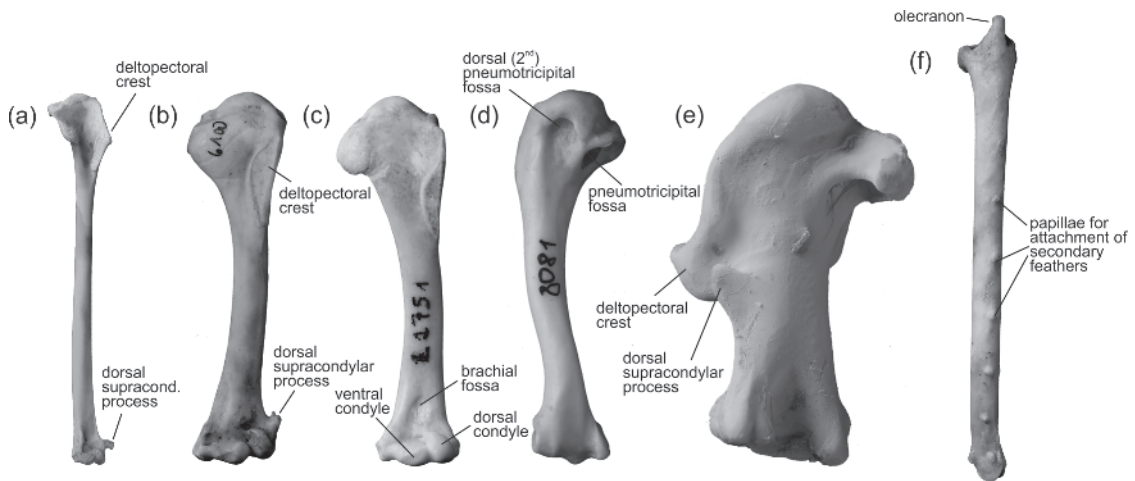


Figure 1.8 (a–e) Humeri of selected neornithine birds. (a) Albatross (*Diomedea*, Diomedidae), (b) crow (*Corvus*, Passeriformes), (c) trogon (*Pharomachrus*, Trogoniformes), (d) partridge (*Arborophila*, Galliformes), (e) swift (*Apus*, Apodiformes). (f) Ulna of *Corvus* in cranial view. Not to scale (a–c: cranial view, d, e: caudal view).

papillae at the attachment sites of these feathers (Figure 1.8).

Birds are characterized by a skeletomuscular mechanism, which couples the elbow and wrist joints during wing movements. This “drawing parallel system,” which is also known as “automatic extension” of the wing, results in a synchronization of the extension and flexion of the elbow and wrist joints, whereby the hand section is drawn in parallel to the humerus during wing movements.

The hand of the avian ancestor had three fingers, which consisted of a metacarpal bone and one, two, and three additional phalanges, respectively. Each of these fingers furthermore bore well-developed claws. There has been, and still is, much debate on the identity of the three fingers of birds (Feduccia 2012; Xu et al. 2014). Dinosaurs primitively had a hand with five fingers, and in phylogenetically basal theropods, such as the late Triassic *Herrerasaurus* and the Early Jurassic *Heterodontosaurus*, the fourth and fifth manual digits are reduced. This suggests that the digits of later three-fingered non-avian theropods, as well as those of birds, are the first, second, and third, with the fourth and fifth digits having been lost. Gene expression patterns also indicate that the three avian digits are the first to third ones (Z. Wang et al. 2011; Xu et al. 2014). From studies of the embryonic development of the hand of extant birds, however, it was concluded that the avian digits are the second, third, and fourth ones, and that the two outermost digits were lost (see Feduccia 2012). Developmental shifts in digital identity were proposed to explain this mismatch, and it was hypothesized that the embryonic tissue of digits 2–4 develops into digits 1–3 of the adults (“frameshift hypothesis”; e.g., Bever et al. 2011).

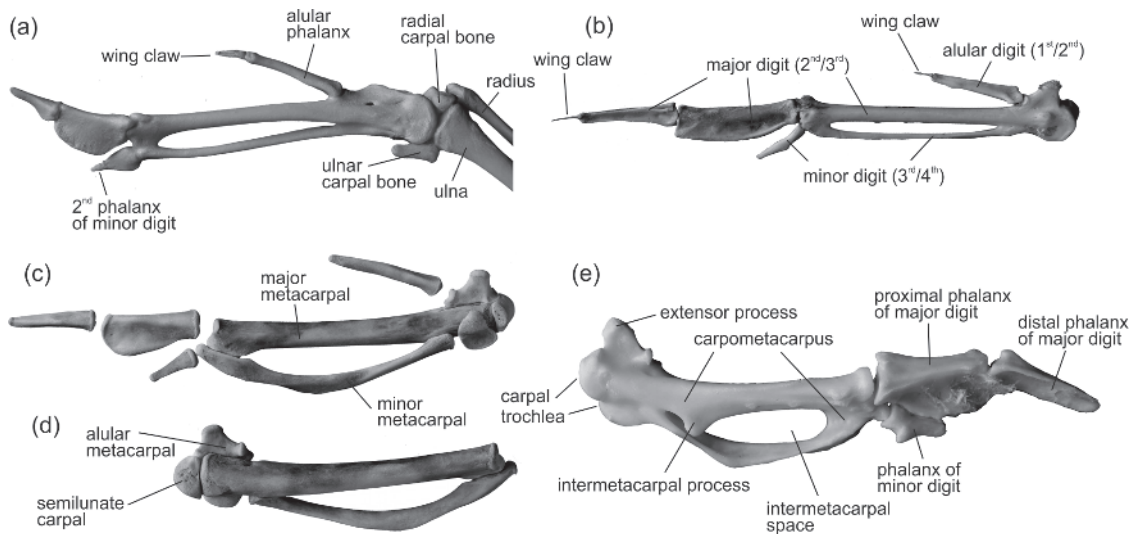
Resolving the issue of digital homology in birds and non-avian theropods is complicated by the fact that the adult morphology of fossil

taxa is compared with **ontogenetic** data from neornithine birds (Xu et al. 2014). Moreover, the two outermost manual digits – that is, the first and the fifth – are reduced in a least one theropod, the Late Jurassic ceratosaur *Limusaurus* (Xu et al. 2009a). Although this taxon is probably too distantly related to birds to bear directly on the identity of digital homology in birds and non-avian theropods, it indicates that there was some **homoplasy** in the reduction of the forelimb digits of theropods. In any case, the hand of *Archaeopteryx* is so similar to that of closely related non-avian theropods that there can be little doubt that the fingers of *Archaeopteryx* are **homologous** to those of, for instance, dromaeosaurs, irrespective of the exact digital identity (Zhou 2004). To account for the uncertainties in digital homology, the fingers of birds and closely related Mesozoic taxa are here termed alular (1st/2nd), major (2nd/3rd), and minor (3rd/4th) digits (Figure 1.9).

Neornithine birds have two free carpal (wrist) bones, which are traditionally considered to be the ulnar and radial carpals (see, however, Botelho et al. 2014a for ontogenetic data that challenge these identifications). Both carpals exhibit complex shapes and guide the movements of the hand. Two further carpal bones are fused with the metacarpals and contribute to the carpal **trochlea** of the carpometacarpus (Figure 1.9). One of these distal carpal bones, the semilunate carpal, is of particular phylogenetic interest, because it represents a key apomorphy (i.e., one of the defining characters) of maniraptoran theropods (e.g., Makovicky and Zanno 2011).

The carpometacarpus is one of the most characteristic avian compound bones (Figure 1.9). Its main portion is formed by the proximally and distally conjoined metacarpals of the major and minor digits, which delimit the intermetacarpal space. The carpometacarpus is the main attachment site for the proximal **primary feathers**. In

Figure 1.9 Major features of the hand skeleton of neornithine birds. (a) Palaeognathous nandu (*Rhea*, Rheiformes), (b) goose (*Anser*, Anatidae), (c, d) juvenile galliform currasow (*Crax*, Cracidae), (e) adult phasianid galliform (*Rollulus*, Phasianidae). Note the presence of wing claws in (a) and (b). All bones are from the right side and not to scale (a–c: ventral view; d, e: dorsal view).



some birds the major metacarpal forms a distinct intermetacarpal process (Figure 1.9), which increases the leverage of a muscle flexing the hand, and which occurs in birds exposed to high aerodynamic forces on the hand section of the wing (Stegmann 1965).

The metacarpal of the alular digit is co-ossified with the carpal trochlea and bears the cranially directed extensor process, on which inserts the tendon of a muscle that extends the wing during flight stroke. The alular digit itself serves for the attachment of the feathers that form the alula. This separate “winglet” constitutes an important device to prevent stalling of the airflow, if the wings are held under a high angle of attack, especially during start and landing. Various groups retain vestigial wing claws on the alular and major digits, which sometimes reach a fair size (Figure 1.9). Whereas the alular and major digits of neornithine birds therefore still show the original phalangeal counts in some taxa, the minor digit is always greatly

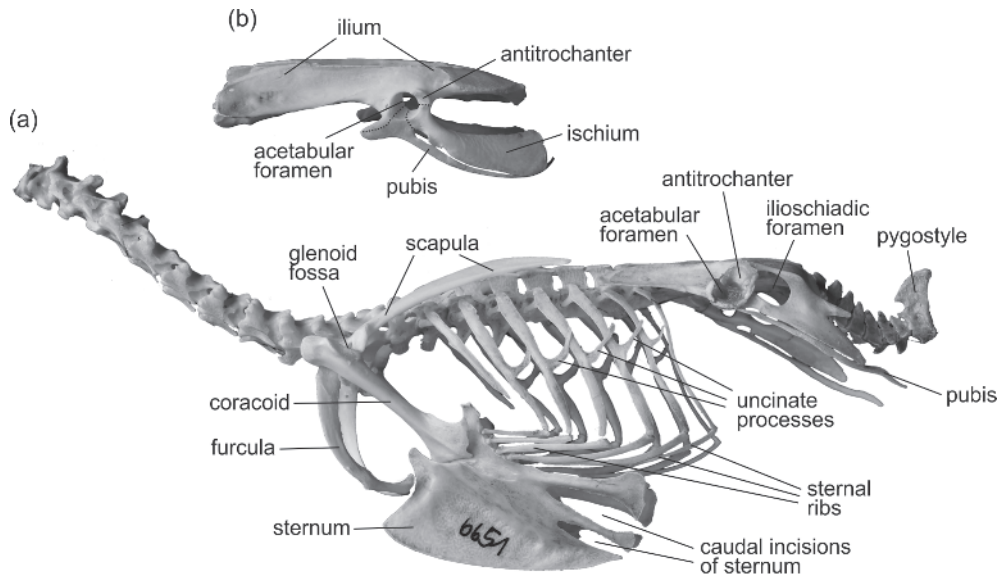
reduced and is usually composed of only a single free phalanx, rather than three as in the avian ancestor.

The axial skeleton, pelvic girdle, and tail

The ribs of most neornithine birds are connected by transverse processes, which provide muscle attachment sites and play an important role in respiration. The length of these “uncinate processes” (Figure 1.10) also appears to be correlated to locomotory habits and they are short in terrestrial birds, but very long in diving taxa (Tickle et al. 2007). The distribution of uncinate processes shows some homoplasy. Such processes are found in several theropods currently placed outside Aves (e.g., some dromaeosaurs), but they are absent in some large flightless Neornithes, such as the extinct Dromornithidae, Gastornithidae, and Phorusrhacidae, as well as in the volant Anhimidae (screamers).

Birds primitively possessed rib-like gastral elements (gastralia) in the caudal portion

Figure 1.10 (a) The trunk skeleton of a roller (*Coracias*, Coraciidae) illustrates characteristics of the body plan of neognathous birds. (b) The pelvis of a palaeognathous tinamou (*Rhynchotus*, Tinamiformes); note the open ilioischadic foramen, and the boundaries between the pelvic bones are indicated by dotted lines. Not to scale.



of the trunk (see Figure 2.1), for which a respiratory function has likewise been assumed (Claessens 2004; see, however, O'Connor et al. 2015a, who hypothesized an involvement in the attachment of pectoral muscles). Gastralia are widespread among archosaurs, but were lost in the evolution towards the crown group. In non-neornithine birds their numbers range between 16 and 4 pairs (O'Connor et al. 2015a).

In *Archaeopteryx* and other basal Mesozoic avians, the pelvis consists of three paired bones: the ilium, ischium, and pubis. The contact zones between these bones delimit the acetabular foramen, which forms the socket for the femur head. In Neornithes, all pelvic bones are fused into a single solid unit; usually they also co-ossify with the synsacrum, a bone formed by fusion of the sacral vertebrae. The pubis is caudally directed in crown group birds, but was more vertically oriented in the earliest avians, in which the

two pubic bones were furthermore conjoined at their tips and formed a pubic symphysis. Neornithes show some diversity of pelvis morphologies, and whereas foot-propelled diving birds have a very long and narrow pelvis, the pelvis is short and wide in highly aerial birds that make little use of their legs.

The earliest avians had a long bony tail, which is greatly foreshortened in neornithine birds, where it consists of only a few vertebrae. The caudalmost ones of these form a plate-like bone, the pygostyle, to which the central tail feathers are anchored.

The hindlimb

Like the wing, the avian leg is divided into three major units; that is, the femur, the tibiotarsus and fibula, and the foot. The major visible leg joint of birds, sometimes falsely assumed to be a reversed “knee,” is an intertarsal joint, which develops between the tarsal (ankle) bones. In Neornithes, these

tarsals are completely fused with the distal end of the tibia and the proximal ends of the metatarsals of the foot (Figure 1.11). The resultant compound bones are termed tibiotarsus (tibia and proximal tarsals) and tarsometatarsus (metatarsals and distal tarsals). Unlike in most other tetrapods, where it swings back and forth, the femur of birds remains largely fixed in the same position during locomotion, and hindlimb movement is mainly driven by the knee (e.g., Allen et al. 2013).

The proximal end of the tibiotarsus bears two so-called cnemial crests, which serve as attachment sites of the shank musculature and are absent in early Mesozoic avians, in which the leg musculature may not yet have been so centralized. The cnemial crests are proximally elongated in swimming and

diving birds, which use their legs for aquatic locomotion and therefore require larger attachment sites of the hypertrophied foot muscles. In long-legged, terrestrial birds the cnemial crests are also well developed, albeit not proximally elongated, whereas they are reduced in short-legged, arboreal taxa. The distal end of the tibiotarsus bears two condyles that articulate with the tarsometatarsus. Just above these condyles, the cranial surface of the bone exhibits a marked sulcus, through which pass the tendons for extensor muscles of the toes (Figure 1.11). This “extensor sulcus” occurred late in avian evolution. In the majority of neognathous birds it is bridged by an osseous arch, the supratendinal bridge, which is secondarily lost in some taxa and primitively absent in most palaeognathous birds.

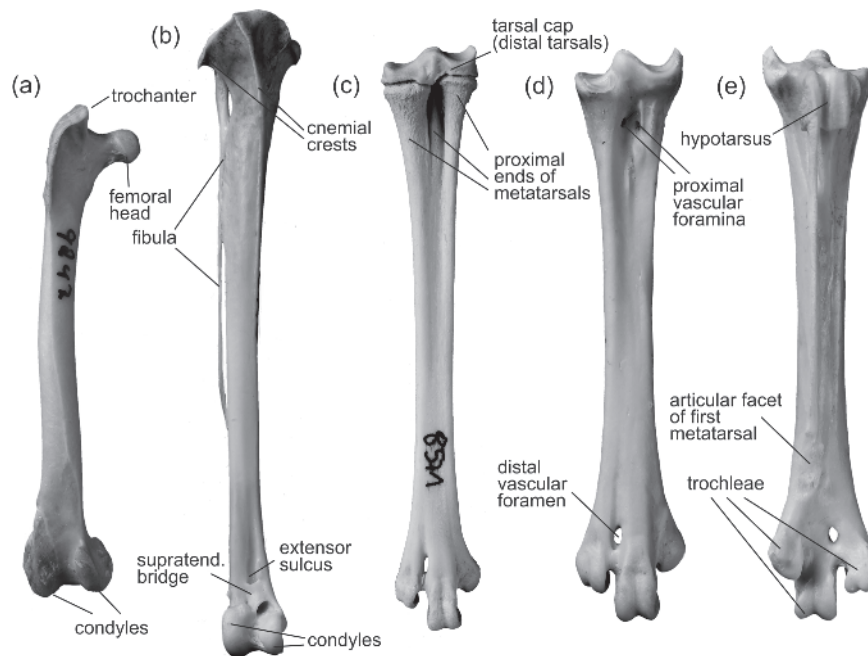


Figure 1.11 Major features of the leg bones of neornithine birds. (a) Femur and (b) tibiotarsus of a rock partridge (*Alectoris*, Galliformes). (c) Tarsometatarsus of a juvenile pheasant (*Lophura*, Galliformes), which shows the incomplete proximal fusion of the metatarsals and the cap formed by the distal tarsals. Tarsometatarsus of an adult rock partridge (*Alectoris*) in (d) dorsal and (e) plantar view. All bones are from the right side and not to scale.

Birds derive from an ancestor with five metatarsals. Even in the earliest avians, however, the fifth metatarsal is only a rudimentary splint, and the bone was completely lost in the evolution towards the crown group. The first metatarsal, which in neornithine birds carries the hind toe, is distally positioned and likewise reduced (Figure 1.12). In the course of avian evolution, the three other metatarsals – that is, those of the second, third, and fourth toes – completely fused with each other and the distal tarsals, thereby forming the tarsometatarsus.

The tarsometatarsus is another characteristic compound bone of extant birds, which greatly varies in its proportions across different taxa. It is particularly short and stout in highly aerial birds and elongated and slender

in wading or **cursorial** ones (Figure 1.12). The proximal end of the neornithine tarsometatarsus bears the hypotarsus, a bony structure that guides the tendons of the flexor muscles of the toes. Early Mesozoic avians lack a hypotarsus and in more advanced non-neornithine birds its structure is very simple, consisting of a single low crest. This plesiomorphic hypotarsus morphology is still found in palaeognathous birds, whereas the hypotarsus of most neognathous birds exhibits well-developed furrows and canals, the configuration of which is often of taxonomic significance (Figure 1.12).

The distal end of the tarsometatarsus also shows distinctive morphologies that characterize various neornithine taxa. The bone usually exhibits a foramen between

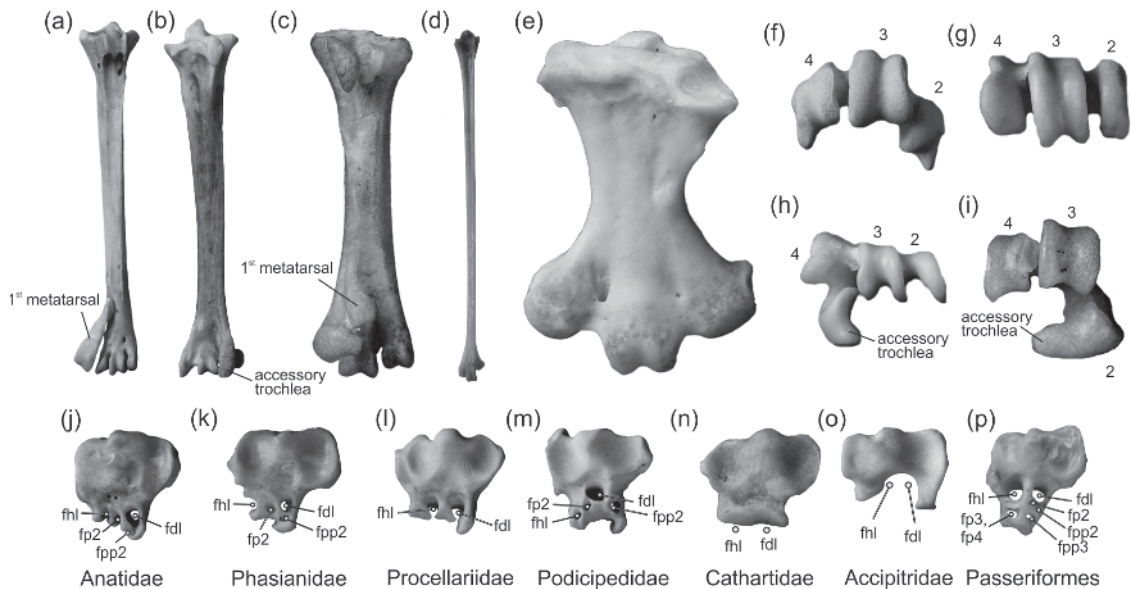


Figure 1.12 Different morphologies of the neornithine tarsometatarsi. Depicted are (a, g) an anisodactyl songbird (*Corvus*, Passeriformes), (b, h) a zygodactyl woodpecker (*Dryocopus*, Piciformes), (c, i) a heterodactyl trogon (*Pharomachrus*, Trogoniformes), (d) a flamingo (*Phoeniconaias*, Phoenicopteriformes), (e) a potoo (*Nyctibius*, Nyctibiiformes), and (f) a phasianid francolin (*Pternistis*, Galliformes). All bones are from the right side and not to scale (a–c: plantar view, d, e: dorsal view, f–i: distal view). (j–p) Different patterns of the sulci and canals of the hypotarsus on the proximal tarsometatarsus end; indicated are the passages for tendons of the muscles flexing the hind toe (fhl), all three fore toes (fdl), and the second (fp2), third (fp3, fpp3), and fourth toes (fp4).

the fused metatarsals of the third and fourth toes, the distal vascular foramen, and forms trochleae for the articulation with the three fore toes. Very rarely is one of these trochleae reduced, and, if it is, it is always that of the second toe, as in the cursorial ostriches (*Struthioniformes*). The configuration of the tarsometatarsal trochleae is variable and reflects different locomotory adaptations. In birds with reversed fore toes (see next paragraph), the corresponding tarsometatarsal trochleae are deflected and often bear accessory trochleae (Figure 1.12). Embryological studies suggest that the arrangement and morphology of the tarsometatarsal trochleae are shaped by developmental constraints, and the occurrence of short and parallel trochleae with narrow incisions, for example, seems to be correlated with the reduction of certain toe muscles (Botelho et al. 2014b).

Besides its locomotory function, the avian foot often serves as a grasping tool and many different kinds of foot specializations exist. Most Neornithes have four toes, three of which direct forwards and one, the hind toe or hallux, is turned backwards. This toe arrangement is termed anisodactyl and represents the primitive condition for neornithine birds. Very rarely are all four toes directed

forwards (pamprodactyl foot). To increase the grasping capabilities of the foot, the fourth toe became reversed in some groups, resulting in a zygodactyl foot. This condition is developed to various degrees in different taxa, and the fourth toe can be moved back and forth in facultatively zygodactyl birds, is laterally spread in semizygodactyl ones, or is permanently directed backwards in fully zygodactyl taxa. Trogons are the only neornithine group in which the second toe is permanently reversed, forming the heterodactyl foot (a putative heterodactyl foot in one specimen of a Cretaceous bird reported by Zhang et al. 2006 is likely to be an artifact of the preservation of the feet in this fossil). The ontogenetic mechanism involved in the formation of zygodactyl or heterodactyl feet is an asymmetric development of some of the muscles of the fourth or second toe, which causes the reversion of these toes (Botelho et al. 2014b).

In summary, therefore, the avian skeleton exhibits numerous specializations and shows a high degree of variation across neornithine birds. Still, it was a long evolutionary way until this diversity developed, and the fossil record allows us to trace many of the steps in between.