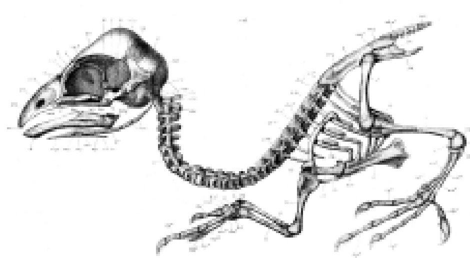
The Inner Bird



GARY W. KAISER

The Inner Bird

Anatomy and Evolution

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For Dr. Alice Wilson,
Dr. Donald C. Maddox, Mr. Herb Groh,
and all the other adult mentors
of the Macoun Field Club,
the Ottawa Field-Naturalists' program
for young people

Contents

Part 3: How Does a Bird Fly?

Appendices

Figures and Tables

Figures

Tables

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Brett vander Kist and I prepared most of the figures except as noted. We concentrated our efforts on images that are not readily available from other sources. Consequently, there are few illustrations of whole birds or dinosaurs. There are huge numbers of informative images of dinosaurs and ancient birds on websites such as the Dinosauricon (http://dino.lm.com/pages/).

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While working on this book, I was privileged to be accepted as a research associate at the Royal British Columbia Museum.

Introduction

Does the world really need another bird book? Ever since Aristotle declared the study of birds to be a useful activity some 2,300 years ago, hundreds of enthusiasts have taken him at his word and written about the experience. You might think from the numbers crowding the world's bookshelves that there are more than enough books to satisfy any conceivable demand, but most deal only with what birds look like. They are guides to the identification of the thousands of different kinds of birds, used as basic reference tools by amateur ornithologists or "birders." There are field guides for every place on earth, but birds are so diverse and widespread that the books have no room for more than a picture and a brief note. This book is not about identification; it deals with the internal structures, how they work, and what they mean to the bird.

The bird portrayed in the field guide is the outward form of an animal whose specializations and sophistications are largely internal. There is far more to a bird than colourful feathers and a cheery song. These are trivial compared with the array of sophisticated design elements in a body plan that has ensured survival since the time of the dinosaurs. Birds have cleverly solved many difficult problems in their long history and found ways to invade most of the world's environments. They may or may not be dinosaurs in some sense,[1] but they are definitely not mammals, and as successful co-inhabitants of the globe, they have much to teach us mammals about alternative ways to exist. To properly appreciate their solutions to life's challenges, we must look at the animal beneath the feathers – the inner bird.

A study of the internal workings of a bird might seem an esoteric and obscure subject, but if you picked up this book you were already in the "bird section" of

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1 For the purpose of clarity, I use an arbitrary definition for birds and dinosaurs based on their ability to fly. The former is a feathered animal that flies, whereas the latter is a non-flying creature that may or may not have feathers. Some representatives of both groups are tiny (less than 100 g) and others mid-sized (about 100 kg), but only dinosaurs produced giants of 100 tonnes or more. All dinosaurs are extinct.

the bookstore or library and probably have a collection of field guides at home. You may even have a basic textbook on ornithology and have noticed that its illustrations and examples have changed little since you were in school. In fact, they have changed little since your grandparents' day. This widespread use of outdated material is misleading and weakens the ability of both professional and amateur ornithologists to apply new discoveries made in other sciences. This book attempts to show how modern discoveries in paleontology, aerodynamics, molecular genetics, and other sciences are affecting our fundamental understanding of the bird and how it lives. Increasingly, the results of modern research are challenging traditional interpretations of avian anatomy.

A hundred years ago, anatomy was the single most important aspect of ornithology, and fully half the chapters in an ornithology text might be devoted to the skeleton. Today's texts squeeze a brief summary of the anatomical information into the introductory chapters and the skeleton is lucky to get more than a page or two. Such extreme condensation has required a great deal of generalization and simplification. Over the years, unnoticed errors and subtle misrepresentations of fact have crept into the accounts, and significant pieces of information have been omitted. More importantly, such highly condensed summaries give the impression that avian anatomy is simple or merely a variation on mammalian anatomy. This is not the case.

A bird's skeleton is not just a lightweight and rather rigid assembly of hollow bones; it may, in fact, be heavier than the skeleton of a similarly sized rodent and it is usually just as flexible. Sometimes the vertebrae of the back are indeed fused into a rigid block, but the extent and occurrence of such fusion is difficult to predict and may vary within a family. A great many birds have independent vertebrae and a flexible backbone. Only the hip region is always fused into a rigid block known as the synsacrum. Similarly, the claim that birds have hollow bones is an oversimplification. Some bird bones may be filled with nothing more than air but, just as in a rabbit or other small mammal, some bones are empty while others are filled with marrow. Even the claim that birds have air sacs extending into the limb bones is not universally true. The sandpipers and their relatives probably descended from birds whose bones were open to the respiratory system, but for unknown reasons their bones are now sealed off.

Some familiar anatomical features show surprising variability. You might expect the wishbone or furcula to be a universal characteristic of birds, but it varies greatly in shape from group to group and occasionally disappears. It is usually described as a thin springlike bone that flexes during flight. In birds with very energetic flight, however, such as hawks, it is a large and robust unit that is too stiff to flex. Owls may look like hawks and also hunt on the wing, but many of them have done away with their wishbone. For whatever reason, it is just not necessary to their flight technique and they make do with a pair of clavicles connected by a long loop of ligament. Similar startling differences in the design of other bones have been successful and have contributed to the great diversity of birds throughout the modern world. New information about the function of skeletal features and other internal structures has not gone unnoticed by the research community. It appears regularly in the technical literature but only a little filters down into more general publications.

The widespread emphasis on the external features and habits of birds also extends to the professional literature. Even at the university level, textbooks devote most of their space to avian ecology, behaviour, conservation, and similar topics. Consequently, it can be surprisingly difficult to find useful information on the internal features of birds. General textbooks offer some basic information on physiologically significant organ systems, but it is very difficult to get beyond the most elementary questions about avian anatomy and the skeleton is often dismissed in a page or two. There are veterinarian guides to the domestic chicken that go into great depth, but you must be prepared to navigate through a very large and very dense professional literature. It is easy to get lost in specialized technical jargon.

The chicken is by far the most abundant and most important bird on the planet, and avian anatomy has traditionally relied on it as a conveniently available example of a bird. There was a time when whole chickens were regularly sold in grocery stores and most people had a passing familiarity with their internal anatomy. The world has moved on. In most places, chicken meat is sold as anonymous, sterile lumps in plastic display packs that intentionally obscure any suggestion that the contents came from a living creature. The disjointed bits are not even useful as elementary introductions to avian musculature. Some textbook editors seem to have noticed this social change and have begun to use illustrations from a wider variety of birds.

Although chickens have great cultural significance, they have always been a poor choice as a typical bird. In the wild, jungle fowl spend most of their time walking on the ground and rarely take flight. Pigeons, starlings, or sparrows might be a better choice today. They at least are arboreal animals that hop about on the ground, behaving in the same way as 90% of the other birds. As unwelcome pests, victims of urban hazards, and common offerings from house cats, they also make a convenient subject for casual anatomical investigation.

In spite of the difficulties in learning more about avian anatomy, a flood of exciting new fossils suggests that the time is ripe for such study. Paleontologists have been busily reconstructing ancient life from the remains of birds and birdlike dinosaurs that seem to turn up almost daily. The most exciting finds are often accompanied by the claim that scientists will be forced to rethink the origin of birds. The more dramatic journalistic claims are foolish but not all are, and the fossil record of birds and their ancestors has proven particularly challenging to the scientific community. Before 1980, no one suspected the existence of undescribed subclasses of fossil birds with very distinctive anatomical features. We now know that the Cretaceous fauna included Confuciusornithes and Enantiornithes as well as modern birds (Neornithes). Other recently discovered fossils have demonstrated that many lineages of dinosaur had feathers and some small forms, such as *Microraptor,* may even have achieved a basic form of gliding flight. Without a basic knowledge of avian anatomy, it is difficult to assess the significance of such new information or understand why some some creatures are classified as birds and others as dinosaurs.

New fossils have not been the only challenge to traditional ornithology. Advances in biochemistry and molecular genetics have begun to chip away at the view of living birds as members of a monolithic group. Anatomical studies have long been used to place ostriches and their relatives in a discrete group within Class Aves. The use of the name Paleognathae implied that they were perhaps more primitive than other birds, but it took biomolecular analyses to confirm that they actually represent an early branch from the main lineage. Similar analyses have shown that the galliform and anseriform birds (chickens and ducks) represent another, major branch. The remaining groups of birds are still lumped together informally as the Plethaves because analyses of anatomical features have persistently failed to produce a convincing family tree. Molecular techniques have also failed to produce a family tree, and their results frequently contradict one another. Nonetheless, they have succeeded in undermining confidence in long-standing ideas about the relationships among the major groups of birds. One recent genetic analysis has called for a division of the Plethaves into two large groups, Metaves and Coronaves. Metaves happens to contain many groups that have been most difficult to classify, and it may represent survivors of an early radiation of modern birds. Unlike some other results of molecular studies, it is not one that was anticipated by students of anatomical features, and researchers are scrambling to find further evidence one way or another.

Such a fundamental division within the Class Aves would have profound significance for our understanding of the group's history, but so far it is based only on variation in a single fibrinogen gene. Nonetheless, such results make it clear that students of both fossil and living birds need to take a fresh look at avian anatomy. One of the objectives of this book is to introduce some of the appropriate background material and suggest some new interpretations for familiar structures.

In many ways, this book is a personal statement about birds and it reflects events in my career as a working ornithologist. Like most of my contemporaries, I am a practical avian ecologist with little academic training in the study of birds. I have spent most of my career dealing with questions of human impact on the environment and never needed to call on biomolecular genetics or paleontology. I dissected the occasional cadaver, searching for ingested lead pellets or other evidence of human-induced mortality, but my work never required more than a basic understanding of avian anatomy.

When I first looked for work as a biologist, I was, if anything, a specialist in insect sensory physiology. After a brief stint bouncing chicken carcasses off aircraft for the Bird Hazards to Aircraft Committee, I began a 33-year career as a Migratory Birds population biologist for the Canadian Wildlife Service and spent a great deal of time counting ducks from low-flying aircraft. In the 1970s, continental management of bird populations depended heavily on information from bird bands, and conservation agencies invested in numerous large-scale capture operations. Consequently, over the years I handled thousands of ducks, geese, auks, and sandpipers, as well as loons, grebes, cormorants, pelicans, cranes, herons, petrels, gulls, and terns. References to some of these birds appear throughout the book because I know them best. Fortunately, my experience was not limited to North America. Over the years, I have been lucky enough to help colleagues with field studies of penguins, boobies, frigatebirds, shearwaters, albatrosses, and other marine birds. I have also done a little work with small forest birds in the tropics. For many years I conducted courses in field ornithology and mist-netted a variety of exotic resident and migrant species in Colombia, Ecuador, Peru, Sri Lanka, Borneo, and the Philippines.

Although I have banded all the North American ducks and most of the world's sandpipers, it was handling tiny tropical species in Colombia that really opened my eyes to the structural diversity of birds. During a series of winter field courses for students from the Universidad de los Andes, I handled everything from huge and furious oropendolas to tiny and docile sword-billed hummingbirds. They were exciting and bizarre creatures but none stands out in my mind more than a giant White-collared Swift caught at 3,300 m in the Sierra Nevada of Santa Marta. It lay stiffly in my hand, more like a model airplane than a living creature. Its body felt heavy and densely muscled, surprisingly reminiscent of Marbled Murrelets that we had been catching in British Columbia during the previous summer. It would be 20 years before I realized just how few high-speed aerial specialists there are among birds and why the swift's internal architecture was so different from that of other high-speed fliers, such as a murrelet or a falcon.

I never touched another giant swift but I still work with the Marbled Murrelet whenever I get the chance. The murrelet was largely ignored by conservation agencies until it was declared a threatened species in the early 1990s. Suddenly there was a demand for information on its nest sites and feeding areas. It proved to have such unusual habits, however, that the only way to study it effectively was either through radio telemetry or tracking on radar. Nonetheless, it soon became one of the most intensively studied species in North America and its biology is discussed regularly at seabird conferences and on dozens of websites. Although few of this book's readers will have seen one of these birds, it is now one of the most thoroughly documented species in North America.

The Marbled Murrelet is a secretive, non-colonial seabird that can be studied only one individual at a time, and working with it changed my perception of birds. It forced me to think of them as discrete organisms instead of masses of animals in populations or communities. The murrelet turned out to be one of the fastest birds in the air, and individuals regularly commute more than a hundred kilometres between the nest and feeding areas at sea. Other auks nest near sea level but the murrelet will lay its egg more than a kilometre up one of the coastal mountains and more than 50 km inland. It is famous for finding the right branch in a forest of branches, in complete darkness. For me, its unusual flight capabilities and special adaptations for life underwater have become useful benchmarks in assessing the performance and structure of other species.

Another intensely documented species has also caught my imagination, although I have never been able to handle a living example. It is the Hoatzin (more or less rhymes with Watson), a tropical species that is about as far anatomically from a murrelet as it is possible to get. It is a large, loose-limbed, and slow-flying chicken-like bird that lives along streams in the Neotropics. It is perhaps best known for the peculiar fingers on the wings of its young. They are suggestively reptilian but are not this bird's only unusual feature. In spite of intensive investigation, it has repeatedly defied classification, confounding both comparative anatomists and biomolecular geneticists.

In 1891, William Kitchen Parker made Victorian naturalists familiar with the peculiar features of the Hoatzin by publishing detailed drawings of the skeleton of a fully developed embryo [155]. Its fingers suggested the intriguing possibility of an evolutionary connection to primitive fossil birds like the *Archaeopteryx,* but its specialized digestive system suggested something much more advanced. It is the avian equivalent of a ruminant, and no other bird has such a hugely enlarged crop for the fermentation of vegetable matter.

Surprisingly, the crop suggests a link to yet another group of primitive birds. In 1981, Cyril Walker described a whole new subclass of fossil birds that he called "Enantiornithes" [221]. These "opposite birds" were a highly successful and widely distributed group until they became extinct with the dinosaurs. The pectoral skeleton of the species that gave the group its name, *Enantiornis,* shared many structural features with the modern Hoatzin, implying that the two birds might also have shared a very similar lifestyle. Could the Hoatzin be an unrecognized living fossil? It is highly unlikely but a Victorian amateur would have found the subject much easier to investigate than his or her modern counterparts. There are no illustrations of the Hoatzin skeleton in modern reference texts or on specialized ornithological websites. A recent study of the Hoatzin's skull is available only in Portuguese.

The Hoatzin and the Marbled Murrelet are among the most specialized birds and are somewhat unfamiliar to most ornithologists. Other species might seem more representative of their class, but these two have been so intensively studied that they have become more useful examples than they first appear. Both are discussed on the Internet and in many books. This book also uses other auks and specialized types of birds, such as loons, grebes, frigatebirds, and albatrosses, to illustrate some of its points. It mostly avoids discussions of songbirds, chickens, or pigeons.

The book is divided into three parts, each of which addresses one of the elementary questions that have been the basis of ornithology since the time of Aristotle: "What is a bird?" "What kind of bird is it?" and "How does it fly?"

Aristotle answered the first question, to almost everyone's satisfaction, some 2,300 years ago. In the last 20 years, however, paleontologists have rekindled interest in it by finding one fossil after another that bridges the gap between birds and dinosaurs. The phrase "birds are dinosaurs" has become a journalistic cliché but it is patently foolish from an ornithologist's point of view, if only because we see living birds every day whereas dinosaurs have been dead for 65 million years.[2] For most avian ecologists, this is far too long a period for dinosaurs to be very relevant in the study of living species. The distinction between birds and dinosaurs is of more interest to evolutionary theorists investigating the origin of birds and their method of flight.

Since the late John Ostrom found the large predatory dinosaur *Deinonychus* and described its birdlike characteristics, there has been increasing acceptance of the idea that birds arose from within a group of advanced carnivorous dinosaurs known as theropods. In this century, a civil court jury would certainly decide in favour of a dinosaur origin "on the balance of probabilities," but there are still enough questions that a criminal court jury might have difficulty deciding "beyond a reasonable doubt."

Ironically, it is Aristotle's comparative method that lies at the root of any ongoing difficulty in distinguishing between tiny birds and giant dinosaurs. For centuries, biologists have compared one specimen with another and used similarity as an indicator of relationship. Unfortunately for those who want simple answers, similarity does not imply causality.

There is an evolutionary process called convergence that strongly limits the usefulness of similarity and is particularly widespread in birds. When otherwise unrelated animals occupy similar habitats and share similar lifestyles, natural selection is likely to increase the similarity of their appearance and they are said to converge. The process is different from mimicry, where an innocuous species gains protection by looking like a dangerous or toxic neighbour. Convergence may occur between animals that live in opposite hemispheres or, like the Hoatzin and *Enantiornis* mentioned above, that are separated by great expanses of time. The degree of convergence can be stunning, and in some cases it has confounded ornithologists for centuries. Only recently have we come to understand that American vultures are a kind of stork even though they look very much like African vultures, which are related to eagles.

Sometimes the true relationships between animals are so thoroughly hidden that they can be resolved only by the use of DNA and gene sequences. It turns out, however, that there is even convergence of DNA, and biomolecular analysts

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2 The subject of dinosaurs and ancient extinctions brings up the issue of geological time scales. I have placed a bird-oriented version in Appendix 2. Readers need only be aware that dinosaurs became extinct at the end of the Cretaceous Era about 65 million years ago, while we live in the Tertiary, which began at that time. Little additional information is needed to understand this book.

must be careful of their own comparisons. Most importantly, DNA cannot be applied to fossils and paleontologists must depend on anatomical details winkled out from confusing fragments of bone. In the last few years, distinguishing feathered dinosaurs from the early reptile-like birds has become one of their greatest challenges.

The question "What is a bird?" is investigated in the first two chapters in terms of the internal structure and architecture of living species. Chapters 3 and 4 look at the same question in terms of a bird's similarities and differences with regard to the animals commonly known as dinosaurs.

The question "What kind of bird is it?" is usually answered with a name, but like a person's name, a bird's name makes sense only in a broader context of family relationships and connections to larger groups. Nonetheless, the name is central to the popular hobby of birdwatching and the basis for the vast number of field guides. For centuries, the question of names was the most important issue in ornithology. After Christopher Columbus and other explorers introduced the rest of the world to the Europeans, huge numbers of unknown species were brought back to Europe. For over 400 years, the description of newly discovered birds absorbed the careers of most ornithologists. By the mid-20th century, the great majority of the world's unknown species had been catalogued and ornithologists, like most other biologists, began to turn their attention to other kinds of study. Many chose to link ornithological studies to experimental forms of science. Today there are more professional ornithologists than ever, but only a handful work on issues of bird identification. Most specialize in bird-oriented components of other fields, such as avian ecology, avian demography, avian physiology, or avian genetics.

This book does not deal with individual species of birds except as representatives of general types. Usually these types have such distinctive and specialized characteristics that they have been placed in distinct families or groups of families known as orders. Generally ornithologists and biomolecular geneticists have had some success at working out the relationships between species and clustering them in large groups, but agreement on the relationships among those larger groups has eluded them. The history of the difficulties in determining ranks for the various groups and the relationships among the families of birds is discussed in Chapters 5 and 6. Many problems remain unresolved; consequently, ornithologists have failed to produce a generally accepted family tree or phylogeny for the birds. Without such a tree there can be no evolutionary story.

Most ornithologists agree that flight capability is the key to understanding avian evolution, and that "How does a bird fly?" lies at the heart of ornithology. This question has had a much greater impact on our culture and history than any issue of bird identity. For centuries our ancestors watched birds and dreamed of achieving flight themselves. Without a basic knowledge of the composition of air, however, it remained a fantasy until science advanced and pioneer aviators solved the problems of generating sufficient mechanical power. Even then, they built aircraft that looked like box kites and few thought that avian flight merited serious scientific investigation.

In the mid-20th century, when aeronautical engineers began to design truly sophisticated aircraft, they also began to reconsider the performance of birds as flying animals and to make systematic investigations of avian flight. It proved to be a rewarding field of investigation, and avian aerodynamics made many important contributions to aircraft design. In return, aeronautical engineers provided ornithologists with new perspectives on the energetics of bird flight and developed mathematical models of avian performance in the air. These models of energy expenditure have enabled ecologists to determine the cost of the various aspects of the bird's life cycle, such as parental investment in reproduction. Energetic factors have key components in conservation plans and assessments of the bird's ability to exploit modified environments. A host of more esoteric questions arising from the mathematical models remain the subject of intense investigation, and new ideas about flight are reported regularly in the *Journal of Experimental Biology* and other scientific publications.

Feathers are central to avian flight but remain the single most difficult element to model or investigate effectively. Their importance is indicated by the energy invested by the bird in preening and sophisticated physiological processes that keep the plumage in good condition. Feathers are so intimately linked to the flight of birds that the discovery of feathered dinosaurs was initially met with controversy and disbelief. None of those dinosaurs show adaptations necessary for flapping flight, but the same can be said about *Archaeopteryx* and some other primitive species. Birds appear to have taken a very long time to develop basic aerial skills. It may have been an expensive or risky process, and some early lineages appear to have abandoned the attempt. The role of feathers and some early experiments in avian design are discussed in Chapters 7 and 8.

The evidence is sparse but it is beginning to look as though birds were surprisingly diverse and abundant in the Cretaceous, and at least some modern groups were around long before dinosaurs died out. Chapter 8 looks at the three major evolutionary experiments undertaken by birds in the Cretaceous: the Confuciusornithes, the Enantiornithes, and the Neornithes, or modern birds. You can tell from the tongue-twisting names that the first two of these very important groups are fairly recent discoveries. They have yet to be given a catchy tag by amateur dinosaur enthusiasts. To help the text flow, I refer to the first group as Confucius birds and the second as ball-shouldered birds.

Many of the Enantiornithes are almost indistinguishable from modern birds except for details of their skeletal anatomy. Their shoulder includes a "ball" that fits into a socket at the base of the shoulder blade – hence, "ball-shouldered birds." Neornithes have a socket in the shoulder that receives a "ball" on the shoulder blade. I suppose they could be referred to as "socket-shouldered birds," but "modern birds" is more meaningful. The Enantiornithes were not recognized as a group until 1981 but they may have been more widespread and successful than the modern birds in the Cretaceous. Why did they become extinct while modern birds survived? The answer may have to wait until we unravel the mysteries surrounding the events[3] that exterminated the dinosaurs and many other life-forms at the end of the Mesozoic.

Chapters 9 and 10 look at the influence of flight on the lifestyles of modern birds. Chapter 9 examines the adaptations of a dozen groups usually described as small forest birds. They include about 85% of all species, but in spite of their numbers, they are remarkably uniform in their basic body plans and flight technique. Ornithologists use details of skull structure and internal anatomy to distinguish the families and orders, but in the field the most striking differences are often limited to superficial matters of plumage colour and feather shape.

Although the great majority of small forest birds are capable of flight, nearly all are pedestrians that earn their living by foraging on the ground or some other substrate. Many fly only when pressed to escape predators or to commute between a roost and a feeding area. Only a small minority of birds have learned to forage on the wing or undertake long migrations, but even these aerial specialists are little different from their more sedentary relatives. Except for the extreme specializations of hummingbirds and swifts, most aerial specialists among the small forest birds show only modest variation in the length and shape of the wing.

Less than 15% of all bird species have developed the specialized flight techniques needed to actually earn a living on the wing. In spite of this small number, they are represented in about half the major lineages or orders of birds. Smaller types, such as hummingbirds, swifts, swallows, nightjars, and the smaller owls, have retained a close relationship with forest habitats. They may forage in open areas but typically return to the forest's shelter to roost or nest. Larger species have more difficulty manoeuvring among the branches and often inhabit open habitats on a full-time basis. Some are terrestrial while others are marine or aquatic. The terrestrial types are typically found on grasslands and estuaries, where they exploit thermal updrafts to soar long distances at only a small energy cost. The thermals enable them to investigate sparsely distributed foraging opportunities across vast areas. A few close relatives of those birds of open country, such as the accipiter hawks and forest-falcons, have returned to the forest, where they use high-speed flight to pursue smaller forest species. Others have learned to swim and make use of the many small lakes and wetlands scattered across the continents.

Only a few groups have been able to move out onto the open oceans, but their spectacular success is one of the major achievements of birds and was never

3 "K-T event" is the usual paleontological shorthand for occurrences that led to the extinction of the dinosaurs and many other lineages at the end of the Cretaceous (K) and before the beginning of the Tertiary (T).

accomplished by dinosaurs. The oceans offer a wealth of opportunities but are a challenging environment, and birds have been forced to undertake an array of novel adaptations in order to survive. Food is often abundant at sea but is usually patchily distributed, so marine birds have been forced to find ways to search over huge areas. Once they locate prey, they must be able to catch it even if it disappears beneath the surface. As a result, birds have learned to dive deeper and faster than their prey.

The most successful groups of seabirds exhibit one of three basic strategies for life at sea. The petrels depend on exceptionally efficient flight to search wide areas without exhausting their energy supply. Penguins have exchanged the ability to fly for bodies capable of storing dense masses of fat that they use to fuel long swimming voyages at sea. Auks look a little like very small penguins but have retained the ability to fly and are neither as large nor as heavy (except for some extinct flightless forms). Like penguins, they use their wings for underwater propulsion. In the air, energetically expensive flight depletes energy reserves much more rapidly than the more efficient flight of petrels and albatrosses. Auks have successfully based their lifestyle on the advantages offered by the combination of high-speed flight and the regular availability of energy-rich prey in the sea.

For many years, ornithologists were unimpressed by the flight capabilities of auks, but advances in avian aerodynamic theory have forced them to change that opinion. Auks were once seen as a mere evolutionary waypoint on the path to becoming as flightless as penguins. Just as modern analyses of DNA suggest that seabirds represent advanced lineages, however, modern aerodynamic theory suggests that their flight is a highly sophisticated adaptation for a specialized existence. The auk's choice of speed and energetic extravagance is just as specialized a flight technique as the grace and efficiency of petrels. In each case, the aerial technique has made demands on the owner's internal structure while facilitating reproductive strategies that are denied to all other types of birds.

Where possible, I have illustrated the ideas in this book with material from my own research and experience, but the great majority of illustrations are based on the publications of other ornithologists. By the mid-20th century, the scientific literature had become so vast that no one library could contain it all, and so cumbersome that it impeded research. For better or worse, the Internet has changed all that. Much of the 19th- and 20th-century technical literature for North America is now available, without charge, through SORA, the <u>S</u>earchable <u>O</u>rnithological <u>R</u>esearch <u>A</u>rchive (http://www.elibrary.unm.edu/sora/index.php). Other science journals have websites where you can browse through the titles of current and past issues. Most will allow you to read the abstract for free and give you the opportunity to purchase a copy of a particularly interesting paper (usually online as a PDF file) for between US$10 and US$30.

The volume of paleontological literature has also become very large. Fortunately, much of it is accessible on the Internet, where it has become a common subject in various dinosaur chat groups. Hard copies of paleontological papers are not as readily available as the bird literature, but SAPE, the Society of Avian Paleontology and Evolution (http://www2.nrm.se/ve/birds/sape/sape001.html.en), offers access to the texts of many recent papers.

Since 1998, dramatic reports of new fossils in newspapers and science magazines have helped rekindle public curiosity about the origin of birds. Debate on this issue has flared intermittently since the discovery of *Archaeopteryx* in 1861 and encouraged the production of such books as *The origin and evolution of birds* (1996) by Alan Feduccia [60], *The rise of birds* (1997) by Sankar Chatterjee [24], *The mistaken extinction* (1998) by Lowell Dingus and Timothy Rowe [50], and *Dinosaurs of the air* (2002) by Gregory Paul [157]. Paul's book is particularly useful because it includes illustrations of many of the important characteristics that have been used to identify the various lineages of dinosaurs and Mesozoic birds. The most recent round of debates also led to the publication of four large compilations of research papers: Michael J. Benton, Mikhail A. Shishkin, David M. Unwin, and Evgenii N. Kurochkin edited *The age of dinosaurs in Russia and Mongolia* (2000); J. Gauthier and L.F. Gall edited *New perspectives on the origin and early evolution of birds* (2001); Luis M. Chiappe and Lawrence M. Witmer edited *Mesozoic birds: Above the heads of dinosaurs* (2002); and Philip Currie, Eva Koppelhus, Martin Shugar, and Joanna Wright edited *Feathered dragons: Studies in the transition from dinosaurs to birds* (2004). Individual papers from these books are cited at various points in the text, and the books are all recommended as a source of technical detail and information on closely related topics.

Throughout this book, I have tried to help the reader find additional information either on the Internet or in the technical literature by giving the names of the researchers whose work forms the basis of my discussion and the correct scientific name for the organism and for its component parts. The specialized terminology does not appear in typical dictionaries so I have included a descriptive glossary among the appendices at the end. Nonetheless, the book is a natural history and not a technical treatise. I have had to compromise between readability and appropriate citation. I have tried to give credit to the scientists who had the most important ideas and did the most innovative work, but the subject is complex and I apologize if I have failed to give full credit to every deserving worker. I hope that there are enough citations that readers can explore the literature further and keep abreast of new developments.

This book touches on many highly specialized fields and there are bound to be mistakes. For those you have my sincere apologies. There will also be claims that you cannot believe – you are not supposed to believe them! Examine them for yourself, in other books, in museums, or even on the Internet.

PART 1

What Is a Bird?

1 The Bird beneath the Feathers

How adaptations for flight allow a bird to earn a living on the ground

There are only four groups of terrestrial vertebrates: amphibians, reptiles, mammals, and birds. The first three usually walk, crawl, run, and jump using a basic four-legged architecture, although a few have been modified for swimming or even for flying. These tetrapods differ in body covering and physiology but they are similar enough in structure that it is easy to imagine them as distantly related cousins. A family relationship between these three and the birds is much more difficult to imagine. Like mammals, birds are advanced, warm-blooded vertebrates. They share some characteristics with specialized mammals, such as the human's ability to walk on two legs or the bat's ability to fly, but it is clear that they have little else in common with that group. Birds may still walk on the ground but are otherwise completely specialized as flying creatures and are clothed in a unique type of body covering that contributes to structural integrity and participates in aerial locomotion.

The body covering or plumage also completely obscures the bird's internal activity and has greatly impeded our attempts to understand it as a functioning animal. The plumage has even made it difficult for writers to find ways of describing bird movement. They always seem to be referring to some sort of solid object that just happens to be moving through space. When writers describe the movement of mammals, whether human athletes or fast horses, they turn to well-worn clichés like "grace in motion." The rippling muscles slide smoothly over one another in ways that capture the eye and the imagination. It does not matter whether the mammal under consideration is a mouse or a hippopotamus because we recognize that their underlying body plans are similar to our own and know that all the component parts will act in a predictable manner. It has been much more difficult to understand the bird. For centuries, we knew little more about a bird's movement than that it was a mystery that we could not imitate but that seemed to be based on the flapping of wings.

Other aspects of avian locomotion added to the early observers' inability to understand the flapping wing. Dense plumage seems to enable the bird to change shape while disguising the movement of the body or limbs. The albatross resting on the sea might be carved from a block of wood until it transforms itself and drifts away effortlessly on hugely extended wings. The squat duck takes off more energetically but it also stretches out its neck and adopts a more streamlined conformation for high-speed flight. Even the backyard sparrow transforms itself from a momentarily tense visitor to a vibrating projectile as it dives into protective shrubbery.

The changes in shape are largely the responsibility of the feathers but feathers do much more than define the bird's external shape. Feathers are found on no other living animal,[1] and, more than any other feature, they give meaning to the word "bird." They protect the fragile body, give it the power of flight, insulate it from the cold, advertise its species, and display its readiness for reproduction. Feathers are also a key element in an architectural strategy that exposes as little as possible of the bird's living body to the outer world. Not surprisingly, they are often the only feature we notice about a bird. Like an inept house cat with a disappointing mouthful of feathers, we often get distracted by externalities and miss the meaty bit underneath. By concentrating on appearance, we lose sight of two fundamental characteristics of birds.

First, almost none of the visible parts of a bird are alive. From one end to the other, birds are covered by tough proteins called keratins that are formed as a lifeless excretion of the skin. Keratins come in several forms. Some form the airy layer of feathers that gives the fleshy parts of the body a flexible covering, while other types create a durable surface for working structures such as the beak, legs, and claws. Even the living surface of a bird's eye lies beneath a glassy layer of transparent keratin.

Avian keratin is unique but similar material forms the patches of hair, fur, and claws in mammals and scales in reptiles. Like the scales of reptiles, the feathers are shed at regular intervals, but the eye covering and leg scales remain for life.

The second fundamental characteristic of birds is that they are pedestrians. Few actually earn their living in the air or spend a great deal of time in flight. Wherever they are, the feathers protect them from excess heat or cold and decrease the risk of mechanical injury. Most birds forage by walking about on the ground, looking for food just like their distant reptilian ancestors. Those that live in forests have traded level ground for more vertical substrates such as trunks, branches, leaves, and flowers, but they still forage on foot. Although the great majority of birds fly only to escape from predators or commute between feeding areas and a roost, the benefits must have made it worthwhile for their ancestors to undergo the complex adaptations that led to aerial flight. In modern birds, almost every anatomical feature reflects the demands of aerial locomotion, but we should never lose track of the bird's heritage as a pedestrian animal.

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[1] The recent confirmation of feathers in some dinosaurs further blurs the distinction between these two groups. In *Dinosaurs of the Air,* Gregory S. Paul sees some of the most advanced dinosaurs as descendants of birds that lost the power of flight [158].

Although the outer cloak of feathers is an important part of the animal, all living functions are the responsibility of the inner bird. The inner bird is a strange goblin-like creature that manipulates its appendages by pulling on long tendons just as the human operator within the muppet Big Bird pulls on a network of internal wires and strings. The puppeteer gets to enjoy an independent existence when he sheds his casing at the end of the workday, but the plumage of the inner bird is part of an integrated whole animal.

Suggesting that we should look at the inner bird as a puppeteer behind a screen of feathers may seem an extreme point of view but it does not overstate the case. The muppet analogy extends beyond the feathered suit to the bird's basic design. In mammals, the limbs are moved by muscles that are distributed over the whole skeleton so that they lie close to the joints they move. There is ample additional room on the limbs for generous blood supplies and even stores of fat. In birds, the muscles are remote from the joints and the limbs often appear thin and sticklike. Even the fleshier wings are little more than nubs, with no more tissue than is needed to carry and manipulate the feathers during flight.[2] The limbs are not one of the places where a bird can store its reserves of fat, and they offer little space for blood vessels or nerves. Because the muscles are collected together in a dense mass and anchored as close as possible to the body's core, they often lie far from their point of action and depend on long tendons to carry out their responsibilities. Tendons from muscles along the breastbone move the wing, while others along the backbone move the tail. Even the muscles that curl the toes are mounted high on the leg.

In mammals, tendons are usually short links of connective tissue that travel in a straight line across a single joint. In birds, tendons are often very long and many cross two or more joints. In some cases, they are responsible for movements that are more complex than the simple bending of a hinge. Perhaps the best-known example involves the supracoracoideus and the pectoral muscles that lie parallel to each other along the keel of the sternum. The large pectoral muscle depresses the wing by pulling directly on the humerus. The smaller supracoracoideus raises the wing because its tendon reverses direction as it passes through a pulley in the shoulder.

Dependence on the forelimbs for flight and the hind limbs for walking has left birds with few options for manipulating prey or other objects that might be worth investigating. Parrots grip food with their feet and raptors kill with their talons, but most other birds are entirely dependent on coordinated interaction of their neck and beak. In effect, the neck has become the bird's equivalent of an arm and the beak is its equivalent of a hand. To meet the demands of this role, the neck must be exceptionally long (Figure 1.1). In mammals, such as the giraffe, this is achieved through the elongation of a small number of vertebrae. The neck of a

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2 The muscles that put a little protein into "Buffalo wings" are found only in chickens. Other birds have replaced them with a lightweight tendon.

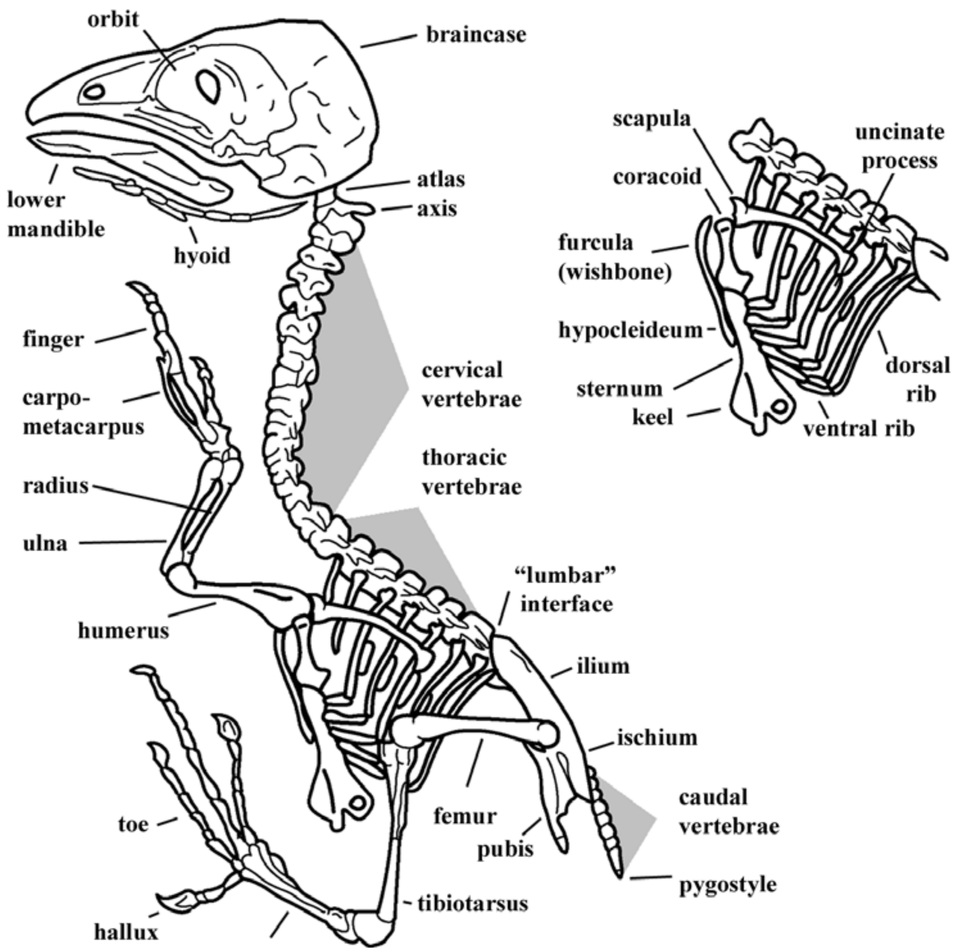

Figure 1.1 Major elements in the avian skeleton. This illustration is derived from W.K. Parker's depiction of a newly hatched Hoatzin [155]. This is not a typical bird but all of the important bones are present. At this stage of development, many are not completely fused and the individual components of some, such as the tarsometatarsus, are visible. In this species, the bones of the fingers are independent and are similar to those in the early ancestors of birds. More typical avian hand bones can be seen in Figure 1.11.

bird, however, is assembled from numerous small components, supported and strengthened by a complex array of muscles, tendons, and ligaments. In many ways, this elaborate structure is reminiscent of the type seen in dinosaurs and other ancient reptiles.

The assignment of manipulative duties to the head and neck has required that birds solve some complex biomechanical problems. Birds often use rapid movements of the head to capture prey, but if the bird's head were heavy, it would generate

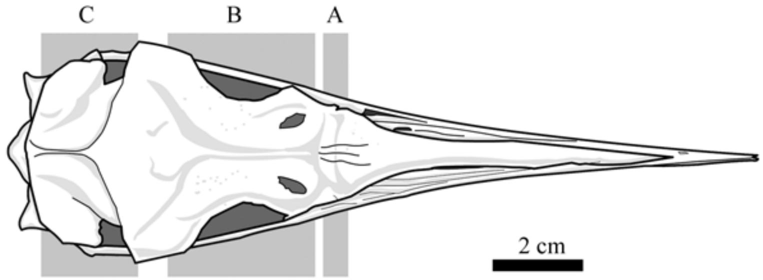

Figure 1.2 Dorsal view of the skull of a Pacific Loon. (A) Flexion zone between beak and braincase; (B) troughs over the eyes for the salt glands; (C) troughs to hold unusually large jaw muscles.

considerable momentum that might strain the neck joints or injure the fragile spinal cord. The ancestors of birds solved this problem by reducing the amount of bony material and soft tissues in the head. The long-necked dinosaurs used the same tactic but birds have carried it to an extreme. Bones in a bird's skull are often paper-thin and have lost much of their protective capacity. Even the jaws have become lightweight structures in spite of the variety of services that they are called on to perform. They lost their heavy teeth early in the bird's evolutionary story, and their muscles have been moved closer to the body core. The muscles lie behind the eyes or beneath the skull, near the top of the neck. The brain and eyes have remained exceptionally large and contribute the greatest amount of weight to a bird's head.

The massive jaw muscles found in many mammals are usually attached to a distinctive ridge along the midline of the skull, called the sagittal crest. Most birds have small jaw muscles and a skull that is a smoothly rounded dome without such obvious sites for muscle attachment. Crests and other structures appear, however, among birds with exceptionally heavy beaks or birds that regularly handle struggling prey. In heavy-billed ibises and fish-eating cormorants, and in boobies, a reinforcing crest of bone creates a distinctive collar near the base of the skull and leads to a trough that contains the jaw muscles. Puffins and petrels have a more modest array of ridges in the same general area, but broad troughs mark the spaces occupied by their jaw muscles. Only loons and large grebes have well-developed, mammal-like sagittal crests along the midline of the skull (Figure 1.2).

Even the most robustly jawed birds can only begin to process food in the mouth. Most birds are satisfied with the ability to orient the food for comfortable swallowing, but some species are able to tear large prey into edible chunks or crack unwanted shells off seeds. There are no teeth or elaborate grinding surfaces in the mouth for chewing. Even the saliva produced by some species lacks digestive enzymes. Both mechanical and chemical reduction is delayed until the food enters the muscular foregut deep within the body. Even there, birds lack a hard grinding surface and, like their distant relatives among the dinosaurs,[3] birds swallow grit or small pebbles to aid mechanical reduction. The grit might not be lighter than a set of teeth but it is stored deep in the body, not in the head.

Long necks, such as those found in all birds, are uncommon in nature because they are vulnerable to attack and radiate valuable body heat. To reduce the risk, birds adopt a protective posture by folding their necks and tucking their heads tightly into their bodies. This pulls the neck's muscles close to the warmth of the central core of the body without limiting the bird's ability to reach distant objects. In flight, the plumage covers the neck and smoothes the angular contours of the shoulders, reducing drag by allowing air to pass smoothly over the body. A few long-necked birds fly with the neck extended. Flamingos and cranes fly so slowly that drag is not a concern, but ducks, geese, and swans achieve higher speeds where drag can significantly increase energetic costs. They are careful to maintain the head in a central position so that it does not increase drag by extending beyond the cross-section of the body.

No characteristics highlight the distinctions between the inner and outer bird more than the structures used by a bird to interact with the world. The continuity of a bird's plumage is broken only by its eyes, beak, and feet, whose shiny, armoured hardness contrasts sharply with the proverbial softness of the feathers. Using only these three external features, the bird has thrived for millions of years while all of its nearest relatives have long since disappeared. Each structure is based on a fragile core of living tissue that protects itself by excreting a tough but lifeless outer case.

Interacting with the External World

Perceiving the External Environment

Eyes and Vision

The eyes of birds are truly vital organs; no bird can fly blind.[4] Although the eyes lie near the base of the beak, they are perhaps the most exposed part of the bird's body. To protect them from normal wear and tear, they are covered by the same tough sclerotic film that lines the lungs and the walls of the hollow bones. This covering is one feature that birds seem to have inherited from reptilian ancestors, but it is different from the transparent scales that cover the eyes of modern reptiles. Snakes and lizards lose their eye coverings in one piece whenever they shed the rest of their skin. Birds keep their eye covering for life, adding to it from within. They also have a third eyelid, the semi-transparent nictitating membrane, which can sweep across the eye to clear it of dust and other irritants.

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3 Dinosaurs will appear regularly in this story. Paleontologists now say that birds are dinosaurs, but for clarity and simplicity, I use the word "dinosaur" in its traditional and original sense as the name of an extinct lineage of ancient reptiles. A bird is a flying (or secondarily flightless) animal that shares the ancestry of *Archaeopteryx,* the earliest known member of its lineage.

4 Oilbirds and some swifts nest in caves and appear to have developed basic skills in echolocation.

Within the bird's eye, there is a ring of a dozen or so small bony plates set around its pupil. Similar structures were found in dinosaurs and other primitive reptiles. The ring appears in all birds but its individual small plates vary slightly in form and number and have occasionally been used as a characteristic in classification. Birds that forage underwater need to modify the shape of their eyes to accommodate the greater optical density of water. The small plates help to protect their eyes from extreme distortion.

Falcons and other hunting birds have long been famous for their keen eyesight but almost all birds have exceptionally acute vision. They achieve it by having exceptionally large eyes. A bird's eye may be larger than that of a much bigger mammal [16], so that the eye of a 200 g owl is as large as or larger than that of a 100 kg human. The eye of the ostrich is the largest of any terrestrial vertebrate and may approach the upper limits of optical effectiveness in a biological structure. Many factors affect the growth of biological materials and organic tissues cannot provide sufficient clarity and consistency of structure to make a practical lens beyond a certain size. In addition, the single lenses in a large eye may have problems with diffraction that are not noticeable in a smaller eye [121].

There are two clear benefits to a large eye. There is ample room for a large receptor field on the retina and a long distance between the lens and that receptor field. As in a digital camera, acuity or resolution is based on the number of activated receptors. A large eye can hold more receptors and therefore has greater potential acuity. The greater the distance between the lens and the retina, the greater the image on the receptor field. In mammals, the eyes are usually spherical so that the size of receptor field is directly proportional to the diameter of the eye. Not all parts of a spherical eye are important to image quality, however, even though they contribute to its weight. Birds have adopted an eye shaped like a flattened disc, which offers a saving in weight without decreasing the diameter of the receptor field (Figure 1.3).

Even unusual eyes require special accommodation in the bird's head and leave little room for other structures in the skull. The eyeballs are so tightly fitted that their backs press on each other and are separated by only a paper-thin sheet of bone. They squeeze the brain into the back of the skull and restrict the neural connections for the olfactory system to a narrow channel along the midline.

The flattened disc is a particularly suitable shape when it comes to fitting a large eye into the avian skull. In general, bird skulls tend to be long and narrow, but some are more exaggerated than others. For instance, cormorants have a particularly narrow skull that is much less bulbous than that of a typical bird. They accommodate their flattened eye discs by placing them more or less back to back so that their maximum diameter lies parallel to the long axis of the skull. The arrangement places the eyes on the side of the bird's head, where they give a very broad field of vision that helps the bird detect threats over a wide arc and provides a good general view of the surrounding environment. Unfortunately, it significantly reduces opportunities for binocular vision and these birds have only a small wedge

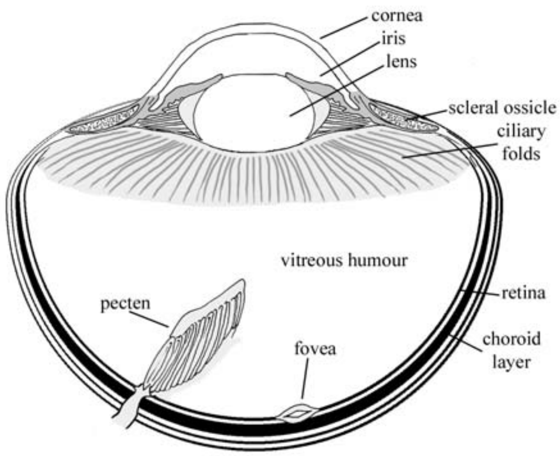

Figure 1.3 The flattened disc of the avian eye in cross-section. The view looks into the right eye. The pectin is an elaborately folded structure with many blood vessels that carries nutrients to the internal tissues of the eye (after G.R. Martin [121]).

of overlap in the visual field, directly in front and above. Such an arrangement is somewhat surprising in an active predator that uses its sight to pursue prey. Perhaps cormorants modify their hunting behaviour to accommodate this shortcoming.

There is evidence for special behaviour in other active predators that depend on effective binocular vision to locate prey in three dimensions. Falcons are high-speed aerial hunters that need the enhanced visual acuity provided by exceptionally large eyes. They have a wider type of skull than a cormorant but must still make do with a much narrower wedge of visual overlap than humans. To get the clearest possible image of a prey item, a predator needs to place the image of its target near the centre of the retina, in the most sensitive part of the eye. In a falcon, that region is not within the area of binocular overlap, so the clearest image can be held in only one eye at a time. If it tried to keep the clearest possible target image straight ahead in its line of flight, it would have to turn its face about 40° to one side. It would then present the side of the head to the oncoming air and increase drag by as much as 50% [210]. To avoid the energetic costs of additional drag, a falcon uses a specialized behaviour that makes the best of its skull design. It attacks obliquely, spiralling in on the prey in a way that keeps the target in the best part of one eye's visual field [211]. Auks are also high-speed predators but they chase fish underwater. Water is a much denser medium than air, making drag an even greater issue. It is not surprising, then, to find that auklets also make use of a spiralling attack.

Predatory birds generally have larger eyes than other species of similar body size [83]. A hawk's eye is about 1.4 times bigger, and an owl's eye about 2.4 times bigger, than that of a grouse. Because a larger eye resolves objects at greater distances, a large predator can see a sparrow at a much greater distance than a sparrow can see another bird of its own size. This kind of increased ability to resolve small objects is particularly useful to birds that attempt to fly through forests at high speed.

Although falcons and hawks are spectacularly effective hunters, their overall design is not very different from that of other birds. In comparison, owls are far more specialized predators and have evolved a suite of unique features. Unusual feather construction gives them nearly silent flight; special facial plumage and modifications to their skull enhances their highly sensitive hearing; and a specialized optical system gives them binocular vision that is exceptionally effective at night. The eyes of other avian predators are merely large versions of the flattened discs found in most birds, but the eyes of the owl have a unique tubular shape (Figure 1.4). Much of the outer disc has been lost, leaving only the central core. Where a ring of small bones, or scleral ossicles, strengthens the flat surface of the eye in most birds, owls have platelets that stand on end to form a tall supporting collar, giving the eye a peculiar columnar shape that looks and functions like a short telescope. It allows the owl's eye to retain a great distance between the lens and the retina while fitting into the limited space in an owl's crowded skull. The narrow tubes lie beside each other on the owl's flat face to give the owl an unusual degree of binocular vision.

Most owls do not fly at high speeds but use their high-resolution eyes to hunt in poor light. Compared with a hawk, their receptor field is rather small for the

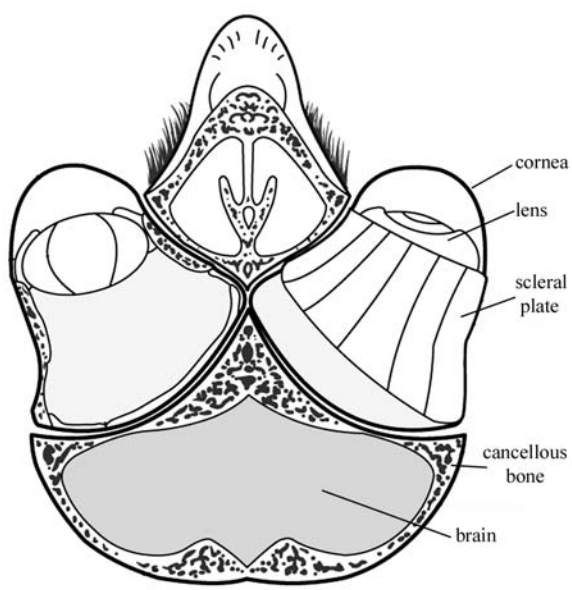

Figure 1.4 The specialized eyes of an owl. The left eye is shown in cross-section (as in Figure 1.3); the right eye is shown with the supporting tube of scleral ossicles in place. Note the relative sizes of the brain and the eyes (after G.R. Martin [121]).

large lens, but the lens concentrates as many photons as possible onto the small retina, providing the owl with an intensely lit image of a small patch of habitat. In combination with excellent binocular vision, this makes the owl an exceptionally efficient predator.

Owls are not the only birds that specialize in nocturnal vision. The tropical Oilbird is a fruit eater that roosts deep in caves where there is no light at all. In the absolute darkness of the caves, it may depend on a primitive form of echolocation and its sense of smell to find its way about, but its eyes are specially constructed to function in extremely low light. "The retina is dominated by small rod receptors arranged in a banked structure that is unique among terrestrial vertebrates. This arrangement achieves a photoreceptor density that is the highest so far recorded (1 million rods/mm^2) in any vertebrate eye" [122]. In fact, the Oilbird has 2.5 times more rods than any other bird; in order to fit, they are arranged in banks like those found in some deep-sea fish. Photons that pass through the first layer of rods appear to be picked up by deeper layers. The structure provides extreme sensitivity at very low light levels. It comes at a cost, however, and the Oilbird may find it difficult to resolve visual information into a detailed image.

The Beak, Taste, and Olfaction

The beak is usually the most prominent of the bird's three exposed structures, and is perhaps the most flexible in evolutionary terms. Its shape offers clues to the bird's food habits and frequently makes a colourful contribution to its owner's repertoire of displays and signals. Probing, tapping, or gaping with the beak is often an important part of courtship behaviour or territorial defence. Nonetheless, it is primarily a feeding apparatus that varies in shape from group to group according to food preferences. Most birds use it as a basic set of pincers or snips, but others may call upon it to function as a chisel, spear, or sieve. Herons, cranes, and storks have simple, elongated beaks for picking up small prey, but the length is important if the bird is to hold struggling prey away from the all-important eyes. From a distance, the long bills of shorebirds look like they might be as hard and sharp as a heron's, but they are sensitive probes. The blunt tip of the beak in a Dunlin is as soft and sensitive as a fingertip and it is well irrigated with blood.[5] It can sense the movement of tiny worms hidden deep in fine mud, and its tip can open, without moving the whole jaw, to pick items from their hiding places. In contrast, the tip of the beak in a goose or parrot is a robust and rigid structure that acts as a hard-edged set of sharp shears that can tear through the toughest vegetable fibres.

Even the most robust beaks include some sophisticated structures and specialized components. Near the tip, there are spaces for tiny taste organs and other sensory receptors that help the bird sort out edible from inedible items. Usually

[5] Artists who work from dead specimens often portray them with needle-sharp beaks because the soft covering shrinks and collapses as the blood in the tip dries.

these sensors are concentrated along the margin of the upper bill, where there is some risk that the continuously growing sheath of the beak might cover them over. They must be kept clear, and birds frequently trim their beaks by wiping their edges against some hard object. The cuttlefish “bone” given to captive parrots helps them wear away the rapidly growing edge of the beak and keep the sensitive areas exposed.

The finches on the Galapagos Islands have perhaps the most famous beaks in history. The structural variety among the beaks was a key piece of evidence in Darwin’s development of the theory of evolution. Recent evidence suggests that they have even more to offer astute observers. The islands undergo long cycles between slightly wetter and slightly drier climates. The seeds that the finches eat get larger under the moist regime and smaller under the dry regime. Apparently, the length of the beak changes within some species so that new generations of birds can handle changes in the size of edible seeds [73].

The hard, smooth surface of the outer beak hides a great deal of internal complexity that is not associated with feeding – at least not directly. The mid section of the upper beak covers and protects any organs of smell that the bird might possess. A number of thin bony plates above the palate often turn the nasal area into a convoluted maze of chambers lined with a thin layer of sensitive tissue that collects odours carried on the inhaled air. The tissue’s blood supply also helps to warm air coming into the body and conserve moisture as it is exhaled. If a sense of smell is unusually important to a bird, this central section will also include large bony nostrils. Large nostrils and large eyes in Old World vultures suggest that they have both a keen sense of smell and keen eyesight, but it is not immediately obvious which sense they use to find their prey. The great medieval ornithologist Frederick von Hohenstaufen tackled the question in some of the earliest experiments of modern science, and concluded that they could not find food by scent alone.

The openings created by the nostrils lead directly to the lungs, and one might expect flooding to be a potential problem for birds that dive underwater. Species that plunge into the sea from 30 or 40 m up, such as gannets, boobies, and pelicans, would face a more extreme challenge if they had not done away with the nostrils by sealing them within the sheath of the beak. Needless to say, such birds hunt by sight alone and have little or no sense of smell. Other seabirds, such as petrels, make great use of their sense of smell to find food across stretches of open ocean, and have large, well-developed nostrils. Birdwatchers sometimes exploit this sensitivity by spreading fish oil on the water to attract petrels within binocular range. Petrels do not plunge violently into the water so there is no high-pressure rush of water into the mouth. When they put their head beneath the surface, a small plug of cartilage beneath the tongue seals the inner airways. It is adequate to protect the air passages of shearwaters and other diving petrels that swim to depths of 70 m or more [229]. A similar simple device protects the lungs of auks and loons.

Although modern birds do not have teeth in adult life, the embryos develop one and sometimes two “egg teeth” before they hatch. The egg tooth is usually a small deposit of white bony material that collects near the tip of the beak and is used by the fully grown embryo to crack the egg's shell. If a second egg tooth develops, it appears near the tip of the lower mandible. Typically, an egg tooth will drop off very soon after hatching, but a fledgling Marbled Murrelet may keep its upper tooth for a month or more after heading out to sea. It is quite large and, when it catches the light, the white flash offers an easy way to distinguish recent fledglings from slightly older birds.

In most birds, the horny beak is no more complicated than a pair of chopsticks. Like the set of chopsticks, it is an excellent example of how an elegantly designed but simple tool is capable of many functions. Like that set of chopsticks, however, the beak is useful only because it is manipulated by a complex and sophisticated hand. The "hand" in this case is the avian jaw, an assembly of small bones that is far more complicated than anything found in mammals. Where mammals have two robust bones that work against each other, birds have nine or more small bones that sometimes work together and sometimes in opposition (see Chapter 2). Special hinges allow the upper jaw to rotate against the skull, and the arms of the lower jaw can flex outward near their midpoints. Both actions increase the gape and enable the bird to cope with inconveniently shaped foods. Unlike the bones in other parts of the skeleton, some bones in the anterior part of the jaw are not attached to muscles. They are passive pushrods or levers bound by ligaments to bones further back in the mouth that do have their own muscles. The action of a bird's jaw has more in common with the shuttling of a mechanical loom than the relatively simple grip of the human hand.

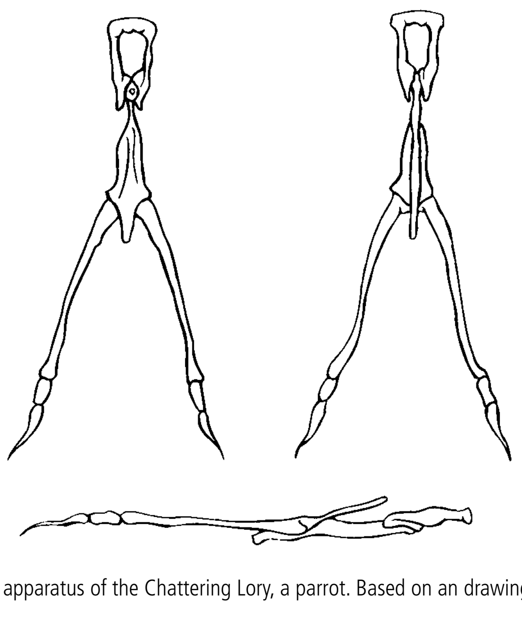

Figure 1.5 The hyoid apparatus of the Chattering Lory, a parrot. Based on an drawing by G.V. Mivart in F.E. Beddard [8].

If a bird's jaw functions as its fingers, the tongue is its thumb. Birds have a very non-mammalian tongue that is useful in the initial stages of handling food. It is neither soft nor fleshy and has its own internal skeleton, called the hyoid apparatus (Figure 1.5). The outer surface of the tongue is sometimes armed with arrays of little spikes that hold food in place or help direct it into the gullet. When a puffin is already holding one fish but wants to catch another, it uses its spiky tongue to hold the first fish against the roof of its mouth until it can chase and catch the next. Sometimes it uses this trick to bring home a dozen small fish to its nestling.

The beak and jaws are useful as a "hand" for the bird because the avian neck is a very capable arm. The structure and function of the neck is discussed with other parts of the skeleton in Chapter 2.

Ears and Hearing

A bird's ears are not marked by external structures. In some owls, facial feathers may reflect sounds towards the ear's opening, but typically there are no external structures, only a narrow canal leading to the inner ear. In spite of the ear's small size, many birds depend on songs and calls for social interaction.

The Avian Head

The concentration of the bird's most important sensory receptors close to its only feeding apparatus has had a profound effect on the design of the head and the organization of its component parts. The avian head is one of the most specialized structures in nature.

As in all vertebrates, the shape of the bird's head reflects the fundamental function of the skull as a case for containing and protecting the brain. In spite of the slanderous implications of the term "bird-brained," the bird's brain is almost as large and well developed as that of a mammal of similar size. In its efforts to contain a large brain, very large eyes, and mobile jaws, the avian skull has gone through a series of evolutionary contortions that are rather similar to those that accommodate the large brain in humans. Our face has rotated "forward" on the skull so that the eyes face front when we stand erect. In strict anatomical terms, our face has rotated ventrally and now lies on the same surface as our belly. This movement allowed our brain to curl and to expand into the spacious dome formed by the skull so that its ventral surface now faces downward. The faces of some birds have also rotated forward, and birds are the only other kind of terrestrial vertebrate with a large spherical head. Their brain has retained its primitive orientation, however.

In a primitive vertebrate, the brain is small and elongated, with a long axis that lies on the same plane as the long axis of the skull. This arrangement offers ample space in the head for eyes and other sensory organs without the need for long neural connections. The bird's brain has retained some of its primitive orientation to the spinal cord in spite of its enlargement. Unfortunately, when the brain of a bird is illustrated in a textbook, it is usually shown in a prone position without the surrounding braincase, and its orientation within the skull of the living animal is not

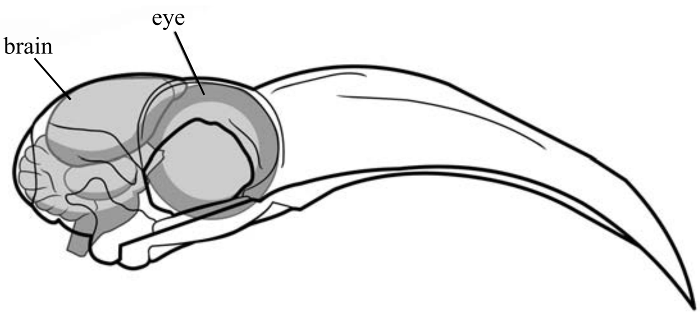

Figure 1.6 Relationship of the brain and eye in the skull of a Yellow-billed Hornbill.

at all obvious. In fact, such illustrations are misleading and unhelpful because the bird's brain typically stands on its end. It is not rotated or folded forward like the human brain.

We have already seen that the bird's eyes are so large that they press against each other at the midline. In many birds, there is no room for the brain to sit between or beneath them. Consequently, the brain sits vertically in the back of the skull, its long axis lying across the long axis of the skull (Figure 1.6). This posture may increase the effectiveness of important neural connections. Vision, the most important sense in birds, depends on the quick integration of vast quantities of visual data. Shorter nerve connections between the sensors in the retina and data processors in the brain speed the bird's response in an emergency or when presented with an opportunity to feed. In the vertical posture, the optical lobes are virtually pressed against the backs of the eyes, so the optic nerve is very short.

The peculiar vertical posture of a typical bird's brain allows it to maintain a simple linear arrangement with the spinal cord that is not much different from the relationship between the brain and spinal cord in the most primitive of vertebrates. In species where the brain's axis lies across that of the beak, only the bones of the skull have changed shape. Those above the eyes have become greatly elongated to allow the beak to rotate forward onto the same surface as the belly. The bones between the ears and around the brainstem have remained more or less unchanged. The most extreme example of these changes appears in the skull of the American Woodcock [32]. If the beak were held horizontally, the back of the skull would be tipped backward about 30° beyond vertical, to the point where the woodcock's brain would be lying on its back. The beak normally points downward in life, however, and the woodcock can enjoy an unequalled view of predators in the sky even as it probes for earthworms in soft soil.

Not all birds have a brain oriented across the beak. As mentioned earlier, cormorants (and some other diving birds) have unusually elongated skulls and their brains and beaks lie on the same plane. Consequently, they look somewhat primitive and often rest with their beaks pointing skyward. In keeping with the simple linear arrangement, the opening for the spinal cord, the foramen magnum, lies

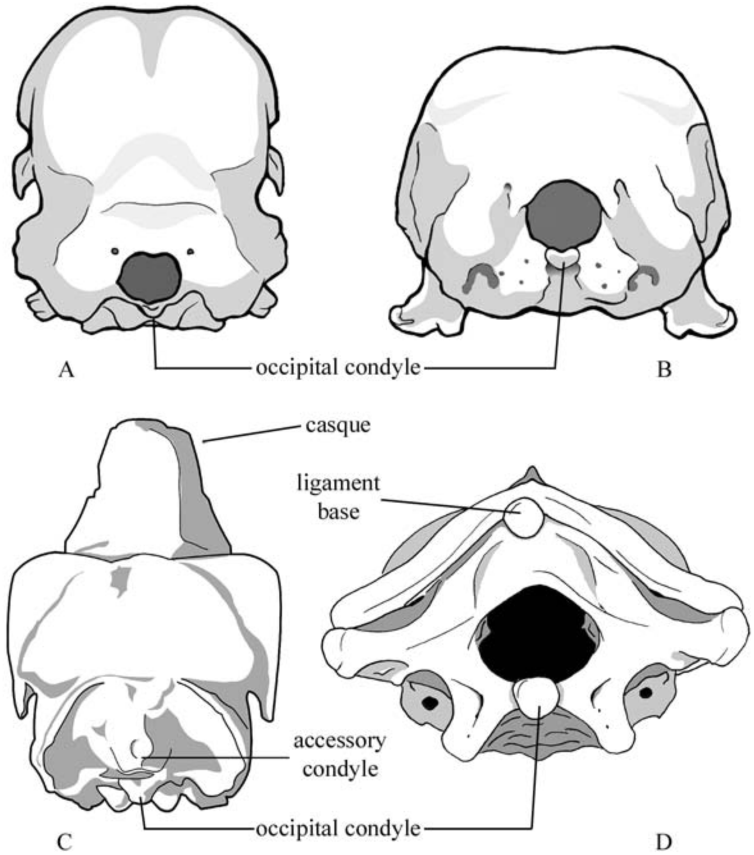

Figure 1.7 Caudal or posterior views of the skulls in four birds, showing the positions of the foramen magnum and occipital condyle. (A) Hoatzin; (B) Black Currasow; (C) Ground Hornbill, with an accessory condyle that articulates with the atlas and supports the weight of a large casque on the skull; and (D) Double-crested Cormorant, with a large boss above the foramen magnum for the attachment of very large neck ligaments (A and B adapted from drawings by M.L. Vidiera Marceliano [218]).

centrally in the base of the skull (Figure 1.7), just above the nub of bone, the occipital condyle, that articulates with the first vertebra of the neck.

In other birds, the expansion of bones in the skull included the forward components of the braincase and it ballooned into a large, smooth dome. Because the bones near the brainstem did not expand, the skull appears to balance across the top of the neck, as it does in humans. The extent of this process has been highly variable; consequently, the foramen magnum and its associated connection to the neck may vary from a position on the "back" of the skull to one that lies beneath it (Figure 1.7). Anatomically speaking, the location of the brainstem has not changed but the bones of the skull have slid into new positions around it. As in humans, the migration of the face onto the ventral surface of the body is the most immediately apparent result of this process.

The compact arrangements of the avian brain and optical systems contrast sharply with the more attenuated arrangements of the olfactory system. Most birds make little use of their sense of smell and it is unlikely to be involved in any sort of emergency response. There is therefore little risk to the bird in having relatively long nerves between the sensitive tissue in the nostrils and the olfactory lobes in the brain. The olfactory impulses from the midsection of the beak must make a relatively long journey to the brain, through an arch of bone on the midline of the skull that passes over the eyes. New Zealand's nocturnal kiwi is one of the few birds that use a keen sense of smell to find its prey. The kiwi's skull is exceptionally long and allows the olfactory tracts to extend far forward towards nostrils at the tip of the beak. The eyes are exceptionally small and leave ample room in the skull for a specialized olfactory system, complete with large and rather mammal-like olfactory lobes.

Moving through the External Environment

Feet, Legs, and Terrestrial Locomotion

Near the tail end of the bird, scaly legs hold the body off the ground. Just as the feathers create the outer bird and mark it as a flying animal, the well-developed legs mark the inner bird as an active pedestrian, descended from a long line of walkers and runners. Legs are a fundamental feature of birds; many species are flightless and some of those are wingless, but no bird is legless.

In the limbs of most vertebrates, long bones of roughly equal length meet at a major hinge formed by the elbow or the knee. In primitive vertebrates and mammals, a large single bone (humerus or femur) is attached to the body and the outer unit consists of paired slender bones (radius and ulna or tibia and fibula). Birds have moved a long way from that basic pattern. Their hind limb includes three large long bones (femur, tibiotarsus, and tarsometatarsus) and the remnant of a fourth (fibula). As a result, birds have two major joints between the hip and the toes (Figure 1.1).

The femur is the leg bone that lies closest to the body. It is deeply buried in a mass of muscles and completely screened from view by a covering of feathers. Many bones found within a bird's body are thin and flexible, but in spite of its position deep in the thigh, the femur is one of the largest and most robust bones in the skeleton. Its strength reflects its importance in transferring the weight of the body to the legs. In a large dinosaur, the femur, like the other bones in the leg, was a simple column; in birds, it is a much more complex structure. It is usually slightly bowed and twisted, suggesting that it is designed to resist an array of conflicting forces. The right-angled ball-and-socket joint that forms the hip generates some of those forces because birds have abandoned the simple upright posture of a dinosaur. When a dinosaur stood erect, its femur, the tibia, and the fibula were held almost vertically; when the bird stands up, in its "at-rest" posture, the femur is suspended at an angle, almost parallel to the ground. This posture is maintained by tension in the thigh muscles, which are attached at several points to the femur, where they generate shearing forces in the bone that can only be accommodated by increased size and strength. The muscles twist the femur against the hip joint and subject it to almost constant strain unless the bird is lying on its belly or floating on water. Because it is held horizontally, the femur contributes little to the bird's length of stride.

Two long bones of roughly equal length make up the externally visible part of the leg. Both are derived from the fusion of several embryonic bones. The one nearer the body includes a bone of the leg (tibia), roughly equivalent to the mammalian shinbone, and a fused collection of small ankle bones (tarsals). It is called a tibiotarsus. The outer segment of the limb is constructed from a mixture of ankle and foot bones (metatarsals) and is called a tarsometatarsus. Frequently, the tarsometatarsus is the only visible portion of the hind limb. The neighbouring tibiotarsus is often hidden by a skirt of long feathers. These specialized lower limb bones have no precise equivalent in a mammalian limb and there are no widely used common names for them.

In very long-legged birds, the tarsometatarsus and tibiotarsus usually have very similar lengths. When the leg bends at the ankle, the equal length of the two long bones allows the body to move straight up and down like a scissors-lift. If the two bones were of different lengths, long-legged birds might have considerable difficulty sitting squarely on the eggs. Instead, they can place the egg between their feet and confidently drop straight onto the nest cup as the leg folds. The normal resting posture of the leg bones may also be of significance before the egg is laid. Because the femur is almost horizontal, the knee lies forward of the main body cavity so that the upper part of the limb can reach around the front of even a very large egg. The space behind the knee allows the egg to be much wider than the hip joint without interfering with the bird's ability to walk. In straight-legged dinosaurs, the eggs could not have been wider than the hip joint. In their case, the egg size was further limited by the passage of the oviduct through a solid ring of bone formed by the pair of pubic bones. In birds, the tips of these bones do not meet.

The great majority of birds are terrestrial pedestrians, so it is not too surprising that many share a similarly shaped tarsometatarsus. It is usually one of the longest bones in the leg but it may be short and stubby, especially in groups that do not do a lot of walking. It is very short in swifts and hummingbirds, which use their limbs only when perching or moving around the nest. They have such tiny feet that they have been placed in the Order Apodiformes, a name that means "footless." The tarsometatarsus is also stubby in the frigatebird, a seabird that not only does not walk but apparently does not swim and spends much of its life in the air. Like the Apodiformes, it uses its feet only when roosting. In waterbirds, such as grebes and loons, that swim actively, the tarsometatarsus is often flattened, as though it were designed to move through water with little resistance (Figure 1.8). One of the

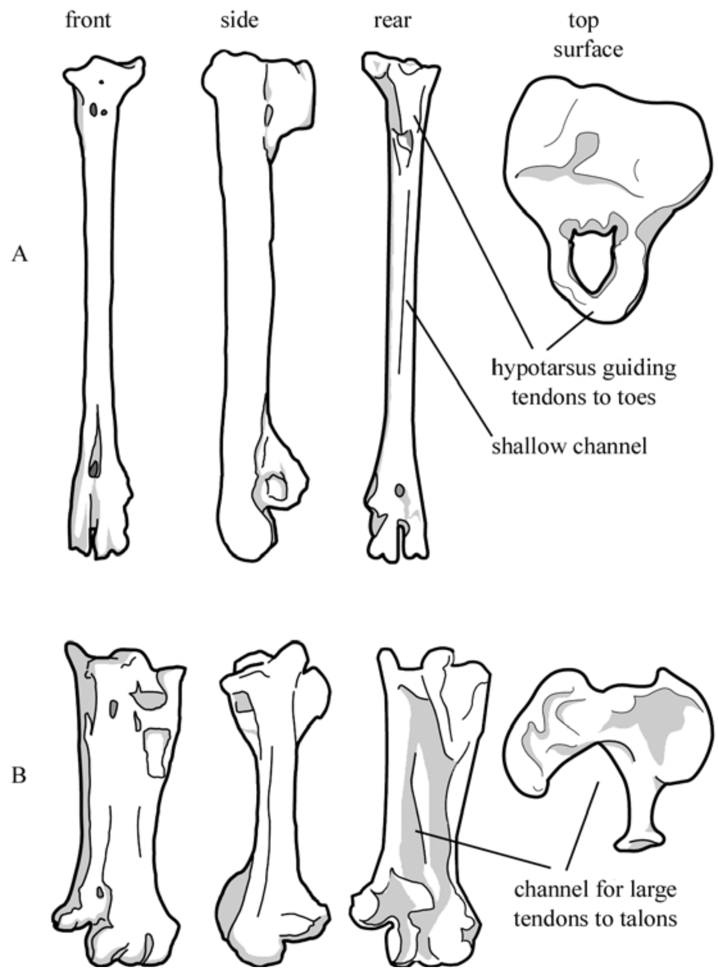

Figure 1.8 Two extremes in the shapes of the tarsometatarsus. In (A), the Yellow-billed Loon, it is a flattened box with modest channels, front and back, for tendons to the toes. In (B), the Northern Hawk Owl, the bone has become a broad, protective trough for the massive tendons that close the talons.

most spectacular modifications occurs in tarsometatarsi of predatory birds. The bone is shaped like a long trough to carry the robust tendons that operate the killing feet (Figure 1.8).

In many familiar land birds, the absence of muscles along the tarsometatarsus makes it look like a particularly fragile and sticklike bone, but it is usually much the same diameter as the neighbouring tibiotarsus. The tibiotarsus, however, is buried within the large mass of muscles that make up the familiar "drumstick" in a chicken or turkey. Except during extreme contortions, the muscle-covered bone is hidden beneath a skirt of long feathers.

The tibiotarsus is accompanied by a thin splint of bone that is all that remains of the fibula. The upper end of this vestige widens to meet the knee, but the lower tip just trails off into gristle without ever reaching the ankle. It is often used as an example of how birds eliminate unnecessary weight in the outer parts of the limbs, where decreased bone mass can help to reduce problems of inertia and momentum during active movement. In dinosaurs, the fibula usually articulated with the ankle bones.

At the outer end of the bird's leg, the toes form the most variable part of the limb. They offer valuable clues to the bird's lifestyle and may vary in number and position as well as shape and size. Typically, the claws and the covering scales are more dramatically modified for special functions than the underlying bones. The toes of raptorial predators are among the most familiar examples. Their tips are armed with long talons and their soles have a thick armour of large, rough scales to secure wriggling prey. These killing feet quickly subdue prey and reduce the risk of injury to the predator's sensitive head. Climbing birds also have curved claws and rough scales on the toes, but they are designed to grip tree bark and the talons are neither as thick nor as sharply curved as those of raptors. Birds that live in the water tend to have short claws; the skin of their feet is soft, especially if the feet are important heat radiators. The thin web between the toes is flexible for swimming but must also be durable enough to withstand the wear and tear of walking on dry land. Grebes are waterbirds that lack webbed feet. Their paddles are formed from expanded scales that grow along the sides of the toes so that each digit acts as a paddle. Similar structures appear in several unrelated groups of birds, such as phalaropes, coots, and fin-foots.

Many seabirds put their webbed feet through real torture tests. The web of skin between their toes must be both soft and tough. Seabirds nest on craggy islets and must be able to walk around on sharp rocks or excavate deep nesting burrows in stony soil. In the breeding season, their claws are worn to blunt nubs, like those of a dog. The young hatch with large, soft feet that are ideal points of attack for the ticks that swarm in many colonies. The webs heal quickly but their surface may bear scars from these parasites throughout the bird's adult life. On the water, most seabirds use their feet only for slow paddling on the surface. Consequently, worn or damaged webs and even serious injury to the foot need not be a serious problem. It is even less of a problem for the many species that use wing-propelled locomotion underwater.

The number and arrangement of toes is one characteristic of birds that varies from group to group (Figure 1.9) but is not a particularly useful tool for classification. There is not a clear relationship between foot structure and other taxonomic characters. The similarity of the toe arrangements may be merely superficial. In the single most common format for toes, three forward and one back, there is a choice of six different arrangements for the underlying plantar tendons that manipulate the digits. In addition, toe arrangements that might be described as rare or specialized tend to be just another unique feature for groups of birds that are

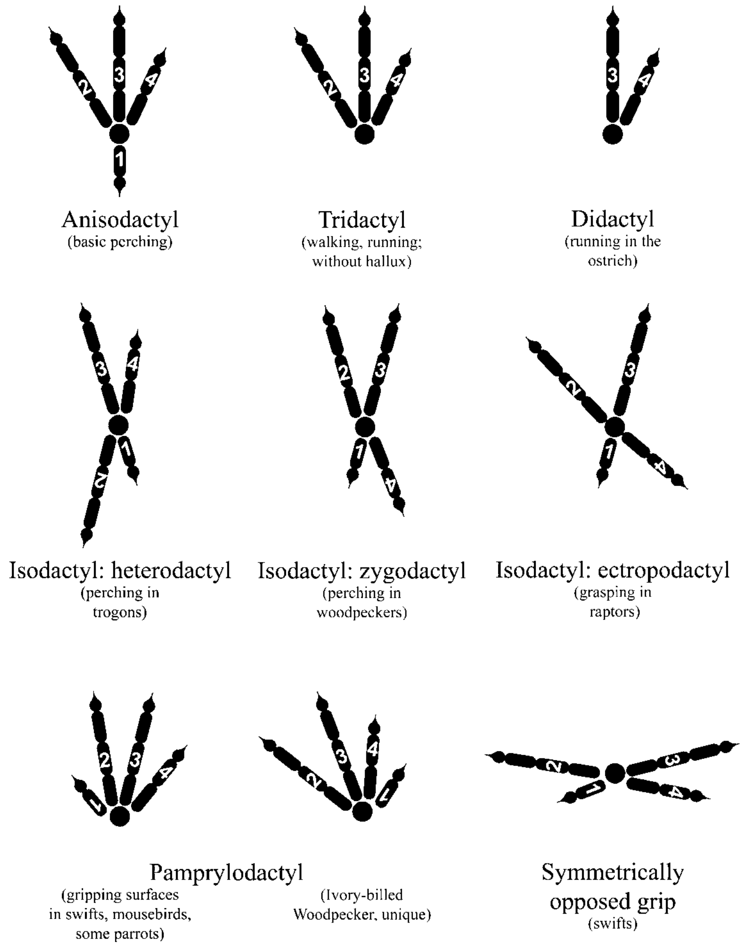

Figure 1.9 The basic arrangements of toes in birds. Most of the isodactyl arrangements appear to be adaptations for perching, but the ectropodactyl form seen in owls and ospreys gives the tips of the talons a very wide spread for grabbing prey. The unusual "opposed grip" seen in swifts is likely a minor modification of the isodactyl type. It is also found in chameleons but is otherwise very rare in nature.

already difficult to classify because they have an abundance of other unique or unusual features.

Two, three, or four toes may fan out from the knuckles of the tarsometatarsus in ways that are better clues to lifestyle than to family relationships. Three-fourths of all birds share the most frequently encountered toe formats, while some closely related families have an assortment of feet. For instance, among the Charadrii-formes, gulls, terns, and auks have webbed feet but sandpipers and plovers include species with and without webs. Phalaropes have lobes on their toes like a grebe, whereas others, such as the oystercatcher, have simple toes but have lost the hallux (digit 1) at the back of the foot.

Wings and Aerial Locomotion

Although much of a bird's skeleton reflects the importance of the pedestrians in its ancestry, it is not the ability to walk or even run and swim that has generated interest in birds; it is their ability to fly. Flight is the key characteristic that has enabled birds to occupy every conceivable terrestrial habitat and has played a major role in their successful invasion of the high seas. One might argue that flight has enabled penguins to invade Antarctica, even though they "fly" only underwater.

Except for the penguin's specialized flipper, the modern bird's forelimb is completely adapted for aerial flight. It, and it alone, provides the motive power for aerial locomotion. Unlike the legs or other structures with which the bird interacts with its environment, none of the wing's living structures are visible. The ancestral bird, *Archaeopteryx,* had naked fingers on its wings, but today only the nestlings of the South American Hoatzin have exposed digits. It is a temporary condition and these curious structures are gradually absorbed as the bird matures. In all other birds, the feathers completely cover the fleshy parts of the limb and provide the lift needed for flight. As in the hind limbs, tendons connect to remote muscles that provide the actual locomotory power. Small muscles lie along the wing bones but these are responsible mostly for subtle changes in feather position or wing shape. The muscles that drive the wings' powerful strokes lie deep within the body, along the breastbone.

Although the forelimbs of birds have been extensively modified to serve as wings, the long bones retain the primitive characteristic of being approximately equal in length. Exceptions usually indicate that the bird has a very specialized flight technique. In wing-propelled diving birds, such as auks and penguins, the humerus is almost 30% longer than the radius or ulna. It is also arched and flattened into a shape not found in any other kind of bird. It has been suggested that the unique shape reduces drag underwater, but the reduction in profile is minimal and the purpose of this design remains a matter of speculation. It will come up again in Chapter 10, in the discussion of underwater wing-propelled locomotion.

The wing skeletons in swifts and hummingbirds are also very unusual (Figure 1.10). The humerus is short, stubby, and robust, like the femur of the leg. Deep sculpting on its surface accommodates tendons and attachments for large muscles, but it is less than 20% of the wing skeleton's length. The paired radius and ulna are also robust but otherwise not highly specialized, while the hand is hugely elongated and accounts for nearly 60% of the wing skeleton's length. No other birds possess such an unusual skeletal arrangement. Swallows soar through the air to forage on flying insects and are somewhat convergent with swifts, but their wing skeleton is similar to that of other small songbirds, with the hand less than 40% of the wing's length.

The short, thick humerus in hummingbirds and swifts may be related to their use of very rapid wing beats. Just as the robust avian femur is designed to bear the stress generated by large muscles in the hip, the stubby humerus may be the appropriate design to absorb unusual forces generated by rapid contraction of the

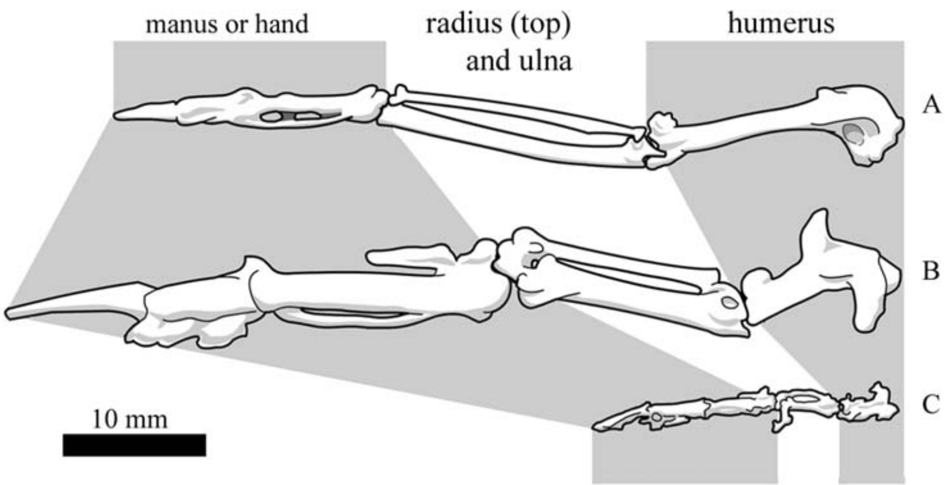

Figure 1.10 Variations in the proportions of the major skeletal elements in the wings of three aerial specialists among small forest birds. (A) A swallow (*Hirundo pyrrhonota*); (B) a swift (*Aeronautes saxatilis*); and (C) a hummingbird (*Selasophorus rufus*).

flight muscles. It is more difficult to understand why both these birds should have such large hands. Intuitively, you might expect to find smaller bones in the outer part of the wing, where the weight of bone might create issues with momentum and inertia. In fact, the size of the hand is misleading and the total contribution of the skeleton to the wingspan in hummingbirds and swifts is less than 40%. In other birds, it usually ranges from 55% to 60%. The remainder is unsupported feather.

Feathers tend to make a large contribution to the wings of highly aerobatic birds. In the swiftlike swallows, the primaries account for about 60% of the wingspan. Storm-petrels, aptly nicknamed sea swallows, are highly manoeuvrable in the air and have an almost butterfly-like flight. Unsupported feathers make up a bit over half the total wingspan. Even though albatrosses are closely related to storm-petrels, their flight style has called for a completely different architectural strategy. They use greatly elongated wing bones that support 70% of the wingspan to achieve highly controlled and efficient flight on wings that have rather short primary and secondary feathers. Other marine and aquatic birds, such as loons, grebes, and auks, tend to fly at high speeds using a very energetically expensive technique. Their wing skeletons are also rather long. In the case of the auks, which use the wings for underwater locomotion, part of that length is due to elongation of the humerus.

Arm bones are remarkably similar among all kinds of vertebrates, but the hands are often highly specialized. The nature of the avian hand skeleton has been a point of contention in the bird/dinosaur debate. Birds have remnants of only three digits, which studies of the developing embryo suggest are numbers 2, 3, and 4.

Some dinosaurs also have a hand reduced to three digits, but the fossil record appears to provide evidence for the sequential loss of digit 5 and then 4, leaving numbers 1, 2, and 3. If both the avian and the dinosaur sequences have been correctly interpreted, the bird's hand did not descend from a dinosaur's. It is not an argument that is going to go away in the immediate future. It is possible that avian digits 2, 3, and 4 slid over into positions 1, 2, and 3 during the early stages of embryonic development, but recent genetic evidence for this "sleight of hand" has not been conclusive one way or another (see Chapter 4).

The difficulty posed by the sequence of avian digits is fairly typical of a range of long-standing problems that remain unresolved in biology. They tend to be based on the observations of prominent 19th-century figures and have been successfully defended against contradictory evidence ever since. The digit sequence was first put forward by the Victorian anatomist Richard Owen and has survived a series of criticisms by embryologists in both the 19th and 20th centuries.

One of the most significant of these long-standing problems has to do with the classification of birds and the development of an evolutionary story for the group. In spite of the development of sophisticated mathematical techniques and biomolecular genetics, ornithologists have not been able to agree on a family tree for the birds. As a result, the 19th-century classification by Max Fürbringer [62] continues to influence our ideas about avian evolution. It has been updated by Alexander Wetmore and others, but its basic framework remains. Fürbringer placed the loon near the base of his tree because it seemed to have more reptilian characteristics than other birds and was remarkably similar to the toothed fossil *Hesperornis.* He placed the songbirds near the top of the tree because they appeared to have more complex anatomy and more advanced behaviour. Today, loons, grebes, and other waterbirds still appear in the opening pages of field guides.

If that were the only significant consequence of Fürbringer's tree, there would be no problem. Even though he was writing 15 years before the successful flight of the Wright brothers at Kitty Hawk, the loon's position has had a subtle influence on thinking about avian flight. It is quite easy to find derogatory comments about the loon's aerial capabilities in both the technical and popular literature. Throughout the mid-20th century, aeronautical engineers struggled with problems of lifting large loads into the air. As a result, it was only natural that biologists of the time were unimpressed with the loon's need to taxi to gain sufficient speed for take-off. It must be remembered, however, that even though the loon's method may be more labour-intensive and energetically expensive than a sparrow's quick spring into the air, high levels of energy expenditure are not necessarily a primitive trait.

We should look beyond the cost of take-off to the loon's ability to carry its heavy body rapidly across an entire continent. The loon takes advantage of a subtle paradox in aerodynamic theory. If a bird can generate enough thrust to fly very fast, it can increase its payload without a proportional increase in energy expenditure. It is already putting so much energy into thrust that changes in the amount of energy going into lift, to carry additional payload, are relatively small. Although the loon may have difficulty getting into the air, its large body can carry a great deal of fuel; once airborne, it can travel long distances very quickly. Modern jet aircraft use the same strategy by trading high fuel expenditure for a short journey. We might look at the loon as the avian equivalent of the Boeing 747, which carries its payload at high speeds but consumes huge quantities of fuel, especially on take-off. No one would argue that the 747 is a type of primitive aircraft.[6]

Victorian notions about avian flight continued to influence ornithology until 1988, when Jeremy Rayner published an important review that made the principles of aerodynamics accessible to ornithologists [176]. It covered his own work on the importance of vortices generated by moving wings and the application of fluid dynamics to avian flight [172, 173] as well as the contributions of C.J. Pennycuick, U.M. Norberg, and other theorists.

The Tail and Aerial Control

Birds often have spectacular fans of tail feathers but beneath this plumage there is little more than a small nub of flesh. Much of the tail's skeleton lies within the body, between rearward extensions of the hipbones. Only the bladelike pygostyle extends into the fleshy nub. In spite of its simple appearance, the tail's internal components give it a great deal of manoeuvrability and make it an important component of the flight apparatus. Tail feathers vary in length from family to family, according to variations in their aerodynamic responsibilities. They tend to be longest in birds that require a great deal of aerial manoeuvrability and use the tail as a rudder. They are unusually short in birds that fly at exceptional speeds or exhibit unusual levels of aerial efficiency. Many of those short-tailed birds are marine or aquatic fliers that steer by making subtle changes in wing conformation or by opening the web between their toes.

The tail of the modern bird is an outstanding example of structural centralization. *Archaeopteryx* and some other ancestral species had long, reptilian tails that may have been flexible but were not an effective shape for an aerial rudder. Also, they must have included a considerable weight of muscle and bone. The fleshy nub of a modern bird's tail contributes to controlled flight even though its movements are controlled by muscles closer to the body's core and it does not contain any muscles of its own.

Conclusion

Although most paleontologists today agree that birds have evolved from a specific group of advanced dinosaurs, just a few years ago it was the topic of heated debate and there are still some unresolved arguments and anomalies. Most ornithologists have stood aside from these debates, partly because paleontologists deal with a level

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[6] We will revisit the speed-versus-efficiency question in Chapter 10 when we look at its effect on contrasting lifestyles among seabirds.

of structural detail foreign to most ornithologists and partly because modern birds seem so far removed from their reptilian ancestors. Paleontologists may never convince ornithologists that the origin of birds has practical significance. The relationship of birds to one group of dinosaurs or another has no demonstrable impact on avian conservation, wildlife management, or endangered species issues. Many similarities and differences between birds and dinosaurs are obvious, however. Perhaps an investigation of the design of one would improve our understanding of the construction of the other, if we can avoid getting lost in the technical jargon of unfamiliar sciences.

Further Reading

The topics in this chapter are covered in some way in most ornithology textbooks. Progress in avian anatomy is generally slow, and older technical books that are often readily available in public libraries may contain information that is still current:

Chamberlain, F.W. 1943. Atlas of avian anatomy: Osteology, arthrology, myology. Michigan State College, East Lansing, MI.

Proctor, N.S., and P.J. Lynch. 1993. Manual of ornithology: Avian structure and function. Yale University Press, New Haven, CT.

Reports on research in avian aerodynamics or mathematical models of bird flight frequently appear in the *Journal of Experimental Biology.* A good start can be made by looking for papers in the 1990s by C.J. Pennycuick, J.M.V. Rayner, and U.M. Norberg. Earlier work can be misleading. Rayner puts much of it in perspective in:

Rayner, J.M.V. 1988. Form and function in avian flight. Pages 1-66 *in* R.F. Johnston (ed.). Current ornithology. Vol. 5. Plenum Press, New York.