THE CORNELL LAB OF ORNITHOLOGY
HANDBOOK OF BIRD BIOLOGY
THIRD EDITION

EDITED BY
IRBY J. LOVETTE AND JOHN W. FITZPATRICK

The **Cornell** Lab of Ornithology

WILEY

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Myrah A. Bridwell, Permissions Editor
Mya E. Thompson, Online Content Director

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Preface

At this very moment, somewhere on earth, the sun is rising and a dawn chorus of birdsong welcomes the new day. This never-ending avian symphony has been performed non-stop for millions of years, yet our scientific understanding of avian biology still improves with every passing year. This third edition of the *Handbook of Bird Biology* is intended as a current and helpful guide into the spectacular richness of bird diversity and the wonderful and varied ways that birds look, behave, display, function, and evolve.

The third edition of the *Handbook* extends a tradition that began in 1972 when the Cornell Lab of Ornithology first offered a Home Study Course in Ornithology to the general public. That early correspondence course comprised nine seminars on different topics, all written by the Cornell Lab's Director at the time, Dr. Olin Sewall Pettingill, Jr, an ornithologist known for helping connect recreational birdwatchers with scientific advances in avian biology. The first Home Study Course students received nine units of mimeographed sheets sent through the mail. Over the subsequent two decades, the materials increased in length and sophistication as the Home Study Course evolved and expanded. More than 10,000 students successfully passed their mailed-in exams and completed the course.

This material was expanded and modernized as it was incorporated into the 2004 second edition of the *Handbook*, which was produced as an impressively hefty single-volume book co-published by the Cornell Lab of Ornithology and Princeton University Press. It became a multi-authored endeavor with 11 chapters written by experts in their respective fields, each of whom lent their own personal style to explaining why birds look, act, and function in the ways that they do. The second edition remained the foundation of the continuing Home Study Course, used by an additional 5000 students from 65 countries. The book was likewise adopted as a textbook for many college-level ornithology courses and enjoyed as a general reference by many

individuals interested in learning more about birds, even outside of any formal or informal coursework.

This third edition, published in 2016, represents an even more extensive overhaul of the content, presentation, and coverage of the *Handbook of Bird Biology*. The new edition's 15 chapters have been authored by 18 expert ornithologists, including five authors who extensively revised their well-regarded chapters from the second edition and 13 who contributed entirely new material. The new content includes extensive and expanded coverage of hundreds of recent discoveries and insights about avian ecology, behavior, evolution, physiology, anatomy, and conservation.

Given that birds are so visually appealing, it is appropriate that the new edition be presented in full color, a first for any general textbook of Ornithology. The 1150 photographs, illustrations, and figure elements depict hundreds of bird species, along with graphs and tables that explain intriguing facets of their underlying biology. The *Handbook* editors and authors express their deep thanks to the many individuals—credited in the figure legends—who generously contributed photographs or artwork to this edition.

Readers familiar with the earlier editions may notice that this edition is now global in its coverage of the world's birds and the people who study and conserve them. It includes examples featuring bird species that are collectively found literally everywhere on earth that birds occur. In addition to the venerable traditions of ornithological research in North America and Europe, exciting new discoveries are now constantly being made by ornithologists from the rest of the Americas, Africa, Asia, Australia, and islands around the world. Our hope is that readers of this book—wherever they might be—will enjoy finding out more about some of the most familiar birds that live around their homes, while also being inspired by learning about species that occur in far-away places.

A special new feature of the third edition is that it is complemented and supplemented by a wealth of online

materials found on the Bird Academy website of the Cornell Lab of Ornithology (web link: **birdbiology.org**). These resources include interactive learning modules on topics ranging from feathers to sexual selection; high-quality video and audio clips chosen to represent behaviors or phenomena discussed in the text; animations that illustrate fundamental concepts in ornithology; longer feature-length coverage of special topics; and much more. The resources are conveniently organized in reference to the corresponding chapters of this *Handbook*. We encourage all readers to use this online material to supplement their readings here. This is especially helpful for the chapters on bird song (Chapter 10) and mating behavior (Chapter 9) where there is no better way to understand these behaviors than to hear or see examples of living birds in action.

In addition to the 18 chapter authors, the creation of this third edition was possible only through the dedicated efforts of the skilled editorial and production teams at the Cornell Lab of Ornithology and Wiley. The Editors express a debt of gratitude to their Cornell colleagues whose expertise and energy brought this book to completion, including Myrah Bridwell (Permissions Editor), Rebecca Brunner (Development Editor), Alexandra Class Freeman (Art Program Editor), Kevin McGowan (Advising Science Editor), Nancy Trautmann (Education Program Director), Mya Thompson (Online Content Manager), Melissa Walker (Citation Manager), and Megan Whitman (Project Manager). We are likewise deeply appreciative of the wise input and skillful management of this project from the editorial group at Wiley, from our initial discussions with Alan Crowden and Ward Cooper and ultimate project oversight by Kelvin Matthews, through to the production oversight by Emma Strickland and David McDade, hundreds of artistic contributions to figures by Debbie Maizels, production management by Rosie Hayden, skillful project management by Jane Andrew and indexing by Terrence Halliday. We feel extremely fortunate to have had the opportunity to work with such dedicated and professional individuals and teams from both organizations.

About the Cornell Lab of Ornithology

This *Handbook* is an educational resource created by the Cornell Lab of Ornithology, a unit of Cornell University located in Ithaca, New York, USA. The Cornell Lab is a world leader in the study, appreciation, and conservation of birds. Our hallmarks are scientific excellence and technological innovation to advance the understanding of nature and to engage people of all ages in learning about birds and protecting the planet. Our mission—which we take to heart and which guides all of our endeavors—is *to interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds.*

Founded in 1915, the Cornell Lab has grown over the past century into an unusual amalgam of a university department, conservation organization, technology and engineering think-tank, and communications agency. Our staff and faculty number nearly 200 individuals, complemented by almost as many undergraduates, graduate students, and postdoctoral scholars from Cornell and from visiting institutions worldwide. Our vibrant broader community includes 400,000 citizen science participants from all walks of life and 14+ million bird enthusiasts of all ages who connect with us online at birds.cornell.edu.

The Cornell Lab is located in the Johnson Center for Birds and Biodiversity and surrounded by the Sapsucker Woods preserve. We invite all readers of this book to come and enjoy our visitor center and to go birding on our trails. If you cannot visit us in person, be sure to take advantage

The Cornell Lab of Ornithology. Located in the Johnson Center for Birds and Biodiversity, the Cornell Lab is both a unit of Cornell University and an international membership organization. Our mission is *to interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds.* (Photograph by Diane Tessaglia-Hymes © Cornell Lab of Ornithology.)

of our web resources, not only the companion site to this book but also our All About Birds website (**allaboutbirds.org**), our live cameras at active bird nests around the world (**cams.allaboutbirds.org**), our award-winning magazine *Living Bird* (**allaboutbirds.org/living-bird-latest-issue**), and our many citizen science projects (**birds.cornell.edu/citsci**) where you can get involved in collecting information that adds to our ornithological knowledge base to inform bird conservation and management.

We especially encourage all birders—from beginners to experts—to discover and use eBird. At ebird.org you can upload your own checklists and access a rich suite of resources designed to enhance your ability to find and identify birds, all at no cost. eBird is a truly global resource with web portals and partners in many languages and most countries.

We also invite all users of this book to become members of the Cornell Lab at **birds.cornell.edu**. As a nonprofit organization, we depend on our members, donors, research, and our other programs for 99% of our operating budget. These resources support the continued development of this *Handbook* and its online enhancements, along with our many other endeavors in science, conservation, education, and outreach. Your engagement supports the advancement of ornithological science and the informed conservation of birds and their habitats worldwide.

Irby J. Lovette
Fuller Professor of Ornithology
Cornell Lab of Ornithology

For additional online material please visit the
Bird Academy website of the Cornell Lab of Ornithology at **birdbiology.org**

Bird Academy Web Resources

This *Handbook* is complemented by extensive online learning resources hosted on the Bird Academy site of the Cornell Lab of Ornithology. Be sure to visit **birdbiology.org** to access the web content associated with each *Handbook* chapter. These include hundreds of videos of wild birds, interactive learning modules and features, animated and annotated sound recordings, and in-depth articles on topics of particular importance about birds and their conservation.

We particularly encourage all readers to use the Bird Academy site when reading *Handbook* Chapter 10 on Avian Vocal Behavior. The spectrogram figures seen as static images in the printed chapter are playable on the Bird Academy site as animated recordings: you can hear the actual sounds and watch the visual display of the sonogram. The direct link to that enhanced Chapter 10 content is: **birdbiology.org/vocalbehavior**.

How to report errors and offer suggestions

We encourage all readers of this *Handbook* to visit **birdbiology.org/suggestions** to let us know if you find errors in the text or have other critiques to offer. At that same web link we also welcome suggestions about additional content that could be covered in future editions, newly published studies with relevant findings and discoveries, and all other kinds of feedback that can help the *Handbook* remain a useful and current resource for individuals interested in avian biology. We pay close attention to this feedback and thank all respondents for offering their input.

For additional online material please visit the
Bird Academy website of the Cornell Lab of Ornithology at **birdbiology.org**

Chapter 1   Why Study Birds?

Irby J. Lovette and John W. Fitzpatrick
Cornell Lab of Ornithology

Birds have a special place in human science and culture: they capture our hearts, arouse our curiosities, and inspire a sense of wonder. We may revel in the diversity and simple beauty of their forms, but birds also fuel fascinations that drive us towards deeper scientific inquiries into their varied ways of life. Every student of ornithology— from recreational birders to career scientists—will find much to learn and appreciate in the extraordinary physical and behavioral adaptations of birds, their rich evolutionary history, and their commanding global presence.

One of the wonderful aspects of enjoying birds is that they are found nearly everywhere. Given that these outwardly delicate creatures must maintain an internal body temperature even higher than our own, their capacity to live in almost every environment on earth is staggering. Birds occupy windswept arctic tundra and harsh antarctic ice, fog-shrouded mountaintops and tropical rainforest understories, the world's driest deserts, and storm-swept high seas. They live amongst us in the most urbanized cities, in suburban backyards, and in the most remote wildernesses. Wherever we travel, birds are our constant companions, and by discovering more about the birds we find around us, we can come to understand many other aspects of the natural world and our relationship to it.

Birds are endlessly fascinating partly because they are so diverse. Birds make use of their myriad habitats with an almost bewildering array of foraging strategies, performing important ecological functions in the process. Many birds capture and eat other animals, from tiny insects to large vertebrates, sometimes including other birds. Some birds hunt by night, and a few even navigate by echolocation. Others hunt high in the sky with eyes far keener than our own, diving down with incredible speed and agility at a moment's notice; many are equally skilled in detecting insects on leaves or worms under the ground. Still others specialize in scavenging, thus speeding up the process of decomposition. Many birds eat nectar, seeds, or fruits, sometimes aiding in plant reproduction by serving as pollinators and seed dispersers.

The breeding strategies of birds are just as varied as their ecological roles. Many engage in complex choreography as a precursor to mating, often presenting highly decorative displays and intricate vocal performances. Some birds pair together for many years or live in extended families, while others mate only for an instant, never to see one another again. Some bird chicks are raised by groups of relatives, some by both parents, others by only their father or their mother, and a few receive no parental care at all. Some birds attempt to raise just one offspring in every alternate year, while other species can raise large broods of chicks several times within a single season. Bird nests come in a dazzling variety of forms, from simple scrapes on the ground, to intricately woven baskets, to messy piles of sticks that may weigh several tons.

Birds flap, hover, soar, glide, stoop, swim, dive, burrow, walk, hop, and even sprint. To us, they often appear—and quickly vanish—as a burst of motion and color. Through their longer movements, birds create living links among the

Opposite: This flock of Greater Flamingos (*Phoenicopterus roseus*) includes both colorful adult birds and whiter juveniles. (Photograph by Ian Davies.)

Fig. 1.01 Conifer needles are the principal food of the Spruce Grouse (*Falcipennis canadensis*). (Photograph by Christopher Wood.)

earth's continents, oceans, and hemispheres. Migratory species know the planet as a north-south stage to be traversed twice each year, generating one of the most remarkable global migration spectacles on earth. The annual return of individual birds to their precise breeding or winter territory seems almost miraculous, and this homing ability is a testament to their underlying adaptations for orientation as birds move across vast distances. Other kinds of birds are nomadic, sometimes wandering in great flocks in search of super-abundant food or prime breeding sites; yet other birds are home-bodies, remaining very close to their hatching site throughout their entire adult lives.

The songs of some birds are among nature's most evocative sounds. Birds make sounds primarily to communicate with other birds, but they do so in a great variety of ways and across a great range of auditory frequencies. For human birders and scientists, learning bird calls and songs is often the key to discovering what species are present in a habitat or location. Going further, we can eavesdrop on the more detailed lives of birds by learning how they use songs to defend territories, advertise to mates, warn of potential dangers, and communicate about their own status.

Beneath all this behavioral and ecological diversity of birds lies a remarkable vertebrate body structure and physiological potential. Birds have unique skeletons: every bird is equipped with specialized forelimbs and fused hand bones that together form a wing. Some birds' wings are proportionally too small for flight; others have wings that are modified into flippers for swimming. All birds have beaks, lay eggs, and breathe via a system of one-way airflow, which permits more efficient capture of oxygen than the in-and-out breathing pattern of mammals. Yet despite these similarities, birds have a wondrous variety of physical forms—from the smallest of hummingbirds to the towering ostriches—that are adapted to different ways of life. Their internal body processes are similarly multifarious: some birds can dive deep into water and remain submerged for minutes, others can fly at great heights where the air is thin and oxygen correspondingly poor. Different birds can extract energy and nutrients by digesting a great range of foods, from tough leaves to fluid nectar, and from tiny invertebrates to rodents swallowed whole. Some birds time their breeding based on subtle shifts in day length that cause cascading effects on their hormones and reproductive systems. Others use specialized areas of their brains to remember the locations of thousands of seeds that they have hidden for later consumption.

The external beauty of birds is enriched by their variety of feathers, which are magnificent in function as well as form.

Fig. 1.02 Scimitar-billed Woodcreepers (*Drymornis bridgesii*) are among the many bird species in which male–female pairs coordinate their songs to produce a synchronized duet. (Photograph by Ian Davies.)

Fig. 1.03 The Rufous-tailed Jacamar (*Galbula ruficauda*) uses its long bill to capture butterflies and other agile flying insects. (Photograph by Benjamin G. Freeman.)

Fig. 1.04 Penguins, like this Gentoo Penguin (*Pygoscelis papua*), have many morphological and physiological adaptations for their aquatic lifestyle. (Photograph by Christopher Wood.)

Feathers are an adaptation found in no other animal group today, but we now know that birds are the living descendants of otherwise extinct dinosaurs that also sported a great variety of feathered plumage. Feathers provide birds with thermal insulation, waterproofing, and, in many cases, facilitate their flight. Feathers come in bold or cryptic patterns, ornamental shapes, incredible shades of color, pure tones, impressive lengths, or, in just the right light, brilliant iridescence. Many birds offer a combination of these features that play a large role in both mate choice and camouflage.

There are enough species of living birds—10,000 or so—to keep the most ardent birders questing after new sightings throughout their lives. This rich diversity has evolved over 150 million years, creating the panoply of avian orders and families that populates our field guides. Over the smaller timescales that can be addressed in field studies, birds have provided some of the best examples of how evolutionary forces play out in time. Scientists have carefully documented how natural selection can change bird populations in just a few generations, and how intense sexual selection can drive the evolution of gaudy plumage and elaborate displays. Birds have therefore played a central role in our general understanding of these most basic processes by which species arise and change through time.

Birds have a similarly influential standing in our efforts to conserve the natural world. Birds serve as flagships for imperiled habitats and ecosystems, and as early warning systems for environmental toxins or other destructive forces. Conservation efforts focused on birds often help preserve many other less conspicuous organisms. And owing to their charisma and popularity with humans, birds can help inspire all of us towards being better stewards of natural systems and biodiversity.

This book is about all of these aspects of avian biology, and more. Thanks to a fortuitous combination of diversity, accessibility, and charisma, birds through the ages have taught humans an extraordinary amount about natural history. Nearly everyone on earth has seen and wondered about a bird, and this familiarity helps give birds their special inspirational power—birds capture our imagination and curiosity by simply being in our presence. Researchers over the years have harnessed this same accessibility of birds to answer questions in the laboratory and in the field with relative ease, especially compared with the challenges of studying most other animals. Dozens of principles in evolution, ecology, biogeography, behavior, neurobiology, life history theory, natural resource management, and conservation biology have been—and continue to be—discovered and refined through studies of birds. This book is intended as a tool to help all of its readers find further inspiration in the birds that form an important part of our lives.

1.1 Engaging with birds in the twenty-first century

Whether we study them as students, casual observers, lifelong learners, or professional scientists, birds can be mesmerizing any time we stop and simply watch them. At the bird feeder, at the city park, in a parking lot, at the beach, or in the woods, these creatures share the planet with us largely in disregard of our fascination with them. Pausing to observe birds employ their adaptations—those that allow them to fly, catch a fish in a flash, or show off gorgeous songs and plumage—is one of the most satisfying ways to connect personally with the details and the larger workings of the natural world. The more we watch them, the more we are likely to want to know about birds.

Today our intrinsic interest in birds can go further than ever before. We can learn, observe, and contribute to a

dynamic and unprecedented collection of knowledge about birds. Significant gaps still exist in our understanding, but by simply watching and recording birds—even the most common ones—individuals and communities can make a big difference. Birds are extremely sensitive indicators of ecosystem conditions and quality. As humans continue to alter the natural world, the status of bird populations can provide clues about the type and scale of our impacts. Which bird species are declining, and which are increasing? Which species are successfully adapting to human-modified habitats, and why? As the planet warms, are birds changing their migratory routes, or spending the winter in different places?

Among all of the ways that we can engage with birds, "citizen science" projects deserve special mention owing to the benefits they generate for both their human participants and the avian subjects of their observations. Many local and regional citizen science endeavors provide enjoyable ways to enhance your engagement with the birds in your area. On a global scale, eBird (**ebird.org**) is the most geographically widespread avian citizen science initiative of all; it is based at the Cornell Lab of Ornithology, the same organization that developed this book, with partnering organizations in many countries and resources available in most of the world's major languages. The eBird project involves simple checklists of bird sightings submitted online by birders from every country in the world. The aggregation of this vast amount of information on bird distributions allows researchers to address questions that have, until now, been impossible to pursue. By sharing observations in the same database, people from all professions and walks of life directly increase global understanding of bird populations, movements, use of habitats, and relationships with humans.

Such studies are particularly crucial as we develop strategies to facilitate the coexistence of human cultures with stable and functioning natural systems. When we take the time to listen and understand them, birds become more than captivating creatures—they reveal themselves as indicators of environmental health. All over the world, humans are taking the pulse of the planet through their interactions with birds.

1.2 A short note on the names of birds

Depending on your place of origin, you may find that some familiar birds mentioned in this book have unfamiliar names, as there is some regional variation in the "official" English names of birds, and even greater variation in their colloquial names. Similarly, there are several authoritative lists of the world's bird species that are generally in high agreement with one another, but that differ in the way they

"lump" or "split" a handful of species or higher taxonomic groups. All English and scientific names of birds used in this book follow the eBird/Clements Checklist version 6.9, which includes taxonomic updates through to August 2014. This Checklist and its more recent updates are freely accessible at **birds.cornell.edu/clementschecklist/**.

In this book, we treat the full English names of bird species as capitalized proper nouns. Group names and other variants are regular nouns and not capitalized. Thus you might read a sentence like: "Among all of the world's species of chickadees and tits, the Great Tit (*Parus major*) is one of the most widely distributed and best studied." The two-word Linnaean name (*Genus species*) is included every time a bird species is mentioned within the text in a new context or as a new example.

1.3 Birds and ornithology are both worldwide

This book is international in scope: birds are found worldwide, and ornithologists have conducted important studies of thousands of species in all of the major habitats and biomes of the earth. The discipline of ornithology is similarly global, as the scientific process of investigation is unconstrained by national boundaries and new discoveries about birds are constantly being published in scientific journals by researchers from all parts of the world.

In choosing examples to be included in this book, the authors and editors have purposefully selected species and studies that span this global breadth. If a particular example

Fig. 1.05 The Red-billed Leiothrix (*Leiothrix lutea*) is native to Asia, but its popularity as a cage-bird has led to introduced populations in other areas of the world. (Photograph by Ian Davies.)

treats a bird that is unfamiliar to you, consider whether any of the species that you know from your own region might exemplify a similar trait or phenomenon. More generally, we hope that this global breadth of examples helps inspire you to learn about the full range of avian diversity in all of its worldwide glory.

Although ornithological expertise is now truly global, in past times the scientific study of birds was centered largely in Europe and North America, and these regions still have more academic ornithologists than do some other areas of the world. The editors and authors of this book are primarily based in North America, with a few from Europe, although most of us have done field studies elsewhere. For these two reasons—ornithological history and our own familiarity—North American and European birds are somewhat overrepresented in this book in comparison to their total fraction of avian diversity. Nonetheless, readers from every other corner of the globe are sure to find examples in this book featuring birds found in their local area.

1.4 Web resources beyond this handbook

We hope that you feel excited and empowered with this book in your hands. We encourage you to treat it as an entry point into the lives of birds, for there is so much more to bird biology than we could squeeze into these chapters. This book is a product of the Cornell Lab of Ornithology, where our scientists and outreach experts have assembled a wealth of supplemental materials that accompany this book and which are free to access online. Using this book in combination with these web resources will enhance your learning about avian biology and simultaneously be a lot of fun. These online resources include video and audio files related to the material covered in each chapter; interactive, visually compelling modules that bring to life many of the principles outlined here; and much more.

Before reading further, be sure to access additional online content for this book at birdbiology.org.

Chapter 2   Avian Diversity and Classification

Irby J. Lovette
Cornell Lab of Ornithology

The more than 10,000 species of modern birds share a common ancestor, birds that probably lived about 130 million years ago (Fig. 2.01). The evolutionary tree that stretches back through time to connect present-day birds with their avian ancestors provides the basis for classifying birds into a series of hierarchical groups, from the Class Aves, which includes all birds, down to the species that form the tips of the tree's branches. These nested groups are important because they provide a system of classification that helps organize avian diversity in a way that is both evolutionarily correct and useful to birders and ornithologists.

This is a particularly exciting time for people interested in the evolutionary relationships of birds. Rapid advances in genetic technologies make it possible to access the entirety of avian genomes, providing a wealth of comparative information about living birds that can be used to reconstruct their evolutionary relationships and learn how their genes control aspects of avian physiology, behavior, and ecology. Meanwhile, spectacular fossil discoveries continue to expand our understanding of ancient birds and their affinities both to one another and to other dinosaurs. A comprehensive picture of the relationships of all living birds, and a good understanding of where they came from, is now within reach.

This chapter concludes with an overview of all orders and families of living birds. These categories are essential tools for organizing avian diversity for both scientists and birders.

2.1 Classifying avian diversity

Today there are slightly more than 10,000 species of living birds, according to the most commonly accepted classifications of worldwide avian diversity. The scientists who study this diversity are called systematists. The field of systematics involves two general pursuits. One is the **classification** of birds and other organisms into a hierarchy of taxonomic levels, such as species and families. This endeavor focuses on describing newly discovered species and on understanding the distinctions between species. The other task of systematics is to uncover the relationships between taxonomic groups and to look back through time to reconstruct their evolutionary histories. Most commonly, this historical investigation involves creating an underlying evolutionary tree, or **phylogeny**.

Classification: in an evolutionary context, the process by which scientists name organisms and assign them into larger groups based on their evolutionary relatedness.

Phylogeny (or phylogenetic tree): a diagram that depicts the evolutionary relationships connecting a set of organisms.

Opposite: Stunning *Tangara* tanager diversity. Many species in this neotropical genus frequently forage together in mixed flocks. Species, clockwise from top left: Black-capped Tanager (*T. heinei*), Brassy-breasted Tanager (*T. desmaresti*), Black-backed Tanager (*T. peruviana*), Green-headed Tanager (*T. seledon*), Silver-throated Tanager (*T. icterocephala*), Red-necked Tanager (*T. cyanocephala*). (Photographers, clockwise from top left: Andy Johnson, João Sérgio Barros Freitas de Souza, Almir Cândido de Almeida, Dario Sanches, Juan Ignacio Zamora Mora, Frank Shufelt.)

Fig. 2.01 All living birds share a common ancestor. Despite their incredible diversity in forms and ways of life, all living birds—including the (A) African Wood-Owl (*Strix woodfordii*), (B) Orange-headed Thrush (*Geokichla citrina*), and (C) Tufted Puffin (*Fratercula cirrhata*)—descend from a common avian ancestor. (Photographs by: A, Roger Wasley; B, Shashi Shankar Hosur; C, Christopher Wood.)

These two endeavors are fundamentally linked to one another. For example, an avian systematist who discovers a bird that could be a new species will likely describe the particular characteristics that help define it as a distinct entity, while also placing the new species within a broader evolutionary tree that includes other related species. Our understanding of both the classification and phylogeny of birds has improved greatly in recent years, in part because of new discoveries and in part because of technological advances.

2.1.1 Avian classification

A quick flip through a typical bird field guide will reveal that the birds in it are organized meaningfully: for example, the ducks and geese are grouped together, and they are clustered separately from other superficially similar waterbirds such as loons, grebes, or cormorants (Fig. 2.02). These groupings are based primarily on studies of museum specimens over the past 150 years

(Boxes 2.01 and 2.02; Chapter 6), and they reflect our understanding of bird evolution and the way it has played out over time as a branching, hierarchical process. For example, the ducks and typical geese are all more related to one another than they are to any members of other groups, and they are therefore classified together in the family Anatidae. Within this family, species that are even more closely related to each other are then placed within the same genus; for example, the genus *Anas* includes several dozen species of dabbling ducks, including the Mallard (*Anas platyrhynchos*) and related species of teals, wigeons, shovelers, and pintails. This classification structure allows us to place birds into increasingly inclusive categories, as shown in Fig. 2.03, in which each level includes all the members of the previous ranks, going back to the common shared ancestor of all birds. Most field guides and other references on bird diversity follow this organizational practice of putting the most closely related species together, usually by grouping together birds in the same family.
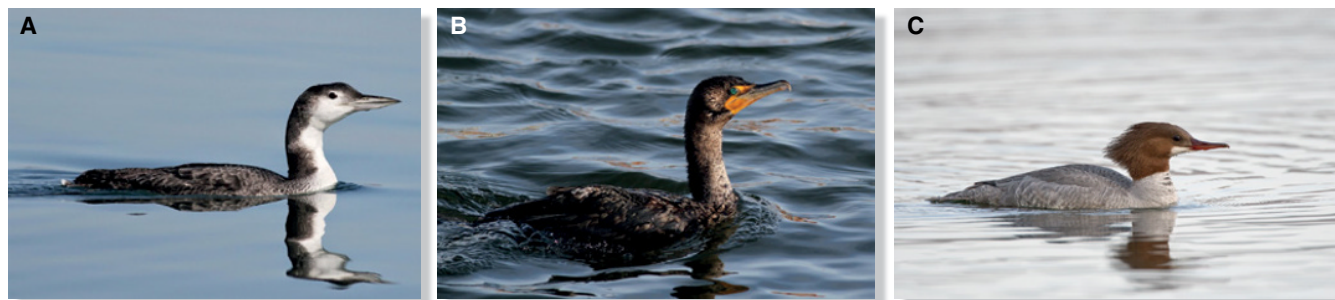
Fig. 2.02 Similar-looking birds in different taxonomic groups. Despite their superficially similar appearances, the (A) Common Loon (*Gavia immer*), (B) Double-crested Cormorant (*Phalacrocorax auritus*), and (C) Common Merganser (*Mergus merganser*) are only distantly related—each belongs to a different order. (Photographs by: A and B, Jay McGowan; C, Christopher Wood.)

Box 2.01 The importance of scientific collecting

Our understanding of living birds is founded on studies of specimens that have been collected and prepared over the past two centuries, and which now are curated in museums around the world. Some of the largest museums hold more than 1 million bird specimens, others only a handful, but all are important for the record of avian diversity they preserve.

A collection of specimens is a physical archive of actual biodiversity that records which birds were present in particular times and places, along with a great variety of information about the birds themselves, such as the habitat they were found in, detailed features of their internal and external anatomy, and the DNA content of each bird's genome. Bird specimen collections therefore are an irreplaceable resource used by a wide range of ornithological researchers and conservation professionals, as well as by students, teachers, and artists.

Although museum curators frequently salvage birds that die from other causes—such as birds that hit windows or cars, or that are caught in commercial fishing nets—and turn them into specimens, most specimens in the world's museums were collected intentionally for that purpose. The era of intense scientific collecting spanned the late 1800s into the mid-1900s, but this endeavor continues today. No ornithologist enjoys intentionally sacrificing birds, but many would argue that when done responsibly, the value of new specimens is high enough to justify the endeavor. Others disagree, and emotions can run high on both sides of the pro-collecting and anti-collecting debate.

One question often asked by first-time visitors to a large museum collection is: "Why do you need so many specimens? Wouldn't one or a few specimens of each species be enough?" For some kinds of research, one specimen is adequate, but for most studies it is important to be able to measure the degree of variation within each species. This broader sampling is especially essential in any study that uses statistics to compare different groups of birds.

A natural related question is: "You have so many specimens already; why do you keep collecting more?" One answer is that birds and their distributions change over time, and having new specimens allows researchers to study these changes. Another answer is that we can glean more data from new specimens than from older material. Current specimen preparators are careful to record every aspect they can about a bird they convert into a specimen, whereas a label on a specimen from the nineteenth century might indicate only the country in which it was obtained. Modern specimens also are accompanied by new types of materials, such as frozen tissue samples, which allow types of analyses that are impossible with older samples.

Fig. 2.03 Avian classification. The Linnaean system categorizes organisms within hierarchical levels based on their relatedness to other taxa, down to the principal unit of species—as illustrated here with the Mallard (*Anas platyrhynchos*). (© Cornell Lab of Ornithology; photograph by Randy E. Crisp.)

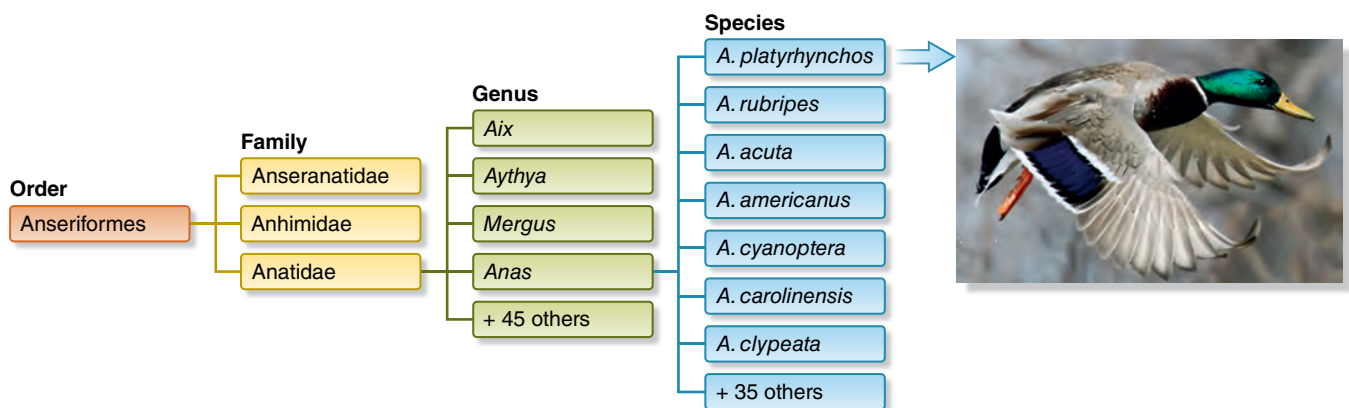# Box 2.02 Preparing bird specimens

When people think of bird specimens in a museum, they often envision the taxidermy mounts in exhibit displays that show birds in realistic postures. Specimens made for research purposes, however, almost never take on this lifelike appearance. Instead, scientific bird specimens traditionally have been prepared in one of three ways: round skins, wet specimens, or skeletons.

Most specimens are in the form of round skins, in which most of the bird's internal parts are removed and replaced with stuffing (Fig. 2.B2.01). The specimen then is dried in a standard stretched-out orientation, with the wings folded at the side and the bill pointing forward. Advantages of round skins include the ease of taking many standard measurements of structures such as the bill, wing, and tail, and the practical utility of fitting many specimens together in one museum drawer.

Making a beautiful round skin requires practice and skill. The parts of the bird that could rot must be removed, and, in the process, the entire skin is turned inside-out, stuffed, and then sewn back together. Once dried, round skins are generally stable: on opening a specimen drawer, it can be difficult to distinguish round skins that are more than a century old from those that were recently collected. Moisture and insects are the greatest threats to round skins.

Museum collections also may include wet specimens, entire birds that are first fixed using formalin—which helps keep their tissues hard—and then stored in jars full of alcohol. Wet specimens are particularly useful for studies of avian anatomy because they preserve the internal structures and organs that are destroyed when making a round skin.

Skeletons are a third common type of bird specimen (Chapter 6). To make a skeleton, first the skin and feathers are removed, along with the organs and largest muscles. Then the remaining carcass often is put into a bin containing dermestid beetles that eat the remaining fleshy tissues but not the bones. The cleaned bones later are numbered and stored in a small box.

Most specimen preparators try to maximize the information that can be gleaned from each specimen, so they also freeze bits of tissue for genetic and other biochemical analyses, and they may also preserve the contents of the crop and stomach for diet analysis.

Laws about possessing and transporting dead birds vary widely around the world. Although some museums are happy to receive carcasses of birds that have died from natural causes, it is critically important to check with them in advance to ensure that no regulations are violated in the process. In any situation in which a dead bird might become a specimen, it is essential to record exactly where and when the dead bird was found. This procedure usually is done by writing these data on a slip of paper and bagging it securely together with the bird before placing it in a freezer.

Fig. 2.B2.01 Round skins in avian research collections. This common type of museum specimen preserves the bird's external anatomy, including the plumage. When kept dry and away from destructive insects, round skins remain useful indefinitely. These specimens—including some that are more than a century old—are from the Cornell University Museum of Vertebrates collection. (Photograph by Jennifer Campbell-Smith.)

Fig. 2.04 Distinctive variants of the same species. Despite their different coloration, these two male Asian Paradise-Flycatchers (*Terpsiphone paradisi*) are members of the same species. Individuals of both forms often occur and interbreed at the same location. (Photographs by: left, Manish Panchal; right, Dr. George Mothi Justin.)

Within this classification system, the **species** is the most fundamental and broadly used unit of avian diversity. As covered later in this chapter, ornithologists have devised many definitions for what exactly constitutes a bird species, but in general terms each bird species looks or behaves differently from related species, tends not to interbreed with members of other species, and has a past history of being evolutionarily distinct from other species.

Below the species level, ornithologists may describe **subspecies**, populations that differ in subtle attributes from other populations of the species. In situations where subspecies are readily distinguished by plumage differences or other distinctive traits, they may be illustrated

Species: the basic unit of biological classification for birds. Criteria for defining bird species vary, but they generally group into a single species the individuals and populations with very similar traits, a history of recently shared ancestors, and the continued ability to fully interbreed.

Subspecies: in birds, a distinct population or group of populations within a more widespread species that is distinguishable from other subspecies on the basis of one or more diagnostic traits.

Monophyletic group: in evolutionary terms, any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

Clade: a synonym for a monophyletic group, referring therefore to any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

separately in field guides. For example, the single Barn Swallow subspecies that breeds in North America (*Hirundo rustica erythrogaster*) has reddish underparts, whereas the subspecies that breeds across much of Europe and Asia (*Hirundo rustica rustica*) has snowy white underparts (Chapter 3). Although some bird subspecies have been defined carefully and show distinctive traits, such regional variants are not sufficiently different to cause them to be treated as fully separate species. Many named subspecies, however, are the result of older studies that do not meet modern standards because of limited sampling, obsolete criteria, or a focus on subjective differences among the subspecies. Still other subspecies are known to have fuzzy boundaries, with one subspecies blending into the next where their ranges overlap; sometimes birds showing this kind of geographical variation are instead referred to as being of different *races* of the same species. Often it is convenient to be able to give a name to a truly distinctive bird population, but many birds can be assigned to a particular subspecies or race only by knowing where they were observed. At an even finer scale, some birds show distinctive variants even within a single location; the forms of these species with distinctive plumage or markings are termed *morphs* (Fig. 2.04).

Above the species level, avian taxonomy is somewhat more straightforward. When the classification is correctly assigned, every higher grouping, from a particular genus—such as the genus *Anas* into which the Mallard falls—all the way to the Class Aves—which includes all birds—includes an ancestral bird species and all of its descendants. This important criterion means that every named group of birds reflects a true evolutionary unit and that these units can be assembled into a hierarchy representative of the underlying evolutionary tree of all birds. In technical terms, these categories each represent **monophyletic groups**, or **clades**. These interchangeable terms refer to the complete

collection of evolutionary lineages past and present that share a common ancestor.

In theory, every split in the evolutionary tree of birds could be used to define one of these taxonomic categories, and some avian systematists argue for exactly this approach. Unfortunately, giving a name to every such split would result in many thousands of avian groups, and the names would change with every advance in our understanding of the evolutionary tree of birds. Instead, most traditional and current avian classifications use a much smaller group of hierarchical categories, such as the familiar levels of genera, families, and orders. Although the placement of the boundaries between these higher ranks is somewhat arbitrary and is highly influenced by past practices and our own organizational convenience, this approach leads to a manageable number of taxonomic categories. As described later in this chapter, our understanding of avian relationships is improving rapidly, so even the traditional taxonomic hierarchy of birds is being modified to reflect new discoveries about how these groups and their constituents are related to one another.

2.1.2 Naming bird species

The concept of hierarchical classification actually predates our modern understanding of evolution. The hierarchical classification system still in use today—the Linnaean System—is named after Carl Linnaeus, the Swedish biologist who in the 1730s developed and popularized a system of nomenclature in which each organism is given a two-word scientific name indicating its genus and species. For example, the scientific name of the House Sparrow is *Passer domesticus*. The first word in this type of **binomial name** refers to the genus in which the species is placed: the House Sparrow is in the genus *Passer* along with more than 20 other Old World sparrow species with which it shares a common ancestor (Fig. 2.05). In a Linnaean binomial name, the first letter of the genus name is capitalized. The second word in the name—*domesticus*—is the species name, which refers only to the House Sparrow; the species part of the binomial is never capitalized.

Although birds are most commonly referred to using this two-word naming system, technical publications on avian diversity sometimes use more elaborate versions with additional levels. For example, a reference to "*Passer domesticus rufidorsalis* Brehm 1855" includes an additional word—*rufidorsalis*—that refers specifically to the subspecies of House Sparrow found in the Nile Valley of Africa, as well as a reference indicating that this subspecies was formally described in an 1855 paper by the German ornithologist Alfred Brehm.

Every bird species is given a scientific binomial name when it is first described formally in a publication. A standardized set of rules set by the International Commission on Zoological Nomenclature (ICZN), the governing body charged with setting the criteria for animal nomenclature, must be followed by the person or team describing the new species. As explorers penetrate the last remote areas of the world, the naming of new bird species is becoming increasingly rare, with only a few such discoveries each year. Sometimes, however, new birds are found in less remote areas, as in the recent discovery of the Cambodian Tailorbird (*Orthotomus chaktomuk*) in the highly populated floodplain of the Mekong River (Mahood et al. 2013) (Fig. 2.06). In contrast to the earlier days of exploration, when it was common to name a species for oneself or in recognition of a sponsor, the scientific names of new species now are based most often on the new bird's region, the local language, a distinctive trait of the species, or the name

> **Binomial name:** a naming system in biology in which each species is assigned a unique name consisting of two parts, the name of the genus and the name of the species, as in the scientific name of the House Sparrow: *Passer domesticus*.

Fig. 2.05 Binomial nomenclature. As indicated by their scientific names, (A) the House Sparrow (*Passer domesticus*), (B) the Eurasian Tree Sparrow (*Passer montanus*), and (C) the Cape Sparrow (*Passer melanurus*) all belong to the same genus, *Passer*. (Photographs by: A, Jay Diaz, KoolPix; B, Johan van Beilen; C, Ian White.)

Fig. 2.06 New birds are still being described. The Cambodian Tailorbird (*Orthotomus chaktomuk*) was first discovered in 2009 as a serendipitous outcome of a research program on avian influenza. (Photograph by James Eaton, Birdtour Asia.)

of an influential scientist. The species name *chaktomuk* of the Cambodian Tailorbird, for example, is based on a Khmer language term for the region near the city of Phnom Penh where the bird was discovered.

In addition to discoveries of previously unknown species, we are steadily gaining a better understanding of variation within and among previously described species. This improved understanding can lead to the **lumping** together of two species formerly considered distinct species into one single species. More commonly, however, populations within a described species are found to be more different than previously thought, leading to the **splitting** of one former species into two or more species. For example, the widespread bird known in Eurasia as simply the Wren and in North America as the Winter Wren was long considered to be the same species (*Troglodytes troglodytes*), but studies of genetic and song differences (Drovetski et al. 2004; Toews and Irwin 2008) recently led to a three-way split that divided the Eurasian Wren (*Troglodytes troglodytes*) from two species in North America, the western Pacific Wren (*Troglodytes pacificus*) and the eastern Winter Wren (*Troglodytes hiemalis*) (Fig. 2.07). As with the split of these wren species, changes in bird classification are usually first

Lumping: informal term for changes in classification that involve merging into one species two or more taxa that were previously each considered to be a separate species.

Splitting: informal term for changes in classification that involve separating into different species populations that were previously considered to be part of a single species.

motivated by scientific studies that present new information on the underlying biology of the species being lumped or split. Ultimately, the formal decision about which species to recognize (and the names they are given) usually rests with regional committees of professional ornithologists that weigh the evidence for each potential change.

2.1.3 English and local names

Although every bird species has a formal scientific name, most people who enjoy birds—including professional ornithologists—refer to a bird by its common name in their local language. Although lists of worldwide common bird names exist in several languages, the most comprehensive common name systems for birds are in English. Worldwide, every bird species has a common English name, and occasionally more than one if it has varying names in different parts of the world. For example, the species scientifically known as *Gavia immer* has long been known as the Common Loon in North America but as the Great Northern Diver in Eurasia. An international group of ornithologists has proposed a standardized list of English names for all birds in order to reduce these regional naming discrepancies (Gill and Wright 2006). In their system, for example, the English name of *G. immer* is a compromise between the North American and Eurasian variations: the Great Northern Loon. Although nobody enjoys changing long-standing and familiar names, the general goal of improving worldwide communication about birds through consistent terminology is laudable.

Bird species often have additional names in local dialects or languages that reflect a direct understanding of that bird's ecology or behavior. For example, in Jamaica, the Snowy Egret (*Egretta thula*) is known as "Golden Slippers," a reference to the bright yellow feet at the base of its black legs (Chapter 8). Likewise, several cuckoos from Jamaica are known as "rainbirds," because they often call before or after downpours (Downer and Sutton 1990).

Comparisons of local names used by indigenous communities with the scientific names given by ornithologists usually reflect very similar patterns of classification. Both groups of observers recognize very similar sets of species and often distinguish nearly each species with a different name. This suggests that both indigenous and scientific communities fundamentally categorize avian diversity very similarly, probably in response to the real biological differences that separate bird species from one another.

2.1.4 Defining species

Ornithologists who classify bird species follow standard criteria to judge whether two bird populations are members of the same or different species. These boundaries usually are obvious and uncontroversial, but sometimes different scientists reach opposing conclusions about where
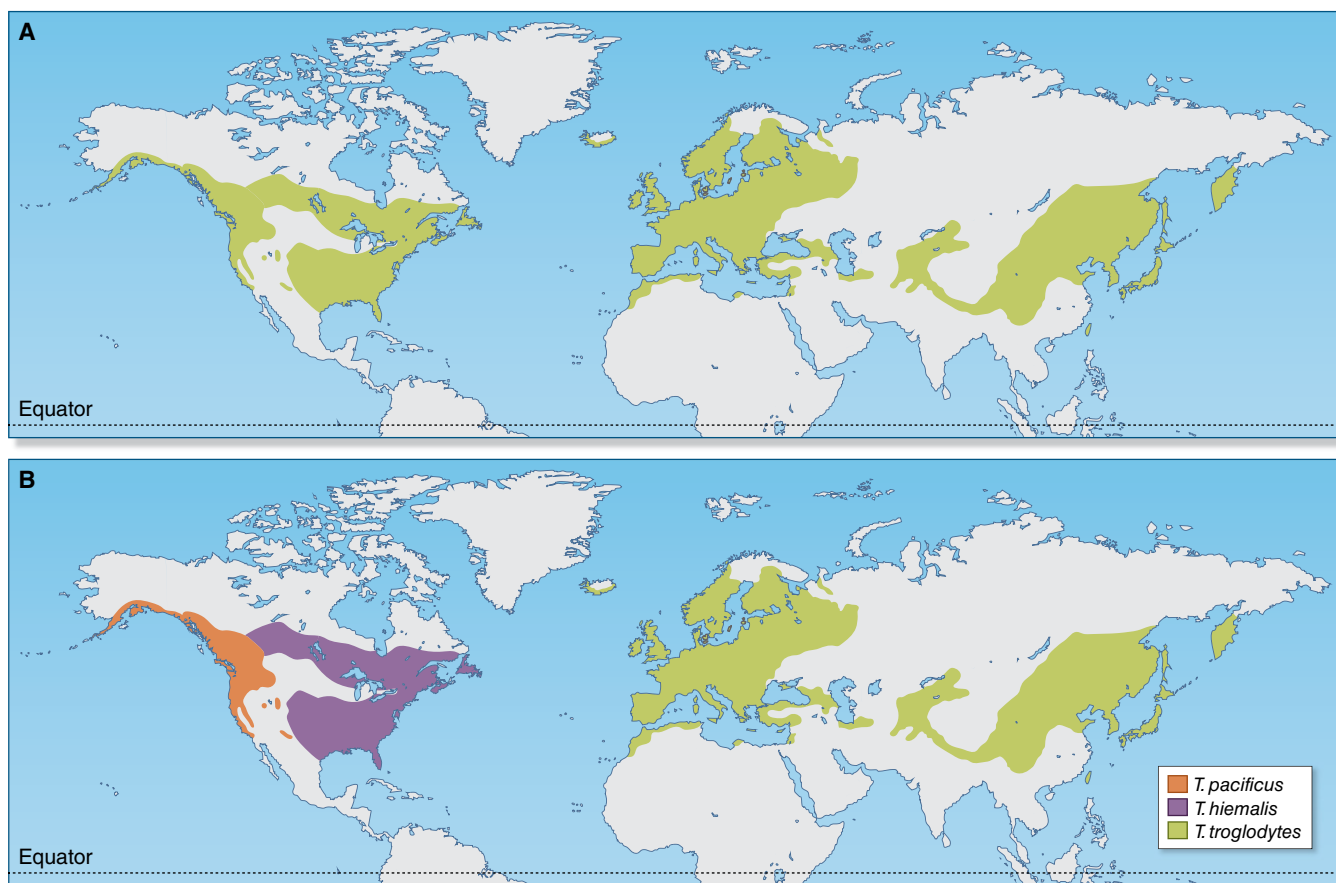
Fig. 2.07 Splitting species based on new evidence. (A) The Winter Wren was once considered to be one species (*Troglodytes troglodytes*) with an extremely broad range (green). (B) On the basis of new behavioral and molecular evidence, these birds have been divided into three separate species: the Eurasian Wren (which kept the original scientific name, *Troglodytes troglodytes*; green), the Pacific Wren (*Troglodytes pacificus*; orange), and the Winter Wren (*Troglodytes hiemalis*; purple). (© Cornell Lab of Ornithology.)

to draw the biological lines delineating different species. In these more complicated scenarios, it is important to remember that the entities we now classify as distinct species all formed over time through the gradual evolutionary process of **speciation** (Chapter 3). Because the speciation process involves one ancestor species gradually splitting into two or more descendant species, it is not surprising that there are points along that evolutionary pathway where conflicting classifications can be drawn, depending on what kind of evidence is considered.

Most birds occur in discrete **populations**, groups of individuals that breed in locations that may be separated in space from other similar populations. Imagine that you have to make a decision about whether the bird populations on two nearby islands belong to the same or different species. The birds from these two islands are generally very similar and clearly closely related, but they also differ in some subtle aspects of their plumage and courtship behavior. What evidence should you examine and what criteria should you use to decide whether they are one or two species?

To define species, biologists refer to **species concepts** that highlight the most important criteria used to decide whether two populations belong to the same or different species. The two most prevalent species concepts in

> **Speciation:** the evolutionary process by which one ancestor lineage splits into two or more descendant species.
>
> **Population:** in ornithology, a group of interbreeding birds of the same species that live in the same place at the same time.
>
> **Species concept:** the precise sets of criteria that systematists use when deciding whether two populations are members of the same species, or two separate species. Different species concepts tend to emphasize different such criteria, sometimes leading to disagreements about classification.

ornithology are the **biological species concept** and the **phylogenetic species concept**. Their respective criteria focus on different aspects of the speciation process. In essence, the biological species concept focuses on current mating compatibility and what might happen in the future. In contrast, the phylogenetic species concept focuses on the history of populations and whether they have been evolutionarily separated in the past.

2.1.5 Birds and the biological species concept

The biological species concept has been adopted broadly across the field of biology, but its roots are in ornithology, as it was first formalized by the ornithologist and evolutionary biologist Ernst Mayr, an expert on South Pacific birds. Mayr's classic definition of a biological species is especially useful because it is both concise and descriptive of a fundamental aspect of biology: a biological species comprises "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). This definition places the emphasis on interbreeding: when populations can no longer interbreed owing to their biological differences, they are considered different species.

The biological species concept is easy to apply when birds found in the same location clearly either interbreed fully (thereby showing that they are the same biological species) or completely fail to interbreed (indicating that they are different biological species). However, individual birds of two species occasionally mate with one another in nature and produce hybrid offspring, and even more can do so when kept together in captivity (Chapter 3). One challenge in applying the biological species concept to birds is deciding what level of hybridization to accept between two populations that are otherwise considered distinct species. In the mid-twentieth century, a small amount of hybridization was considered enough to lump populations into a single species, even when those populations had other distinctive traits. For example, collections made in the 1950s showed that the species known as Baltimore (*Icterus galbula*) and Bullock's (*I. bullockii*) Orioles hybridize in a narrow region of the North American Great Plains (Chapter 3). This evidence of consistent hybridization led to their official reclassification into one species, the Northern Oriole, in 1983. However, subsequent research showed that these forms do not exchange genes as effectively as their levels of hybridization might suggest, as the hybrids appear to have lower fitness than non-hybrids and therefore are poor conduits for the exchange of genes between the two species. On a continent-wide scale, these two orioles therefore remain essentially genetically isolated, and since 1995 they have once again been formally classified as two separate species despite their ability to hybridize.

Biological species concept: a classic species concept that is still widely used in ornithology; it places the greatest emphasis on whether or not the members of two populations retain the ability to interbreed.

Phylogenetic species concept: a species concept that focuses on the history of a related set of organisms, in which a species is usually defined as the smallest group descended from a common ancestor that shares some kind of distinguishing feature that separates them from other such groups.

Allopatric: populations that occur in separate regions with no geographic overlap.

Similar populations that live in separated places, such as populations of landbirds on islands separated by wide stretches of ocean, pose another practical challenge to the application of the biological species concept. Their isolation means that they cannot interbreed with one another, even if they would otherwise be reproductively compatible. In theory, ornithologists could test whether these populations are different species by introducing birds from one island to the other, and watching to see if the immigrants breed with the residents. For a host of practical and ethical reasons such experiments are rarely conducted, and, instead, ornithologists generally use other, more indirect, forms of evidence to predict what would happen if the populations somehow came together. In such cases, alternative criteria are used to delineate species, including differences in plumage and song traits that are important to mate choice, and the degree of genetic difference relative to other populations that are known to be distinct biological species (Box 2.03). Demarcating species' boundaries in these situations usually requires judgment calls about the divergence between **allopatric** populations relative to that between reproductively isolated populations that occur together.

2.1.6 Birds and the phylogenetic species concept

The phylogenetic species concept is an alternative way of defining species that considers their past evolutionary histories. Under this approach, a species is the smallest cluster of individuals in an evolutionary tree in which all members share at least one distinctive, inherited trait that is absent in other groups. The shared trait provides evidence of the common ancestry of the individuals grouped together into one species, whereas the absence of the trait in other organisms provides evidence that they have diverged along a different branch of the avian evolutionary tree. The phylogenetic species concept thereby focuses on past levels of

Box 2.03 Birds with complicated distribution patterns

Some bird species, particularly those in tropical regions, have a complicated mosaic of populations with widely varying traits. Often, in such situations it is difficult to determine whether forms should be considered variants within one species or, alternatively, as separate and distinct species. Ornithologists often refer to such groups as "species complexes" to reflect this uncertainty.

The White-browed Brush-Finch (*Arremon torquatus*) forms one such complex along its distribution from Costa Rica south to Argentina. Plumage traits in this group vary dramatically, particularly with regard to the presence and extent of a white superciliary stripe on the head, and the presence or absence of a black band on the breast. In some cases, similar-looking brush-finch populations are found in widely separated locations, but interspersed in between are brush-finch populations that look quite different (Fig. 2.B3.01). This "leapfrog pattern" of plumage variation is seen also in other birds with long distributions along the Andes mountain
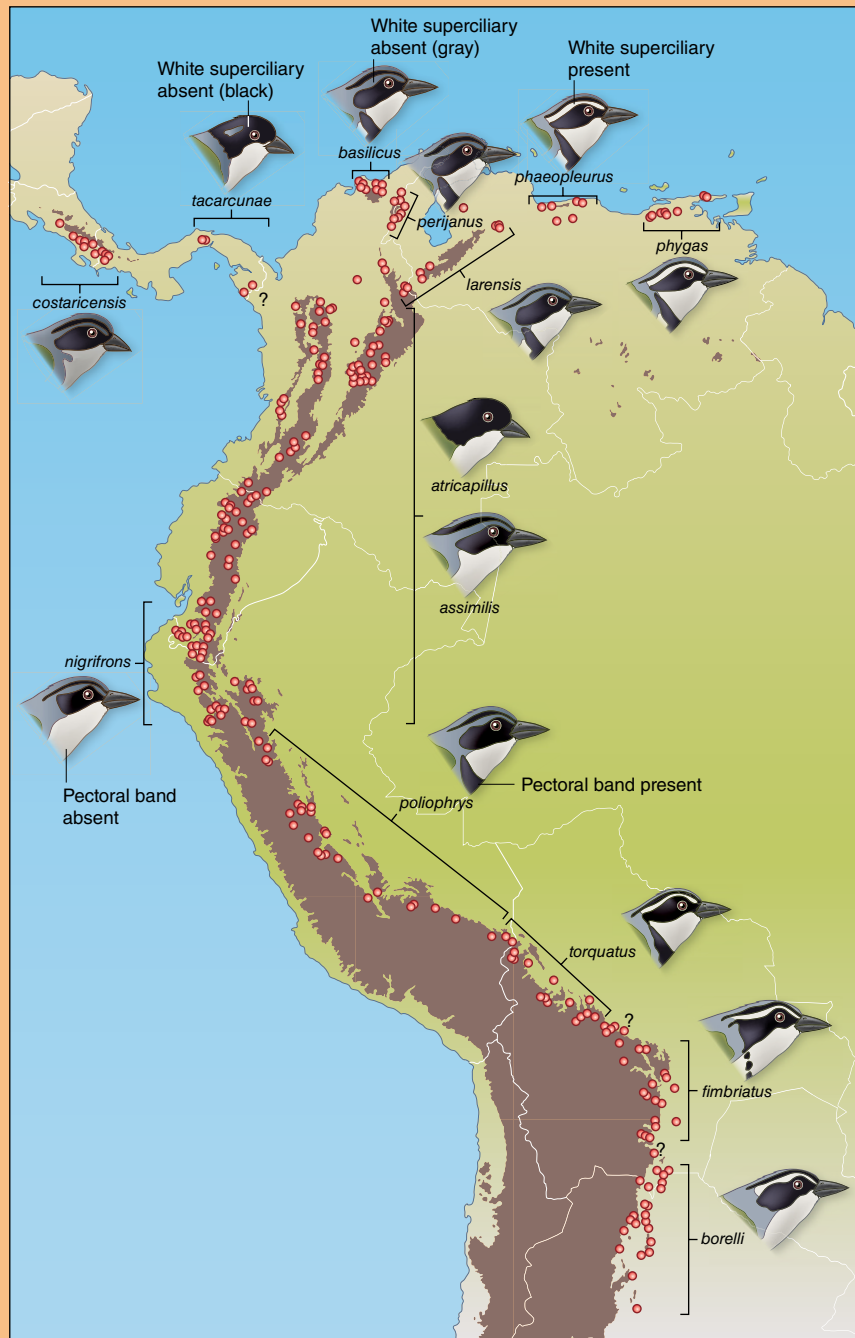
Fig. 2.B3.01 Distribution and plumage variation in a species complex. Various populations of White-browed Brush-Finches (*Arremon torquatus*) show great variation in plumage traits, including the presence/absence of the black pectoral band and white superciliary feathers. Gray shading indicates range; Latin names paired with illustrations refer to subspecies. (Cadena et al. 2011. Reproduced with permission from John Wiley and Sons.)

range. Researchers have long wondered about how this pattern originated: did the similar but separated populations evolve those plumage types independently, or are they similar because they are more closely related to each other than they are to their adjacent but differently plumaged neighbors?

The Colombian ornithologist Carlos Daniel Cadena and his collaborators used a combination of techniques to test these hypotheses in brush-finches. Using DNA sequences, they reconstructed a phylogeny for the different populations and found that each population had evolved its particular

combination of plumage traits independently and that these plumage changes occurred at a relatively fast rate during the complex's evolution (Cadena et al. 2007, 2011). Similar-looking populations are therefore not particularly closely related to one another, suggesting that the leapfrog pattern arises when distant populations separately evolve similar appearances. Additional comparisons of habitat preferences and song variants in these populations suggest that the populations are in the process of diverging into as many as eight distinct species (Cadena and Cuervo 2010).

genetic connection, an intrinsically historical perspective, rather than on reproductive compatibility, an intrinsically biological perspective.

The phylogenetic species concept has both advantages and disadvantages. One benefit lies in its fine-grained approach, which demands high levels of specificity and thereby avoids lumping together as one species the larger groups that share traits inherited from a more ancient common ancestor. For example, among living organisms, all birds share the trait of having feathers, but clearly the trait of *has feathers* is not useful in defining the breakpoints among individual bird species. More problematically, however, any bird populations that have been geographically isolated—especially small populations—are likely to develop some distinctive traits fairly quickly. A strict application of this species concept in birds would result in the recognition of far more than 10,000 living bird species, because many geographic populations of the same biological species have subtle but distinctive shared traits that could be used to classify them as separate phylogenetic species. Despite these challenges, the phylogenetic species concept has a solid basis in evolutionary theory, and it has many proponents among professional ornithologists.

2.2 Phylogenetics: the evolutionary tree of birds

All birds, living or extinct, are connected in a master evolutionary tree—a phylogeny—that reaches back to their common ancestor, which (as described later in this chapter) was probably a theropod dinosaur. The avian phylogeny therefore is the result of many millions of years of evolutionary change, speciation, and extinction. It has thousands of connected branches, some of which lead ultimately to the species that exist today, and others that terminated in the past in lineages that have gone extinct without leaving any descendants. A primary goal of avian phylogenetics is to reconstruct this evolutionary
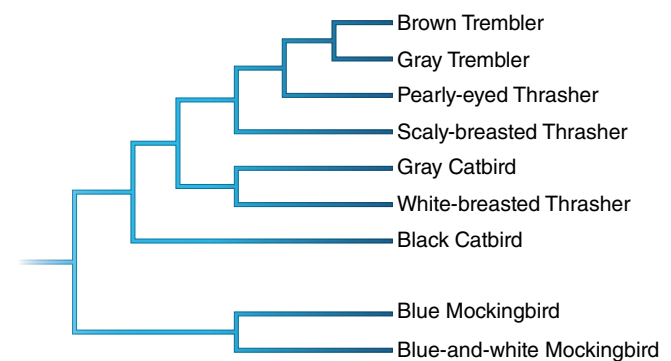
Fig. 2.08 Evolutionary trees. Also called phylogenies, these trees represent hypotheses about the historical relationships among past and present birds. Based on evidence from DNA, this phylogeny depicts the evolutionary relationships among nine of the many living species in the family Mimidae. Branches convey levels of relatedness within a clade: for example, the Brown (*Cinclocerthia ruficauda*) and the Gray (*Cinclocerthia gutturalis*) Tremblers are sister taxa, followed by the Pearly-eyed Thrasher (*Margarops fuscatus*), which is equally related to them both. (From Lovette et al. 2012. Reproduced with permission from Elsevier.)

history to produce a complete picture of how and when bird diversity originated.

2.2.1 What is a phylogeny?

At one level, a phylogeny is a diagram that represents the history of evolutionary connectedness among a group of organisms. For example, Fig. 2.08 shows a phylogeny for a group of nine species within the avian mockingbird and thrasher family, Mimidae. Although there are many other living species in this family, genetic and other evidence demonstrate that these nine species are each other's closest living relatives, thereby forming a monophyletic group, or clade.

Phylogenies are depictions of evolutionary connections. Although any one phylogeny can be drawn in many alternative orientations, phylogenies typically comprise lines
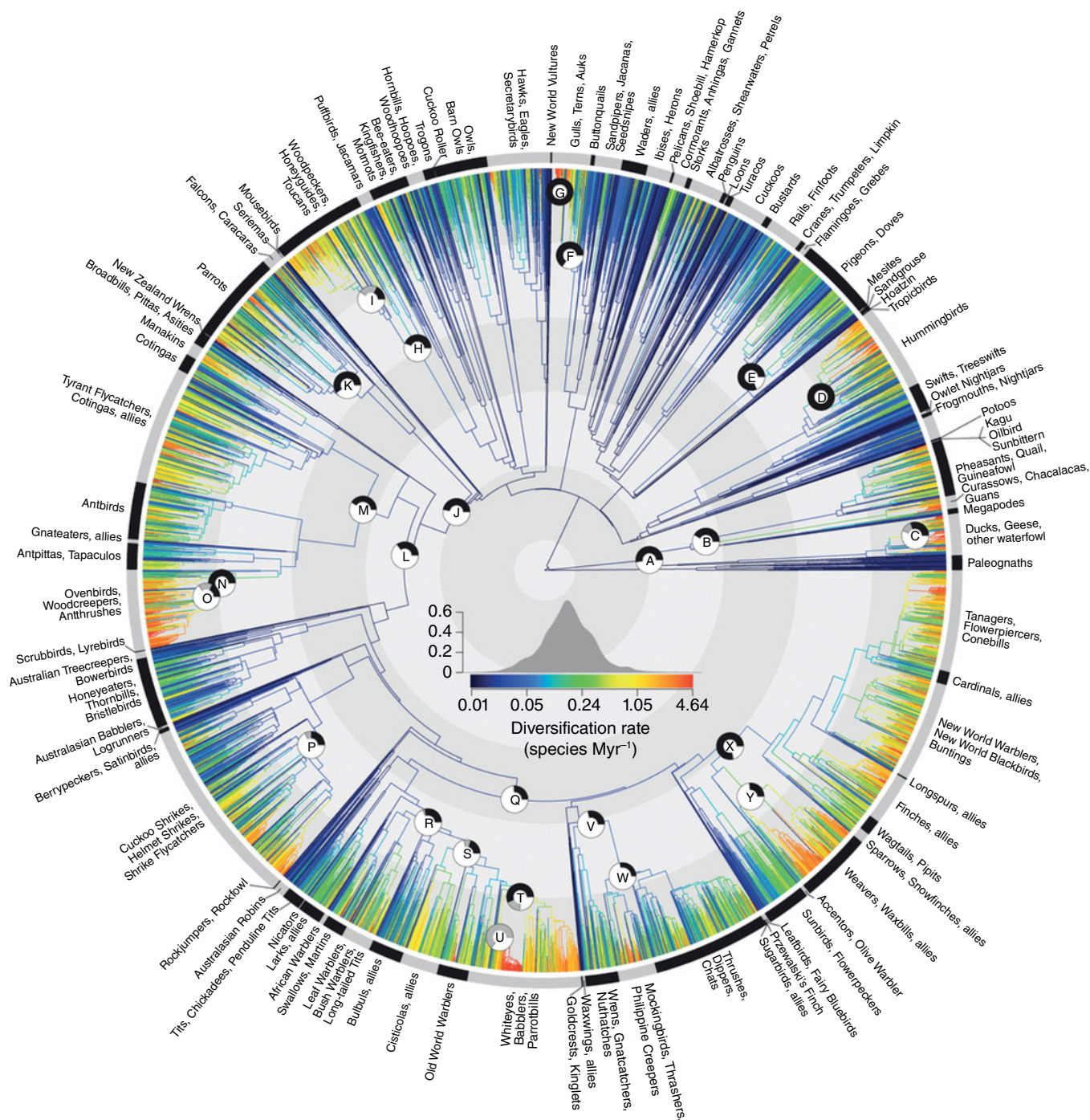
Fig. 2.09 Diversification of all modern bird groups. This circular evolutionary "tree" tracks rates of speciation across space and time, and is one of the first to include all recognized species of extant birds. Reddish branches indicate groups with particularly high speciation rates. (From Jetz et al. 2012. Reproduced with permission from Macmillan Publishers Ltd.)

called **branches** that join together at points termed **nodes**. The branch lines represent evolutionary lineages that have persisted through a period of time, and nodes represent points in the past when one ancestral lineage split into two or more descendant lineages. Though there are phylogenies that include nearly every living species of bird (Jetz et al. 2012) (Fig. 2.09), most phylogenies of birds show the

Branches: the lines on a phylogeny that trace the pathway of evolutionary lineages through time.

Nodes: the points on a phylogeny where branches separate, usually representing points where an ancestral lineage splits into two or more descendant lineages.

relationships only of a certain group—the species within a particular genus, the families within an order, and so on. For example, the phylogeny in Fig. 2.08 shows only the connections between a group of living species; although there are likely to have been additional species in this clade that are extinct and unknown to us, they cannot be shown in the phylogeny. The phylogeny's branches connect bird species and illustrate their level of evolutionary relatedness, as in the tree in Fig. 2.08 where the Gray Catbird (*Dumetella carolinensis*) is most closely related to the White-breasted Thrasher (*Ramphocinclus brachyurus*). In that tree, these species therefore represent **sister taxa**, a pair of species with no closer relatives.

2.2.2 Phylogenetic data and techniques

Historically, early experts on avian relationships drew phylogenies based on their general perceptions of how bird groups were related. In modern studies, however, avian phylogenies are based on careful analyses of specific characters that are shared or variable among groups. Many kinds of traits can serve as useful characters, including the presence of a particular patch of plumage, a distinctive behavior, or a DNA variant at a particular location in the genome. Before genetic technologies became available, all avian systematists studied morphological **characters**, and much of our understanding of avian relationships derives from their early insights. Today, systematists who study living groups of birds most often use genetic characters because genomes of different birds vary at millions of points in their DNA sequences, and these differences can be used to infer their relationships. Despite science fiction movies that show scientists working with ancient dinosaur DNA, most genetic characters cannot be recovered from fossils, because DNA molecules degrade over time. The oldest bird DNA successfully analyzed thus far is less than 20,000 years old and comes from the bones or eggshells of extinct moas from New Zealand (Box 2.04). Therefore, avian systematists who study fossil birds still most commonly analyze and compare morphological characters measured from preserved bones or feathers.

Technological advances make it increasingly easy to generate and analyze large datasets of genetic characters from samples taken from extant birds (Box 2.05). Most research museums maintain collections of frozen tissues taken when specimens are collected, and these well-preserved tissues are excellent starting material for genetic studies. Newer laboratory techniques also make it possible to perform genetic studies with older museum materials, such as bits of dried tissue snipped from traditional museum skin specimens.

The genetic characters targeted in these phylogenetic studies have changed as laboratory methods have grown more powerful. The first large-scale phylogenetic studies of avian genetic characters were conducted in the 1960s through the early 1980s and were based on differences in egg-white proteins, as those proteins were relatively easy to isolate from recently laid eggs. These protein investigations were followed in the 1980s by an important series of studies that used a technique called DNA-DNA hybridization, influentially synthesized by ornithologists Charles Sibley and Jon Ahlquist (1990). The phylogenies generated using this method were far more comprehensive than any earlier genetic surveys of birds, and led to many discoveries about previously unsuspected avian relationships; for example, the DNA-DNA hybridization work showed for the first time that the Old World starlings are most closely related to the New World mockingbirds and thrashers. Today, however, the technical limitations of the DNA-DNA hybridization method along with methodological controversies about its application to birds have rendered it obsolete.

In the late 1980s it became possible to determine the precise sequence of DNA building blocks (the four **nucleotides** abbreviated as A, G, C, and T) within a region of DNA (Box 2.06). Many studies of avian phylogenetics conducted since then have been based on relatively short **DNA sequences** from the genes found in **mitochondrial DNA**, a part of the genome passed from a mother bird to her offspring. In the 2000s, many researchers started to include DNA sequences from other regions of the avian genome into their analyses to create evermore robust phylogenetic studies. For example, using DNA characters, one research group produced an influential phylogeny for all major groups of songbirds (Passeriformes) (Barker et al. 2004). Other researchers studying the deeper relationships among avian families and orders similarly generated a tree for 169

Sister taxa: two groups (often but not always two species) that are each other's closest evolutionary relatives.

Character: in avian systematics, any heritable trait that can be compared among different groups of birds.

Nucleotides: the basic molecular building blocks of DNA and RNA.

DNA sequence: the precise order of the nucleotides in a region of the DNA molecule.

Mitochondrial DNA (or **mtDNA**): in birds, the DNA that is found not in the cell nucleus, but rather in the cell's mitochondria, a structure involved in generating energy within the cell. Mitochondrial DNA is passed down only from mother birds to their offspring.

Box 2.04 Ancient DNA and the extinct moas of New Zealand

Approximately 700 years ago, the first humans who traveled to the islands now known as New Zealand encountered a world where birds were the dominant animals. They would have seen an eagle far larger than any known today, as well as its giant prey: the moas, a group of giant birds related to kiwis, ostriches, emus, cassowaries, and the other ratites. Moas had never experienced hunting by a terrestrial predator, and they were highly vulnerable to human exploitation; the entire moa family went extinct shortly after humans colonized New Zealand. Today, physical evidence of moas comes from fragmentary remains found in fossil deposits or old human campsites, and from caves and gullies that have preserved desiccated moa feathers and body parts. Fortunately, these remains often hold moa DNA, which researchers can use to reconstruct the diversity and relationships of this extinct family. DNA from fossil specimens is fragmented and degraded, so laboratory work on ancient DNA must be done very carefully in specially designed facilities to reduce the risk of contamination by modern DNA from bacteria, the researchers themselves, or the lab in which the study is performed.

Using these techniques, researchers have successfully sequenced DNA from hundreds of moa specimens, including bones, eggshells, and skin fragments. Their studies show that at the time of human discovery of New Zealand, there were between 9 and 11 moa species (Fig. 2.B4.01). These species can be clustered into three groups based on their phylogenetic relationships (Baker et al. 2005), and all probably shared a common ancestor about 6 million years ago (Bunce et al. 2009). By using these DNA samples to determine the sex of each of the moas that left these fossil remains, researchers further discovered that some moa species had extreme sexual size dimorphism, with adult females weighing more than twice as much as adult males. Based on this extreme size difference, many moa specialists had previously believed that the large and small moas represented different species (Bunce et al. 2003). Distinctive male moa DNA found on the outer parts of preserved eggshells even suggests that the smaller male moas incubated the eggs, as do males of various other ratites like ostriches (Huynen et al. 2010).
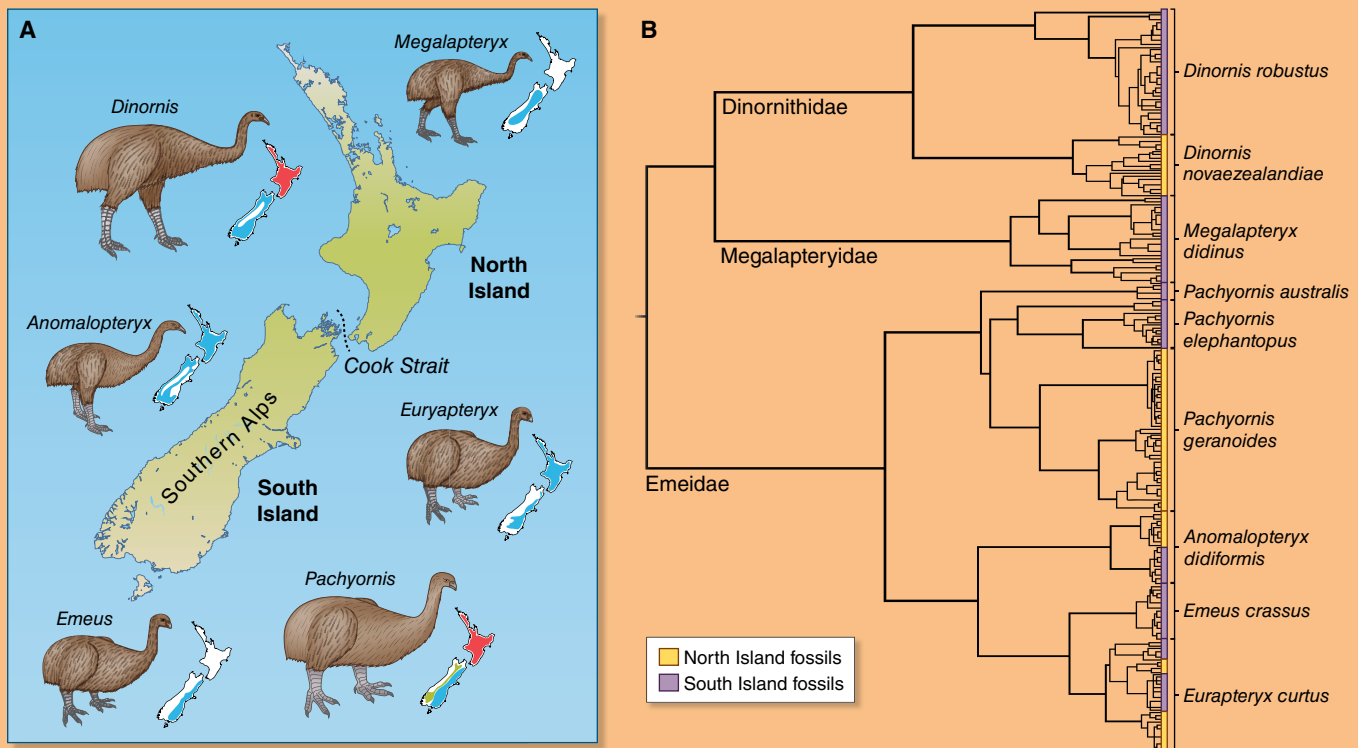
Fig. 2.B4.01 Moa distribution and phylogenetics. (A) The distribution of extinct moa genera on the islands of New Zealand. Species' ranges are depicted on each genus map. If a genus includes more than one species, their distributions are distinguished with different colors. (B) Reconstruction of phylogenetic relationships based on DNA recovered from moa fossil remains. (From Bunce et al. 2009. Reproduced with permission from National Academy of Sciences, USA.)

Box 2.05 The theory behind evolutionary trees

The study of bird relationships has benefited greatly from advances in the way phylogenies are reconstructed from data on morphology, DNA, or other traits. The single greatest innovation was the formalization in the 1960s of an approach termed "cladistics." In an evolutionary tree based on a cladistic analysis, a trait shared by two or more avian lineages provides evidence to group them together, under the assumption that such shared traits are present in those lineages because they were also present in their common ancestor. Only traits that have changed at some point and then been passed down—derived traits—are useful evidence in this cladistic framework, because these "shared derived traits" identify subgroups within the hierarchical nodes of the tree. Cladistic methods had a transformative role because they based phylogenetic analyses on a sound and logical theoretical footing.

Today, many avian phylogenies are made instead using a statistical approach called "maximum likelihood," in which the analysis evaluates the fit between the characters that vary among the species in the phylogeny (nowadays, these

characters are usually but not always based on DNA variation), a model of how those characters change over time, and the resulting evolutionary tree. These and related analyses are particularly useful for studies that involve huge datasets that must be analyzed on advanced computer systems.

An ongoing challenge in DNA-based phylogeny studies is that the correct phylogeny based on a particular subset of the genome—termed a "gene tree"—can differ somewhat from the average phylogeny of the entire genome—the "species tree." This discordance can arise from several sources. One is when a part of the genome is inherited differently from the rest; for example, the mitochondrial DNA in birds and most other organisms is passed down only from a mother to her offspring, so mitochondrial DNA gene trees do not reflect any gene flow caused by males dispersing from one area to another. Fortunately, now it is possible to generate thousands of independent gene trees as part of a phylogenetic study and to use statistical approaches to find the overall species tree that is best supported by this abundance of information.

Box 2.06 DNA barcoding of birds

Studies of DNA variation have become central to our modern understanding of bird diversity, as genetic similarities and differences can be used to reconstruct how various lineages of birds are related to one another. Different regions of the avian genome are better suited to different kinds of phylogenetic analysis. At the level of populations and species, genes that evolve quickly are particularly useful, because they are more likely to have evolved distinctive differences even during relatively short and recent periods of evolutionary separation.

Genes from the mitochondrial genome have long been the workhorse for studies of recent divergences in birds. An international consortium of scientists is attempting to assemble a database of mitochondrial DNA sequences—which they term "DNA barcodes"—for all bird species (Lijtmaer et al. 2011). By gathering together sequences of the same gene from as many bird species as possible, this DNA barcode database makes it possible to compare and

match any new sequence to the archive of known sequences. As demonstrated by hundreds of studies from long before the term "DNA barcode" was coined, mitochondrial DNA is a good genetic starting point for discovering genetic breakpoints within individual species and for assembling phylogenies of closely related species. Hypotheses based on mitochondrial DNA then can be explored in depth with more powerful sources of data from throughout the genome.

DNA barcodes are particularly useful in forensics to identify the source of an unknown avian sample. For example, DNA barcodes have been used to identify the mangled remains of birds that have passed through aircraft engines, as well as the sources of illegally collected live birds or feathers. Avian DNA barcodes recovered from bird blood in the stomachs of midges, mosquitoes, and blackflies have even been used to discover which bird species these insects feed upon under natural conditions.

avian species based on sequences from 19 different genes (Fig. 2.10). The resulting phylogenetic hypothesis generated by this international team was broadly considered to be that decade's most important advance in avian systematics (Hackett et al. 2008). Together with numerous phylogenetic studies of smaller groups of living birds, these new

and expansive perspectives on avian diversity inspired ornithologists to address broad-scale questions such as the origins of avian behaviors, and the times and places at which avian diversification has been unusually rapid.

DNA sequencing also has made it possible to determine the affinities of unusual bird species, and has revealed many

Fig. 2.10 Phylogenies based on DNA. One of the first avian evolutionary trees based on large amounts of DNA sequence data, this phylogeny reconstructs the relationships among 169 species from most major groups of birds using sequences from 19 different genes. (From Hackett et al. 2008. Reproduced with permission from AAAS.)
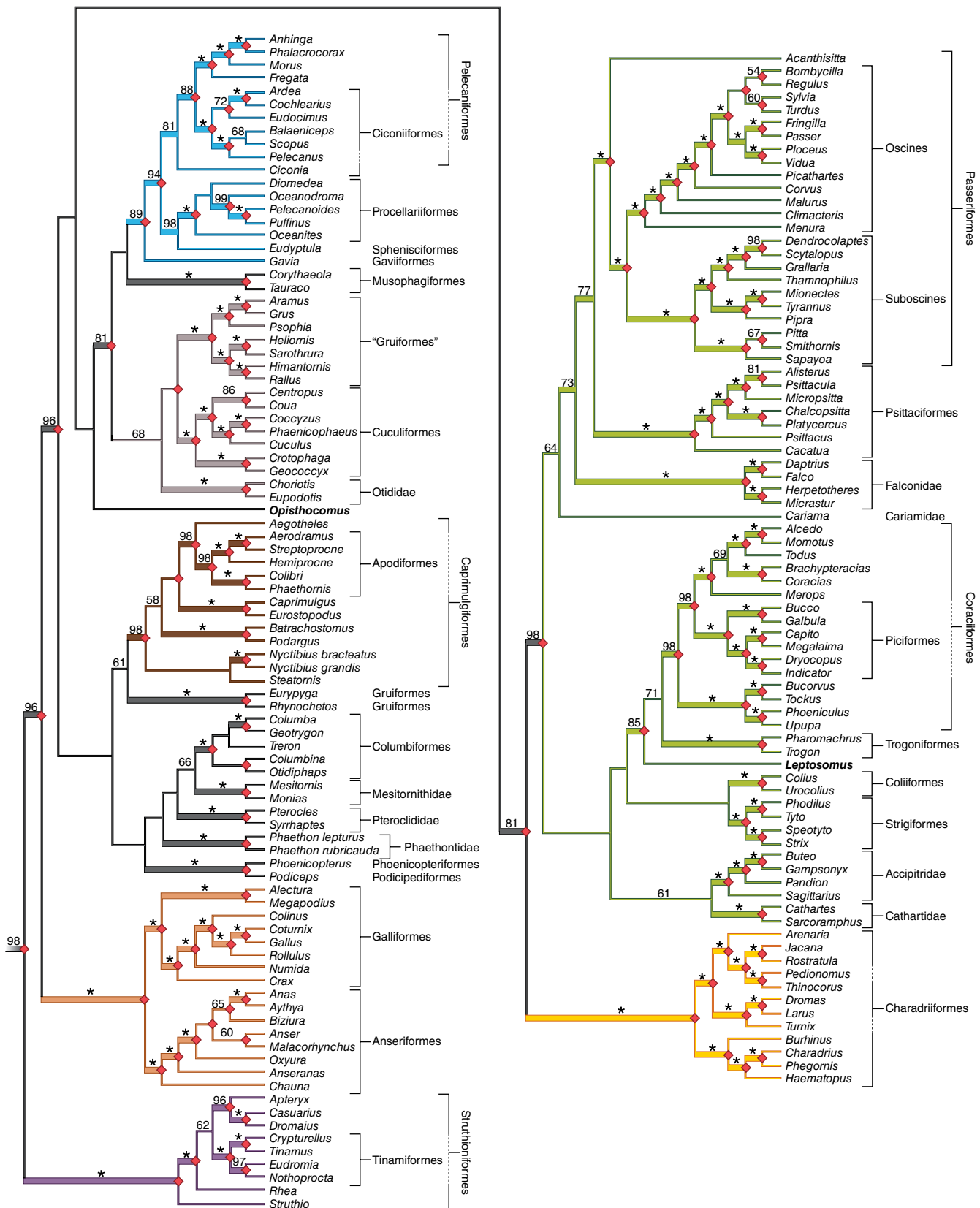
Fig. 2.11 Phylogenetics can reveal surprising relationships. For years, (A) the Sapayoa (*Sapayoa aenigma*) was assumed to be closely related to similar-looking birds that are also found in the neotropics such as (B) the Greenish Schiffornis (*Schiffornis virescens*), until genetic evidence revealed that the Sapayoa is actually more closely related to Asian broadbills. (Photographs by: A, Nicholas Athanas; B, Dario Sanches from São Paulo, Brazil (FLAUTIM (*Schiffornis virescens*). CC-BY-SA 2.0. http://creativecommons.org/licenses/by-sa/2.0.)

Fig. 2.12 Morphology can be misleading. Many bird species were originally named according to morphological similarity to other known species. For example, Hume's Ground-Jay (*Pseudopodoces humilis*) is not actually a jay, but rather an unusual member of the chickadee and tit family. It has since been renamed the Ground Tit. (Photograph by Fung Wai Choy.)

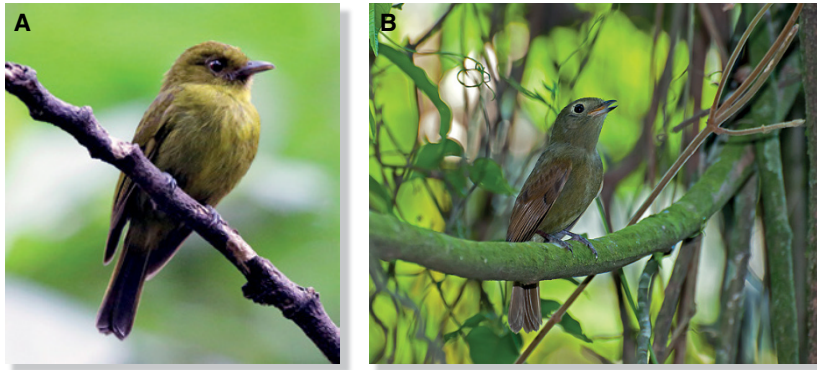surprises involving birds with previously uncertain relationships. For example, the Sapayoa (*Sapayoa aenigma*) is a drab songbird that nests along lowland streams in Panama, Colombia, and Ecuador (Fig. 2.11A). Based on its general resemblance to other groups of birds found in the neotropics (Fig. 2.11B), the Sapayoa was often thought to be an aberrant manakin or flycatcher. It was therefore notable and surprising when phylogenies based on genetic data showed conclusively that the Sapayoa is instead the sole New World representative of the broadbill radiation, an ancient group of songbirds that is otherwise restricted to Africa and Australasia (Fjeldså et al. 2003; Chesser 2004; Moyle et al. 2006). Similarly, a bird of the high Tibetan Plateau previously called Hume's Ground-Jay (*Pseudopodoces humilis*) (Fig. 2.12) was long considered an unusual member of the crow and jay family, as reflected by its common name. When DNA-based phylogenies showed that really it is an atypical member of the chickadee and tit family, it was accordingly renamed the Ground Tit (James et al. 2003). In a final example, several birds from South

Asia—the White-bellied Erpornis (*Erpornis zantholeuca*) and the shrike-babblers (genus *Pteruthius*)—were long thought to be part of the babblers, but DNA-based phylogenies determined them to be the only Old World members of the vireo family (Jønsson and Fjeldså 2006; Reddy and Cracraft 2007), revealing a previously unsuspected connection between the avifaunas of Asia and North America.

This process of phylogenetic discovery continues, and future studies undoubtedly will bolster many of the current phylogenetic hypotheses about avian relationships while refuting others and making new discoveries. We are moving into an era of expanding phylogenetic scope, in which reconstructions of the relationships among living birds will be based on comparisons of their entire genomes and in which giant phylogenies will be assembled that include thousands of bird species (Hugall and Stuart-Fox 2012). An ultimate goal of these advances in analytical methods and resources is to create well-supported phylogenies that include all living birds.

2.2.3 Genetic variation within bird species

In addition to phylogenies that illuminate the connections between species and higher taxa of birds, more subtle genetic variation also exists among populations of the same bird species. Bird populations start to become phylogenetically distinct when they are able to diverge genetically from one another, which most often happens when the populations are separated from one another geographically and few or no individuals move between them, allowing each population to evolve its own set of genetic differences. This process of divergence occurs more readily if the populations are small, and it becomes more and more pronounced when the populations have been geographically isolated for longer periods; ultimately, this same process can lead to full speciation of the two populations. Therefore, recently separated populations are likely to be very similar to one another genetically, whereas long separated populations are likely to show more differences in DNA characters and other traits.

Fig. 2.13 Geography and gene flow. Colored sampling points from a genetic study of Arctic Warblers (*Phylloscopus borealis*) show how populations spanning from northern Europe to Alaska are closely related (blue points), whereas those in the remote Kamchatka region of Russia (yellow points) and more southerly islands of Japan (red points) are each genetically distinct. (From Saitoh et al. 2010. CC-BY-2.0. http://creativecommons.org/licenses/by/2.0.)

When many birds move between two such populations, the high level of gene flow tends to mix the populations genetically, thereby slowing their genetic divergence. For this reason, bird species that undertake movements such as long-distance migration tend to be genetically similar across broad distances. For example, migratory populations of Yellow Warblers (*Setophaga petechia*) sampled from across much of North America are very similar to one another genetically, whereas non-migratory populations of this same species on different tropical islands often are genetically distinct from each other (Boulet and Gibbs 2006; Chaves et al. 2012). A similar pattern is found in the Arctic Warbler (*Phylloscopus borealis*), in which populations spanning northern Europe to Alaska are quite similar, but populations from the remote Kamchatka Peninsula in Russia and the islands of Japan are each genetically distinct (Saitoh et al. 2010) (Fig. 2.13).

Variation among bird populations is particularly obvious in bird species with wide but patchy distributions, because their disjunct populations often have evolved independently for a period of time. **Range disjunctions** are especially prevalent in birds that occur on islands or in birds restricted to habitats that act like islands within a matrix of other habitat types. For example, birds that require high-elevation habitats may be restricted to isolated patches on different mountains, a pattern that occurs in many parts of the world and in many groups of birds. The White-starred Robin (*Pogonocichla stellata*) of central and eastern Africa follows this pattern, breeding only in montane regions above 1500 meters (Fig. 2.14). Populations of this species from different mountain ranges show plumage differences that have led them to be classified as different subspecies, and genetic surveys have confirmed that many of these

populations are genetically distinct, although not at the level that that would lead most ornithologists to classify them as separate species (Bowie et al. 2006).

Studies of finer scale geographic variations that use phylogenetic methods to understand past connections within species, either among individuals or populations, fall within the discipline of **phylogeography**. Avian phylogeographers explore relationships among bird populations and test hypotheses about the processes that lead them to diverge. The most powerful such analyses compare phylogeographic patterns across many bird species. For example, Burney and Brumfield (2009) looked at genetic variation within 40 South American bird species, comparing populations from either side of a major barrier such as the Andes Mountains or a wide river (Fig. 2.15). They found that bird species in the forest canopy consistently had fewer genetic differences among their separated populations than did bird species that use lower parts of the forest understory. This finding links a phylogeographic pattern—lower differentiation in canopy birds—with the ecological process that likely generates it: the higher dispersal ability of birds that inhabit

Range disjunction: a pattern of geographic distribution in which two or more occupied areas are separated by substantial intervening areas where the species is not found.

Phylogeography: the scientific study of the evolutionary relationships of populations and species across space, usually as inferred from genetic information.
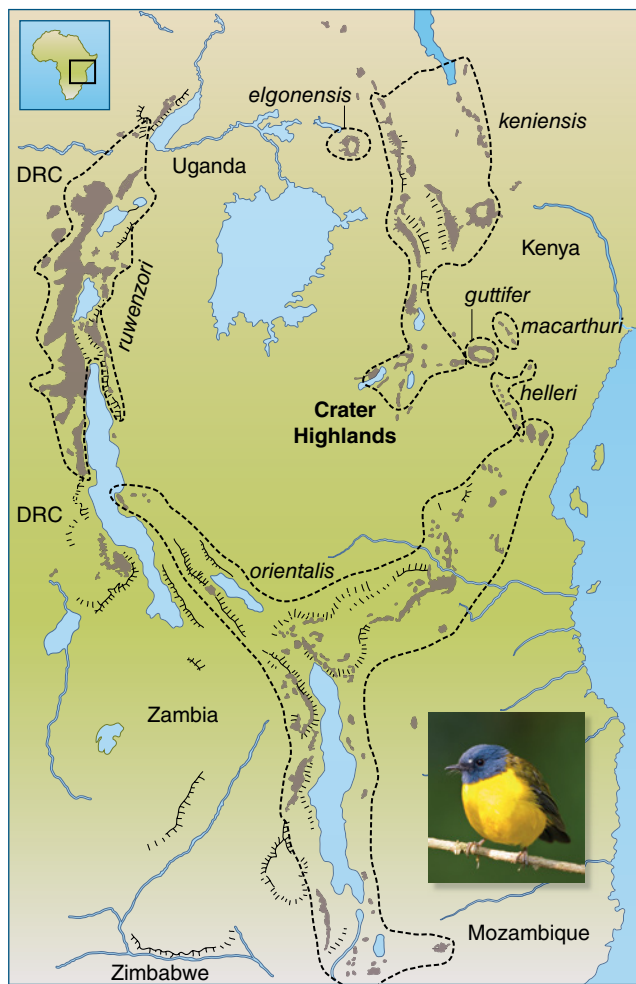
Fig. 2.14 Range disjunctions and genetic divergence. Species with fragmented ranges often show genetic variation among their constituent populations. For example, the White-starred Robin (*Pogonocichla stellata*) breeds only in montane regions above 1500 meters (depicted as the solid gray areas). Populations that occupy different mountaintops have become genetically distinct (dotted lines) over time. (From Bowie et al. 2006. Reproduced with permission from Elsevier. Photograph by Ronan Donovan, www.ronandonovan.com.)

the more open parts of the environment and that are adapted to moving long distances in search of fruit or other widely spaced resources.

2.3 Global patterns of avian diversity

Some of the variation in the diversity of bird communities arises from ecological forces like the availability of niches, competition among species, and the presence or absence of particular resources (Chapter 14), but other patterns
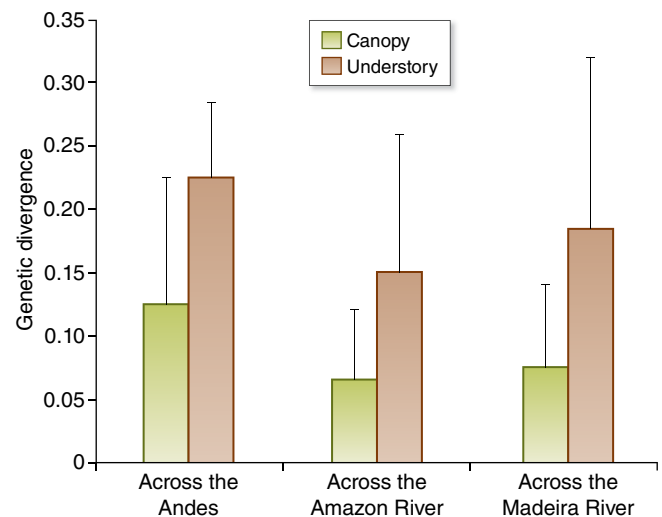
Fig. 2.15 Dispersal ability affects genetic differentiation. In the neotropics, canopy species tend to disperse more readily than birds of the forest understory and thus canopy species generally maintain higher levels of gene flow across potential barriers. For example, understory birds on each side of three major barriers (the Andes Mountains, the Amazon River, and the Madeira River) tend to have higher genetic differentiation than do canopy species. (Adapted from Burney and Brumfield 2009.)

occur on a larger biogeographic scale and allow us to make several concrete generalizations about bird diversity worldwide.

First, all else being equal, bird diversity increases with area. As summarized in more detail in Chapter 14, there are multiple reasons for this nearly universal pattern. Larger areas within a region are likely to contain more habitat types, which in turn can host a larger variety of bird species. Larger areas are better targets of colonization, so that bird diversity builds up over time. Larger areas generally support more individuals of each species, thus lowering the risk of local extinction. Finally, large areas can support populations of rare or wide-ranging species that are unable to persist in smaller regions.

Second, bird diversity is greatest near the equator and lowest at the earth's poles, a phenomenon termed the **latitudinal diversity gradient.** This pattern is one of the most conspicuous in avian biogeography, but it has no single cause; rather, it arises from a combination of past and

Latitudinal diversity gradient: the general rule that in most groups of organisms, species diversity is greatest in the tropics and steadily decreases towards the earth's polar regions.
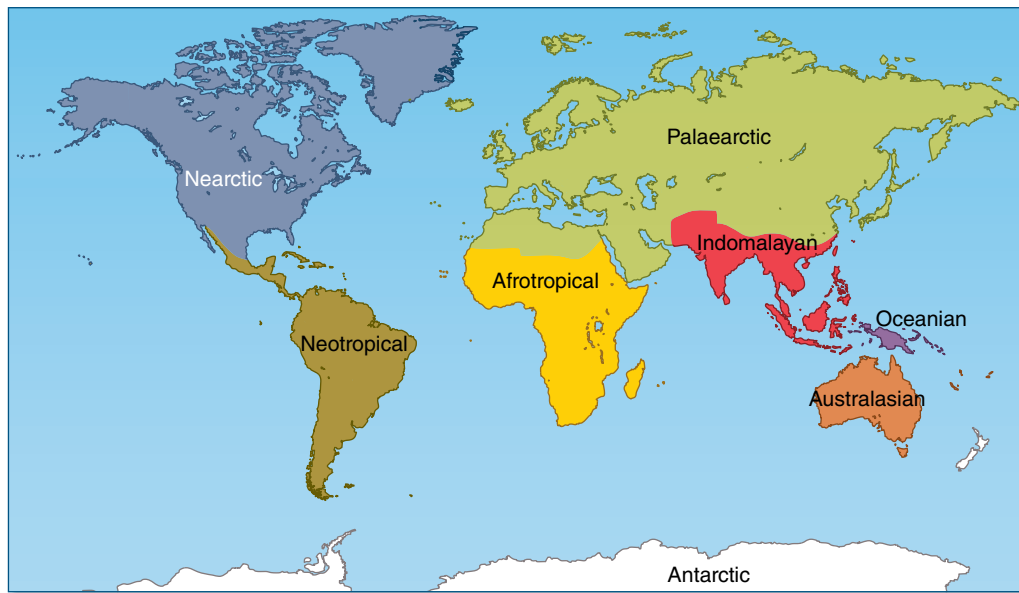
Fig. 2.16 Biogeographic realms. Avian biogeographers traditionally subdivide the world into eight primary realms based on the distributions of birds endemic to each region. (© Cornell Lab of Ornithology.)

present forces. On an evolutionary scale, the tropics are more diverse because they have a higher overall ratio of speciation to extinction than areas at higher latitudes, so that the number of tropical species increases over time. At an ecological scale, the tropics are more diverse because a given area of habitat can support more bird species, probably because tropical habitats typically have a higher diversity of plants, insects, and other resources important to birds. Furthermore, as discussed in Chapter 14, there is more turnover in bird species across tropical habitats, a pattern that boosts diversity when it is measured regionally rather than at a single point in space.

Third, islands support fewer breeding bird species than continental areas of the same size. This phenomenon is a manifestation of the same processes that cause bird diversity to scale with area more generally. Further, not all types of birds can colonize islands successfully, and extinction rates on islands are higher because their isolated populations are not as readily replenished by dispersal from other populations (Chapter 13).

2.3.1 Birds and biogeographical realms

Avian biogeographers have traditionally divided the world into eight primary **biogeographic realms** based on bird distributions (Fig. 2.16). Although similar systems have been developed for other organisms, this type of classification was first suggested in the 1850s by the British ornithologist Philip Sclater, the leading expert of his time on songbird classification and diversity. As Sclater and his successors recognized, each biogeographic realm has a distinctive avifauna with a unique mix of avian families and orders.

Not surprisingly, the boundaries of each realm coincide with general barriers to the dispersal of birds. Many families of birds are found in only one of the eight biogeographic realms and a visit to a new realm often provides the first chance for a birder or ornithologist to see entirely new branches of the avian evolutionary tree. At the same time, many groups of birds that are good at dispersing are found in two or more biogeographic realms. The realm system is therefore more relevant for landbirds, because waterbirds and seabirds tend to disperse more easily across the water barriers that often separate different realms.

The most famous barrier between biogeographic realms occurs at the shared boundary of the Australasian and Indomalayan realms (Fig. 2.17), where there is a sudden change in faunas at the junction known as "Wallace's Line." Alfred Russel Wallace, the biologist who first proposed it, was a founding figure in biogeography. Wallace's Line runs along a deep sea channel that separates the island of Sulawesi from Borneo and the island of Lombok from Bali. The channel is so deep that, even during past periods of low sea levels, there was no land bridge connecting these nearby islands.

> **Biogeographic realms:** a traditional classification of the earth's terrestrial regions that groups them by their broadly similar faunas, floras, and evolutionary histories.
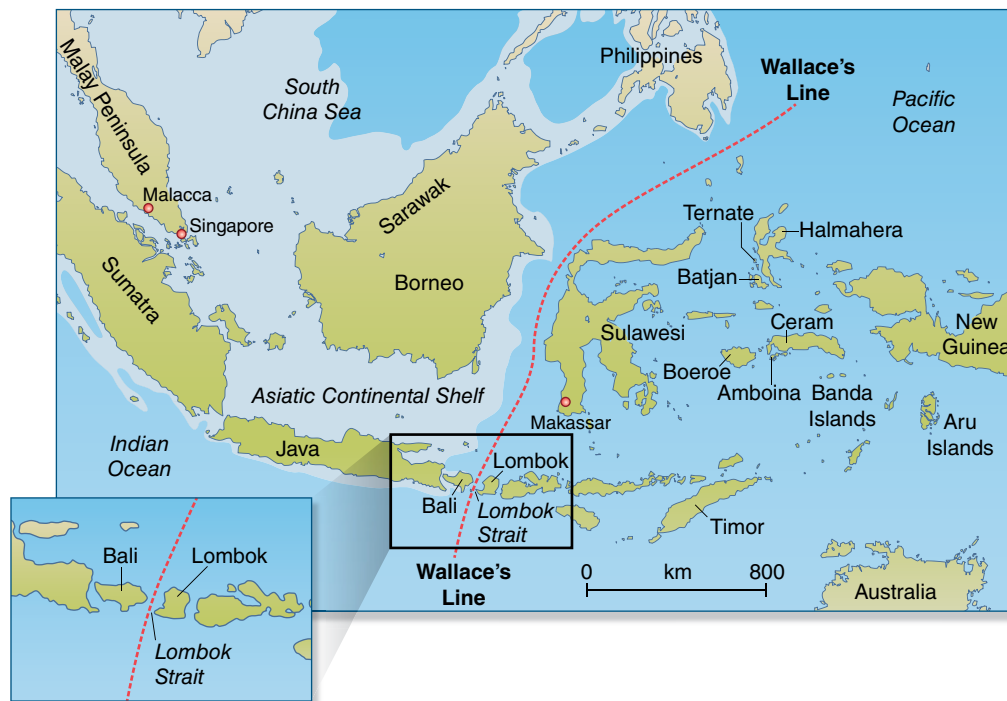
Fig. 2.17 Wallace's Line. The most famous barrier to dispersal between distinct biogeographic realms, this line occurs at the shared boundary of the Australasian and Indomalayan tectonic plates. (Map by Leanne Olds, in *Into the Jungle* by Sean Carroll (2008), courtesy of the author.)

Many families of birds found to the north have distributions that stop at Wallace's Line, whereas bowerbirds (Ptilonorhynchidae), owlet-nightjars (Aegothelidae), birds of paradise (Paradisaeidae), and others are found only to the south.

Past isolation has resulted in some realms having unique families and orders. However, a number of broadly dispersing bird lineages cross between realm boundaries and are represented in multiple realms. For example, the nearctic and neotropical realms have exchanged many birds, and today there is no single, clear breakpoint to indicate where their bird faunas diversified. Topographically, one might expect this breakpoint to occur at the Isthmus of Panama, a land bridge connecting North and South America that emerged from the sea about 3 million years ago. The formation of the Panama land bridge had a profound effect on non-flying animals such as most mammals, because it allowed the previously isolated faunas to mix rapidly, a phenomenon known as the **Great American Interchange**. Genetic studies, however, have shown that its effect on

> **Great American Interchange:** the exchange of animals that commenced about 3 million years ago when a land bridge first connected the previously isolated continents of North and South America.

birds was more varied: members of avian groups that disperse easily over water had moved between these continents many times previously and were relatively unaffected by the advent of the land bridge, but the new dispersal corridor created opportunities for birds such as antbirds and woodcreepers that do not normally disperse across water (Weir et al. 2009).

2.3.2 Avian distributions and their limits

No bird species can be considered to have a truly worldwide distribution since no species is found on every continent. The Peregrine Falcon (*Falco peregrinus*), which is found on all continents except Antarctica, has the broadest natural breeding distribution of any landbird. Runners-up include the Barn Owl (*Tyto alba*), which is found on five of the seven continents, and the Barn Swallow (*Hirundo rustica*), which breeds on four, and visits two more during other parts of the year. Among waterbirds, the Wilson's Storm-Petrel (*Oceanites oceanicus*) (Fig. 2.18A), Arctic Tern (*Sterna paradisaea*) (Fig. 2.18B), and Sooty Shearwater (*Aedenna grisea*) are among the most wide-ranging species; all have annual migration cycles that span most of the world's five major oceans.

It can be surprisingly difficult to define the precise geographic range of a particular bird species. The easiest

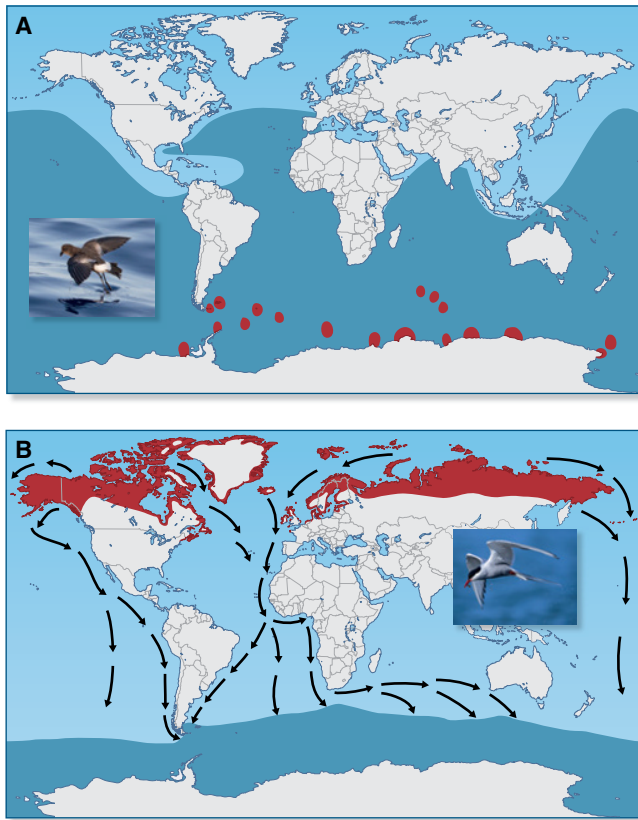**Fig. 2.18 Seabirds with worldwide distributions.** Some pelagic seabirds spend much of their lives away from land, such as (A) Wilson's Storm-Petrel (*Oceanites oceanicus*) and (B) the Arctic Tern (*Sterna paradisaea*). Their expansive ranges cover most of the world's oceans. Wintering areas are shown here in darker blue; breeding areas are depicted in red. (A, Shyamal, https://en.wikipedia.org/wiki/File:OceanitesDistribution.svg. CC0 1.0; photograph by Olli Tenovuo. B, Andreas Trepte, http://en.wikipedia.org/wiki/File:Sterna_paradisaea_distr_mig. png. CC-BY-SA 2.5; photograph by Arto Hakola.)

situations occur when a bird is found exclusively on a small island or in a very specific type of habitat; in these cases, the bird's distribution corresponds directly to the area of the island or the distribution of its specialized habitat. More commonly, however, birds have complex distributions, with populations that vary in abundance in both time and space. Nomadic birds might be common in a region one year but completely absent the next. Migratory birds similarly move around during their annual cycle. Many bird species are relatively common in a core part of their breeding distribution but then become increasingly rare towards the edges of their range. Even within a region, a bird is likely to be present in certain habitats but absent from others. Distribution maps therefore are particularly sensitive to the scale at which they are drawn, as discussed in Box 2.07.

Some factors that determine the limits of a particular bird's distribution are readily apparent. Range limits often are dictated by where the species' preferred habitat occurs or by the availability of other fundamental resources such as particular foods or nesting sites. Similarly, many birds are physiologically adapted to certain climate conditions and are found only in areas with appropriate temperatures and water availability. Changes in climate therefore may cause changes in avian range limits, both over evolutionary timescales and during recorded history. One clear example comes from surveys conducted 100 years apart in the Sierra Nevada Mountains of California (USA), where changes in temperature and rainfall patterns over the course of a century are well documented. Of the 53 bird species surveyed, 48 showed range shifts that corresponded to these long-term changes in temperature and rainfall, demonstrating that the distributions of these birds are determined at least in part by these fundamental environmental attributes (Tingley et al. 2009).

In many settings, range limits can be mysterious, and it is common for a bird species to be absent from areas where it may seem well suited. In these cases, the range limits may be a legacy of the past, for example if the species has gone locally extinct or never had the opportunity to disperse into the region. Alternatively, a species might be limited by hidden environmental features, such as the presence of parasites, diseases, or predators. Or it might be generally suited to the local environment but unable to compete successfully with other species that are even better adapted to those conditions. Many birds have range limits that are dictated by several factors simultaneously. For example, studies of range limits in birds of the Himalayas have suggested that climate variation and the presence or absence of competitors all strongly influence the distribution of each individual bird species (Price et al. 2011).

2.3.3 Variation in the diversity of living birds

Bird groups demonstrate an enormous range in their levels of diversity. For example, the largest order of birds—Passeriformes—includes more than half of all living bird species, whereas several other orders that have existed for equivalent lengths of time contain only a few species. Ancient but low-diversity lineages include the strange Hoatzin (*Opisthocomus hoazin*) of South America, the only member of its order (Opisthocomiformes), and the three species of mesite from Madagascar, which together form the order Mesitornithiformes.

There are several complementary explanations for why some groups of birds are richly diverse while others have only a few species. Fossil evidence demonstrates that some groups with low diversity today were once far more widespread and numerous. For example, all five species of living mousebirds (which together form the order Coliiformes) are restricted to Africa, but the fossil record shows that

Box 2.07 Bird distributions from far and near

The geographic breeding distribution of a particular bird species often is complex, particularly when observed in fine detail. Birds that breed in colonies, such as many seabirds, may range widely when foraging or during the non-breeding season, but their breeding sites usually are highly localized. Non-colonial landbirds usually have a more even distribution across space, but even these species usually are restricted to a particular set of habitats. Indeed, no widespread bird species occurs everywhere within its range.

Classic distribution maps for birds, such as those found in many field guides, do not capture much of this heterogeneity in bird distributions. Such maps usually use shading to indicate the outline of the entire region in which a particular species might be found. Colors can be used to distinguish areas where the species is a permanent resident, migratory breeder, migrant, or non-breeding visitor. For mapmakers, the boundaries of these colored zones often are challenging to draw, because many species become rarer at the edges of their range. Deciding exactly where to place the distribution lines therefore becomes a matter of judgment, and map users need to consider their knowledge of each species' habitat use when looking for birds at a particular location.

With advanced mapmaking techniques, ornithologists can create atlases of bird distributions on a much finer scale than ever before. These approaches take advantage of huge, worldwide datasets derived from satellite observations, climate measurements, and land-use assessments.

They also integrate precise information on locations where bird species are found, as recorded on museum specimens or reported by birders. The power of this approach is that it is not necessary to know every location where a bird species occurs. Instead, sophisticated mathematical models are created to determine what environmental parameters best predict these locations, and then the predictions are expanded to determine a species' entire range. Because these predictions are expressed as probabilities, it is possible to generate a probability map of each species' distribution (Fig. 2.B7.01) in which the intensity of the color on the map codes the probability that the species occurs at that point. These more detailed maps are of obvious interest to birders, but they also have great utility in any setting where fine-scale knowledge of a species' distribution is important for conservation, management, or land-use decisions.

The quality of these predictive maps is highly dependent on the quantity of bird observations that underlie them. Birders have contributed hundreds of millions of observations to this endeavor by participating in citizen science projects such as eBird (www.ebird.org), the source of the heatmaps shown here. However, many places still exist where observations are sparse, and additional observations will improve maps even for well-covered areas. Anyone with an interest in birds can make valuable contributions to our scientific knowledge by participating in this kind of citizen science project, while simultaneously improving resources for birders and aiding bird conservation.

Black-throated Gray Warbler

Dickcissel

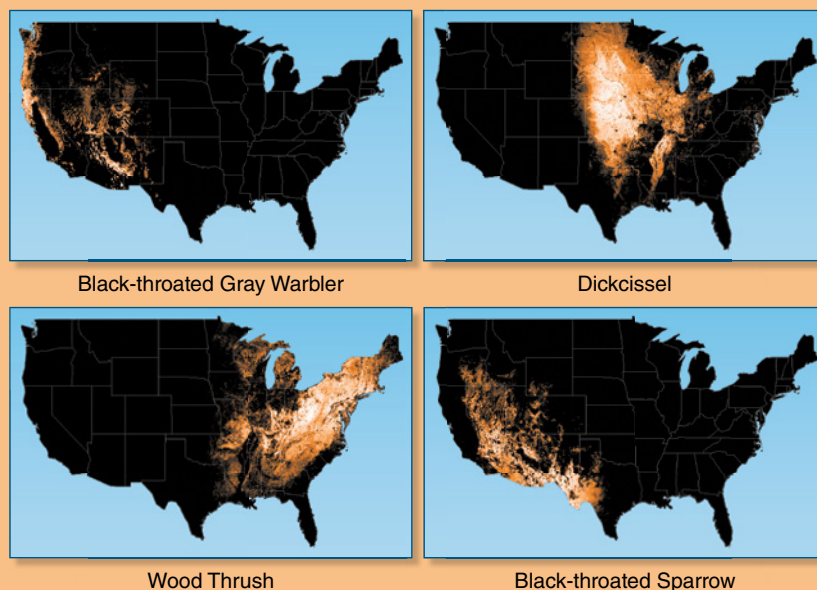Wood Thrush

Black-throated Sparrow

Fig. 2.B7.01 Heatmaps of bird abundance. These breeding distribution maps of four North American bird species were generated from bird counts submitted by bird watchers to the eBird website. Lighter/whiter colors indicate a greater likelihood of a particular species occurring at that location. (© Cornell Lab of Ornithology.)
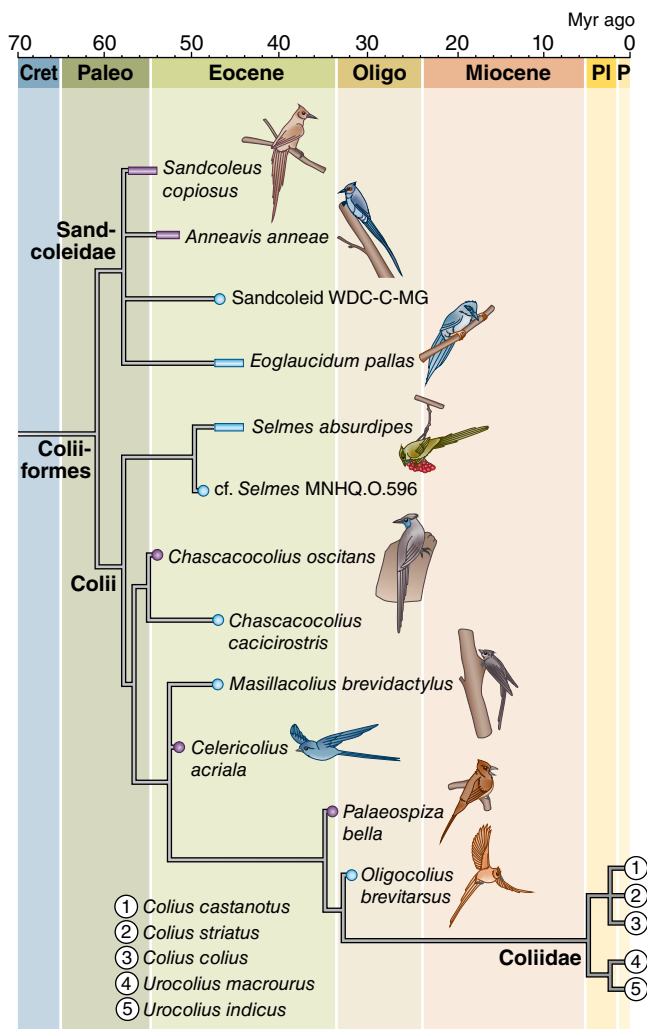
Fig. 2.19 Evolutionary expansion and contraction. Fossil evidence reveals that mousebirds were once extremely diverse with a worldwide distribution. Only five mousebird species (bottom right) occur today, all in Africa. (From Ksepka and Clarke 2010. Reproduced with permission of John Wiley and Sons.)

other lineages of mousebirds were once very diverse components of North American and European bird faunas. It is not clear why mousebirds eventually died out everywhere except Africa (Ksepka and Clarke 2010) (Fig. 2.19).

A more complete fossil record would allow us to track such changes in detail for all groups of birds and to study how their patterns of diversity have waxed and waned over time. In the absence of such a detailed record of the past, diversity can be explored by comparing groups of living birds with high and low diversity to determine whether certain aspects of their biology are associated with their differing levels of diversity. Biologists often have wondered if **key innovations** drive diversity; that is, whether the occasional evolution of an important new trait allows a lineage to diversify as new species expand into additional locations or avail themselves of new resources.

Most obviously, the ability to fly almost certainly was a fundamental key innovation that contributed to the diversity and long-term success of birds in general. Potential key innovations for particular groups of birds include the ability to learn songs and other mate-attracting or territory-protecting behaviors, the presence of high levels of sexual dimorphism and sexual selection, and behaviors related to migration and dispersal ability.

Phylogenetic data can be used to compare the pace of diversification in different groups of birds. The fastest rates of generation of new species often occur when birds colonize island archipelagos, as has happened in the Galápagos finches and Hawaiian honeycreepers (Chapter 3). White-eyes in the genus *Zosterops* are another instructive example of just how fast avian diversification can occur, given favorable circumstances. These birds are distributed across much of tropical and semitropical Africa and Asia, including many islands in the Indian and Pacific Oceans. Phylogenetic studies show that birds in this family have diversified steadily over the past 10 million years, but the approximately 80 species of the *Zosterops* group result from a notable explosion of diversification during only the past 2 million years (Moyle et al. 2009). One cause of the diversification of *Zosterops* is this small bird's propensity for colonizing new and often remote locations, where small, isolated populations can diverge quickly to become new species.

Many groups of living birds share a common pattern of diversification: a pulse of early and rapid speciation followed by a decreasing pace of further speciation over time (Phillimore and Price 2008). There are at least two potential explanations for this pattern. One starts with the dispersal of the group into new and somewhat isolated areas: the colonization of new places initially provides these populations with the raw material for speciation, but eventually the newly available locations are all colonized, and the rate of speciation slows. The *Zosterops* white-eyes exemplify this pattern, since their pulse of speciation seems to have followed from one very widespread wave of dispersal 2 million years ago, after which fewer new species were generated (Fig. 2.20). These geographic opportunities and limits on speciation are most prominent in allopatric groups, in which new species form in different locations. The second possible reason involves the eventual competition among the resulting species. Particularly in settings where many existing bird species within a group occur

> **Key innovation:** a newly evolved trait that allows a lineage to take advantage of new ecological opportunities, and which results over time in that lineage diversifying into multiple species that are specialized for those new ecological niches.
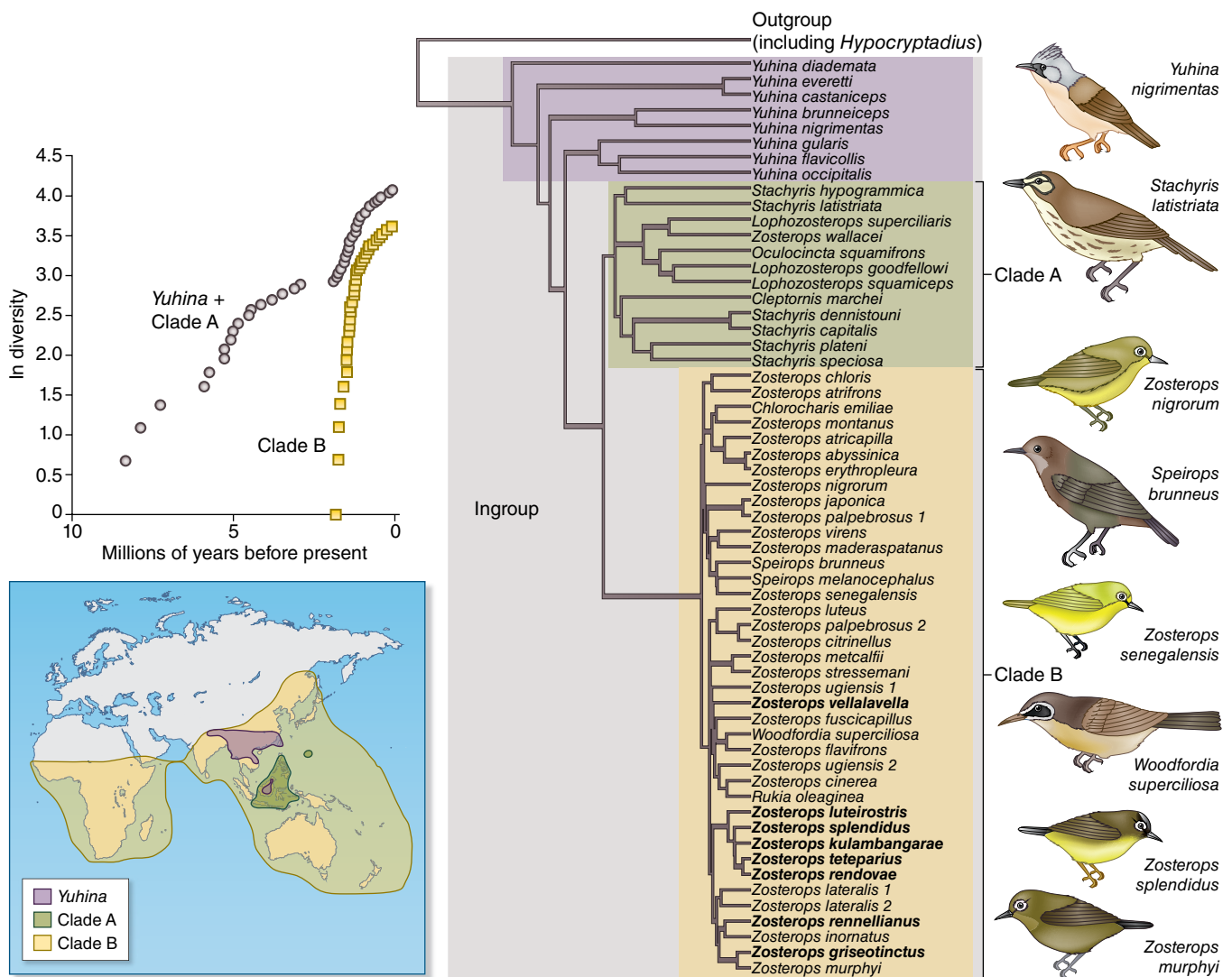
Fig. 2.20 Rapid speciation. This evolutionary tree for the genus *Zosterops* and its close relatives can be used to plot the increase of white-eye species through time. Several pulses of diversification occurred as this group spread through continental regions and colonized many isolated groups of islands. Colors on the map depict the areas inhabited by the groups with the same color codes on the evolutionary tree. (From Moyle et al. 2009. Reproduced with permission from National Academy of Sciences, USA.)

together in **sympatry**, their ecological competition with one another can place limits on their opportunities to diversify further. For example, many species in the North American wood-warbler *Setophaga* group likely diverged during past periods of geographic separation, but many breed in the same places and habitats today, and phylogenetic studies show that speciation in this group has slowed markedly since its origin (Rabosky and Lovette 2008). This pattern of diversification slowing through time suggests that there is feedback between existing diversity and the origin of new species—especially when the species that occur together are in competition with one another: the more species present, the less likely it is that new species will arise. This general phenomenon is termed

density-dependent diversification, and its prevalence and potential causes across different groups of birds are intriguing yet not fully understood.

> **Sympatry:** refers to organisms or groups of organisms that occur in the same place.
>
> **Density-dependent diversification:** the somewhat controversial concept of a feedback loop in which speciation within a group slows down over time as the number of species increases, since the presence of existing species blocks opportunities for new species to arise.

2.4 Origin of birds

Few topics in all of ornithology have engendered more debate than the origin of birds, and those arguments continue today. Fortunately, new information from both fossils and DNA has helped to clarify the relationship between birds and other dinosaurs and defined the timescale over which birds most likely originated and diversified.

2.4.1 Birds are theropod dinosaurs

Nearly all experts now feel confident that birds are the living descendants of dinosaurs, a diverse group of reptiles that originated about 230 million years ago and which subsequently became the dominant group of land animals until the mass extinction at 66 million years ago that ended the Cretaceous Period. Earlier researchers often suggested that birds might be more closely related to various non-dinosaur groups of reptiles or that birds represent a very early offshoot of the dinosaurs. Many lines of evidence—including traits seen in fossils and shared aspects of their inferred physiology and behavior—now strongly support the idea that birds form a subgroup of the dinosaurs, one that arose fairly late from within the broader dinosaur radiation (Fig. 2.21).

Even though birds are traditionally classified into a Class Aves that is separate from the reptile Class Reptilia, in evolutionary terms dinosaurs and birds are both more correctly considered a subset of the reptiles, a group that also includes living turtles, crocodiles, snakes, and lizards. Reptile diversity was even higher in the past, because the group includes not only all dinosaurs but also a number of other long extinct lineages such as plesiosaurs, ichthyosaurs, and the flying pterosaurs. Therefore, it is technically correct to say that "birds are living dinosaurs" or that "birds are reptiles," but it is incorrect to claim—as still happens in the popular media—that these statements are scientifically controversial.

The evolutionary affinity between birds and dinosaurs was first recognized in the 1860s, when British biologist Thomas Huxley popularized the idea that the fossil *Archaeopteryx* (covered later in this chapter in more detail), which had been recently discovered, represented an evolutionary transition between these groups. In the early 1900s, however, influential scientists challenged the dinosaur–bird link, emphasizing specific differences in a small number of traits seen in fossils. Their cornerstone argument was based on the idea that dinosaurs had lost the fragile bones called clavicles, which are present in more ancient groups of reptiles and also in birds, which have fused clavicles that
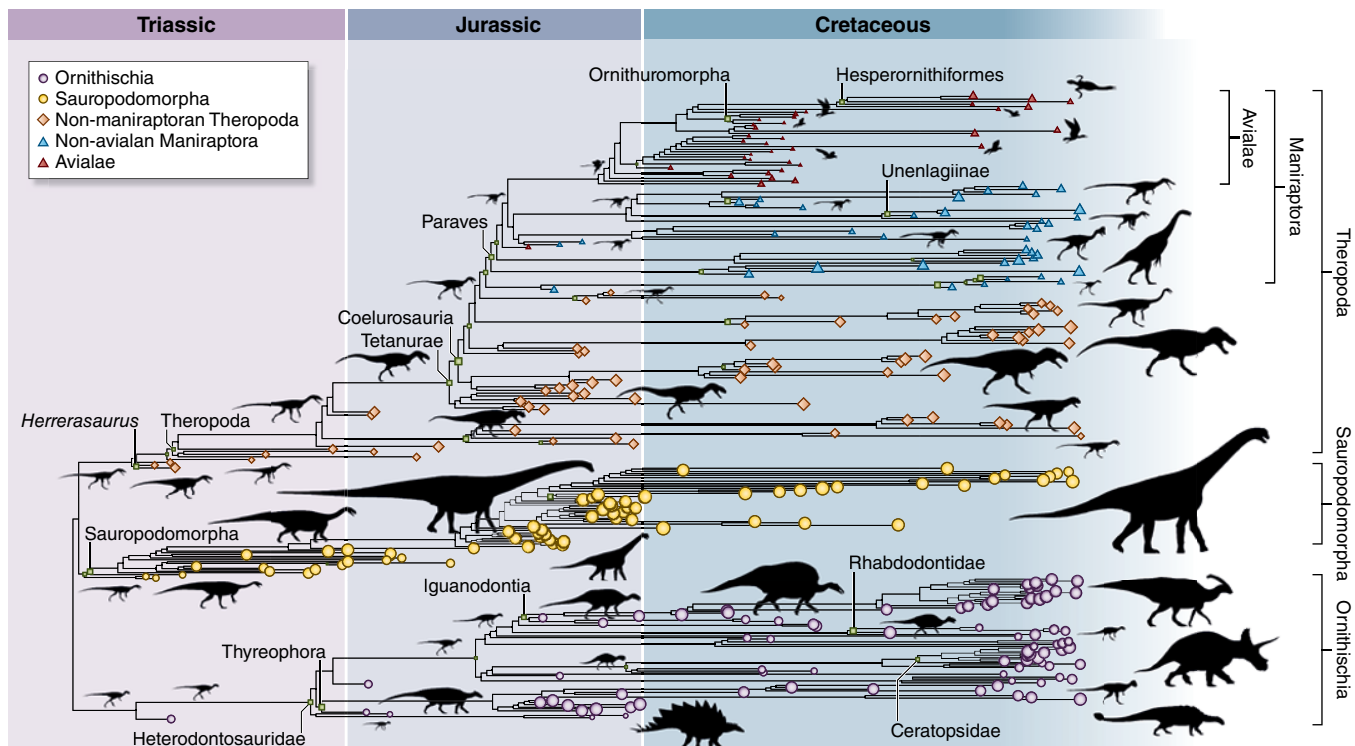

Fig. 2.21 Birds form a subgroup of dinosaurs. This phylogenetic tree shows one widely accepted view of how modern birds (top right) might have evolved from carnivorous dinosaurs. Key evidence for this version of the avian evolutionary tree comes from late Jurassic fossils unearthed in China and South America. (From Benson et al. 2014.)

Fig. 2.22 *Tyrannosaurus rex* **was a theropod dinosaur.** This spectacular specimen in the Field Museum (Chicago, USA) is the largest and most complete *T. rex* fossil ever found. (Photograph by Connie Ma, http://en.wikipedia.org/wiki/File:Sues_skeleton.jpg. Used under CC-BY-SA 2.0.)

form the furcula, or wishbone (Chapter 6). Under the assumption that birds would not have re-evolved a complex structure that was lost in their immediate ancestors, birds were thought to be descended from one of the older, non-dinosaur reptile groups with clavicles. For 50 years, this targeted focus on clavicles and a few other similar traits distracted researchers from the many other features shared by dinosaurs and birds.

Researchers started to adopt a more synthetic view of bird origins in the late 1960s, sparked in part by advances in the reconstruction of evolutionary relationships based on the similarities and differences between organisms. Based initially on the insights of paleontologist John Ostrom, many other morphological traits were identified that revealed evidence for the shared ancestry of birds and dinosaurs. At the same time, new fossil discoveries expanded our knowledge of the diversity of both dinosaurs and early birds. A critical later finding was that dinosaurs did have clavicles after all, and that the fusion of clavicles into a furcula is a trait found not only in birds but also widely in the theropod group of dinosaurs that includes the well-known tyrannosaurs, among others (Nesbitt et al. 2009). The presence of clavicles was overlooked previously because these fragile bones do not fossilize well, and because some dinosaur clavicles were misidentified.

Debate has persisted longer over which subgroup within the dinosaurs gave rise to birds. One possibility is that birds originated relatively early in the radiation of the **archosaurs**, the group that includes all of the dinosaurs and crocodiles, as well as birds. Previously it was thought that birds were more closely related to crocodiles than to

dinosaurs, but this possibility has been refuted by newer fossil evidence. Alternatively, birds might be embedded deeply within the dinosaurs, within the theropod dinosaurs, or within or near one of the other dinosaur groups. Variants of this latter possibility have long been championed by the paleontologist Alan Feduccia (2012) and his colleagues, but among most other avian paleontologists there now is nearly universal agreement that birds originated from within the theropods (Dyke and Kaiser 2011).

The earliest theropod dinosaur fossils date from the Late Triassic Period about 225 million years ago, when several major groups of dinosaurs first arose. Throughout the subsequent 160 million years of the Jurassic and Cretaceous Periods, theropods were the dominant terrestrial carnivores. The most famous theropod species was the fearsome *Tyrannosaurus rex* (Fig. 2.22). However, although many theropods were huge meat eaters, the theropods also included a diverse range of smaller-bodied dinosaurs, some of which were likely herbivores or insectivores. Within the bipedal theropods, birds probably arose within a group termed the **Maniraptora**, which was distinguished by bird-like features such as long arms. Fossil evidence suggests that some non-avian maniraptorans could also fly

Archosaurs: a large group of reptiles that includes the non-avian dinosaurs, pterosaurs, crocodiles, and birds.

Maniraptora: a group that includes birds and their closest relatives within the theropod dinosaurs.

Fig. 2.23 Maniraptorans likely gave rise to birds. These dinosaurs had many bird-like features, suggesting that the earliest birds might have arisen within this group. (Illustration by Jane Kim, Inkdwell.)

Fig. 2.24 Present-day archosaurs. Crocodiles are the nearest living relatives of modern birds; these two groups represent the only extant archosaurs. (© Shane Moore/Animals Animals.)

or glide; indeed, because of their similarities to birds, there is still debate about whether some maniraptoran fossils should perhaps be reclassified as early birds. More generally, however, it is likely that the lineage that ultimately gave rise to modern birds was just one of many similar maniraptoran lineages that had features once thought to be found only in birds and their direct ancestors (Fig. 2.23).

From the broader archosaur group that once included the non-avian dinosaurs and other extinct groups, only birds and crocodiles have survived to the present day. Therefore, among living organisms, birds and crocodiles are each other's closest present-day relatives (Fig. 2.24).

2.4.2 Feathers and other dinosaur traits in birds

Birds and theropod dinosaurs share many traits, some of which are also found in other dinosaur groups. From a historical perspective, feathers are one of the most surprising features that birds and other dinosaurs have in common, because the presence of feathers was long thought to be a trait that unambiguously distinguished birds from all other animals. Starting in the 1990s, an important series of fossil discoveries produced increasingly clear evidence that most lineages of theropod dinosaurs sported feather-like quills and plumes (Chapter 4). Many of these new discoveries came from exceptionally well-preserved dinosaur and early bird fossils found in Liaoning Province, China, where fine volcanic ash fell about 125 million years ago and preserved not only bones but also impressions of soft external parts of the animals entombed in the ash deposits (Fig. 2.25). Evidence of feathers now has been found in dozens of fossil theropods from China as well as a few from North America and Europe; feather-like structures also have been identified in some non-theropod dinosaur fossils. Although today feathers are a feature restricted to living birds, in the past feathers were widespread among the dinosaur ancestors and relatives of birds.

In addition to feathers, birds and theropod dinosaurs share many other morphological traits, including the furcula formed by fused clavicles. Like birds, some theropods had bones that were tube-shaped and hollow, or **pneumatized**. Feathers and pneumatized bones were long considered avian adaptations arising from selection for flight, but we now know that these features evolved in non-flying dinosaurs, the ancestors of birds. Instead, the hollow bones of theropods may be evidence of a respiratory system in which the spaces within the bones serve as part of the air-sac network, similar to that of modern birds (Chapter 6). Comparative studies suggest that pneumatized bones evolved separately in different groups of theropods; in the largest such dinosaurs, these bones may have served to reduce the weight of the huge skeletal structures needed to support their massive bodies. In the non-avian theropod lineages related to birds, these air spaces and the lighter bones were more likely related to an active, fast-moving lifestyle (Benson et al. 2012).

Although no ancient dinosaur DNA survives to be analyzed, fossil evidence suggests that birds and the other theropod dinosaurs share the trait of having a small **genome** relative to most other vertebrates. In an elegant paleontological detective story, researchers realized that in living

Pneumatized: filled with small air cells.

Genome: the complete set of genetic material—DNA—within an individual bird.
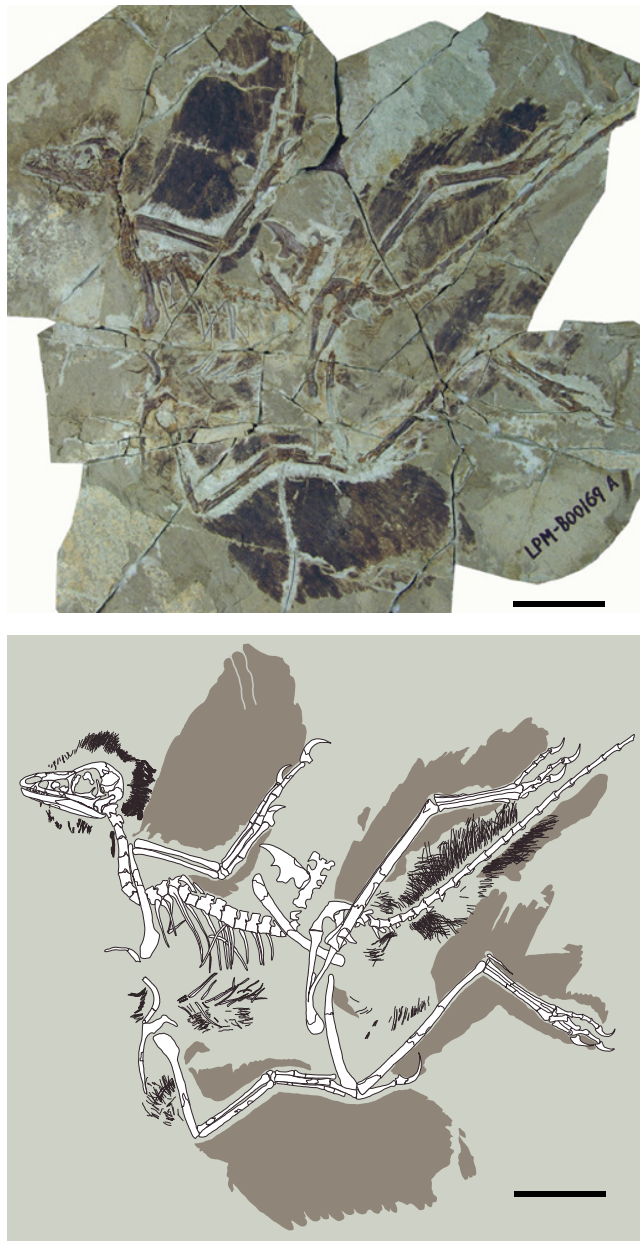
Fig. 2.25 Feather impressions in fossils. Numerous fossils of non-avian dinosaurs include preserved impressions of feathers. This fossilized theropod dinosaur from Liaoning Province, China has visible remains of feathers around the tail and limbs, indicated by the dark gray areas in the illustration. Scale bar = 5 cm. (From Hu et al. 2009. Reproduced with permission from Macmillan Publishers Ltd.)

Fig. 2.26 Birds and other theropod dinosaurs have small genomes. The colored branches on this evolutionary tree indicate the genome sizes of various groups of tetrapod vertebrates. The orange and red branches indicate the smallest genomes and are found in birds and their theropod dinosaur relatives. Genome size here is measured in picograms (pg), or one-trillionth of a gram. (From Organ et al. 2007. Reproduced with permission from Macmillan Publishers Ltd.)

vertebrates, the size of certain bone cells correlates strongly with the size of an animal's genome: larger genomes result in larger bone cells. The diameter of these bone cells can be measured in some particularly well-preserved dinosaur fossils, which shows that genome size became reduced during the early evolution of theropods. This reduction is therefore another trait that birds probably inherited from their theropod ancestors (Organ et al. 2007) (Fig. 2.26).

Birds and the other theropod dinosaurs further share many physiological and behavioral traits: an upright, bipedal posture; the rapid growth rate of young individuals; and details of the structures of their calcified eggs. Fossil trackways of dinosaur footprints and fossilized theropod nest sites show that at least some theropods were social and that they likely guarded or incubated their eggs, similar to most modern birds. Debate persists about whether these other theropods, like modern birds, were endothermic—metabolically able to maintain their core body temperature at a level higher than their surroundings—but it is possible that they also share this trait.

2.4.3 *Archaeopteryx*, the earliest known bird

The fossil bird *Archaeopteryx* is one of the most famous of all extinct organisms. *Archaeopteryx* fossils are known only from 150-million-year-old limestone deposits in southern Germany. The species name of *Archaeopteryx lithographica* derives from the fact that most specimens come from rock quarries that were mined for use in lithography, a printing process. Fossils of *Archaeopteryx* and thousands of other Jurassic Period organisms were discovered when quarry workers split slabs of this stone to make lithographic plates.

Several of the earliest *Archaeopteryx* specimens found in the 1860s and 1870s were nearly complete skeletons, with clear impressions of feathers surrounding the arms and body. One of the most spectacular of these fossils is now in the natural history museum at Humboldt University in Berlin, Germany; it accordingly is referred to as the "Berlin specimen" (Fig. 2.27). Another famous exemplar known as the "London specimen" is in the British Museum. The limestone sediments in which all *Archaeopteryx* fossils have been found were formed in a shallow, tropical sea dotted with islands. Other flying vertebrates coexisted there with *Archaeopteryx*, including a variety of the flying reptiles known as pterosaurs. Pterosaur fossils are much more common in these deposits than are *Archaeopteryx* fossils.

The early *Archaeopteryx* fossils were—and remain—sensational finds because they reveal an organism with a mosaic of traits showing linkages to both theropod dinosaurs and modern birds. Bird-like traits in *Archaeopteryx* include the structure of its plumage, its relatively large brain, and many details of its skeletal anatomy. Features that link it to its non-avian theropod relatives include its many small teeth, a long tail with a bony midline, claws on the ends of its three finger bones in the wings, and additional skeletal details.

There is still great debate about the behavior and flying ability of *Archaeopteryx*. The largest specimen of this species had a wingspan of about half a meter, and various features of its feather and wing anatomy suggest that it could fly, but it is not clear how well (Fig. 2.28). The claws

Fig. 2.27 *Archaeopteryx*, an early bird. One of the most famous of all fossilized organisms, this Berlin specimen of *Archaeopteryx lithographica* provided early evidence that modern birds are derived from dinosaurs. (Photograph by H. Raab, http://commons.wikimedia.org/wiki/File:Archaeopteryx_lithographica_(Berlin_specimen).jpg. Used under CC-BY-SA-3.0.)
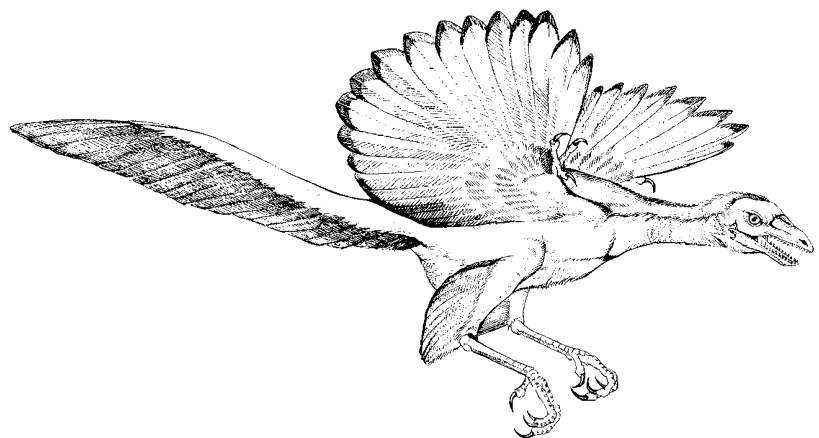

Fig. 2.28 *Archaeopteryx* reconstruction. An illustration depicting how *Archaeopteryx* may have appeared in life. (Illustration by Jane Kim, Inkdwell.)

on its wings have featured prominently in reconstructions of *Archaeopteryx* as a climbing, arboreal specialist, but other anatomical features suggest that it may have spent much of its time on the ground (Chiappe 2007).

Despite the clear affinities of *Archaeopteryx* to both modern birds and extinct groups of dinosaurs, we now understand that *Archaeopteryx* is not a direct missing link between these groups. This is because *Archaeopteryx* is not a direct ancestor of modern birds, but rather a representative of an extinct evolutionary offshoot of early birds, a side branch of the large diversity of early birds that originated earlier in the Jurassic Period. A different—and presently unknown—early bird present at this time was more likely the direct ancestor of all modern birds. Nonetheless, *Archaeopteryx* is generally considered to be the oldest known organism that is clearly a bird (Lee and Worthy 2012). New discoveries of contemporaneous theropods with avian attributes highlight the great diversity of such lineages in the late Jurassic fauna. As in all situations where diverse lineages occur at a time of great evolutionary transition, and because all fossils are inherently incomplete, it can be challenging to distinguish the early birds from non-avian theropods with many similar traits (Xu et al. 2011).

2.4.4 Other early birds from the Mesozoic

Animals that were unquestionably birds diversified greatly during the last part of the Mesozoic Era, in the Cretaceous Period from 66 to 145 million years ago. However, most of the fossil birds from this time are not the direct ancestors of birds alive today; instead, they are offshoots of the avian evolutionary tree that left no direct descendants. Of the dozens of avian groups present in the Cretaceous that are now extinct, four merit special mention.

Discovered in 1993, the crow-sized *Confuciusornis* is now one of the best understood Mesozoic birds due to the exquisite level of anatomical detail preserved in some fossils. Although they are known only from the Liaoning deposits in China that date to about 120–135 million years ago, hundreds of *Confuciusornis* specimens have been studied by avian paleontologists; unfortunately, hundreds, or perhaps thousands, of additional specimens have been sold (often illegally) to collectors and are not available for research. The skeletal anatomy of *Confuciusornis* has many avian characters but lacks adaptations seen in later birds, such as an extensive keel on the sternum (Chapter 6). Its wings were long and pointed, and its wing feathers were highly asymmetrical, as seen in modern flying birds. Instead of the long, bony tail seen in earlier birds such as *Archaeopteryx*, *Confuciusornis* had a pygostyle, the knot of fused vertebrae that support the tail feathers in modern birds (Chapter 6). Although *Confuciusornis* did not have the full, fan-shaped tail seen in most living birds, many specimens preserve two dramatically long tail plumes (Fig. 2.29). These feathers are reminiscent of sexually selected ornaments seen in many groups of living birds and suggest that female birds of various species have been selecting mates with long tails for at least 140 million years.

Some groups of Mesozoic birds, including *Hesperornis* and its relatives in the order Hesperornithiformes, have

Fig. 2.29 *Confuciusornis* **reconstruction.** An illustration depicting *Confuciusornis* (120–135 MYA), an early bird known from Mesozoic deposits in China. (Illustration by Jane Kim, Inkdwell.)
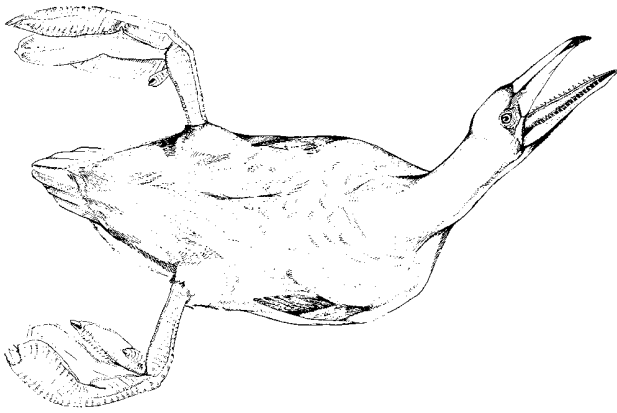
Fig. 2.30 *Hesperornis* reconstruction. An illustration depicting *Hesperornis* (80 MYA), a waterbird of the Campanian that left no close living relatives. (Illustration by Jane Kim, Inkdwell.)

Fig. 2.31 *Ichthyornis* reconstruction. An illustration depicting *Ichthyornis* (85–93 MYA), a tern-like bird of the Cretaceous that may be closely related to the ancient lineage that gave rise to modern birds. (Illustration by Jane Kim, Inkdwell.)

been known to paleontologists for much longer than *Confuciusornis*. *Hesperornis* fossils were discovered in western North America in the 1880s. These birds were all highly specialized swimmers with long, torpedo-shaped bodies (Fig. 2.30). Their reduced wings indicate that, like modern penguins, they had lost the ability to fly. With large, lobed feet and strong leg muscles, they could move swiftly underwater to catch fish in their long, toothed jaws. More fragmentary remains of related species suggest that *Hesperornis* is but one representative of a larger radiation of birds with similar features that went extinct at the close of the Cretaceous Period.

Fossils of one of the most diverse and successful groups of Mesozoic birds, the Enantiornithes, are found on all modern continents except Antarctica. The diversity of enantiornithine birds may have rivaled the varied morphologies and foraging specializations seen in modern songbirds. Enantiornithes were similar in body size to today's songbirds, and details of their skeletons suggest that many were strong fliers. Although their finger bones had claws, the general structure of enantiornith wings shares many features—including the presence of an alula (Chapter 4)—with modern birds. Considered as a group, the Enantiornithes had diverse ecologies, including both aquatic and terrestrial lineages. Fossil evidence from tiny droplets of amber indicates that at least one species had an unusual diet: fossilized tree resin found in the bird's digestive tract suggests that this enantiornithine species fed directly on tree sap (Dalla Vecchia and Chiappe 2002).

Ichthyornis is another well-known bird from the Mesozoic (Fig. 2.31). Compared with Enantiornithes, *Confuciusornis* (Fig. 2.29), and *Hesperornis* (Fig. 2.30), *Ichthyornis* is probably more closely related to the lineage that gave rise to modern birds, although it too is not their direct ancestor. *Ichthyornis* was a strong flier, a fish-eating equivalent of modern seabirds, and was the size of a modern
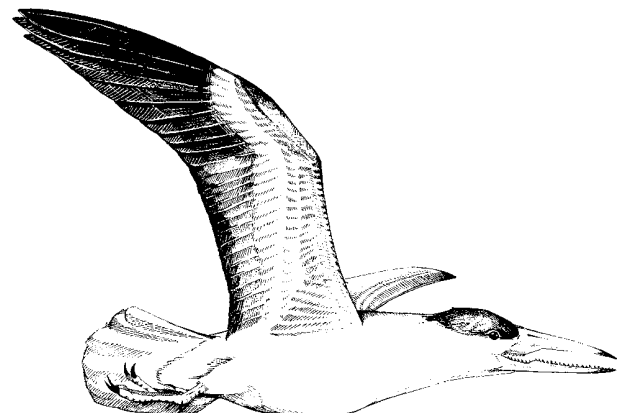
tern. Its wing structure and breastbone with a large keel were similar to those of modern birds. Many *Ichthyornis* specimens were collected in western North America in the late 1800s, and, along with *Hesperornis*, these discoveries of early birds with teeth became well known. In 1880, Charles Darwin wrote a letter to an American paleontologist noting that these archaic birds provided some of "the best support to the theory of evolution" since his publication of his *Origin of Species* (Clarke 2004).

Despite the recent dramatic discoveries in fossil lineages of Mesozoic birds, we have only fragmentary evidence for the full diversity of early birds and other bird-like dinosaurs from this time period. Only a single lineage from the entire radiation survived until the present day to become the lineage of modern birds.

2.4.5 Mass extinction and the origin of modern birds

There is ongoing debate as to when the lineages of birds living today originated and started to diversify from one another. The devastating mass extinction event that ended the Cretaceous Period at 65.5 million years ago is most famous for causing the extinction of all dinosaurs except for birds. This end-Cretaceous event also caused the demise of many other groups of terrestrial and marine organisms, and it may have sparked the diversification of many of the bird lineages that still exist today.

Although the causes of this mass extinction are long obscure, evidence suggests that the impact of a huge asteroid, which produced the Chicxulub crater near Mexico's Yucatan Peninsula, resulted in sudden shifts in climate worldwide. However, independent events happening at the same time, such as sharp rises in volcanic activity and sea levels, may have contributed to the mass extinction.

Fossil deposits from just before the asteroid impact are particularly important for pinpointing whether the extinction was rapid—as would be expected if it resulted primarily from the asteroid impact—or more gradual, as would be expected if there were multiple factors. The few deposits with avian fossils from just before 65.5 million years ago suggest that the asteroid impact was devastating
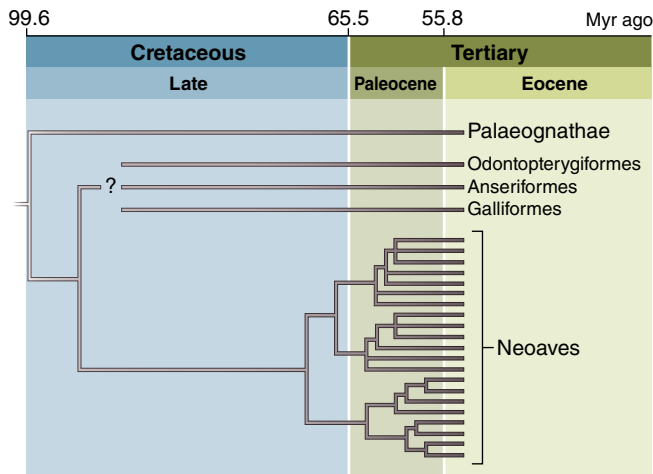
Fig. 2.32 Bird diversity before the Tertiary Period. Substantial uncertainty still exists regarding how many groups of living birds originated before the mass extinction at the end of the Cretaceous Period. Few fossils of modern birds have been found in Cretaceous deposits, but dates derived from DNA comparisons often suggest that many modern birds had Cretaceous origins. This tree shows one hypothesis in which a few modern lineages had Cretaceous origins, but most radiated later on in the Tertiary. (From Dyke and Kaiser 2011. Reproduced with permission from John Wiley and Sons.)

to the birds present in the late Mesozoic. For example, analyses of avian bones from sites in North America and Madagascar have revealed a wide diversity of Mesozoic birds, including representatives of the Hesperornithiformes and Enantiornithes, and *Ichthyornis*, that persisted until the very end of this period but not beyond (O'Connor and Forster 2010; Longrich et al. 2011). In contrast, these surveys did not identify any bones that could be assigned to orders of birds still living today, suggesting that the diversification of most modern groups of birds started after the mass extinction event (Fig. 2.32).

In fact, there is only one known fossil from the entire Cretaceous that unambiguously falls within a group of still living birds: the fossil duck relative *Vegavis* (order Anseriformes). Many other Cretaceous fossils from sites around the world have been linked tentatively to groups of living birds, but these associations usually are uncertain and often based on single bones. In contrast, the *Vegavis* fossil specimen is a nearly complete skeleton, except for the skull. The *Vegavis* fossil was found in Antarctica in 1992, but was not recognized as a waterfowl until detailed analyses were conducted a decade later (Clarke et al. 2005). The presence of a duck relative in the late Cretaceous has important implications, because we know from other phylogenetic evidence that ducks, geese, and their relatives in the Anseriformes split from the group that includes living chickens, grouse, and pheasants (order Galliformes) after an earlier split that divided the paleognaths (ostriches, emus, kiwis, tinamous, and their relatives) and all other living birds. The fossil *Vegavis*, therefore, shows that these two earlier splits must predate the end of the Cretaceous, despite the current lack of fossil evidence for these modern lineages during the Mesozoic (Slack et. al. 2006) (Fig. 2.33).
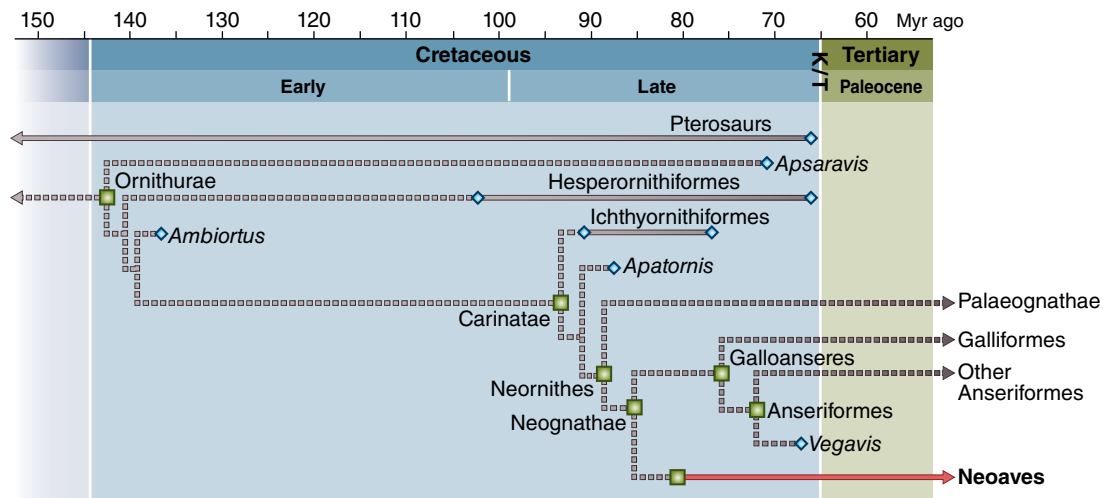
Fig. 2.33 One hypothesis of modern bird origins. This avian phylogeny shows the possible placement of lineages that likely went extinct at the end of the Cretaceous, along with the few known early fossils of modern birds, including the early duck *Vegavis*. (From Slack et al. 2006. Reproduced with permission from Oxford University Press.)

Fossils representing many modern orders are found in subsequent deposits from the early Tertiary Period, after the mass extinction. However, many archaic bird lineages that were common in the late Cretaceous are absent in the Tertiary. This pattern of sudden turnover in the avian fossil record further suggests that nearly all bird lineages were wiped out in the mass extinction at the junction between the Cretaceous and Tertiary. Under this line of reasoning, the few groups of surviving birds then diversified rapidly in the very early part of the Tertiary as the environment became more hospitable, refilling many avian ecological niches (Chapter 13) opened up by the mass extinction. This period of very rapid radiation in the early Tertiary gave rise to many modern orders and families.

In contrast to the later, Tertiary radiation implied by the near absence of most modern birds from the earlier fossil record, studies based on genetic comparisons consistently point to a much earlier origin of modern birds. These DNA dates are based on evolutionary trees calibrated using fossils from deposits of known age. Dates from a few well-documented fossils can help calibrate the timescale for more extensive phylogenies that are mostly based on DNA comparisons among still living species. This **molecular clock** method is useful for back-calculating the point in the past when two bird lineages diverged from one another. Different mutations accumulate over time in each descendant lineage once they separate from their common ancestor; therefore, if you know the overall average rate of mutational change, you can use the amount of DNA difference between two living species to estimate the time when their ancestors separated. In practice, this process is not very precise, in part because different parts of the genome have different average mutation rates, because well-dated fossils are absent for many groups of living birds, and for other technical reasons. Many of these procedural issues can be addressed through statistical analyses that take these underlying sources of variation into account to provide a window of the most likely time for each evolutionary split, rather than pinpointing one exact age.

Using the molecular clock approach to date the origins of groups of organisms was originally controversial when the method was introduced several decades ago, but today it is widely applied and broadly accepted among evolutionary biologists. Controversies involving the outcomes of molecular clock analyses still exist, however, including the general discrepancy between the fossil and DNA dates for the origins of most groups of modern birds. For reasons that remain uncertain, dates estimated using molecular tools are almost always much earlier than the corresponding earliest fossils known for those groups. Even the most advanced DNA-based estimates suggest that the earliest split within the evolutionary tree of living birds—the split between the paleognaths and all other living birds—occurred in the earlier part of the Cretaceous, at roughly 130 million years ago (Cooper and Penny 1997; Haddrath and Baker

2012). Some studies further suggest a Cretaceous origin for many living orders, yet the earliest equivalent fossils of nearly all of these groups are from much later in the Tertiary Period.

When both the fossil and genetic evidence are considered, it seems clear that at least a few lineages of modern birds arose before the mass extinction at the Cretaceous–Tertiary boundary. The extent of the Cretaceous radiation of modern birds remains uncertain, but future fossil discoveries may provide direct evidence for the existence of the **ghost lineages** in the Cretaceous whose existence currently is inferred from phylogenies but which are physically missing from the known fossil record. Additional genome-wide DNA data, analyzed in concert with improved molecular clock analyses and calibration, alternatively might show that most of the diversification in modern birds occurred in the Tertiary, as these lineages expanded into niches opened during the previous mass extinction. Reconciling these two possibilities remains an important challenge in avian systematics.

2.4.6 Diversification of living birds

The groups of birds that diversified just after the mass extinction at the close of the Cretaceous Period include representatives of most extant avian orders. Few fossils from this early part of the Tertiary can be linked to modern birds at the family level, however, because most avian diversity in this early period occurred in families that later went extinct.

At the family level for living birds, fossils clearly assignable to **crown groups**—groups that consist of the common ancestor of living representatives and all its descendants—generally date to the Eocene Epoch (55 to 33 million years ago). Fossils assignable more specifically to genera of living birds are younger, generally originating 2–25 million years ago.

A dramatic feature of the Eocene avian fossil record is the surprisingly broad distribution of some groups that later became restricted to certain parts of the globe. Some

Molecular clock: the idea that DNA changes accumulate at a relatively steady rate, and that the genetic differences among organisms can therefore be used to estimate the time in the past when they started to diverge from one another.

Ghost lineages: an evolutionary lineage that is inferred from a phylogeny, but for which no fossil evidence has been found.

Crown group: a special type of monophyletic group (i.e., clade) that includes all organisms descended from the last common ancestor of all *living* members of a larger clade.

Box 2.08 Ancient hummingbirds in surprising places

All 335 living species of hummingbirds are found exclusively in the Americas. These birds astounded the European naturalists who first encountered them zipping about the tropics. Ever since, the logical assumption has been that this family of tiny, hovering birds originally evolved in the New World. Therefore in 2004 it came as a great surprise when fossil bird expert Gerald Mayr recognized that several 30-million-year-old remains from a site in southern Germany were actually fossil hummingbirds. Mayr carefully described those fossils, clearly documenting that hummingbirds occurred in the Old World during an earlier part of their evolutionary history.

Mayr's specimens were conclusively hummingbirds: features of their bone structure showed that they could rotate their wings to hover, and their elongated bills suggested that they fed on flowers. However, these first-known European hummingbirds differed from all present-day hummingbirds in various details of anatomy, suggesting that they were an early part of the hummingbird evolutionary tree.

Another spectacular hummingbird specimen from the same early period was found in southern France (Louchart et al. 2008). The skeleton of this ancient hummingbird is nearly complete, and the rock matrix around its bones even reveals the outline of the bird's feathers, making it possible to discern its wing and tail shape (Fig. 2.B8.01).

The French specimen is more similar to modern hummingbirds than the fossils first discovered by Mayr, providing

Fig. 2.B8.01 Early Eocene hummingbird fossil from France. Hummingbirds today are restricted to the Americas, but they were more widespread 30 million years ago. (From Louchart et al. 2008. Reproduced with permission from Springer Science + Business Media.)

even stronger evidence that important aspects of hummingbird evolution occurred outside of the Americas. Mayr and his French colleagues point out that the presence of ancient hummingbirds in what is now Europe does more than provide a radically new perspective on our ideas of where and when these birds evolved: because hummingbirds often coevolve with the plants they feed on, some modern plants in Europe and Asia may retain attributes from the time when they evolved to attract hummingbirds as pollinators.

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of the best and most diverse fossil deposits from this period, for example, are found in Europe (Box 2.08). They record the presence of birds closely related to todies, hummingbirds, and New World vultures, yet today these groups are found only in the Americas. Similarly, the deposits contain frogmouths, which now are restricted to Australasia; and relatives of the Secretary-bird (*Sagittarius serpentarius*), mousebirds, ground-rollers, and turacos, all of which are now found only in Africa (Mayr 2005).

The most diverse and widespread order of living birds—the passerines or songbirds (Passeriformes)—is conspicuously absent from most Eocene deposits in the northern hemisphere. The earliest fossil passerines known are a few Eocene-age bones found in Australia (Boles 1994, 1997). This finding parallels other lines of evidence suggesting that passerines first evolved in the southern hemisphere. Passerine fossils appear in northern hemisphere deposits in the Oligocene (34 to 23 million years ago), but do not become common until the Miocene (23 to 5 million years ago), at which point they constitute a major part of most fossil avifaunas (Box 2.08).

2.4.7 Relationships of living avian orders

There is strong phylogenetic evidence that many orders of living birds originated during a brief period, although, as described earlier, the timing of that burst of diversification is uncertain. The rapidity of this diversification has impeded attempts to reconstruct the precise phylogeny connecting these avian lineages, although some parts of that overall tree are well resolved.

The earliest split in the tree of living birds separates the **ratites** (Fig. 2.34) and the tinamous (collectively termed

Ratite: a group of flightless birds defined by their absence of a keelbone (or carina), including the ostriches, kiwis, rheas, cassowaries, emus, and recently extinct moas and elephantbirds.

Fig. 2.34 Two examples of living ratites.
Tinamous and the large, flightless ratites—
including (A) the Greater Rhea (*Rhea americana*)
and (B) the Emu (*Dromaius novaehollandiae*)—
form the sister group to all other living birds.
(Photographs by: A, Christopher Wood;
B, Chris Burns.)
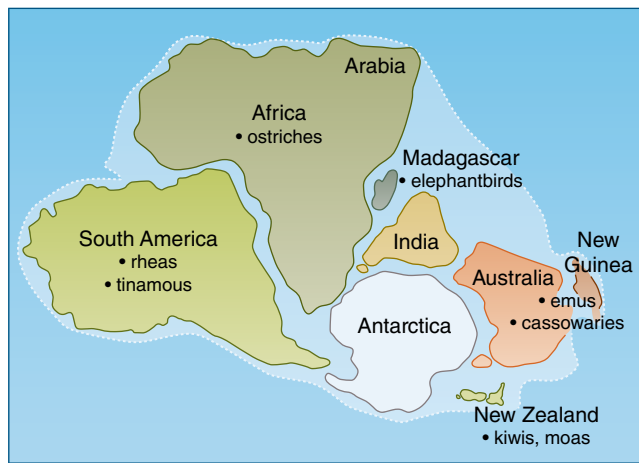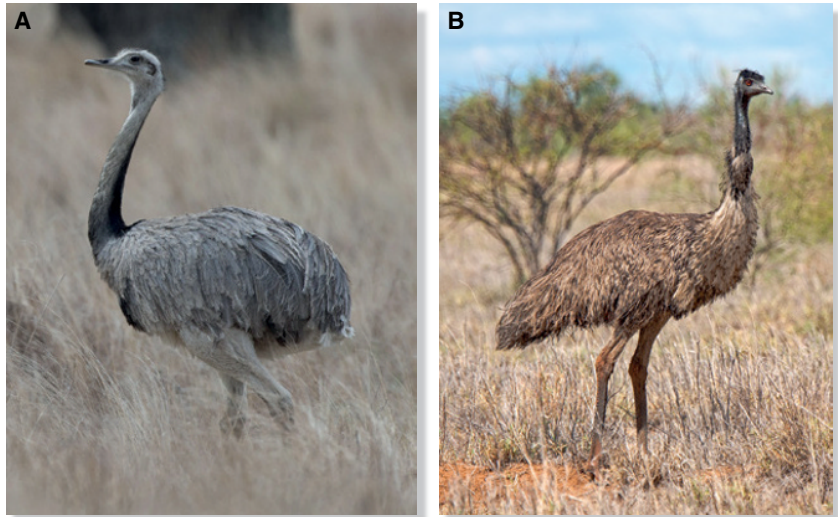
Fig. 2.35 Gondwana. A map of the super-continent of Gondwana about 170 million years ago, before it began to break apart into the smaller continents and islands we know today. (From Gibbs 2006. Reproduced with permission from Craig Potton Publishing.)

within this group as the sister to the moas (Haddrath and Baker 2012; Smith et al. 2013). It now seems most likely that there were multiple losses of flight within the paleognaths after they were present on their respective present-day continents. Under this new scenario, it remains uncertain how the ancestors of today's flightless ratite lineages might have originally dispersed between the continents and islands on which they are now found.

Within the living neognaths, the earliest split separates the group comprising ducks, geese, megapodes, chickens, and their relatives (Galloanseres) from the remaining groups (Neoaves). As described above, the fossil waterfowl *Vegavis* shows that the Galloanseres already had started to diversify before the mass extinction at the end of the Cretaceous. Today, members of this group are found worldwide.

Relationships among the many deep lineages of neognaths remain uncertain. Fig. 2.09 depicts one possible reconstruction of their evolutionary tree, but the details likely will change as we gather more information. In general, however, some traditional groupings find little support in modern DNA-based phylogenies. The list of orders and families in Box 2.09 represents a synthesis of the current phylogenetic information about avian relationships.

paleognaths) from all other birds (termed **neognaths**). With the exception of the flying tinamous, the paleognaths are all large and flightless, and exist on current fragments of the ancient supercontinent of **Gondwana**: ostriches in Africa, rheas in South America, emus and cassowaries in Australia, and kiwis and moas in New Zealand. This distribution of heavy, flightless birds was long thought to be the result of their separation when Gondwana broke up into the present-day smaller continents during the Cretaceous Period, because these non-flying, non-swimming birds would have had difficulty dispersing across the seas separating the new continents. Phylogenetic studies have overturned this hypothesis, however, by showing that the common ancestor of these groups lived more recently than the Gondwana breakup (Fig. 2.35). Furthermore, the flighted tinamous fall well

Paleognaths: one of the two groups of living birds, containing all ratites as well as the extinct elephant-birds and moas.

Neognaths: one of the two groups of living birds, containing all living birds except the ratites.

Gondwana: the name of the ancient southern super-continent of 180–600 million years ago that included most of present-day Africa, Antarctica, Australia, India, Madagascar, New Zealand, and South America.

Box 2.09 A survey of avian orders and families
Contributed by Shawn M. Billerman

One of the joys of Ornithology is encountering an entirely new group of birds for the first time. An exploration of avian diversity best begins with an understanding of the diversity of living birds that we classify into the various orders and families. Many college-level ornithology courses therefore cover the bird families that occur in the local region, or sometimes even the entire set of bird families from across the world. The remainder of this chapter provides a brief introduction to this worldwide diversity of living birds based on the classification of Winkler et al. (2016), a reference that provides more in-depth coverage of each of these groups.

Struthioniformes. The ratites and tinamous together form this ancient and diverse order of terrestrial birds found primarily in the southern hemisphere. Recently extinct forms include the moas of New Zealand and the elephantbirds of Madagascar. Taken together, the members of this order are the sister group to all other living birds. All except the tinamous have lost the ability to fly.

Struthionidae. The Ostrich (*Struthio camelus*), the largest living bird, is found today only in sub-Saharan Africa. The flightless Ostrich is an extremely fast runner. Males care for the eggs and chicks of many females simultaneously.

Rheidae. The rheas include a pair of species found in the grasslands of South America. Although large and flightless, the rheas are more closely related to the smaller and flighted tinamous than to the other ratites.

Tinamidae. Tinamous are a diverse family of flying but ground-dwelling birds from South America with relatively plump bodies and small heads. Generally secretive, many tinamous are more often heard than seen.

Casuariidae. The cassowaries and the Emu (*Dromaius novaehollandiae*) are a small family of large, flightless birds from Australia and New Guinea. The cassowaries, covered with stiff, black, hair-like feathers, inhabit dense rainforests. The Emu is found in drier parts of Australia.

Apterygidae. The kiwis are a small group of small- to medium-sized, flightless birds found only in New Zealand. Covered in fine, brown, hair-like feathers, kiwis are mainly nocturnal and forage primarily on earthworms. They lay the largest egg proportional to their body size of any living bird.

Galliformes. Members of this large and diverse order of fowl-like birds are found worldwide from the arctic tundra to the tropical rainforest. Galliformes range in size from the tiny quail to the robust turkey. The most familiar species of this group are domesticated, including chickens, turkeys, guineafowl, and quail. Males of many galliform species use elaborate displays or exaggerated plumages to attract females.

Megapodiidae. The megapodes are found in tropical regions of Southeast Asia and Australia. Unlike all other birds, megapodes provide no care to their young after the eggs are laid; instead, megapode eggs are incubated by heat from the decomposing matter of large organic mounds piled up by the males or other sources.

Cracidae. An entirely New World radiation, the tropical guans and curassows are diverse. Many are threatened with extinction caused by over-hunting, and they are especially susceptible to being lost from fragmented habitats. These wary birds can be difficult to see but are often heard.

Numididae. A small family of African upland birds, some species of guineafowl have been domesticated. Their raucous calls, intricately patterned plumage, and bare, colorful heads make them instantly recognizable.

Odontophoridae. A diverse family of small, upland birds that often congregate in large coveys, the New World quail are recognizable by their distinctive calls and bold patterns. They are found in a wide range of habitats, from dry deserts to tropical rainforests.

Phasianidae. The pheasants and their allies are found worldwide and include a number of commonly domesticated species, including the chicken. Species in this family come in a wide range of shapes, sizes, and colors, ranging from the diminutive Old World quail to the large turkey. Many species have intricate and exaggerated plumages and use bizarre displays, including dances and booming calls, to attract females.

Anseriformes. A large, diverse, and very familiar group with three families, Anseriformes are found worldwide, primarily in wetland habitats from the arctic tundra to the tropics. They inhabit bodies of water ranging in size from small inland ponds to the open ocean.

Anhimidae. The large South American screamers are found in wetlands, where—as their name suggests—they fill the air with their loud calls. These birds are an avian anomaly in terms of anatomy: they have no feather tracts but do have air sacs under their skin. They have large, heavy bodies, long legs, and tiny heads, and feed primarily by grazing on vegetation.

Anseranatidae. The Magpie Goose (*Anseranas semipalmata*) of Australia and New Guinea nests in large colonies where one male often has a harem of several females who lay their eggs in a common nest. Magpie Geese may be nomadic in their search for suitable wetland conditions for feeding and nesting.

Anatidae. This familiar group of ducks and geese is found worldwide, usually associated with ponds, lakes, oceans, and other wetlands. Many species have distinctly flattened bills, often with serrations or grooves to help them filter or grasp food.

Podicipediformes. This order contains only one family, the grebes.

Podicipedidae. A diverse family of fish-eating waterbirds, grebes are found worldwide. They are well adapted for their life in the water, with lobed toes and feet set far back on their bodies to enable foot-propelled diving.

Phoenicopteriformes. This order contains only one family, the flamingos.

Phoenicopteridae. Flamingos are found in a range of shallow wetlands, mostly in the tropics. Famous for their pink coloration and oddly shaped bill that is specially adapted for filtering tiny food, flamingos are most closely related to grebes.

Columbiformes. This order contains only one family, the doves and pigeons.

Columbidae. Doves and pigeons are found worldwide in a wide variety of habitats, ranging from dry deserts to urban cities. Feeding mostly on seeds, doves and pigeons feed their chicks "crop milk," a substance comprised of water, proteins, and fats.

Mesitornithiformes. This order contains only one family, the mesites.

Mesitornithidae. The mesites are a small family of largely terrestrial birds endemic to Madagascar. Relatively little is known about their natural history, and their relationships with other birds are similarly unclear.

Pterocliformes. This order contains only one family, the sandgrouse.

Pteroclidae. The sandgrouse are found in some of the most arid environments in the world, throughout sub-Saharan Africa and central Asia. Sometimes forming huge flocks, sandgrouse can fly long distances to find water. Adults carry water to chicks by saturating their feathers.

Caprimulgiformes. This is a large order containing both nocturnal and diurnal families. Nocturnal families include the nightjars, potoos, owlet-nightjars, frogmouths, and the frugivorous, cave-dwelling Oilbird (*Steatornis caripensis*). Diurnal Caprimulgiformes include the aerial, insectivorous swifts and treeswifts, and the highly diverse but mostly nectivorous hummingbirds of the New World.

Steatornithidae. The Oilbird is found in the tropical forests of South America. Roosting primarily in caves, it uses its excellent vision and echolocation to navigate in almost complete darkness. Oilbirds are completely frugivorous and use their excellent sense of smell to locate fruiting trees.

Nyctibiidae. The potoos are found in the tropics of South and Central America. Large and cryptically patterned, they sit motionless on trees, resembling the broken ends of branches. Largely nocturnal, they feed mostly on insects.

Podargidae. The frogmouths are found in the tropics of Southeast Asia and Australia. Large and cryptically patterned, they are difficult to find by day, when they sit motionless, resembling the ends of broken branches. At night, they are more active and feed on a wide variety of insects and small vertebrates.

Caprimulgidae. The nightjars are a diverse and worldwide group of nocturnal, aerial insectivores. They have extremely wide mouths and fly around with their mouths open to capture insects. Cryptically patterned, they nest primarily on the ground. Although difficult to see, many species have vocalizations that can be heard at a great distance.

Aegothelidae. Owlet-nightjars are found in a variety of forested habitats in Australasia. They usually roost in tree cavities during the day, and, at night, feed on insects by picking them from the air.

Hemiprocnidae. The treeswifts are small, aerial insectivores found in the tropical forests of Southeast Asia. Most treeswifts have crests or whiskers, which distinguish them from the similar and closely related swifts. Treeswifts do not build nests but instead simply glue their egg to a branch with their saliva.

Apodidae. The swifts are a large radiation of aerial insectivores with a global distribution. Swifts spend much of their life in the air, and have poorly developed feet and legs. Most species nest on vertical or nearly vertical surfaces, and use their saliva to glue nesting material and eggs to the nesting substrate.

Trochilidae. Hummingbirds, named for their unique hovering flight, are small, often brightly colored birds of the New World. With their long, thin bills, hummingbirds famously feed on the nectar of flowers, but also take many small insects and spiders.

Cuculiformes. This order contains only one family, the cuckoos.

Cuculidae. Cuckoos are a diverse group of birds with a global distribution. They are found in a wide variety of habitats, from deserts to tropical savannas. Some cuckoos are nest parasites and notoriously lay their eggs in the nests of other bird species, but many cuckoo species build nests and care for their own young.

Musophagiformes. This order contains only one family, the turacos.

Musophagidae. Turacos and go-away-birds are found in sub-Saharan Africa in a variety of forested habitats, from acacia savanna to tropical rainforest. They are large birds with long tails, and feed on both fruits and leaves. The feathers of many species are extraordinarily colorful, with some species sporting pigments found only in this family.

Otidiformes. This order contains only one family, the bustards.

Otididae. Bustards are medium-sized to very large terrestrial birds found across open grasslands and savannas of the Old World. The bustards include the world's two heaviest flying bird species: the Great Bustard (*Otis tarda*) of Europe and western Asia, and the Kori Bustard (*Ardeotis kori*) of sub-Saharan Africa.

Opisthocomiformes. This order contains only one species in its own family, the Hoatzin (*Opisthocomus hoazin*).

Opisthocomidae. The Hoatzin of tropical South America is an enigmatic bird in many ways, and its relationship to other birds is still debated. The Hoatzin is the only bird that eats only leaves, which it digests using unique foregut fermentation akin to that found in ruminant mammals.

Gruiformes. The gruiform order includes the cranes, the rails, the trumpeters of South America, the finfoots, and the

Limpkin (*Aramus guarauna*). Although much reduced by recent extinction, rails once were the most diverse family in the world, with more than 2000 species. Found worldwide, many species in this order have loud and recognizable vocal displays.

Heliornithidae. The finfoots are a small group of birds with lobed feet. They are found in slow-moving waterways of the tropics, where they are shy and secretive.

Sarothruridae. The flufftails, which consist of the genera *Sarothrura* and *Canirallus*, are highly secretive birds from sub-Saharan Africa. Inhabiting wet woodlands, grasslands, and marshes, the flufftails were long thought to be part of the large rail radiation, but recent data have shown that they are more closely related to the finfoots than to the rails.

Rallidae. An extremely diverse and widespread group, until recently the rails were likely the most speciose family of birds, with a great number of flightless species found on isolated oceanic islands. The 140 or so extant species are found in a wide variety of wetland and terrestrial habitats.

Psophiidae. Trumpeters are a small family of largely terrestrial birds from the Amazon Basin rainforests of South America. Trumpeters are named for their loud call, and their habit of forming large, noisy flocks. Although they forage on the ground, mainly for fruit, trumpeters nest in tree cavities.

Aramidae. The Limpkin is a wading bird found in the marshes of the tropical Americas. Limpkins have a long, decurved bill that is specially adapted for feeding on their main prey, apple snails.

Gruidae. Cranes are a widespread and charismatic group of birds, with some species known for their spectacular courtship dances. Absent only from South America and Antarctica, cranes are found in a variety of open habitats, from drier grasslands to marshes. Many species form huge flocks during migration and on wintering grounds.

Charadriiformes. This extremely diverse order is second only to passerines in number of families and species. Although known by the collective name "shorebirds," members of this group are found in almost every terrestrial habitat in the world, and many also occur in pelagic habitats. With a truly global distribution, the shorebirds are notably varied in their breeding strategies and mating systems. This group includes some of the world's most extreme

migrants: some species fly non-stop for thousands of kilometers. The order also includes the quail-like button-quail and seedsnipe, the wading shorebirds, the penguin-like auks, and the gulls and terns.

Burhinidae. The thick-knees are a small family of terrestrial "shorebirds" found in tropical and subtropical regions of the world, often in relatively dry, open habitats such as savannas. Thick-knees are cryptically patterned and typically nocturnal.

Chionidae. The sheathbills are a small family of seabirds found in the southern oceans, primarily near offshore islands and coastal Antarctica. Resembling large, white pigeons, the sheathbills feed on penguin eggs and chicks, carrion, and other refuse.

Pluvianellidae. The Magellanic Plover (*Pluvianellus socialis*) is a rare wader that has been placed into its own family based on behavioral and molecular evidence. It is a small shorebird of southern South America with bubblegum-pink legs. Using their short, stout bills, these birds flip small rocks and dig into the ground in search of invertebrate prey.

Pluvianidae. The Egyptian Plover (*Pluvianus aegyptius*), found along freshwater bodies of northern and central Africa, is a boldly patterned shorebird that feeds mainly on invertebrates. Once thought to pick food from the mouths of crocodiles, this habit has never actually been well documented. Nesting on sandbars, Egyptian Plovers must actively cool their nest and chicks.

Haematopodidae. Oystercatchers are a small family of large shorebirds that are found along the coasts of much of the world. They use their long, chisel-shaped, coral-red bills to pry or hammer open shellfish and other marine invertebrates.

Ibidorhynchidae. The sole member of this family, the Ibisbill (*Ibidorhyncha struthersii*), lives along fast-moving mountain streams of central Asia. With its long, decurved bill, the Ibisbill searches for invertebrate prey under large boulders and amidst cobbles.

Recurvirostridae. Stilts and avocets are long-legged shorebirds that have a global distribution. They forage for small invertebrates in both fresh- and saltwater marshes.

Charadriidae. Plovers are a large and diverse group of small to medium-sized shorebirds. Found worldwide in a wide variety of open habitats from tundra to tropical savanna, plovers feed on a variety of terrestrial and benthic invertebrates.

Pedionomidae. The Plains-wanderer (*Pedionomus torquatus*), the only member of this family, is a small, rare, and declining terrestrial shorebird from the outback of Australia. Largely nocturnal, the Plains-wanderer feeds mainly on seeds and insects.

Thinocoridae. A small family of odd shorebirds that resemble grouse and quail more than sandpipers, the seedsnipe are found both above the treeline in the Andes and in the open grasslands of southern South America. Unlike most shorebirds, seedsnipe feed mainly on seeds and other vegetation.

Rostratulidae. Painted snipe are a small group of small shorebirds of tropical and subtropical marshes. Often difficult to detect due to their cryptic patterning, painted snipe feed on a variety of aquatic and benthic invertebrates.

Jacanidae. The jacanas are a small group of medium-sized shorebirds. With their extraordinarily long toes, jacanas can wade across surface vegetation in tropical freshwater marshes as they forage for invertebrates. Unlike most birds, male jacanas provide all parental care for the eggs and chicks.

Scolopacidae. The sandpipers and their allies are the largest and most speciose family of shorebirds. They are diverse in their natural history as this family includes species with a wide variety of mating systems and diverse feeding ecologies. They also have varied migration behaviors, with some species flying non-stop for thousands of kilometers.

Turnicidae. The Old World buttonquail are a small group of tiny groundbirds. Seeming more akin to quail than to their actual shorebird relatives, the buttonquail were a longstanding taxonomic mystery until genetic work clarified that they are members of the shorebird group. Buttonquail are terrestrial, cryptically patterned, and feed primarily on seeds and insects.

Dromadidae. The only member of this family, the Crab Plover (*Dromas ardeola*) is a strikingly patterned black-and-white, medium-sized shorebird that breeds along the coasts of east Africa and the Middle East. Crab Plovers construct burrows in the sand where they nest and roost.

Glareolidae. The pratincoles and coursers are the two distinct groups of this family, both of which feed primarily on insects. Pratincoles are swallow-like and catch insects on the wing. Coursers are terrestrial birds and are usually found in dry, open habitats.

Laridae. Gulls, terns, and skimmers together are a widespread family found on every continent. Although largely associated with water, many species also are found in terrestrial environments, and some have adapted well to urban settings.

Stercorariidae. The skuas and jaegers are seabirds found in oceans worldwide, but they restrict their breeding to high latitudes. They feed primarily by pirating food from other birds, particularly gulls and terns.

Alcidae. The auks are a small but diverse family of seabirds of the northern hemisphere. Unlike penguins, which they superficially resemble, auks are fully capable of flight, although they also are accomplished wing-propelled divers. Some auks have brightly colored bills or ornate feathers around the head.

Eurypygiformes. This new order was formed when the former Gruiformes group was split. It contains only two families, each with a single species. Although both species have characteristically colorful wing patterns, they are otherwise quite different.

Rhynochetidae. The Kagu (*Rhynochetos jubatus*) is a flightless landbird endemic to the remote Pacific island of New Caledonia. Found in dense forest, its population is declining. Males display by erecting their long crest and spreading their wings to expose their striking pattern. A cooperative breeder, Kagu helpers defend the territory while the parents care for chicks.

Eurypygidae. The Sunbittern (*Eurypyga helias*) is a striking bird most often found near streams in the tropical lowlands of Central and South America. Sunbitterns are cryptically patterned until they are threatened, which triggers them to spread their wings to reveal the spectacular plumage for which they are named.

Phaethontiformes. This order contains only one family, the tropicbirds.

Phaethontidae. The tropicbirds are a small family of graceful tropical seabirds with white-and-black plumage and long tail streamers. The tropicbirds were long thought to be related to various other seabird families but instead seem to be relatives of the Eurypygiformes.

Gaviiformes. This order contains only one family, the loons.

Gaviidae. The loons (also known as divers) are a small group of birds found only in the northern hemisphere. They breed on northern lakes and ponds, and winter primarily along the coasts of North America and Eurasia. Loons are specially adapted to an aquatic lifestyle: they feed on fish, and their feet are placed far back on their body for foot-propelled diving.

Sphenisciformes. This order contains only one family, the penguins.

Spheniscidae. The penguins are a group of flightless seabirds that are well adapted for swimming and diving. Penguins are most diverse in the southern oceans near Antarctica.

Procellariiformes. The petrels, shearwaters, albatrosses, and storm-petrels are a diverse order of tubenose seabirds found across the world's oceans. They range in size from the small storm-petrels to albatrosses, which have the largest wingspan of any bird. They feed on a wide variety of prey, from small plankton to fish. Many tubenoses have an acute sense of smell that they use to find food and to locate their nests after being away at sea.

Oceanitidae. The southern storm-petrels are a small family of tubenose seabirds that breed primarily on islands in the southern hemisphere, but may be found in the northern oceans when they are not breeding.

Diomedeidae. Albatrosses are a group of large seabirds that range widely across the world's oceans, returning to land only to breed. At 3.5 meters, the Wandering Albatross (*Diomedea exulans*) has the widest wingspan of any living bird.

Hydrobatidae. The northern storm-petrels are a small family of tubenose seabirds that breed primarily on islands in the northern hemisphere. Like southern storm-petrels, northern storm-petrels feed by fluttering over the water and picking items from its surface.

Procellariidae. The petrels and shearwaters are tubenose seabirds found across the world's oceans. They range in size from small diving-petrels to large giant-petrels. They feed on a wide variety of prey, from small plankton

to fish. They use their acute sense of smell to find their nests when returning from sea.

Ciconiiformes. This order contains only one family, the storks.

Ciconiidae. Storks are wading birds that are most diverse in the Old World tropics. Primarily found in marshes, storks inhabit a variety of open habitats, from dry acacia savanna to urban landscapes. Many species have bare skin on their heads and necks. They feed on a variety of prey, from carrion and insects to fish and small mammals.

Suliformes. Members of this order of seabirds are found throughout the world's oceans. Suliformes lack external nostrils, an adaptation to their aquatic lifestyle. Families in this order employ a variety of foraging techniques: frigatebirds pirate food from other species, gannets and boobies are plunge divers, and cormorants and darters swim underwater to take fish. Many species are colonial breeders, sometimes nesting in huge concentrations.

Fregatidae. Frigatebirds are the pirates of the tropical oceans. Found across all tropical waters, frigatebirds often feed by stealing food from other birds such as terns and gulls. Nesting mostly on islands, males perform elaborate courtship displays in which they inflate their massive, red gular pouch.

Sulidae. Boobies and gannets are large seabirds that capture fish by plunging into the water from the air. Found in all the world's oceans, species in this family often nest in huge colonies, primarily on islands. Gannets are larger than boobies and are found in temperate waters, whereas the slightly smaller boobies are found in tropical waters.

Phalacrocoracidae. Cormorants are a diverse and widespread group of waterbirds. Found worldwide, the cormorants swim and dive for fish in both freshwater and marine environments. Cormorants do not have oil on their feathers and thus must dry their wings by flapping and airing them out after diving.

Anhingidae. Like cormorants, the Anhinga (*Anhinga anhinga*) and darters are waterbirds that swim and dive to catch fish. Found mainly in tropical and subtropical wetlands, this small group of birds stabs their prey with their dagger-shaped bill. Like cormorants, they do not have oil on their plumage and must dry their feathers after being in the water.

Pelecaniformes. This order of wading birds includes the herons, egrets, ibises, and spoonbills. It also includes the pelicans, recently found to be closely related to the Shoebill (*Balaeniceps rex*) and Hamerkop (*Scopus umbretta*). Most pelecaniform species are associated with aquatic habitats, ranging from wet meadows to marine environments, and feed on aquatic vertebrates, implementing a variety of foraging techniques.

Threskiornithidae. A diverse family of wading birds, the ibises and spoonbills include many members with spectacular plumage. Both ibises and spoonbills have specially adapted bills; ibises use their long, decurved bills for probing, and spoonbills use their flattened, spatulate-shaped bills to take prey from water.

Ardeidae. The herons and egrets are a diverse and widespread family of wading birds, found worldwide and in many habitats, from dry grasslands to dense rainforest. Most species feed in or along the water, probing and stabbing prey with their dagger-like bills; others feed on insects picked from grass and other vegetation.

Scopidae. The Hamerkop (*Scopus umbretta*) is a medium-sized, brown wading bird from sub-Saharan Africa that uses its bill to take frogs, fish, and other prey from the water. Hamerkops build the largest nest of any bird, a mass of sticks in a tree with an inner nesting chamber.

Balaenicipitidae. A large wading bird of the marshes of central Africa, the Shoebill (*Balaeniceps rex*) has a large, blocky head and a large bill reminiscent of a wooden clog, which it uses to catch lungfish and other aquatic prey. On hot days, adults may use their bills to scoop up water to cool their chicks.

Pelecanidae. Pelicans are widespread waterbirds mostly found on interior lakes and wetlands; some are found along continental coastlines. They use a large bill with an expandable gular pouch to scoop up many fish at one time.

Cathartiformes. This order contains only one family, the New World vultures.

Cathartidae. New World vultures are a small family of raptorial birds ranging from temperate North America to extreme southern South America. The New World vultures feed primarily on carrion, and some species have an excellent sense of smell. The New World vultures are only distantly related to the Old World vultures.

Accipitriformes. These diurnal raptors include the hawks, eagles, kites, and the long-legged Secretary-bird (*Sagittarius serpentarius*). Members of this order are found worldwide

in almost every terrestrial habitat from the arctic tundra to the tropical rainforest.

Sagittariidae. The Secretary-bird is an odd raptor of sub-Saharan African savannas. With long legs, a long tail, and elaborate crest, the Secretary-bird stalks through the grass searching for mammalian and reptilian prey, which it may kill with sharp kicks.

Pandionidae. The Osprey (*Pandion haliaetus*), the only member of this family, is a large raptor that specializes in eating fish. Found on nearly every continent, the Osprey has adaptations, including rough foot-pads and a reversible outer toe, that help it grasp its slippery prey.

Accipitridae. The hawks, eagles, and kites are a large and diverse family of diurnal raptors that prey on animals from insects to monkeys. Found worldwide in nearly all terrestrial habitats, they range in size from the Tiny Hawk (*Accipiter superciliosus*) to the Great Philippine Eagle (*Pithecophaga jefferyi*).

Strigiformes. The owls and barn owls are typically nocturnal predators found across the world.

Tytonidae. The barn owls are a small family of nocturnal predators with a global distribution. Similar in many ways to the typical owls, barn owls have a distinctive, heart-shaped facial disc.

Strigidae. The typical owls are a large, diverse group of mainly nocturnal predators found across the world. Owls feed on a wide range of prey, from insects to fish. Unmistakable the world over, owls have superb nocturnal vision and acute hearing.

Coliiformes. This order contains only one family, the mousebirds.

Coliidae. Mousebirds are a small group of birds restricted to sub-Saharan Africa. They have soft, gray-brown plumage, fluffy crests, and long tails. Mousebirds are highly social and will huddle together in groups for warmth. When foraging, they may scramble through dense brush, often hanging from branches.

Leptosomiformes. This order contains only one species in its own family, the Cuckoo-Roller (*Leptosomus discolor*).

Leptosomidae. The Cuckoo-Roller is endemic to tropical and subtropical forests in Madagascar. Relatively little is known about this large sit-and-wait predator, which feeds on animals ranging from insects to small vertebrates.

Trogoniformes. This order contains only one family, the trogons.

Trogonidae. Trogons are a diverse family found in tropical and subtropical forests around the world. Fantastically colored in iridescent greens and blues above, and bright reds and yellows below, trogons often sit motionless for long periods.

Bucerotiformes. This small order of three families is found primarily in the Old World tropics; the Eurasian Hoopoe (*Upupa epops*) occurs in Europe and central Asia. These three families are found in a variety of habitats, from dense tropical forest to open savanna.

Bucerotidae. The hornbills are a diverse family of medium to large birds found in tropical and subtropical Africa and Asia. They have bold plumage and large bills, often topped with a horny casque. Most female hornbills are walled into their nest cavities and fed by their mate until their nestlings are well grown.

Upupidae. Hoopoes are found in Eurasia and Africa in a variety of relatively open habitats. With large, movable crests; long, thin, decurved bills; and broad black-and-white patterned wings, hoopoes are highly distinctive. They nest in cavities and forage primarily on insects.

Phoeniculidae. Woodhoopoes are closely related to hoopoes but are restricted to forested and scrubby habitats of sub-Saharan Africa. With long decurved bills, long tails, and glossy black plumage, woodhoopoes probe bark and branches for insects.

Coraciiformes. The Coraciiformes are a diverse order of birds, most of which are brightly colored. Found worldwide, the order includes the rollers, bee-eaters, motmots, todies, and the diverse kingfishers. Species are found in a wide variety of habitats, ranging from marsh to open savanna. They are mostly sit-and-wait predators of vertebrates and insects, and all nest in cavities or burrows.

Meropidae. Bee-eaters are brightly colored and boldly patterned aerial insectivores. Found in the Old World, many species live in relatively open habitats, although some live in dense forests. Many are highly social and nest in burrows, often in large colonies.

Coraciidae. Rollers are a small Old World family of bright, colorful, sit-and-wait predators. Named for acrobatic flight displays during which some species roll their body back and forth, rollers are found in a variety of open habitats where they prey mainly on insects and small vertebrates.

Brachypteraciidae. Ground-rollers are endemic to Madagascar. Boldly marked and patterned, they are found from arid thorn scrub to tropical rainforest. Ground-rollers feed on invertebrates and nest in burrows.

Todidae. The todies are tiny, brightly colored, sit-and-wait insect predators found only in forested habitats on the Greater Antilles islands of the Caribbean. Todies have bright emerald-green backs, but they can be difficult to spot when they sit motionless on a shaded branch.

Momotidae. The motmots are boldly patterned, sit-and-wait predators from Central and South America. Named for their calls, motmots have serrated bills that they use to grasp large insects and small vertebrate prey. Most motmots have long, racquet-tipped tails that they wag back and forth.

Alcedinidae. Kingfishers are a diverse family with worldwide distribution. Although their name suggests that they feed on fish, and many species do, a number of species are found in dry habitats where they feed on insects, small rodents, reptiles, or amphibians. Most kingfishers are boldly patterned, and some are very brightly colored.

Piciformes. The Piciformes use a variety of foraging techniques: woodpeckers drill and probe bark whereas puffbirds and jacamars use a sit-and-wait predation strategy. With a nearly global distribution, the Piciformes are found in a wide variety of habitats and nest exclusively in cavities or burrows. The honeyguides are obligate brood parasites; all other families raise their own young.

Galbulidae. Jacamars, found in the lowland tropical forests of South and Central America, are sit-and-wait predators famous for preying on butterflies and dragonflies. Many species have iridescent green and rufous plumage, and long, pointed bills.

Bucconidae. Puffbirds, closely related to jacamars, are sit-and-wait predators found in the lowland tropical forests of South and Central America. Puffbirds have large heads; are boldly patterned in black, white, and brown; and have heavy bills for catching large insects and small invertebrates.

Capitonidae. New World barbets are found in the tropical forests of South and Central America. Brightly colored and boldly patterned, barbets have large bills and feed primarily on fruits. Like other barbets, New World barbets nest in tree cavities.

Ramphastidae. The toucans are found in the subtropical and tropical forests of Central and South America. Most toucans are boldly patterned and have massive, brightly colored, serrated bills. Although primarily frugivorous, toucans also feed on insects and small vertebrates, and raid the nests of other birds for eggs and nestlings.

Semnornithidae. Prong-billed barbets are represented by only two species, the Toucan Barbet (*Semnornis ramphastinus*) of South America and the Prong-billed Barbet (*Semnornis frantzii*) of Central America. The prong-billed barbets primarily eat fruit and, like other barbets, nest in tree cavities that they excavate themselves.

Megalaimidae. The Asian barbets are found in the tropical and subtropical forests of south and southeastern Asia. Brightly colored and boldly patterned, barbets have large bills and feed primarily on fruits. Like other barbets, Asian barbets nest in tree cavities.

Lybiidae. The African barbets are found in a variety of habitats in sub-Saharan Africa, ranging from acacia scrub to tropical forest. The African barbets vary in size and have diverse features: some have the stout bills typical of other barbets, but others have slim bills and feed more extensively on insects.

Indicatoridae. Honeyguides are an odd family of birds: they are all obligate brood parasites, and they are able to eat and digest beeswax. They are most diverse in sub-Saharan Africa but are also found in Southeast Asia. One species is famous for reportedly leading humans and other large mammals to beehives.

Picidae. Found on most continents, but notably absent from Australia, woodpeckers have a suite of adaptations that allow them to use their chisel-like bills to hammer into trees in search of invertebrate prey.

Cariamiformes. This order contains only one family, the seriemas.

Cariamidae. There are only two species of seriemas, both in central South America. With long legs, curved bills, and short crests, seriemas walk the savannas in search of food, feeding primarily on insects but also taking seeds, fruit, and small vertebrates.

Falconiformes. This order contains only one family, the falcons and caracaras.

Falconidae. Falcons and caracaras are a diverse family of diurnal raptors. Recently found to be closely related to parrots and songbirds, falcons are found worldwide. Most falcons are swift aerial predators that catch their prey in their talons, often in mid-air. Caracaras are restricted to the New World and are largely scavengers.

Psittaciformes. The parrots and cockatoos are largely restricted to tropical and subtropical regions, but are popular the world over as pets. Many species are brightly colored.

Strigopidae. The New Zealand parrots are a small family of large parrots restricted to New Zealand and its small surrounding islands. All species have large, strongly hooked bills. They occupy a wide range of habitats, from forest lowlands to alpine habitats. This family includes the largest parrot, the flightless Kakapo (*Strigops habroptila*).

Cacatuidae. Cockatoos are relatively large parrots restricted to Australia and Southeast Asia. They bear distinct crests and feed primarily on fruit and seeds. Most cockatoos are either white or black, with patches of yellow or pink.

Psittacidae. Parrots are largely restricted to tropical and subtropical regions. Popular as pets, parrots are diverse and many are brightly colored. With strong, hooked bills and strong feet, parrots can easily grasp and feed on a wide variety of fruits, seeds, and nuts.

Passeriformes. This huge order of 137 families contains more than half the bird species in the world. The passerines are found around the world in almost every terrestrial habitat. They are also called the perching birds or, more often, songbirds because many species use complex vocalizations and songs. The passerines are hard to generalize: they range in size from large ravens to small kinglets.

Acanthisittidae. New Zealand wrens are found, as their name suggests, only in New Zealand. With relatively long legs, a thin bill, and hardly any tail, New Zealand wrens are energetic insectivores. They represent the ancient sister lineage to all other songbirds.

Pittidae. The pittas are the most diverse family of Old World suboscines. Largely terrestrial, pittas have relatively long legs, short tails, and an upright posture. Most pittas are spectacularly colorful and intricately patterned in a palette of colors including yellow, blue, green, red, and white.

Philepittidae. The asities are endemic to Madagascar. With widely divergent bill shapes, the asities feed primarily on fruit and nectar. During the breeding season, males sport brilliantly colored sky-blue and apple-green wattles.

Eurylaimidae. The broadbills are brightly colored, boldly patterned birds found in the tropical forests of Africa and Southeast Asia. Broadbills feed mainly on insects caught in sallying flights.

Sapayoidae. The Sapayoa (*Sapayoa aenigma*) is a dull, olive-green bird with a fascinating taxonomic history. Part of an ancient, otherwise Old World, radiation of birds, the Sapayoa is found in the lowland tropical forests of southern Central America and northern South America. Sapayoas forage by sallying from branches for insects.

Calyptomenidae. The green broadbills are perching birds from Southeast Asia and sub-Saharan Africa. Most species have large, rounded heads and iridescent, apple-green plumage. The green broadbills, like other broadbills, sally from perches to catch insects.

Thamnophilidae. Antbirds are an extremely diverse group of songbirds from Central and South America. Many are boldly patterned in black, white, and gray. Some species follow army ant swarms to forage on the insects that the ants flush.

Conopophagidae. Gnateaters are a group of small songbirds from the forested neotropical lowlands. With their brown and black plumage, gnateaters are like tiny antpittas (Grallariidae), but with relatively long legs and small, rounded bodies. They usually forage for invertebrates in the branches of understory shrubs.

Melanopareiidae. The crescentchests are songbirds found in scrubby habitats of South America. Boldly patterned in browns and blacks, crescentchests, like wrens, cock their tails as they forage for invertebrates.

Grallariidae. Found in a variety of forest types in the neotropics, antpittas are the duller, New World equivalent of the Old World pittas (Pittidae). Antpittas have a wide range of body sizes, but all are largely terrestrial. With their long legs and upright posture, they often hop when foraging for terrestrial invertebrates.

Rhinocryptidae. Tapaculos are a moderately diverse group of cryptic songbirds found in a wide variety of habitats across South America. With loud but simple whistled songs, tapaculos are more often heard than seen. They are largely terrestrial, and many nest in tunnels dug into the ground.

Formicariidae. Antthrushes are songbirds of lowland tropical forests in Central and South America. More often heard than seen, antthrushes walk on the forest floor with their short tails cocked as they forage for insects.

Furnariidae. The ovenbirds and their allies are an extraordinarily diverse collection of songbirds from Central and South America. Although not colorful, this family sports an incredible diversity of nest types, bill

shapes, and habitat use, from the altiplano of the Andes to the lowland tropical rainforest of Amazonia.

Pipridae. The manakins are small, colorful birds found in neotropical forests where they feed largely on fruits. Some manakins are famous for their lekking displays in which groups of males gather to perform elaborate courtship dances for females, often accompanied by wing-snapping and other mechanical noises.

Cotingidae. Cotingas are a diverse set of songbirds found primarily in neotropical lowland forests. Most cotingas feed only on fruit. Many species in this family have elaborate lek-based courtship displays in which males use spectacular vocalizations and their bright, often iridescent, plumage to attract females.

Tityridae. The tityras and becards, songbirds found only in the neotropics, feed largely on invertebrates by sallying from a perch. These birds have an upright posture, and many are patterned with gray, white, and black.

Tyrannidae. With more than 300 species, the tyrant flycatchers are the most diverse family of birds in the world. They are found only in the New World but occur there in most terrestrial habitats. Many species feed primarily on insects, but some species also eat fruit.

Menuridae. Lyrebirds are found in the eastern forests of Australia. They are arguably the most accomplished avian vocalists and have been known to mimic chainsaws, camera shutters, and cell phones. Male lyrebirds have long tail plumes that are used in their courtship displays.

Atrichornithidae. Scrubbirds are a small family of songbirds with a very restricted range in the coastal scrub of Australia. Cryptically plumaged in brown with extensive barring on the wings, tail, and flanks, they scramble through the scrub and leaf litter in search of invertebrates. Scrubbirds, unlike most birds, lack a furcula (wishbone) and are very poor fliers.

Ptilonorhynchidae. The bowerbirds are found in a variety of forested habitats in Australia and New Guinea. Male bowerbirds construct elaborate bowers, usually from sticks, and decorate them with shells, flowers, fruit, and other items to impress females. Bowerbirds generally are found in the understory and forage for invertebrates and fruit.

Climacteridae. Australasian treecreepers are found in Australia and New Guinea. Although they lack the stiff tail feathers and sharp, chisel-shaped bill of woodpeckers, these treecreepers fill the general niche of woodpeckers in Australia where they scale trees and glean insects from bark and branches.

Orthonychidae. Logrunners are largely terrestrial songbirds found in Australia and New Guinea. Unlike most birds, the logrunners forage in leaf litter by kicking leaves outward to the side, instead of behind them, in search of invertebrate prey.

Pomatostomidae. The Australasian babblers, found across Australia and New Guinea, are highly social songbirds. With decurved bills, strong legs and feet, and long tails, these babblers forage for invertebrates and seeds on the ground and glean tree bark. Adapted to an arid climate, many species have never been observed drinking and are believed to get most or all of their water from food.

Maluridae. The fairy-wrens and grasswrens are a diverse group of small songbirds in Australia and New Guinea with complex breeding systems. Ranging from the bright colors and bold patterns of the fairy-wrens to the cryptic, brown, streaked plumage of the grasswrens, this family is found from tropical forest to Australian scrub desert.

Dasyornithidae. A small family of dull brown Australian songbirds, the bristlebirds are named for the bristle-like feathers above their eyes. They occur in dry scrubby habitats where they feed primarily on insects and seeds gathered from the leaf litter.

Meliphagidae. Honeyeaters are a diverse family found in Southeast Asia, Oceania, and Australia. With thin, pointed bills and tongues with special, brush-like tips, honeyeaters are well adapted for feeding on nectar, although they also eat invertebrates and fruit. Found in a broad range of habitats, many honeyeaters are brightly colored and boldly patterned.

Pardalotidae. These tiny, brightly colored and intricately patterned birds occupy forested habitats in Australia. With short, stout bills, pardalotes feed primarily on invertebrates and on the sap of trees and plants. Unlike many Australian songbird families, there is no evidence of cooperative breeding in pardalotes.

Acanthizidae. Australasian warblers, like many other warbler-like families of the Old World, are a diverse family of small insectivores found in a wide variety of habitats. Most have relatively dull plumage. Many species are cooperative breeders in which the young from previous nesting attempts help parents raise their younger relatives.

Mohouidae. A small family of three species endemic to New Zealand, the mohouids are small songbirds that inhabit a variety of forested habitats. Long considered part of the whistler family (Pachycephalidae), recent

work has shown that these three songbirds represent their own lineage.

Eulacestomidae. The Wattled Ploughbill (*Eulacestoma nigropectus*), whose genus name means "plough-share bill," is a small songbird from the montane forests of New Guinea. Named for their laterally compressed bill and the male's pink wattles, little is known of the biology of this species.

Neosittidae. The two species of sittellas are found in Australia and New Guinea. Sittellas are small songbirds with strong feet and chisel-shaped bills, which they use to scale trees, often upside-down, as they search for invertebrate prey.

Oriolidae. The Old World orioles and figbirds are found in a variety of habitats ranging from gardens to dense forest. Often brightly colored and boldly patterned in black and yellow, orioles feed mainly on fruits and invertebrates. The figbirds typically have duller, olive plumage. All species weave pendant nests hung from branches.

Paramythiidae. This family containing only two species, the Crested Berrypecker (*Paramythia montium*) and the Tit Berrypecker (*Oreocharis arfaki*), is restricted to the montane forests of New Guinea. Both species feed primarily on fruit.

Oreoicidae. This hodgepodge family consists of three species—the Crested Bellbird (*Oreoica gutturalis*), Rufous-naped Bellbird (*Aleadryas rufinucha*), and Crested Pitohui (*Ornorectes cristatus*)—that are grouped on the basis of phylogenetic studies. The Crested Pitohui, like other distantly related poisonous pitohuis, incorporates toxins into its feathers; neither the bellbird nor whistlers do so.

Cinclosomatidae. The quail-thrushes and jewel-babblers are found in Australia and New Guinea. Quail-thrushes are cryptically patterned in browns, black, and white; jewel-babblers are brightly colored and boldly patterned in blue, black, and white. Feeding mainly on invertebrates and seeds, these species forage in the understory of tropical forests.

Falcunculidae. The Crested Shrike-tit (*Falcunculus frontatus*), once part of the large and diverse whistler family (Pachycephalidae), is found in eucalyptus forests and woodlands in Australia. This distinct and boldly patterned songbird uses its strongly hooked, parrot-like bill to tear bark from trees in search of insect prey.

Pachycephalidae. The whistlers and their allies are an extremely diverse family that has colonized many oceanic islands; they are found through Australia, New Guinea, and Southeast Asia. They are brightly colored and many have beautiful songs. Included in this family are many pitohuis, which sometimes have highly toxic plumage.

Psophodidae. Whipbirds and wedgebills are found from arid scrub to tropical rainforest in Australia and New Guinea. With earth-toned plumage, long tails, and a distinct crest, most species are largely terrestrial. Their distinct, whip-like vocalizations are a characteristic sound of eastern Australia.

Vireonidae. The vireos, shrike-babblers, and White-bellied Erpornis (*Erpornis zantholeuca*) are a diverse family with its core diversity in North and South America. Phylogenetic studies recently found that the shrike-babblers and erpornis of Southeast Asia group into this otherwise New World family. With straight, hooked bills, the vireos and their allies feed primarily on insects and other invertebrates.

Campephagidae. Cuckooshrikes occur in a variety of forest types from sub-Saharan Africa through Southeast Asia and Australia. Their long, sleek body and long, graduated tail give them a general appearance similar to cuckoos, but they have the strong, hooked, predatory bills more characteristic of shrikes.

Rhagologidae. The Mottled Whistler (*Rhagologus leucostigma*) is endemic to the montane forests of New Guinea. Once considered part of the large and diverse whistler family (Pachycephalidae), recent work has shown this species to be more closely related to other songbird groups. Little is known of the biology of this brown, streaked songbird.

Artamidae. The butcherbirds and woodswallows are found in Australia and Southeast Asia. Woodswallows, as their name suggests, are aerial insectivores. Butcherbirds have strong, hooked bills and feed on insects and small vertebrates.

Machaerirhynchidae. Boatbills are a small family of two species of small, flycatcher-like birds with relatively long, straight, flattened bills. Brightly colored and boldly patterned in black and yellow, they are found in the tropical forests of northeastern Australia and New Guinea.

Vangidae. The vangas, helmet-shrikes, and wood-shrikes are a morphologically diverse family found mainly in sub-Saharan Africa, with a small group in Southeast Asia. Vangas are found in Madagascar and have evolved a wide array of bill types, including long, decurved bills; short, chisel-shaped bills; and large, inflated bills.

Platysteiridae. Batises and wattle-eyes are tiny but feisty songbirds from sub-Saharan Africa. Batises are boldly patterned in black and white. The wattle-eyes are named

for the brightly colored, fleshy wattle around their eyes. Species occur in habitats from dry acacia scrub to montane tropical forest.

Aegithinidae. Ioras are yellow and black songbirds found in Southeast Asian forests and gardens. With their sharp, thin bills, ioras forage for insects and other invertebrates by gleaning from branches and foliage.

Pityriasidae. The sole member of this family, the Bornean Bristlehead (*Pityriasis gymnocephala*), is a bizarre songbird from the tropical forests of Borneo with a black body, bright red head, and bare crown with yellow bristles. Traveling in social groups, bristleheads feed mainly on large invertebrates.

Malaconotidae. Bush-shrikes are brightly colored and boldly patterned predators found in sub-Saharan Africa. Usually seen hunting from a perch, they feed mainly on insects but also take small vertebrates. Bush-shrikes are well known for the duets males and females sing back and forth to each other.

Rhipiduridae. With their core diversity in Australia and New Guinea, the fantails stretch into Southeast Asia where they are found in a wide variety of habitats. They are relatively small birds with thin, straight bills, and typically drab brown plumage. Fantails are named for their long tails, which they often spread as they forage in order to startle insects.

Dicruridae. Found in the Old World tropics, the drongos are flycatcher-like birds with glossy black plumage and characteristically ornate tail feathers. Found in a variety of habitats, ranging from forest to acacia scrub, drongos catch their insect prey by sallying from perches.

Ifritidae. This family consists of just a single enigmatic species, the Blue-capped Ifrita (*Ifrita kowaldi*). The Blue-capped Ifrita is endemic to the montane forests of New Guinea, where it forages up and down branches for insects, in a manner similar to the widespread nuthatches (Sittidae). The Blue-capped Ifrita is also one of the few species of bird in the world that is toxic, sequestering compounds in its feathers from insects it eats.

Monarchidae. The monarch flycatchers are a diverse Old World group of tropical insectivorous birds ranging from the streamer-tailed paradise-flycatchers of Africa and Asia to the more subdued black-and-white monarchs of Australasia.

Platylophidae. The Crested Jay (*Platylophus galericulatus*), the sole member of this family, is a striking species from the tropical lowland forests of Southeast Asia. With a superficial similarity to many jays (family Corvidae), the Crested Jay is colored black to dark brown with a distinct white neck patch and long crest.

Laniidae. Colloquially termed "butcherbirds" for their habit of impaling their prey—insects and small vertebrates—on thorns, shrikes are a widespread family of birds. They are most diverse in Africa but also are found in North America and Eurasia. Many species are patterned in gray, black, and white with a distinct, dark mask.

Corvidae. The crows and jays are an extremely diverse family of birds that range in size from the large Common Raven (*Corvus corax*) of the northern hemisphere to the Dwarf Jay (*Cyanolyca nanus*) of Mexico. Found worldwide and in nearly all terrestrial habitats, crows and jays have powerful bills, complex social systems, and varied diets.

Melampittidae. Endemic to the montane forests of New Guinea, the Melampittidae consist of two poorly known species, the Greater Melampitta (*Melampitta gigantea*) and Lesser Melampitta (*M. lugubris*). These black, terrestrial songbirds forage for insects and other small arthropods on the forest floor, digging and tossing leaves aside as they search.

Corcoracidae. The White-winged Chough (*Corcorax melanorhamphos*) and Apostlebird (*Struthidea cinerea*) of Australia are highly social cooperative breeders. Although very different in terms of morphology, both species build highly distinctive bowl-shaped nests of mud. Found in open woodlands, these two species forage on the ground for invertebrates and seeds.

Paradiseidae. Found throughout the forests of New Guinea and northeastern Australia, the birds-of-paradise are an extremely diverse family and are a textbook example of the power of sexual selection to create bizarre plumages and display behaviors.

Callaeidae. The wattled crows comprise two highly distinct species from New Zealand. Both the Kokako (*Callaeas cinereus*) and Saddleback (*Philesturnus carunculatus*) have distinct, colorful, fleshy wattles. These two forest-dwelling species feed on insects, fruits, leaves, nectar, and seeds.

Notiomystidae. The Stitchbird (*Notiomystis cincta*) is small and boldly patterned in yellow and black. Closely related to the wattled crows, the Stitchbird has a bizarre mating behavior. An endangered species, the Stitchbird is currently restricted to predator-free islands off New Zealand.

Melanocharitidae. The berrypeckers are a small family of dark-plumaged songbirds endemic to the forests of New Guinea. Berrypeckers feed mainly on insects, fruit, and nectar; their bills range from short and thin to long and decurved.

Cnemophilidae. The satinbirds are a small family of brightly colored songbirds endemic to montane forests on New Guinea. They have a confusing taxonomic history and previously were placed in several other families. Satinbirds feed mainly on fruit and females build dome-shaped nests and care for the chicks alone.

Picathartidae. Rockfowl are represented by only two species, both restricted to the tropical forests of western Africa. These large songbirds have dull gray plumage, but their heads are completely bare with brightly colored skin. Rockfowl build their mud nests in caves and on cliff faces.

Eupetidae. The sole member of this family—the Malaysian Rail-babbler (*Eupetes macrocerus*)—is a strange, largely terrestrial songbird found in the lowland tropical forests of Malaysia. With a long tail and relatively long legs with strong feet, the Malaysian Rail-babbler is patterned in rich browns. Its bizarre vocal display includes the enlargement of two blue air sacs on its throat as it delivers a single long whistle.

Chaetopidae. A relict lineage, the rockjumpers are represented by only two species, both found among high rocky outcrops in southern Africa. Boldly patterned with black, gray, and cinnamon, rockjumpers scramble among rocks with strong feet in search of invertebrate prey.

Petroicidae. The Australasian robins are a diverse family of small songbirds. Found in a variety of habitats in New Guinea, Australia, and New Zealand, these small songbirds feed mainly on insects. Most are have dark plumage above, but some species are spectacularly colorful below, sporting pink, red, or yellow breasts.

Hyliotidae. The hyliotas are warbler-like songbirds from sub-Saharan African forests and woodlands. These insectivores have dark, often glossy, backs and pale, cream-colored underparts.

Stenostiridae. Fairy flycatchers are small songbirds that occur from sub-Saharan Africa through Southeast Asia. Sallying to catch insect prey, these small, often colorful, birds are found in forested and scrub habitat.

Paridae. The tits and chickadees are small, energetic, and vocal songbirds with boldly patterned plumage found across the northern hemisphere and into Africa and parts of Southeast Asia. They often forage in flocks for seeds, fruit, and invertebrate prey in a variety of forested and shrubby habitats.

Remizidae. Most penduline tits are found in the Old World, with one representative in North America. Small, drab birds with short, sharp bills, the penduline tits are named for their woven, often fuzzy, pendulous nests.

Alaudidae. Larks are a large and diverse family of generally dull-colored, cryptically patterned birds that are found worldwide, typically in dry, open habitats. What larks lack in color, they make up for in song, with many species having elaborate aerial vocal displays. Most larks have thin, straight bills and feed mainly on insects, but also eat seeds.

Panuridae. The Bearded Reedling (*Panurus biarmicus*), the sole member of this family, is a small songbird found in marshes across Europe and Asia. Reedlings have long tails, and males have distinct black plumes on their faces. They are highly social and may forage in large flocks for insects and other invertebrates, as well as seeds in the winter.

Nicatoridae. The nicators are a family of only three species in the forests of sub-Saharan Africa. With relatively large, hooked bills, the nicators feed on a variety of invertebrates and small vertebrates. Patterned largely in olive-green with bright yellow spots on the wings, nicators are more often heard than seen.

Macrosphenidae. The crombecs and African warblers are a small family of small, insectivorous birds of sub-Saharan Africa. Found in a variety of habitats, from rocky scree slopes to tropical forest, this group has been recently recognized based on phylogenetic data.

Cisticolidae. A large and diverse family, the cisticolas are found throughout the Old World but reach their peak diversity in sub-Saharan Africa. Usually small, active, warbler-like insectivores, the cisticolas and their allies range from brown and streaked to boldly patterned with gray, black, and yellow. The family is found in a wide range of habitats, from marsh to arid scrubland.

Acrocephalidae. Reed-warblers are small, warbler-like insectivores found throughout the Old World; one species has reached Hawaii. Many reed-warbler species live in marshes and reed beds, but other species occur in a variety of forested and shrubby habitats. Reed-warblers generally have dull plumage, but many are spectacular singers with elaborate, complex songs.

Pnoepygidae. Cupwings, also known as pygmy wren-babblers, are very small songbirds found in Southeast Asia. Occupying the dense forest understory, cupwings generally have dark brown plumage and a very short tail. With a thin, straight bill, cupwings feed on invertebrates.

Locustellidae. Grassbirds and their allies are small, warbler-like insectivores found throughout the Old World. Occupying more open, shrubby, and grassy habitats than other "warbler" families, the grassbirds and their allies generally are brown, some with bold streaking on their breast and back.

Donacobiidae. The Black-capped Donacobius (*Donacobius atricapilla*), the sole member of this family, is a large and conspicuous bird of the lowland Amazon Basin marshes. Pairs sing loudly together from exposed perches. The Black-capped Donacobius is boldly patterned, dark above and buffy below. With a thin, slightly decurved bill, it feeds mainly on invertebrates.

Bernieridae. A small radiation of small, active, warbler-like insectivores, the Malagasy warblers are endemic to Madagascar. With plumage ranging from drab yellow-olive to brown, they are found in a variety of wooded and forested habitats.

Hirundinidae. Swallows are a large and diverse group of aerial insectivores found worldwide. Boldly patterned, generally dark above and pale below, swallows are fast, agile fliers. Swallows construct and use a wide variety of nest structures, from mud domes on cliff faces to tunnels dug into banks.

Pycnonotidae. Bulbuls and greenbuls are a large and diverse family of songbirds from Africa and southern Asia. Found in a variety of forested habitats, members of this family feed on fruit, seeds, insects, and small vertebrates. With relatively long tails, bulbuls and greenbuls generally have plain plumage in browns and olives, but many have brighter faces or undertail patches.

Phylloscopidae. Small, yellow-olive insectivores, the leaf-warblers are a speciose family of birds that for the most part look much alike. With small, thin bills, the leaf-warblers actively glean insects from leaves and branches. They are found in a variety of Old World forested habitats.

Scotocercidae. Bush warblers are small, brown, secretive insectivores. Like many other "warbler" groups around the world, the bush warblers are active birds with thin, straight bills. They are found in a variety of forested habitats from southern Europe through central and south Asia and northern Africa.

Aegithalidae. The bushtits and long-tailed tits are very small, highly energetic birds with dull black, brown, and white plumage, found from western North America through Europe and Asia. The bushtits and their allies are highly social, foraging for insects in wooded habitats.

Sylviidae. Until recently, the sylviids included many groups that now are assigned to other families. The sylviids still include various small warbler-like birds with thin bills for feeding on insects, and the parrotbills with their thick, seed-crushing bills. Members of this family are found in a wide variety of habitats throughout the Old World; one species occurs in western North America.

Zosteropidae. White-eyes and yuhinas are a radiation of small, active, warbler-like insectivores found from Africa through southern Asia and Australia. Variable in plumage pattern, from bright yellow and olive with bold white eye-rings to duller earth tones, the white-eyes and yuhinas are found in a variety of habitats from forest to arid scrubland. Although they feed primarily on insects, many white-eyes also eat fruit and drink nectar using special brush-tipped tongues.

Timaliidae. The tree-babblers and scimitar-babblers, once part of a much larger "babbler" family that has now been subdivided into multiple families, are found in Southeast Asia. With bills ranging from straight and short to long and decurved, they feed primarily on insects and other invertebrates gleaned from leaves and branches. Most species have earth-toned plumage, and build domed or globular nests.

Pellorneidae. Fulvettas and ground-babblers are a diverse group found in Southeast Asia. Occupying a variety of forested habitats, they forage mainly for insects in dense understory vegetation or on the ground with rather short, straight bills.

Leiothrichidae. The laughing-thrushes and their allies are a diverse group of mainly insectivorous birds found from Africa to Southeast Asia. Ranging in size from warbler-like to thrush-sized, and with a dazzling array of blue, yellow, green, and red colors, the laughing-thrushes and their allies are found in a variety of habitats from forest to open acacia–savanna.

Certhiidae. Small, bark-probing birds, treecreepers scale the trunks of trees in search of insect prey. Although they have bright white bellies, most treecreepers are extraordinarily cryptic, with mottled brown upperparts that resemble lichen-covered bark. Treecreepers are found in forests across the northern hemisphere.

Sittidae. Nuthatches are distributed in forests throughout the northern hemisphere. With straight, chisel-shaped bills, most nuthatches forage for insects by descending tree trunks headfirst. Generally, nuthatches are patterned in grays and blacks, but some species are brighter, with blue and rufous coloration.

Polioptilidae. Gnatcatchers are very small insectivores with thin, squeaky voices found in a variety of forested and scrubland habitats from North America to tropical South America. Largely gray with some black patterns, gnatcatchers are known for decorating their small nests with lichen.

Troglodytidae. The wrens are found largely in the New World; a single species is found in Eurasia. Wrens are largely insectivorous, and most are accomplished singers;

many species are known for their complex duets. Wrens can be boldly patterned with browns, blacks, and whites. They often hold their tails upright.

Buphagidae. The two species of oxpecker are found in the savannas of sub-Saharan Africa. Oxpeckers have stout, bright red or yellow bills. They specialize in foraging on the backs of large domestic and wild mammals, from which they pick ectoparasites such as ticks, and eat skin from around wounds.

Sturnidae. Starlings and mynas are diverse across the Old World, although some species have been introduced elsewhere. They are found in a wide range of habitats, from arid scrubland to dense forest, and have similarly diverse diets including nectar, fruit, seeds, insects, and small vertebrates.

Mimidae. Mockingbirds and thrashers are New World songbirds well known for their vocal mimicry abilities and beautiful songs. Found primarily in open, shrubby habitats, the mockingbirds and thrashers feed on a variety of invertebrates and small vertebrates.

Cinclidae. The dippers are remarkable for being the only songbirds that forage underwater, usually in fast-moving mountain streams of the New World and Eurasia. Relatively fat with short, upright tails, dippers walk on the streambed in search of aquatic invertebrates.

Turdidae. The diverse thrushes are found in a wide variety of terrestrial habitats worldwide. Many thrushes have remarkable songs. With straight, thin bills, thrushes feed on fruit, some seeds, and invertebrates. Many species are largely terrestrial and are patterned in earth tones; others are more arboreal and aerial, and some of these are brightly colored.

Muscicapidae. The chats, Old World flycatchers, and allies are a diverse assemblage of songbirds found mostly in the Old World. With a range of feeding ecologies, from small, sallying birds to terrestrial, thrush-like birds, members of this family typically have thin, straight bills and feed largely on insects and other invertebrates.

Regulidae. Kinglets are very small, highly active insectivores of northern hemisphere forests and woodlands. Generally olive-yellow, most kinglets have bright patches of color in the crown, usually yellow, red, or orange. These tiny, vocal, and aggressive birds are able to overwinter in frigid environments by huddling together at night to keep warm.

Dulidae. The Palmchat (*Dulus dominicus*), the only member of this family, is endemic to the island of Hispaniola, where it constructs huge stick nests high in trees that are occupied by multiple pairs. The Palmchat has brown, streaky plumage and forages in groups, primarily on fruit.

Hypocoliidae. The Hypocolius (*Hypocolius ampelinus*), with its pale, gray-brown plumage and distinct black mask, is endemic to the Middle East. It feeds on fruits and insects. The Hypocolius is the sole species of this family; it breeds in loose colonies and gathers in groups during the non-breeding seasons.

Hylocitreidae. The Hylocitrea, or Olive-flanked Whistler (*Hylocitrea bonensis*), is a little-known bird of Sulawesi (Indonesia). Until recently, it was thought to be a member of other families, but phylogenetic work has shown it to be a distinct lineage. This dull, olive-yellow plumaged bird is found in montane forests.

Bombycillidae. Waxwings are a small family found in various forested and shrubby habitats throughout the northern hemisphere. With their silky brown plumage and distinct crest, waxwings are named for the red, wax-like tips of their secondary feathers. Waxwings feed primarily on fruit during winter months but consume invertebrates during the warmer seasons.

Ptilogonatidae. Silky-flycatchers are found from the southwestern USA through Central America. With upright posture, silky plumage, and distinct crests, the silky-flycatchers occur in forested and shrubby habitats where they feed on fruits and sally for insects.

Elachuridae. This newly described monotypic family is found in dense, broadleaf forests in Southeast Asia. Once part of the large babbler family, the Spotted Elachura (*Elachura formosa*) is more often heard than seen, spending much of its time in dense underbrush, where it forages for insects.

Promeropidae. Sugarbirds are endemic to the fynbos habitats of southern Africa, where they specialize in feeding on the nectar from *Protea* flowers with their long, slightly decurved bills. Generally dull brown with faint streaking and yellow on the rump, male sugarbirds have spectacularly long tails.

Modulatricidae. An odd collection of three species without a collective common name, the Spot-throat (*Modulatrix stictigula*), Dapple-throat (*Arcanator orostruthus*), and Gray-chested Illadopsis (*Kakamega poliothorax*) are found in montane regions of sub-Saharan Africa. These three species forage mainly for invertebrates in the dense undergrowth.

Irenidae. Fairy-bluebirds are mid-sized songbirds from the tropical forests of Southeast Asia. Male fairy-bluebirds are spectacularly colored, with bright patches of pale blue contrasting with black and brown. Commonly kept in zoos and aviaries, fairy-bluebirds feed mainly on fruit, but also take insects.

Chloropseidae. Leafbirds are found in the forests of Southeast Asia. As their name suggests, leafbirds generally