



THE
UNFEATHERED BIRD

Katrina van Grouw

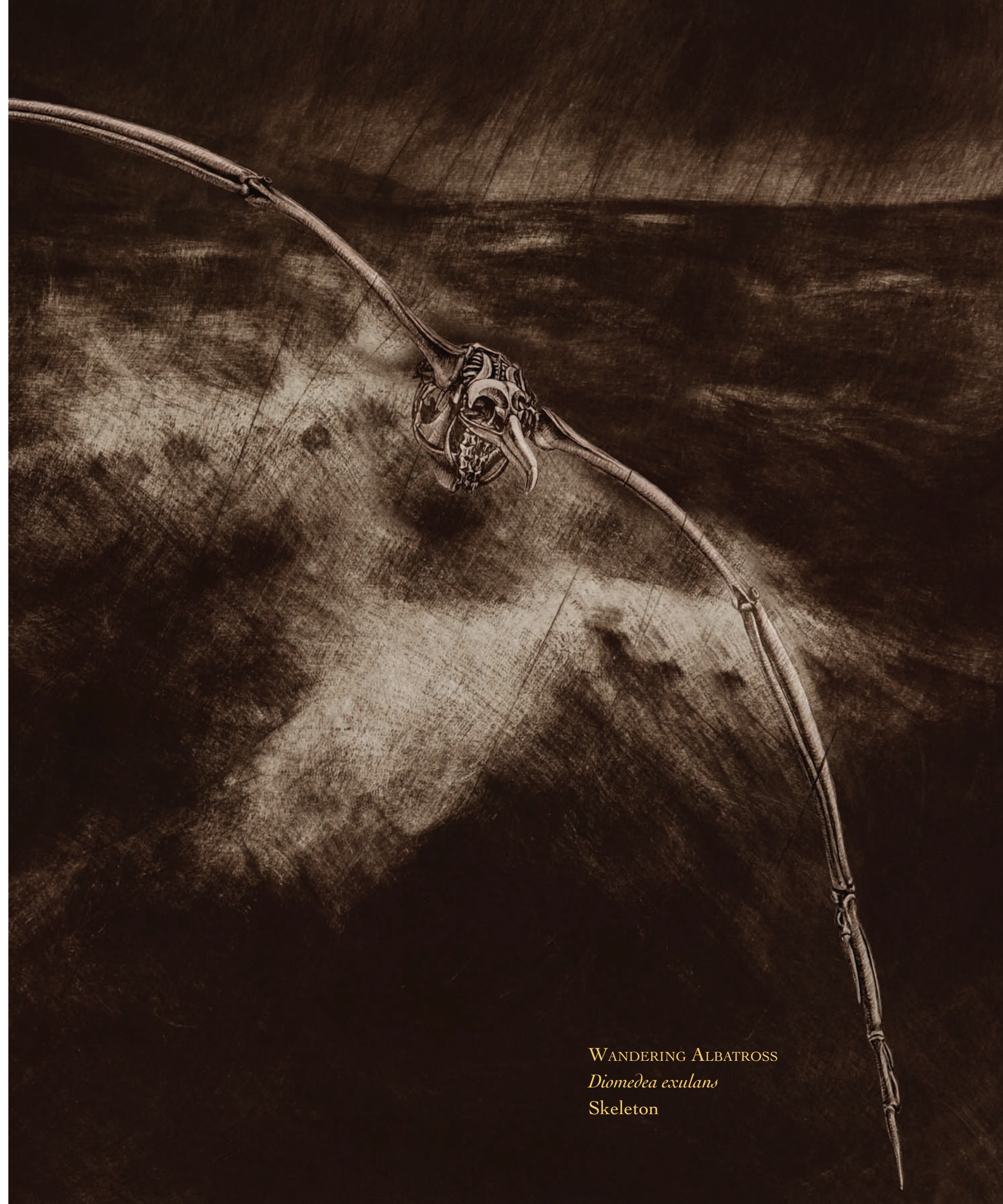
THE UNFEATHERED BIRD

The background is a dark, textured surface, possibly a piece of wood or a canvas, with a horizontal line of light in the upper right corner. The texture is visible throughout the image, with various shades of brown and black.

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Katrina van Grouw

PRINCETON UNIVERSITY PRESS
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WANDERING ALBATROSS
Diomedea exulans
Skeleton



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GREEN BROADBILL
Calyptomena viridis
Skull.

To Amy

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~ Acknowledgments ~

This book was begun twenty-five years ago. Broken down, that roughly constitutes: five years of innocent research, little expecting what it would lead to; one moment of inspiration; fifteen years hoping to convince someone else that it was a good idea; and several more years of *very* hard labor.

Publishers are like buses—no sign of one for ages, and then two come along in quick succession. So it was in this case. Thus my opening acknowledgment goes to Ian Langford, of Langford Press, for being the first publisher to believe in *The Unfeathered Bird*, although this relationship was ultimately not to be. And of course my heartfelt thanks to Robert Kirk, of Princeton University Press, for being the second. The day of our serendipitous meeting was a blessed day for me indeed. It would be impractical here for me to thank everyone at Princeton who has helped and supported me, but the copy editor Jennifer Backer, designer Lorraine Betz Doneker, and production editor, Mark Bellis, deserve special mention.

At this stage I must assure readers that no birds were harmed during the making of this book. I relied exclusively on the goodwill of birds dying naturally in places where they could be found and on the goodwill of a great many people who picked them up for me. Also on people who tolerated my unsavory activities.

Kenneth James Ferguson, my first long-term partner, put up with bad smells and a flat full of seabirds, and I fear he never recovered from the incident with the swan on the sitting room floor. Dave Butterfield made it his mission in life to retrieve every bird that died in the Scottish Highlands—and hid them all in the family freezer labeled as pies belonging to the neighbors. Brian Etheridge, of the RSPB Highland Region, donated the ones that Dave Butterfield missed. Mark Dugdale demonstrated his ardor for me by wading up to his waist in a fetid African swamp to bring me a decomposing pelican. And David Norman and Ian Wallis did no end of paperwork to enable me to legally import it to the UK. Other birds found dead were passed on to me by David Bolton, Keith Grant, Peter Potts, Jill Ford, and Sue Rowe. From the lovely Lucy Garrett I received a long-dead tropicbird as a souvenir from some far-flung Indian Ocean island. And Adrian Skerrett tried valiantly to find me a dead frigatebird on the Seychelles.

Norman McCanch, the late, great, Don Sharp, Barry Williams, James Dickinson, and especially Bas Perdijk—all professional taxidermists—kindly passed many specimens on to me from their own frozen stock. Bas has helped in countless other ways, providing tools and materials and, in collaboration with Johan Bink, loaning me a whole crate of bird skulls. I also borrowed skulls from Richard Smith, John Gale, and George Beccaloni. Barry's son, Luke Williams, volunteered the use of his beetle colonies to clean the smallest bird specimens. And of course there's the New Zealand taxidermist Noel Hyde, who happened to have a fresh kiwi just when I needed one.

Then there are the aviculturalists, pigeon fanciers, poultry farmers, and other keepers of domestic and exotic birds: Hans Bulte, Craig Stanbury, Taco Westerhuis, Colin Ronald, Kees Verkolf, Theo Jeukens, Hans Ringnalda, and Campbell Murn of the Hawk Conservancy Trust. Al Dawes and David Waters of the Great Bustard Group exchanged a dripping bag of putrefied bustard soup for a beautifully cleaned and reassembled skeleton for their educational displays, meanwhile treating me and my husband like visiting royalty. And I cannot forget Scott Dyason, the Ostrich farmer who didn't bat an eyelid at my request for spare body parts. I'd be in trouble if I failed to mention my mum, who has kept many of these birds in her freezer all these years, even farming them out to neighbors when her own freezer broke down. Mum also takes care of my dog, Feather, for me during my innumerable museum visits.

I also received plenty of help of a more conventional kind. Martin Spink and Jonathan Eames, the owners of two of the drawings, very kindly removed them from their frames so that they could be scanned. David Miller—sub-aqua wildlife artist—gave me more photos of auks underwater than I knew what to do with. And every time my pile of drawings outgrew their storage box, David's wife, Lisa, sent more by first class post. Thanks also to Sophie Wilcox, the librarian at the Edward Grey Institute, Oxford, and Alison Harding at Tring. And a whole host of colleagues and friends who have cheered me on to the finish line.

All my drawings are from actual specimens. Photographs were sometimes used as additional reference but never in place of the real thing. Wherever possible I drew from skeletons prepared at home for the purpose of the book. That way I could be sure of knowing if any bones were missing and of getting the posture of the bird correct. But inevitably it was often necessary for me to use museum specimens. Special thanks are therefore due to Malgosia Nowak-Kemp and Matt Lowe for allowing me to make repeated visits to the scientific collections of the university museums of Oxford and Cambridge, respectively, and for making me feel so welcome; Georges Lenglet in Brussels and Christine Lefèvre in Paris; and Jo Cooper and my husband, Hein, at the Natural History Museum's ornithology collections at Tring, and in his former incarnation as collections manager in charge of birds and mammals in Leiden.

Thanks, too, to David Willard at the Field Museum, Chicago, for sending several specimen loans to the UK. Your help is very much appreciated. And Tom Trombone, Paul Sweet, Peter Capainolo, and Matt Shanley for providing photographs of specimens from the American Museum of Natural History in New York. Last but not least, thanks go to Kaitlin Evans of the Bishop Museum, Hawaii—I'm sorry I allowed your honeycreepers to be ousted by vangas at the final cut.

Spouses and partners are the pillar of rock behind every book. It is they who take over the household duties, provide encouragement, mop up the tears, are endlessly called upon to discuss the work and offer opinion, suffer torrents of stress-fueled abuse, and put their own life on hold as though it were less important. My own husband, Hein van Grouw, has been all of that and more. So much more.

If this is heralded as a great book rather than a good one, it is because of Hein. He has made the difference. Hein took over all the specimen preparation to leave me time to write and draw. He boiled and cleaned the bones. It was he who sifted through the bustard soup. He, who put together nearly fifty skeletons in beautiful, lively, and accurate postures. He, who plucked and skinned and set birds up on Audubonesque wires for me to draw. Hein suggested the inclusion of domestic birds and called upon many of his own contacts and colleagues to provide examples of the rare breeds whose skeletal anatomy is virtually unknown.

Again and again we shared in the excitement of discovering for ourselves some little-known anatomical feature. With Hein by my side, my task became an adventure, and I pushed my standards higher and higher.

If any book can be described as a labor of love, this is it—my twenty-five-year love for my idea, our mutual love of birds, and my husband's love for me.

~ A Note about Names ~

Here and there throughout *The Unfeathered Bird* I've referred to bird groups (called taxa) by their scientific names. Although I've attempted to qualify these wherever possible, I thought it useful to include a few words about the different groups and how to recognize them. Not all the divisions are used in the book, but I have listed them here anyway.

KINGDOM—Animalia: all animals.

PHYLUM—Vertebrata: animals with backbones (mammals, birds, reptiles, etc.).

CLASS—Aves: all the birds.

ORDER—ending in -iformes: e.g., the Anseriformes (waterfowl and screamers).

FAMILY—ending in -idae: e.g., the Anatidae (waterfowl = geese, swans, and ducks).

SUBFAMILY—ending in -inae. Only large and diverse families are divided into subfamilies and tribes: e.g., Anatinae (the ducks).

TRIBE—ending in -ini; e.g., Anatini (the dabbling ducks).

GENUS—always begins with a capital letter. Called the generic name. Plural—genera: e.g., *Anas* (a group of very similar dabbling ducks).

SPECIES—always begins with a lowercase letter. Called the specific name. Always preceded by the genus or the genus shortened to its first letter (when this will not cause ambiguity). Think of genus and species in the same way as surname and Christian name: e.g., *Anas platyrhynchos* or *A. platyrhynchos* (the Mallard).

SUBSPECIES or RACE—a geographically distinct population of a single species. It is written as a third name and also begins with a lowercase letter: e.g., *A. p. platyrhynchos*. This population inhabits most of the Palearctic and Nearctic region. It was the race described by Linnaeus in 1758, and because it was the one first described and bears the same name as the species, it is known as the nominate race.

It was Linnaeus who first applied the system of giving organisms a generic and specific name (called binomial nomenclature = two names). Until then animals and plants were known only by colloquial names that varied from region to region, so it was impossible to know if you were talking about the same thing. It was a stroke of genius. Latin was chosen as a language that could be universally understood (though most birds have Latinized versions of Greek names), and the system is still in use today, providing a rigid, uniform, unambiguous identity to all living things.

At least that's the Holy Grail that all taxonomists strive for.

In practice, things are slightly different. Scientific names are in a constant state of flux, ever-changing, according to the latest taxonomic theories and methods. And until we know unequivocally how each species or population is related, scientific nomenclature will continue to evolve. Sometimes the trend is to lump groups together, giving fewer species with more races, sometimes to split them apart into a greater number of species. So even *with* scientific names, it's important to know which school of thought is being followed.

Although I have maintained a rigidly noncommittal stance as far as taxonomy goes, the nomenclature used in *The Unfeathered Bird* is that used in the third edition of the *Howard and Moore Complete Checklist of the Birds of the World*, edited by Edward C. Dickinson (2003).



SOUTHERN CASSOWARY
Casuarius casuarius
Skeleton.

W. H. L.

~ Introduction ~

This book is not an anatomy of birds.

That is to say, you won't find any difficult Latin words or scientific jargon. You won't learn much about the deep plantar tendons of the foot or the comparative morphology of the inner ear. Nothing beneath the skeleton is included—no organs or tissues; no guts or gizzards. There's no biochemistry and very little physiology.

In fact, this is really a book about the *outside* of birds. About how their appearance, posture, and behavior influence, and are influenced by, their internal structure.

Originally intended as a book for artists, it didn't take long to realize that it would have wider appeal. Nothing similar exists. Modern ornithological textbooks sometimes provide a cursory line drawing showing the parts of bird; some even show the skeleton or a view inside the body cavity. But these are diagrams as opposed to works of art—dry, academic, and not at all pleasing to the eye. The illustrations in historical works tend to be rather more aesthetically stimulating, if sometimes a little highbrow for the general bird-lover. But when complete skeletons are shown, their appeal is more often than not counteracted by placing them in the most unlikely postures, bearing little resemblance to their attitude in life. Hardly surprising, considering that the anatomists of the past had seldom seen these birds alive.

This book attempts to combine the visual beauty and attention to detail of the best historical illustrations with an up-to-date knowledge of field ornithology; for the first time showing the internal structure of many species engaged in natural behavior.

Most of the major bird groups of the world are included, especially where their anatomy is of particular interest, though, sadly, it was not possible to include them all. Domestic birds have a place here, too, and provide some of the most bizarre and unlikely revelations in the whole book.

Much anatomical writing—at least in ornithology—is an impenetrable forest of basipterygoid processes and occipital fontanelles, so little wonder that readers often give it a wide berth. I have attempted to take the mystery out of a subject until now shrouded in long words. I've done this by looking down the wrong end of the binoculars, so to speak—allowing the illustrations to speak for themselves when it comes to the fine details and concentrating my descriptions on the birds' most obvious adaptations to their particular environment.

Now nature has a tendency to reinvent itself. For example, webbed feet are useful for swimming, and a hooked beak is useful for tearing flesh, so features like these have arisen independently in groups that are not necessarily closely related. This is called convergent evolution—otherwise known as the taxonomist's worst nightmare. The features that do give genuine clues about evolutionary relationships, those that are not influenced by adaptations to a particular environment or way of life, tend to be the subtle things—the structure of the palate; the coiling of the intestines; or an extra tendon or muscle here and there. Once the primary weapon against the problems of classification, this brand of comparative anatomy is now just a tiny part of the taxonomist's armory; an armory that includes egg-white proteins, DNA hybridization, digestive enzymes, feather structure, and vocalizations—to name but a few.

So are we now close to establishing a universally accepted “natural” classification of birds?

Not really.

I wanted *The Unfeathered Bird* to remain firmly on the fence through the swampy territory of taxonomic debate. After all, it's concerned with outward appearances and adaptations, not with tracing evolutionary

pathways. And it's supposed to be enjoyable. But this of course led to a problem—which order do I use? At all costs I wanted to spare myself and my readers a slavish trudge through each taxon in turn. My answer—a somewhat unorthodox one—was to turn modern classification on its head and to base my order of chapters on a system that is concerned *only* with outward structural appearances; on the first truly scientific classification of the natural world—the *Systema Naturae* of Linnaeus.

Thus my rapacious birds, swimming birds, gallinaceous birds, and so on are grouped together according to convergent evolution under their respective chapter headings in part 2, and I've attempted to place groups that are superficially similar next to each other for ease of comparison. Thus storks are next to cranes and swifts next to swallows. The *actual* relationships are discussed within the text at some length.

Part 2, by the way, in true Linnaean fashion, is entitled “Specific”—looking at birds group by group—while the much shorter part 1 is “Generic”—dealing with the anatomical features common to all birds.

I've attempted to make *The Unfeathered Bird* a convergence of art and science; accessibility and erudition; old and new—without compromise and without apology. I hope it finds its niche.



HEAVY-FOOTED MOA

Pachyornis elephantopus

Preserved partial foot, viewed from underside.

PART ONE:
generic

The Trunk

All birds evolved from flying ancestors. That applies equally to the Ostrich, penguins, the Dodo, and even the long-extinct giants—the moas and Elephant Bird.

Flight makes rather specific demands on the physical engineering of an animal. The skeleton needs to be of a lightweight structure, with large flattened surfaces for the attachment of muscles, and to have tremendous rigidity and the strength to support the entire weight of the animal while airborne. The components are highly specialized and once a satisfactory blueprint has been achieved there is very little room for modification. The paradox, then, is that although the birds represent the largest class of all the vertebrates—approaching ten thousand species—they are fundamentally rather uniform; though with some very surprising variations!

The adaptation for flight is the most important factor behind the structure of birds and can provide an explanation for virtually all of their anatomical characteristics—even those that seem to have nothing to do with flying. For example, with wings instead of front legs, birds need two strong hind limbs and a modified posture to balance on them. And with a body rigid enough to cope with the demands of flapping flight, it's vital to have a long and flexible neck to compensate for the loss of movement. But it's important to remember that birds didn't learn to fly first and develop these perfections afterward. Many of these qualities had long been present in the birds' Theropod ancestors—the upright dinosaurs that walked on two legs—and only through a constant process of adaptation and counteradaptation spanning millions of years did it become possible for the feathered dinosaurs to survive and take wing.

The trunk of a bird's body is rigidly immovable. It's more or less egg-shaped; larger and rounded at the front end and more pointed at the rear, with a central depression below the neck like the cleavage in a peach. Some are rather flattened vertically; others horizontally; some elongated, depending on the bird's lifestyle. There is a good deal of variation between the bones of various species and in their posture and carriage. But no matter what the bird is doing, the body always remains virtually the same shape.

The thorax—the front end of the trunk—is composed of the ribcage, breastbone, and pectoral girdle, which together support most of the machinery for flight. The breastbone, or sternum, is enormous—far larger than it is in other vertebrates—and is uniquely furnished with a plate-like keel along its midline, just like the keel of a ship, providing a broad surface for the attachment of the flight muscles. In general (in nondomesticated birds, that is), the stronger the flier, the broader the breastbone and the deeper the keel. And in birds whose capacity for flight is reduced, the keel is reduced also. One group of birds (the Ostrich, Emu, etc.) that lost the power of flight very early on in its evolutionary history lacks this keel altogether. *Their* breastbone (to continue the nautical theme) is more like the underside of a raft than the hull of a ship and so they have been given the name of “ratites,” meaning “raft-like.”

It may seem surprising that almost all of the flight muscles of birds are concentrated on and around the breastbone—on the underside of the bird's body and not on the wings themselves. For aerodynamic reasons, it's better to keep the wings as slender and as lightweight as possible, so birds have long tendons that may even span several joints, so they can keep the majority of their musculature concentrated toward the center of their frame. The muscles along the forearm are minimal and mainly control the more subtle movements of the wrist and hand.

The primary force in flight is the downward pull exerted by the large pectoral muscles that lie at the surface of the breast on either side of the keel, and these are attached to the lower surface of the wings. This is the main locomotory thrust that propels the bird forward. Beneath these, however, lies another, smaller set of muscles that pulls the wing up again. Their tendons pass through a gap between the bones at the base of the wing and are attached to the wing's *upper* surface.

Traveling through air doesn't demand much from this upward motion, and it's really little more than a recovery stroke to prepare the wing for the next downward thrust. Water presents a different problem, however, and birds that propel themselves underwater using their wings need power on the upstroke as well as the downstroke. In these groups the muscles responsible are rather better developed and may even be supplemented by others attached to the shoulder blades.

Three pairs of bones connect the wings with the body, and collectively these are known as the pectoral girdle. They are the shoulder blades or scapulars (which in birds are usually long and narrow), the wishbone or furculum, and a pair of stout struts called coracoids that are firmly attached to either side of the breastbone and brace the wings apart. The wishbone corresponds with our collarbone and is similarly composed of two sections that meet—or usually meet—in the middle. The wings are attached at the junction of these three pairs of bones by a joint that seems impossibly shallow but allows a good range of movement.



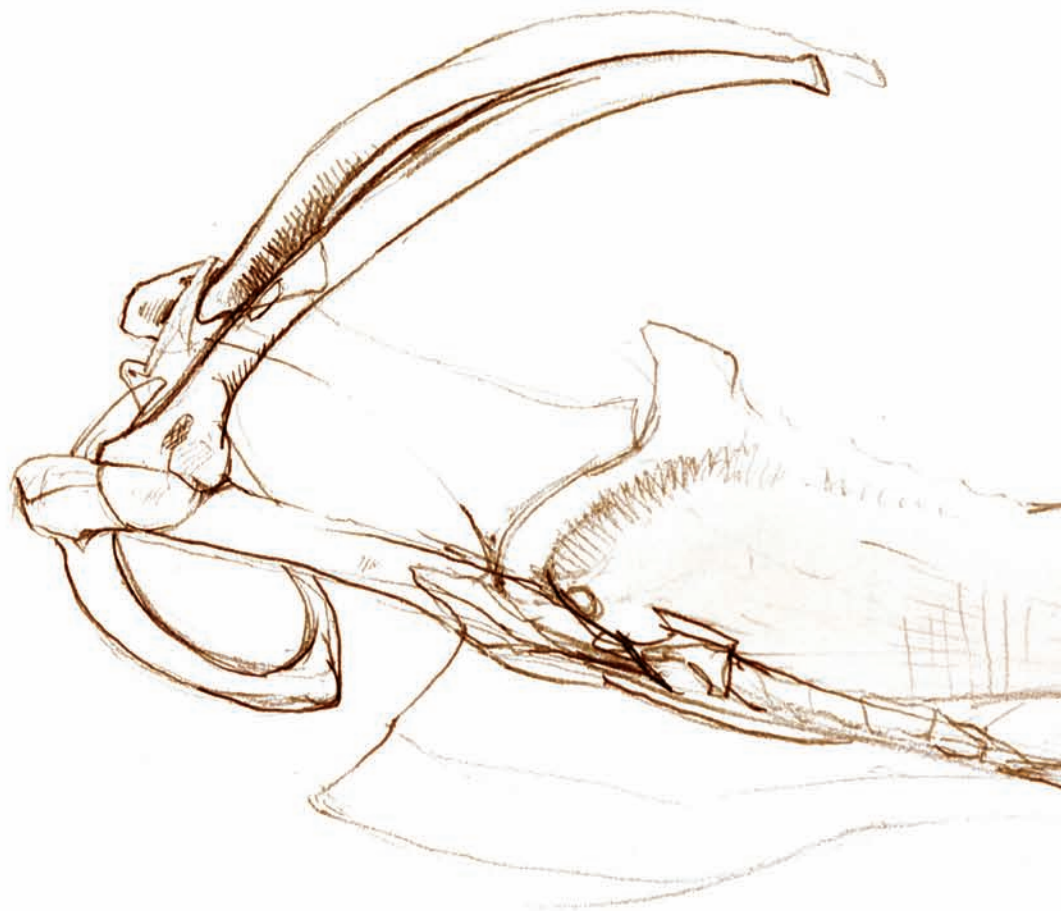
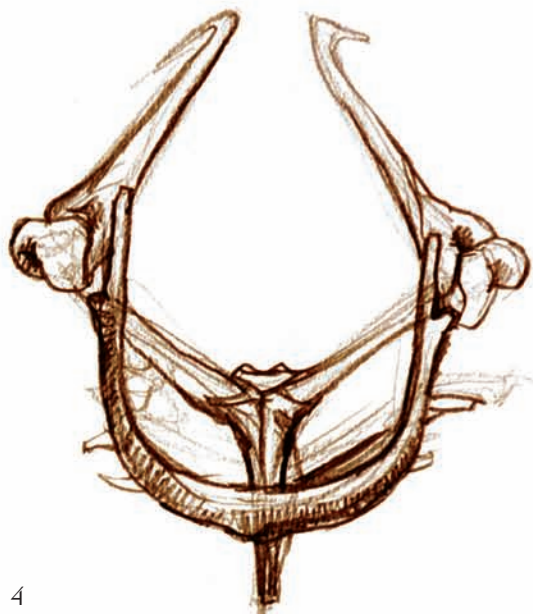
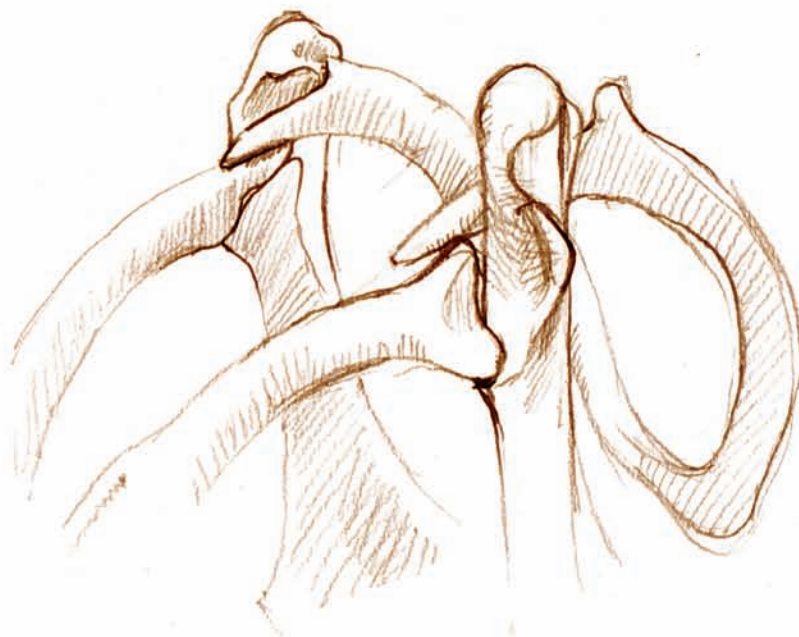
COMMON MOORHEN

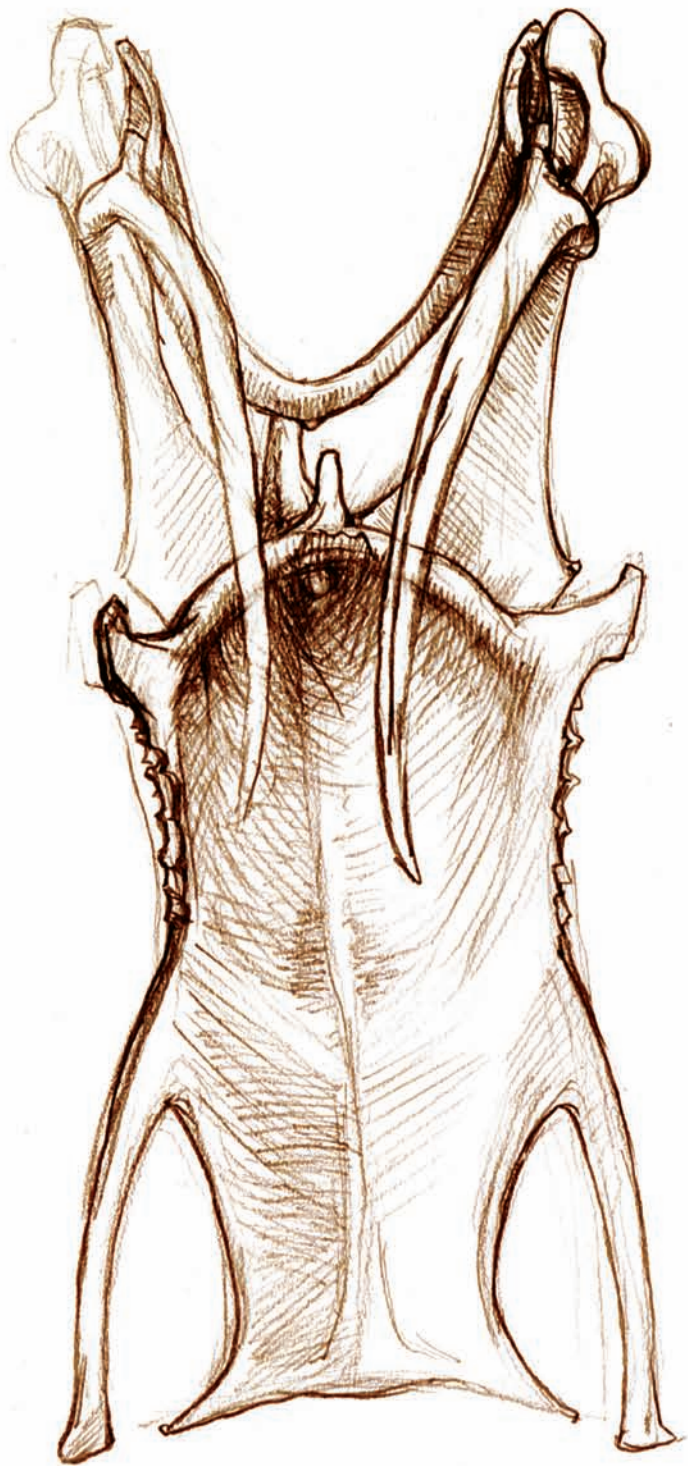
Gallinula chloropus

Trunk with skin removed.

There's little skeleton to see on the underside of a freshly skinned bird, however. The breast muscles dominate everything. They engulf the entire breastbone and keel, overlap onto the ribs, and cover the coracoids completely, extending all the way to the edges of the wishbone where they round out majestically to their insertion points on the wings. This leaves, in the angle of the wishbone, the aforementioned cleavage—the furcular pit. The space provides a comfortable lodging for the lower curve of the neck, as well as the crop (though by no means all birds have one), and is why birds' necks appear so deceptively short in life, especially with the contours smoothed by a thick layer of feathers.

A bird may possess up to nine pairs of complete ribs. Each is composed of two sections that meet at an angle: one attached to the spine and the other to the breastbone. In the mammalian ribcage the section attached to the breastbone is formed of cartilage instead of bone. But birds need the extra strength to cope with the powerful contractions of those enormous flight muscles. Both sections are made of bone, and there are even additional bony projections called uncinat processes that overlap from each vertebral rib to the one behind





to bind the ribcage into a single inflexible unit. By no means are all the ribs formed in such a way. Several at the front or back may be incomplete and may articulate instead with the nearest adjoining rib; with the pelvis; or with the breastbone. Only a proportion of the ribs possess uncinate processes, and one bird family does not possess them at all.

Even the backbone of birds becomes rod-like and rigid soon after it has left the neck and entered the thorax. Indeed in some groups many of the thoracic vertebrae are fused together into a single bone. One or two free vertebrae come next—presumably to act as a shock absorber—before the serious fusion begins. All the vertebrae, from the middle of the back to the base of the tail, along with the pelvic girdle (itself a fusion of several pairs of bones), are welded together to form the synsacrum—here referred to simply as the pelvis.

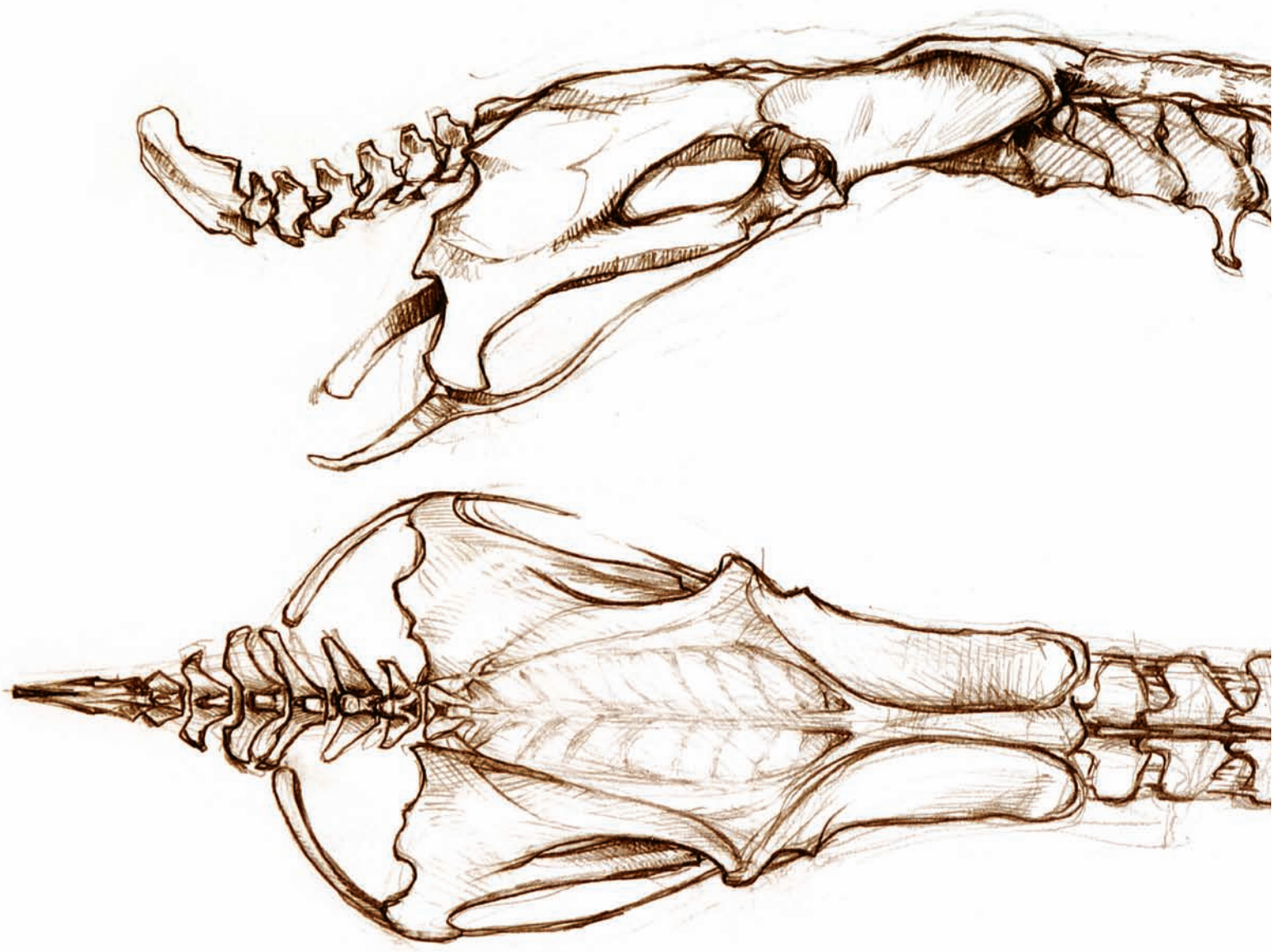
Fusion of bones is extensive in the avian skeleton. It has the dual function of reducing the weight of the bird and helping provide that all-important rigidity. Like the breastbone, the pelvic region provides a large surface area for the attachment of muscles and has the strength needed to support the weight of the entire bird when walking. The sides of the pelvis widen out into laterally spreading wings, the hindmost of which curves downward to partially enclose and protect the abdomen. There is also a slender bony projection—one on each side—called the pubis, or pubic bone. The backward-sweeping orientation of these bones is unique among living vertebrates, only having been detected in fossils of the “bird-hipped” dinosaurs. It’s one of the great ironies of natural history that birds descended not from these but from the “lizard-hipped” Theropod dinosaurs.

Birds excrete all their waste material from a single orifice called the vent or cloaca—a name derived from the Latin word meaning “sewer.” The raised opening lies behind the arc of the pubic bones and just in front of the tail. Birds also copulate via this orifice, though some have an extendable phallus. It takes only a few moments for sperm to be transferred from the male to the female and the brief act has earned the rather grotesquely corny name of “cloacal kiss.”

MALLARD

Anas platyrhynchos

Breastbone and pectoral girdle.





MALLARD
Anas platyrhynchos
Vertebral column and pelvis.



The Head and Neck

With a rigidly immovable body, a long, flexible neck is an absolute must. A neck must be long enough to allow the bird to preen all its feathers, not to mention reaching the preen gland above the tail. It has to be capable of swift movement to locate and follow prey (birds hunt by sight, but their eyeballs have little maneuverability). It has to be able to raise the head above tall vegetation to spot the approach of predators and to be withdrawn again to remain out of sight; to reach the ground in long-legged birds or to reach the bottom in surface-feeding swimming birds. It has to provide the power for a spear-like thrust and absorb the impact of hammering blows. Such a neck is a fundamental requirement for being a bird.

Of course, some birds have a longer neck than others, and more vertebrae don't necessarily mean a longer neck. Some birds with relatively few neck vertebrae have a very long neck indeed. But what sets birds apart from mammals is not the length of the neck alone but its flexibility. Imagine a giraffe that could coil up its neck like a flamingo! Whatever the species—whether bat, giraffe, whale, or human—mammals have only seven neck vertebrae, whereas birds have a variable number and always more than mammals.

The joints between the vertebrae are also different in birds, and their smooth sliding surfaces allow the greatest degree of movement between the bones. It is these that dictate the characteristic “S” shape of the neck, giving free forward movement at both ends and backward movement in the middle, as well as some rotational movement to the sides. This “S” shape is evident even when the neck is fully extended. Usually, of course, much of the neck's length is hidden by feathers, and the bottom of the “S” sits in the cavity formed by the wishbone, making the neck appear far shorter than it really is. The neck connects with the skull in a sweeping curve and enters it, with few exceptions, at the back, rather than from beneath, forming a continuation of the streamlined “S” shape with the same smooth forward movement. Although the size of the vertebrae tapers somewhat toward the head, the surrounding muscles smooth out the transition and give support to the skull.

The upper part of a bird's skull can roughly be divided into thirds: the braincase, the orbits, and the upper mandible of the bill. Birds inhabiting a particularly saline environment may have shallow depressions above their eye sockets, in which the salt excretion glands are situated. In many birds these glands respond to the amount of salt in the environment and may become larger or smaller within the bird's lifetime. The upper mandible is comprised of three strips of bone—one at the top and one on each side—that converge toward their tip. The nostrils lie within the angles formed by these strips. Birds also have internal nostrils that open into the nasal cavity situated within the palate between the bones of the upper mandible. The bones of both jaws are perforated with numerous tiny holes through which blood vessels and nerves pass, particularly in the highly sensitive bill tip.

The lower jaw runs the entire length of the skull, with the two sides joining at the bill tip to form a “V” shape. It articulates with the braincase—not directly, as it does in mammals, but by an independent bone, one on each side, called the quadrate. Now mammals, when they eat, bite, or even talk, move only their lower jaw. Birds, however, are capable of moving the upper part of their bill, too. They do this by means of a complicated pushing mechanism of all the little bones that connect, directly or indirectly, with the quadrates

within the skull, and the thin bone—the jugal bar—that runs alongside the lower jaw. This means that birds can either flip up their entire upper mandible, as parrots do, or grip a worm deep underground, using only the bill tip, like a woodcock. There are many variations in between, and which action a bird is capable of depends on the position of “elastic zones” within the upper mandible. These may take the form of a definite hinge or zone at the base of the bill or as an area of flexible bone tissue farther down its length. In the latter case, the pushing forces are transmitted via the nostrils, so birds with longer, slit-like nostrils can usually flex just a portion of their upper mandible whereas rounded or oval nostrils are usually an indication of a basal hinge in which nostrils play no part.

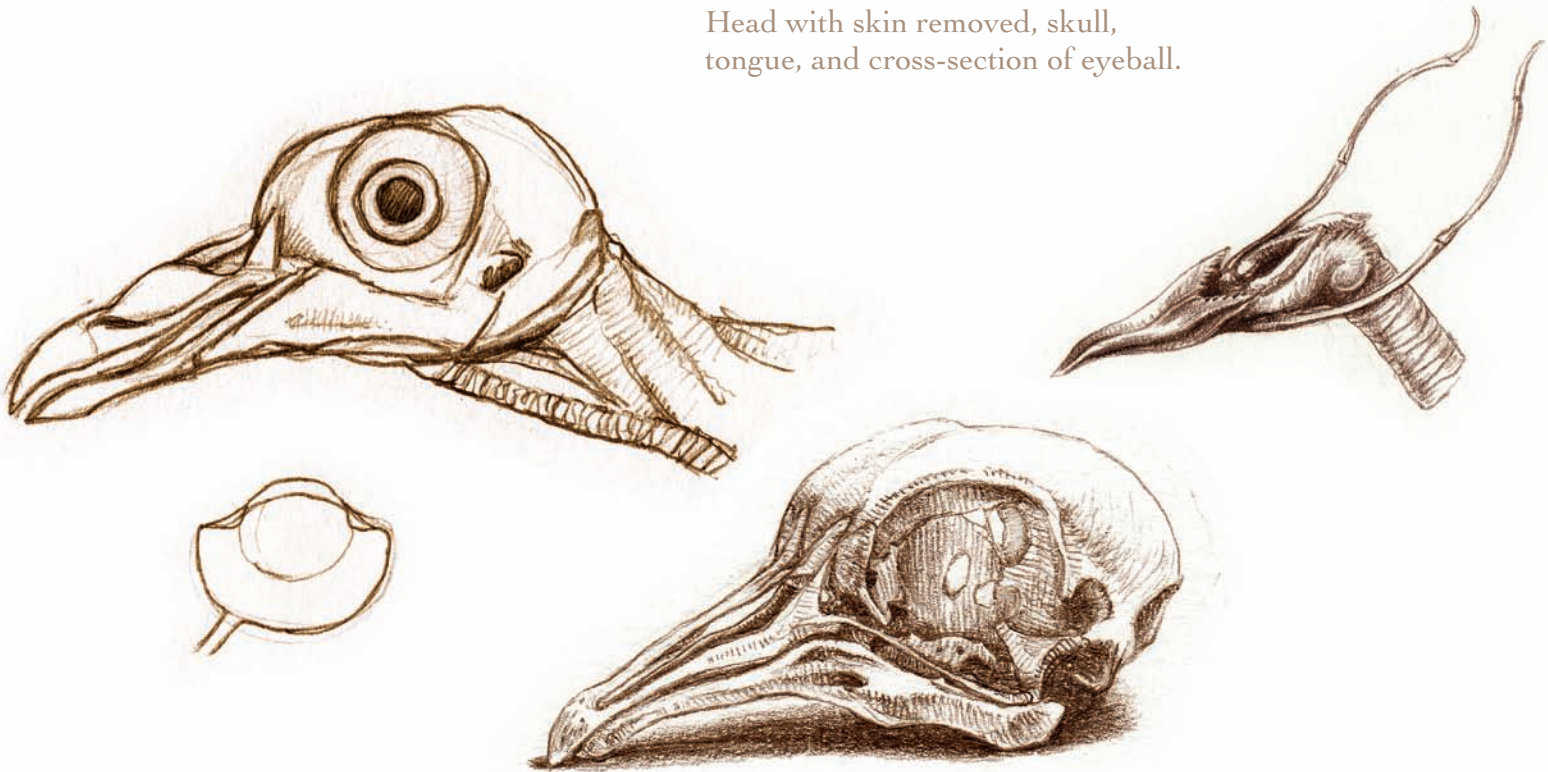
In the overwhelming majority of birds, a sense of smell is negligible. Kiwis and petrels are notable exceptions and, in their nocturnal activities, their olfactory sense has filled the niche usually occupied by their eyesight. Some New World vultures also have a well-developed sense of smell, being able to locate carrion screened from the sight of circling birds by the forest canopy.

As most of what birds see on the ground is, quite literally, a bird’s-eye view from far overhead, excellent vision—and, in particular, long-distance vision—is essential. Birds therefore have eyeballs divided into two hemispheres: a small cornea—the clear “window” that lets light in—and a large retina onto which the image is projected. The eyeball is consequently considerably bigger than it seems when seen through the eyelids of the feathered bird. Although this is an excellent solution for sharp vision over long distances, the dual-hemisphere avian eye is less stable than the spherical eye of mammals and is only made viable by the retention of a reptilian characteristic: a ring of tiny plates of bone that forms a supporting ridge around the circumference of the cornea. This bony ring, and the irregular shape of the eyeballs fitting closely within their orbits, restricts the rotation of the eyes, which means that most birds need to rely on the flexibility of their neck in order to look around in all directions.

WOODPIGEON

Columba palumbus

Head with skin removed, skull,
tongue, and cross-section of eyeball.





PALM COCKATOO

Probosciger aterrimus

Skull showing hinge and bill-opening mechanism.

Birds have two true eyelids, one upper and one lower, fringed with eyelashes. These are not hairs but modified feathers. Unlike human eyelids, however, it is the lower lid that is drawn upward to meet the upper when sleeping. Owls and some nightjars are the exception, with eyelids capable of independent movement. A “third eyelid,” the nictitating membrane, can be drawn across horizontally from the bill side to protect the eye from damage, and in some diving birds such as gannets and kingfishers, this membrane is transparent so as not to lose visual contact with prey while plunge-diving into the water.

Birds have ears, too, though they are seldom visible beneath the feathers. The “ears” of owls, pheasants, grebes, and so forth are simply decorative or camouflaging tufts of feathers and have nothing whatever to do with hearing. The true ears are situated just above the angle of the jaw and are usually visible as a small oval hole, lacking the external flap of skin and cartilage so characteristic of mammals.

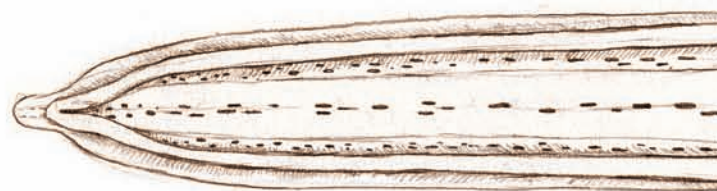
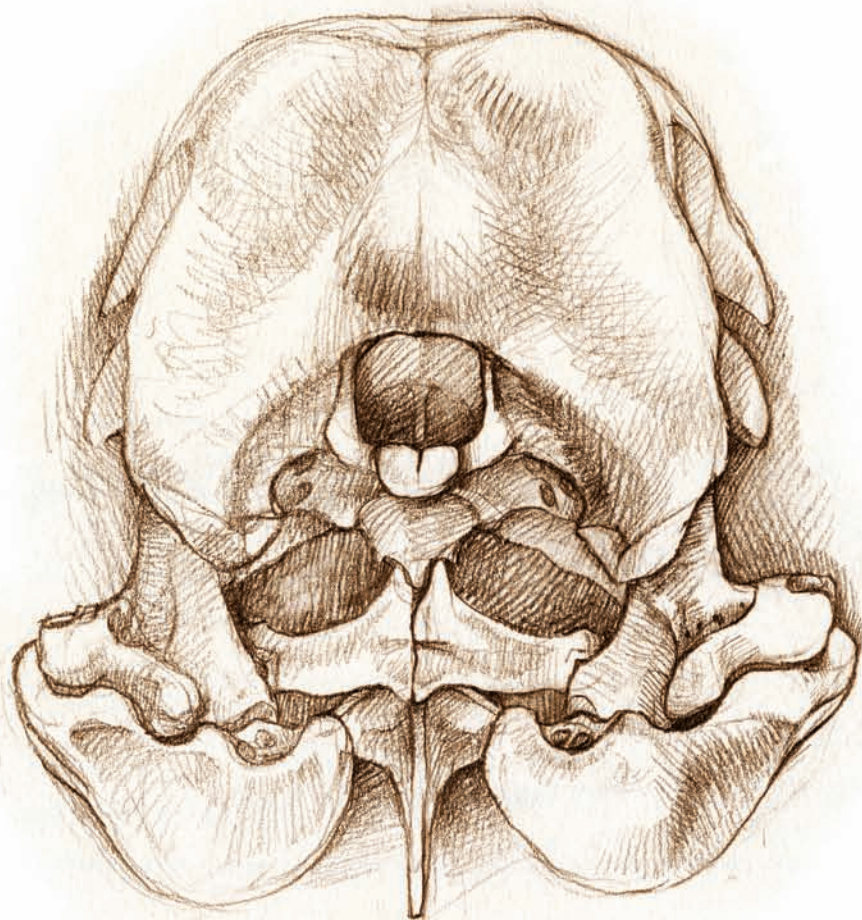
Where a bird’s skin meets the bill, it is thickened to form a horny or leathery sheath called the rhampotheca, completely covering the bone. As this is technically part of the skin, the rhampotheca has been removed for the majority of skeleton drawings in this book in order to more clearly show the underlying structure of the jaws, though in some cases particular bill characteristics are thereby rendered less obvious.

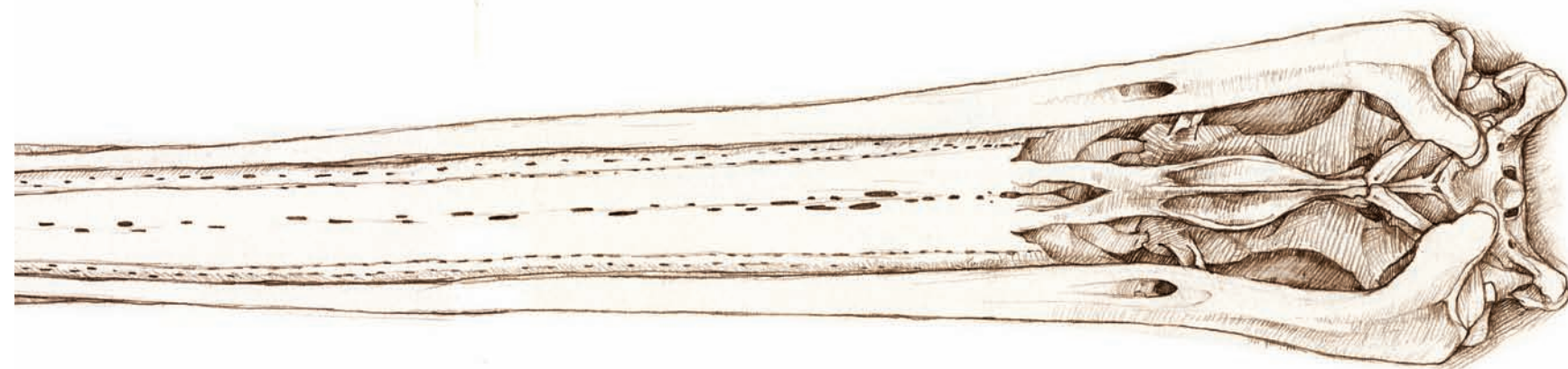
The tongue sits on the floor of the mouth, within the angle formed by the sides of the lower mandible. Bird tongues are highly diverse in structure and appearance though distinctly different from those of other animals. They—like those of many vertebrates—have bones. The tongue itself is supported by a short pedestal, which, in turn, is positioned at the apex of a pair of thin, whip-like structures called hyoid horns. These extend backward, encircling the base of the lower jaw and curl upward again to hug the rear of the braincase.

Beneath the tongue and within the angle formed by the lower jaw is an area of soft skin called the gular region, which may in some species be distended to form a pouch for food, prior to swallowing, or may be inflated in display. But birds have other inflatable regions in their neck, too. Some may blow up their esophagus like a balloon, or specialized branches of the esophagus, or they may inflate their air sacs—the lungs’ supplementary air supply.

Once swallowed, food passes down the length of the esophagus and may be temporarily stored in a crop that sits in the cavity formed by the wishbone, beneath the curve of the neck. Not all birds have a crop, but when present it is essentially a little bag—just a widening of the esophagus—which stores food prior to digestion in the stomach, or gizzard. Particularly heavy meals can be seen as a distinct bulge, clearly visible through the feathers. Alongside the esophagus runs the windpipe or trachea, which transports gases to and from the lungs and the air sacs. The trachea is formed of many interlocking rings of cartilage or bone. It begins its downward path just behind the base of the tongue, symmetrically central within the angle of the jaws, but soon crosses over to the side of the neck; usually to the right side. From here it continues toward the thoracic cavity where it divides to enter the lungs. Birds do have a larynx in their throat, as we do, but their vocalizations are made at this dividing point of the trachea—called the syrinx—by a series of membranes and pads that vibrate when air is passed across them. Although the syrinx, and everything else within the body cavity, is outside the territory of this book, some birds give additional volume to their calls by having a windpipe that is essentially too long for them. And this may lie outside the body cavity, within the bone structure itself, or even just beneath the skin.

GREAT WHITE PELICAN
Pelecanus onocrotalus
Skull and bony eye ring.





The Hind Limbs

With the front limb modified into wings, birds have only two legs to stand on; two points of contact with the ground, on which to balance. Their distant reptilian ancestors would have had legs that projected out to the sides of the body rather than underneath it, like a crocodile—clearly not a feasible option for sustained bipedal locomotion. But long before birds became birds, Theropod dinosaurs were walking the earth on two legs, which had changed their orientation to support the body from beneath.

In order to maintain balance, the posture of the body also needed to change. The knees needed to be rotated upward with the thighs lying almost horizontally, to bring the legs forward and thereby place the center of gravity above the feet.

Birds' legs are structurally just like those of any other terrestrial vertebrate—give or take the loss of a bone here or the fusion of bones there. They have all the same component parts and the joints articulate in the same directions. But because the thighs of a bird lie close to the ribcage, the top part of the leg is enclosed within the skin of the body and is barely discernible on the feathered bird. This leads to all sorts of confusion farther down the leg and even professionals who really ought to know better frequently refer to the “thighs” when they mean the lower leg, the “knees” when they mean the ankle, and so on. Consequently, many people believe that birds' legs bend in the opposite direction to our own. They don't!

The thigh bone, or femur, is relatively short, thick, and robust. It's surrounded by the majority of the muscles that control the legs and feet, and these muscles have points of attachment spanning virtually the entire back end of the bird. The thigh itself is therefore capable of little movement at its articulation with the pelvis, and its principal function is to maintain the position of the feet beneath the center of gravity. Most of the movement of the leg is from the knee joint. This is mostly a backward-and-forward swinging motion, though there are also lateral muscles that rotate the body to cover the supporting limb when the bird is standing on one leg or walking. A knee bone is present in most but not all groups and is usually rather well developed in water birds.

The lower leg is, like our own, composed of two bones—the tibia and the slender, tapering fibula that lies along its outer edge and ends in a sharp point. The latter is the one conveniently used as a toothpick when we eat roast turkey. In birds, however, the lower end of the tibia is fused with one of the tiny bones from the ancestral ankle, the tarsal bones, making its correct name the tibiotarsus. The remaining ankle bones are fused with the foot bone or metatarsus, and again its correct name is a similarly complicated fusion—the tarsometatarsus—though referred to in the remainder of this book simply as the tarsus or foot.

At the back of the tarsus is a raised platform-like process, its surface deeply furrowed with grooves and crests and perforated by canals. These act as channels for the tendons that close the foot. (Those that open the foot run along the front edge of the tarsus.) When the bird is crouched, the joint is flexed, producing the tension on the tendons required to lock the foot into position, a particularly useful configuration that has enabled birds to roost high in trees without the risk of falling. Ridges on the tendons of the toes also help by forming a ratchet mechanism triggered off by the weight of the bird and thus preventing accidental loosening of the grip.

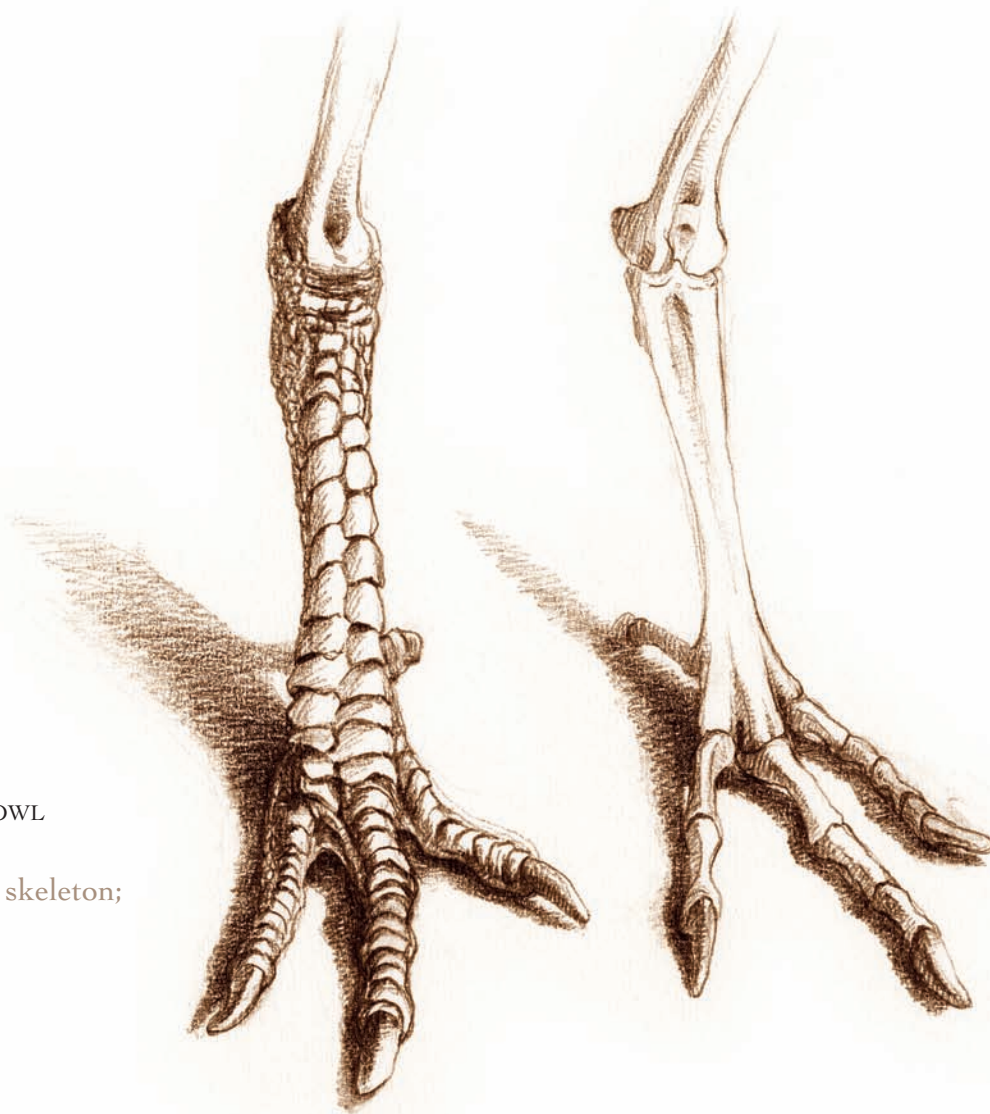
Because of the position of the thigh, mentioned earlier, many people regard the tarsus as a portion of the leg and consider the toes alone as constituting the foot. This is incorrect. At its most basic level, the tarsus is the solid part of a bird's foot, before the toes, and directly comparable with our own foot bone. It's comprised of three parallel sections—one for each of the forward-facing toes—though in the majority of birds (penguins are the exception) this is only apparent at its farthest end.

The hind toe is something of a misnomer, though it is the term that is adhered to, for the sake of simplicity, throughout this book. Although indeed it usually faces backward, or nearly backward—to balance the bird when walking and to oppose the forward-facing toes when perching—it arises not from the back of the tarsus but from the inside edge. It may be at the same level as the other toes in more arboreal species or raised above the ground or even absent altogether in terrestrial birds. Its correct name is the hallux, but it is often referred to as Digit I, with the other toes numbered II to IV consecutively outward.

Not all birds have four toes, though all derived from a four-toed avian ancestor. Some cliff-nesting, wading, or fast-running species and even a few woodpeckers have lost a toe or are in the process of losing one. Ostriches have even lost two. In such cases the hind toe is usually the first to go; Ostriches have lost the hind and inner toes. But a minority of species—some kingfishers and even a single passerine—have retained the hind toe for perching and lost one of the forward-facing toes.

HELMETED GUINEAFOWL
Numida meleagris

Pair of feet: left foot, skeleton;
right foot intact.



Dorsal.



Ventral.

