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2. PROTRACTED & NAKED JAWS (THE BEAK)

OLDEST AND YOUNGEST

Long, long ago, when the world was still very young, the Titan king of all the deities, Kronos, god of destruction and of time itself, was in a quandary. It was foretold that among his offspring would be one who would eventually overthrow him. Kronos could relate to that as he'd overthrown and slain his own father, Uranus, and didn't want to suffer the same fate. What was a god to do?! So, he formed a plan, and when in time his wife, Rhea, gave birth to a child—a beautiful and placid baby daughter she named Hestia—Kronos ate it. He ate all their children, three girls and two boys, until Rhea, pregnant with their sixth child, decided to hide it away and raise it to someday become the instrument of her revenge. The plan was a success. Rhea tricked her husband into swallowing a boulder instead, which the Titan god took to be just a heavy child, and with the help of Gaia, Mother Earth, she raised her son, whom she named Zeus, in secret. When fully grown, Zeus, disguised as a cup-bearer, returned to the court of Kronos and poisoned him, making him regurgitate, in reverse order, first the boulder, then all of the children he'd consumed. First out was Poseidon, closest in age to Zeus. He was to become the god of the sea. Then there was Hades, the god of the underworld. Then Hera, the youngest of the girls and Zeus's future wife. After her came Demeter, the goddess of fertility. And finally, the lovely Hestia, goddess of the hearth and home; least celebrated of all the Olympian deities, but the one most cherished and held dear. Hestia; the first and the last, the oldest and the youngest.

Not so long ago, around 80 million years, towards the end of the Cretaceous when the dinosaurs had already reached their heyday, some of the carnivorous dinosaurs, the theropods, had become very small and feathered and were even able to fly. One day, or maybe over several days, along the edge of a slow-flowing creek in an open sandy area in what is now southeastern Brazil, a vast flock of tiny flying dinosaurs perished.

Countless millions of dinosaurs and other animals had lived, died, decomposed, and disappeared without trace, broken into atoms by the action of wind, water, and other organisms. Just occasionally, if conditions were exactly right, their bodies would be mineralised, turned to stone, deep within the sediment that covered and encased them, as these sand and mud layers, too, were compressed and turned to stone. Down through the layers of strata into Deep Time the history of the planet is written in fossil forms; just impressions, an echo, an earth-memory, primeval murmurings of extinguished beings haunting every horizon since the dawn of complex life.

Fossils from the Late Cretaceous, just before the asteroid impact which would change the world and its inhabitants forever, are as rare as they are important. They alone can tell us why some lineages of animals survived into the next era—the Paleogene—and others didn't. Big dinosaurs fossilise relatively readily, but it takes a very special set of circumstances—the finest sediments, the freshest and most intact corpses, the most tranquil conditions, and just the right amount of pressure—to preserve the intricate details of fragile tiny creatures without crushing them to atoms. Of the fossilised few, the overwhelming majority will remain in darkness. Deep underground they lie still, entombed beneath mountains and beneath cities. Perhaps some will return to the surface in another 80 million years; perhaps never; perhaps tomorrow.

The little dinosaurs that died that day in Brazil were 'opposite birds'—Enantiornithes—not direct ancestors of modern birds, but birds nevertheless, and closely related enough to shed some light on the evolution of modern avian characters. Against all the odds, the many delicate bodies were quickly buried in fine clay and silt and, although the skeletons were broken up into pieces, they were exquisitely preserved as fossils in a rich bone bed crammed into an area of less than six square metres, eventually exposed to human eyes after 80 million years of internment. Miraculously, among the jumble of fragments, as intact and perfect as if it had emerged from the mouth of Kronos himself, was a tiny skull.

On first inspection it could easily pass as the skull of a modern bird: with large eye orbits, a toothless bill, a rounded shape to the back of the cranium, and the hole for the neck insertion situated on the rear corner, angled downward.



↑ Head and neck skeleton of a domesticated fowl *Gallus gallus*, showing the major anatomical regions.

↔↔ The enantiornithine fossil bird *Navaornis hestiae* from the Late Cretaceous of Brazil, specimen MPM-200-1, Museu de Paleontologia de Marília, Brazil. The near-intact toothless skull combines a mosaic of ancient and modern features hinting at the order in which these characters may have evolved in birds.

A cranium of *Homo sapiens*—a human.
All vertebrates share essentially the
same skull structure, and all the
components in the beak of birds are
present in our own skull.



A closer inspection, however, would reveal elements that don't fit at all; elements you'd associate with proto-birds like *Archaeopteryx* and the non-avian dinosaurs further down the phylogenetic tree. Further studies of the internal cavity of the skull also revealed a brain that was birdlike in shape, but with an un-birdlike distribution of brain regions¹.

'Missing link' is the term often used for fossils which seemingly fill evolutionary gaps. It's a terrible term, because it suggests that evolution is a linear progression, like a chain, or a ladder, with single-celled organisms at one end and humans at the other. If you began this book by reading the introductory section *Of Names and Clades* you'll know that there are no ladders in evolution; only trees. It also suggests that all the characters of the creature in question will be intermediate between those of the animals assumed to be on either side. Evolution seldom works like this either, and especially not in large and complex machinery like entire bird skulls. Instead, the various elements—or modules—change independently, rather like one of those Victorian picture games where you combine different parts of several images to get a whole plethora of variables. It's known as 'mosaic' evolution. Some elements change more readily than others, so you get a mixture of new (called 'derived', or 'apomorphic') traits, and inherited (called 'ancestral', or 'plesiomorphic') traits in any single taxon. Working out which of these characters are ancestral and which are derived is the challenging part, and the logic behind the reconstruction of phylogenetic trees.

No, the little skull from Brazil is not a missing link. As an enantiornithine it occupies a different branch on the phylogenetic tree of life from its sister group—the euornithines, the clade to which modern birds belong—so the presence of birdlike characters can mean either of two things: 1. that both lineages evolved the characters independently, by what we call convergent evolution. (Convergence is very common in birds and they did, in fact, evolve many characters independently, like their toothless beak².) Or, 2. that the characters were already present in the common ancestor of

¹ Chiappe, L. M., Navalon, G., Martinelli, A. G. et al., 2024. Cretaceous bird from Brazil informs the evolution of the avian skull and brain. *Nature* 635(8038): 376–381.

² Xu, L., Buffetaut, E., O'Connor, J. K. et al., 2021. A new, remarkably preserved, enantiornithine bird from the Upper Cretaceous Qiupa Formation of Henan (central China) and convergent evolution between enantiornithines and modern birds. *Geol. Mag.* 158: 2087–2094.

both, suggesting that they evolved at least 50 million years earlier, before the two lineages diverged. And of course, the combined birdlike characters may be a mixture of derived and ancestral. The little bird, named *Navaornis hestiae* after the Greek goddess Hestia, is not an intermediate, not a grey area partway between extremes. Its skull and brain combine a mosaic of features modern and ancient, hinting to us the order in which these characters may have evolved in birds and to what extent each is reliant upon another. Small and unremarkable though the fossil seems, it's so important it's been described as a Rosetta Stone of bird evolution³ and is so much more than the sum of its parts. Simultaneously the oldest and the youngest, the first and the last, *Navaornis hestiae* is wholly deserving of its divine appellation.

A JAW THAT OPENS AND CLOSES

We'll return to discuss the brain of *Navaornis hestiae* and its significance shortly, but meanwhile it's time I introduced the main subject of this chapter: the “protracted and naked jaws” of Linnaeus's description—the beak, as he added in parentheses afterwards. Indeed, to speak of the beak is to speak of the skull itself. There's nothing new in the bony components of a bill; a beak isn't something strapped on to the skull, like a plague mask. These components were already present in non-avian dinosaurs and can be recognised today in the toothed snout of crocodiles—birds' closest living relatives. They're present, too, in our own skull. We have a jaw that opens and closes, nasal bones, palate bones, and maxillary bones that hold our upper teeth. We even have tiny premaxillary bones behind our upper incisors. All these bony elements are shared by all other vertebrates, and all variation between them—between anteaters and antbirds, tyrannosaurs and tenrecs, crocodiles and cobras—are the result of expansion, reduction, separation, relocation, or modification of the relative elements.

³ Domínguez, N. 2024. An intact 80-million-year-old fossil is the 'Rosetta Stone' that promises to decipher bird evolution. *El País* 18 Nov. 2024.

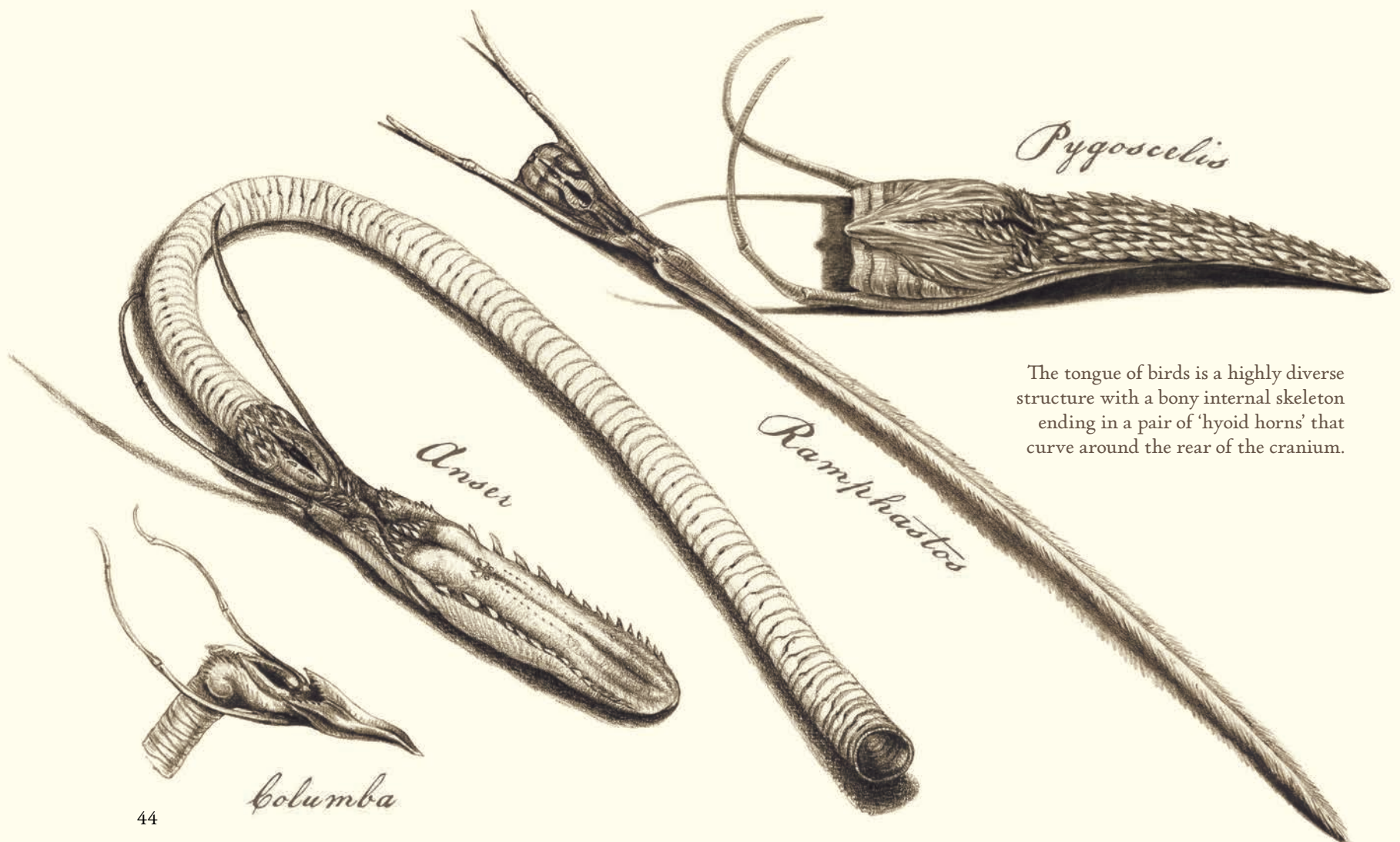
Although the chelonians—the turtles, tortoises, and terrapins—possess a beak, it's very different from the beak of birds. The avian upper jaw is formed mostly from a single enlarged premaxilla, while the chelonian premaxillae are paired structures separated by a suture and confined to the very tip of the jaw, directly beneath the nasal opening. This is a Green Sea Turtle *Chelonia mydas*.



Many vertebrates besides birds even possess a toothless beak (think of turtles or platypuses) or they may have combined a toothless snout with grinding teeth at the rear of the jaw like many of the ornithischian dinosaurs, or the ancestral platypuses of the Miocene. The pterosaurs, the flying reptiles of the Mesozoic, evolved both toothed and toothless clades. Where the beak of birds differs, however, isn't in its toothlessness, but in the proportions of the various elements, and in the movability—kinesis is the correct word—of the upper jaw, independently of the cranium.

One of the difficulties in writing this chapter is the interrelatedness of all the component parts because the bill and skull of birds function and evolve as one complex machine. It's therefore not possible to think of the bill without the braincase, the kinetic (moveable) palate of most birds without the akinetic palate of the few, the parts as they are now without the parts as they used to be, or the beak of birds without the beak of other animals and the stages of their jaws through their evolutionary history. Introducing just the bill of a bird is therefore rather like describing the steering wheel of a car while trying not to get sucked, all at once, into the mechanics of the entire chassis, wheels, and engine. Thus, this chapter has, more by accident than by design, evolved like the skull itself in a modular yet integrated way, interweaving between the separate yet interconnected elements, between the present and past—oldest and youngest.

If you look at a living bird, the bill is covered in a horny or leathery sheath called the rhamphotheca which abuts the soft-skinned and feathered face. The rhamphotheca can therefore be said to define the limits of the beak, but this is a rather arbitrary delineation as it covers just a small portion of the workings of the jaws. You'll often see diagrams at the beginning of bird books showing the different parts of a bird's external surface, and these invariably label the upper and lower parts of the beak as the upper and lower mandibles. This is, however, only partially correct. The upper part of the bill isn't a mandible; it's correctly called the rostrum. Only the lower jaw is the mandible, and only a part of it, the dentary, is covered by the rhamphotheca and forms the beak section. The mandible extends the entire length of the skull, so when a bird opens its beak it does so from far back behind the eyes, towards the rear of the cranium. Only





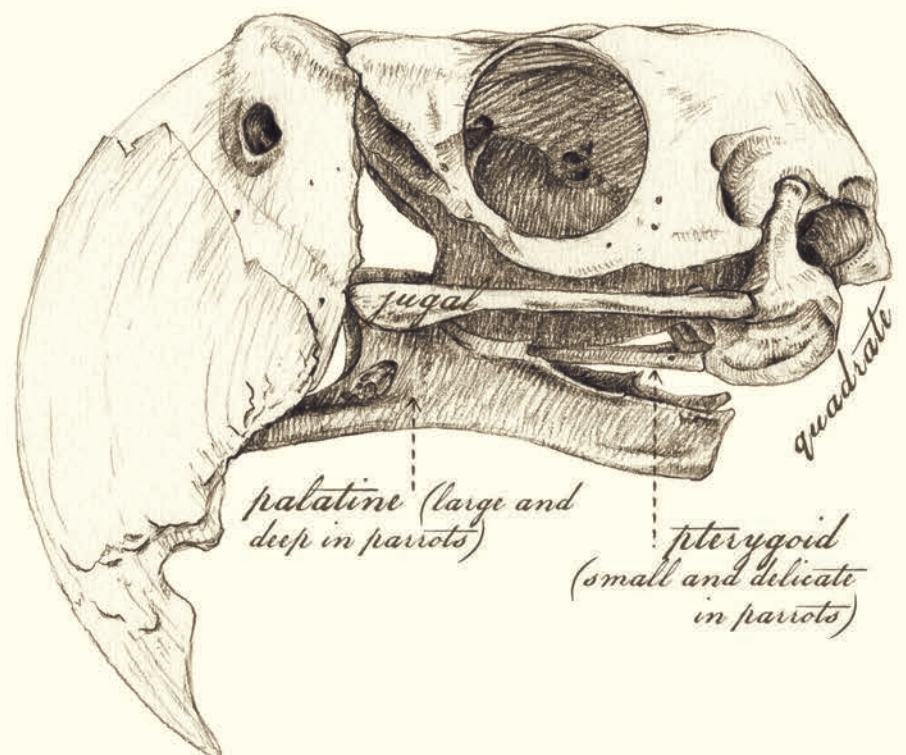
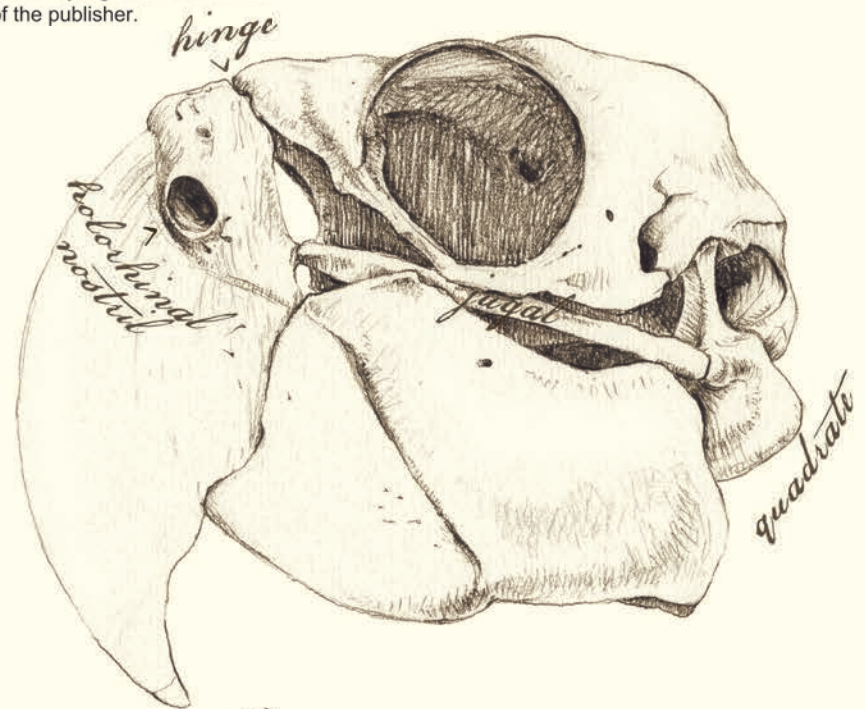
the rostrum can be raised and lowered at the border of the feathered face. There's no hinge along the lower jaw for the bill to open where the dentary meets the feathers—a frequent error in illustrated and animated birds with a symmetrical articulation with the lower part of the beak mirroring the upper.

The mandible's two sides, or 'rami' (the singular is 'ramus', which means 'branch'), meet at the bill tip where they converge at a sharp angle to give a pointed 'V'-shaped beak (think of chickens) or in a gentle curve to give a 'U'-shaped bill (think of ducks). In side view the fusion of the rami slants upwards to give a tapered tip at an area called the gonys, and it's the only place where the two rami meet. You can see the angle of the gonys clearly marked by the red spot on the bill of some large gulls which is very conspicuous in such a formidable-looking weapon, but gently tapering mandibles produce a more delicate and slender bill in which the gonys angle is barely discernible at all. The area between the two rami is floored with the soft and rather elastic skin of the chin—the gular region—in some species, a useful storage sack for holding and carrying food. In general, the smaller the gonys, the larger the gular sac, and nowhere is this more notable than in the pelicans. Pelicans use their gular sac as a trawling net, and have flexible zones along the rami that can be bowed outward at the sides to maximise the catch, in a manner convergent with rorqual whales⁴.

⁴ Field, D. J., Lin, S. C., Ben-Zvi, M. et al., 2011. Convergent evolution driven by similar feeding mechanics in balaenopterid whales and pelicans. *Anat. Rec.* 294(8): 1273–82.

Palm Cockatoo *Probosciger aterrimus* skull showing the mechanism for cranial prokinesis—the movement of the upper jaw at a 'hinge' joint at its junction with the skull.

In birds with a prokinetic skull the nostril is usually rounded, or 'holorhinal'.



The tongue sits within the angle between the rami, a highly diverse structure with a bony internal skeleton ending in a pair of 'hyoid horns' which curve around the rear of the cranium.

The gonys is exclusive to modern euornithines—the Neornithes—but in the toothed Mesozoic Euornithes like *Ichthyornis* and the wingless diving bird *Hesperornis*, the two sides of the mandible were unconnected, instead being united by an entirely separate element, a tiny conical bone called the prementary, giving the skull an oddly truncated look, as though their bill tip had been accidentally snapped off and stuck back on again. It's possible that the prementary bestowed a degree of kinesis on the toothed jaws⁵. *Hesperornis* was a foot-propelled diving bird probably very similar to modern grebes and loons, so one can speculate that the evolution of a jaw with pincer-like bill tips enabled the catching, and perhaps even the carrying, of several fish at once, the way modern puffins do. Some Enantiornithes, as we can see from *Navaornis hestiae*, had a mandible joined by a gonys at the tip, as it is in modern birds, though the similarity is convergent.

Past the gonys the upper and lower edges of these slender branches are more or less parallel along the length of the beak, increasing somewhat in height beyond the dentary where they support the muscles that power the jaw. At its rear end, the mandible flattens out from top to bottom to form a hinge joint—appropriately known as the 'articular'—which articulates with the cranium. In most vertebrates it does so directly, but in birds the cranial part of the hinge has separated into a pair of independent bones called quadrates. Only in mammals has the mandible articulation changed to a new and more proximal position. The quadrate and articular regions are still present, however, counter-adapted (the correct term is exapted, as opposed to adapted) to a new role as the tiny incus and malleus bones—the 'anvil' and 'hammer'—of the middle ear.

Quadrates in birds are 'go-between' bones; a sort of telephone exchange, connecting and controlling the various elements of the skull and the movements of the lower—and upper—jaw. They're so-called because they have four points of articulation: one with the mandible, another with the cranium itself, one for the slender jugal bar—the avian equivalent of our zygomatic arch, or cheekbone—which connects with the sides of the rostrum, and a fourth, on the inside of the skull, with a pair of rod-like palate bones called pterygoids, part of the complex machinery of kinesis.

⁵ Bailleul, A. M., Li, Z.-H., O'Connor, J. K. et al., 2019. Origin of the avian prementary and evidence of a unique form of cranial kinesis in Cretaceous ornithuromorphs. *Proc. Nat. Acad. Sci. USA* 116(49): 24696–24706.

Parahesperornis, a flightless—and wingless—foot-propelled diving bird from the Late Cretaceous of North America. Like other members of the Hesperornithes, its lower jaw, and the maxillary section at the rear of the upper jaw, were armed with a row of backward-pointing curved teeth. Presumably, the pointed tip of the snout, the premaxilla, was covered in a horny or leathery rhamphotheca like the bill of modern birds. Cast specimen at South Carolina State Museum.

When we, as mammals, open our mouth, we can only do so by depressing our lower jaw. Our upper jaw is a fixed and inflexible part of the skull. Rabbits and hares have a little more movement, but nothing approaching the flexibility of bird skulls. Most birds are able to articulate their palate bones independently, with a combined function to raise and lower the upper part of the bill, either from a hinge at its base or partway along its length. The pushing forces applied by the quadrate to the pterygoids—and then in turn to the palatines, to which they connect, and the jugal bars at the sides—are transferred from the palate to the bill, which then rotates upward at one or more flexible zones along its upper surface. Once again, it's important to stress that all of these bones were already present in the comparatively rigid skull of non-avian dinosaurs. The difference is in their separation into individual independent components.

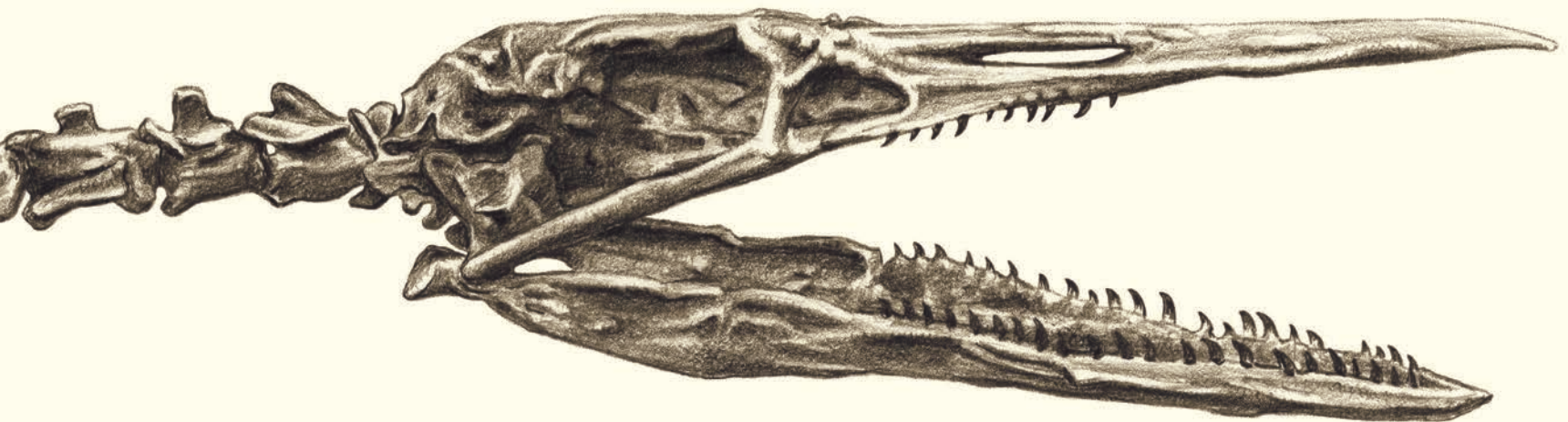
While the postcranial skeleton of birds (everything apart from the skull) was undergoing large-scale fusion, the reverse was happening in the skull itself. The solid and immobile regions separated into individual elements capable of complex and fine movements; precision machinery for a beak that would be able to weave elaborate nests of grasses or gossamer, extract prey from deep down in heavy wet sand, carry multiple small fish from a single dive, build elaborate gardens of gathered flowers, and ensure that each and every barb and barbule of their feathers zips tightly to a smooth, waterproof, and aerodynamically efficient contour around their body.

ENDOCRANIUM QUARTET

You may be wondering how we know what the brain of *Navaornis hestiae* was like. After all, it isn't fossilised. It would have decomposed along with the rest of the soft tissues 80 million years ago. The answer is that the brain develops within the skull, and the skull develops to fit the brain⁶. It's a snug fit, with barely any space in between. So, by making a cast of the space inside the braincase (the endocranium) it's possible to get a highly accurate physical model of the brain's surface structure—an endocast.

Historically this was achieved by filling the braincase with plaster or silicone, or sometimes an endocast could be formed naturally. There are lots of holes opening onto the brain cavity where nerves and blood vessels enter and leave, not to mention the large hole, the foramen magnum, for the attachment of the neck. These holes let in sediment

⁶ Fabbri, M., Mongiardino Koch, N., Pritchard, A. C., et al. 2017. The skull roof tracks the brain during the evolution and development of reptiles including birds. *Nature Ecol. & Evol.* 1(10): 1543–1550.



which over time is mineralised into stone. There are two problems with this. One is getting the cast out again, which necessitates damaging the specimen. The other is being limited to fossils that are not embedded in a stony matrix. Fortunately, modern CT scanning (CT stands for computed tomography) and its associated software allow us to create *virtual* endocasts—digital models that can be studied on screen, or even 3D printed at any size. It works by firing X-rays at an object. The X-rays penetrate all the way through, allowing us to visualise it in slices as a series of thin segments. By this method you might think that sediments and debris within and around the skull would create an obstruction. Braincase filled with rock? No problem! The matrix will usually (hopefully) be of a different density from the bone, allowing it to be manually removed on-screen, one tenth-of-a-millimetre-thick slice at a time, in a mind-numbingly tedious operation called ‘segmentation’. If you survive the ordeal, the software *might just* reward you with a reassembled and perfectly detailed three-dimensional rendering of a multi-million-year-old brain, never before seen with human eyes.

This technique has enabled scientists to study the brain shape not just of *Navaornis*, but also of *Archaeopteryx*⁷, the alleged ‘first bird’, dating back 150 million years to the Jurassic, and of *Ichthyornis*⁸, a euornithine seabird from the Late Cretaceous around 85 million years ago. Add to this trio of long-extinct taxa a skull of a modern bird for comparison and we can begin to form a picture of the transformations which may have shaped the evolution of their radically altered brain and sensory abilities.

Don’t be fooled into thinking that bird behaviour is a result of instinct alone. Birds are highly intelligent animals able to learn from their experiences, solve complex problems, integrate into social communities, form emotional bonds, and navigate with an advanced spatial memory. All this, and more, takes place in the forebrain—the cerebrum—and in modern birds it’s enormous, sometimes rivalling its relative proportions in apes and other primates⁹. The cerebrum of birds is so large it dominates the entire upper portion of the braincase. Birds’ primary sense is their eyesight, so their optic lobes, part of the mid-brain region, are also considerably larger. The brain has an olfactory lobe too, which processes scents. It’s often said that birds have a poorly developed sense of smell, which is an unfair reflection on their better-developed visual acuity. They don’t, and in some groups, like kiwi, petrels, storm petrels, and New World vultures, it’s extraordinarily good¹⁰.

Whether as a result of the enlargement of the cerebrum, the optic lobes, or from another, independent, cause, the regions of the brain have also shifted their relative positions in birds. Instead of the linear, end-to-end arrangement of forebrain, midbrain, and hindbrain that we see in *Archaeopteryx* and non-avian theropods, the midbrain and optic lobes of modern birds have been shunted down to a position beneath the cerebrum, so that the cerebrum’s rear edge is instead in direct contact with the hindbrain, the cerebellum. The net result of this is that the overall brain shape has, in many birds, flexed, giving the rear of the skull a more rounded shape and changing the angle of attachment of the spinal column from its posterior position at the back of the skull to a more ventral one¹¹.

This dramatic transformation was assumed to have occurred very recently in bird evolution, possibly even within Neornithes, the crown bird group that exists today, but exactly when, in what order, and how, brain and skull transformations were intertwined, remained a mystery. Enter *Navaornis*. The perfectly preserved skull, 80 million years old, revealed a brain that’s flexed just as it is in modern birds, although the cerebrum is less enlarged¹. Although this might suggest the exciting possibility that the flexed brain had already evolved before the divergence of Enantiornithes

7 Domínguez Alonso, P., Milner, A. C., Ketcham, R. A., et al. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* 430(7000): 666–669.

8 Field, D. J., Hanson, M., Burnham, D., et al. 2018. Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head. *Nature* 557(7703): 96–100.

9 Emery, N. J. 2006. Cognitive ornithology: the evolution of avian intelligence. *Phil. Trans. R. Soc B* 361(1465): 23–43.

10 Corfield, J. R., Price, K., Iwaniuk, A. N., et al. 2015. Diversity in olfactory bulb size in birds reflects allometry, ecology, and phylogeny. *Frontiers in Neuroanatomy* 9(102): 1–14.

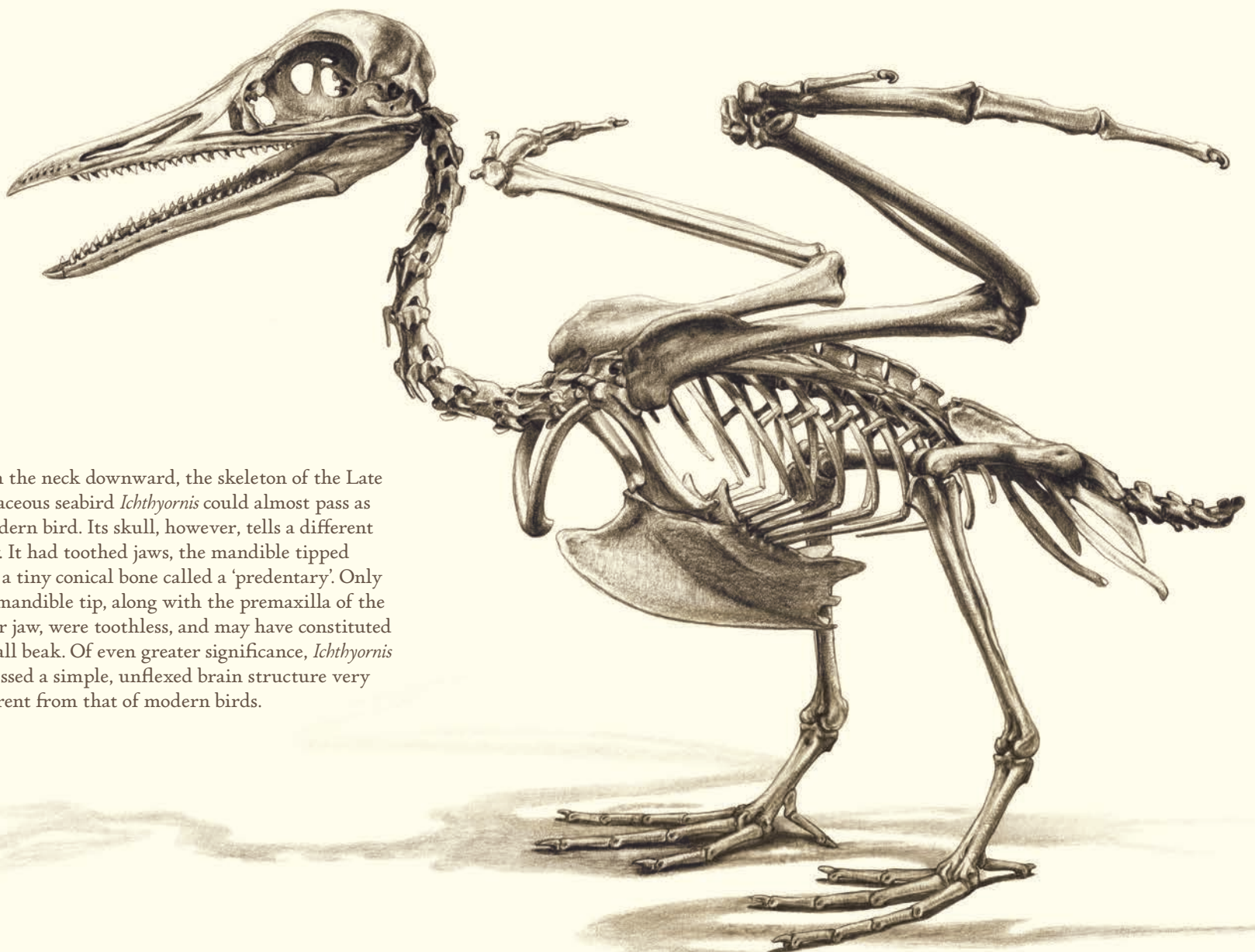
11 Torres, C. R., Norell, M. A., & Clarke, J. A. 2021. Bird neurocranial and body mass evolution across the end-Cretaceous mass extinction: the avian brain shape left other dinosaurs behind. *Sci. Adv.* 7(31): eabg7099.

and Euornithes 130 million years ago, the fourth endocranium in this quartet is yet to make its appearance and potentially blow this theory out of the water. Enter *Ichthyornis*.

Despite having teeth, and hand claws, *Ichthyornis* is far more closely related to modern birds than is *Navaornis*. It's a member of the Euornithes (meaning literally, 'true birds'). All taxa more closely related to modern birds than to Enantiornithes—the 'opposite birds'—are, by definition, Euornithes. So, if the flexed brain and ventral neck attachment are ancestral for both groups, it's logical to expect that *Ichthyornis* would possess these characters too. Cue the drumroll...

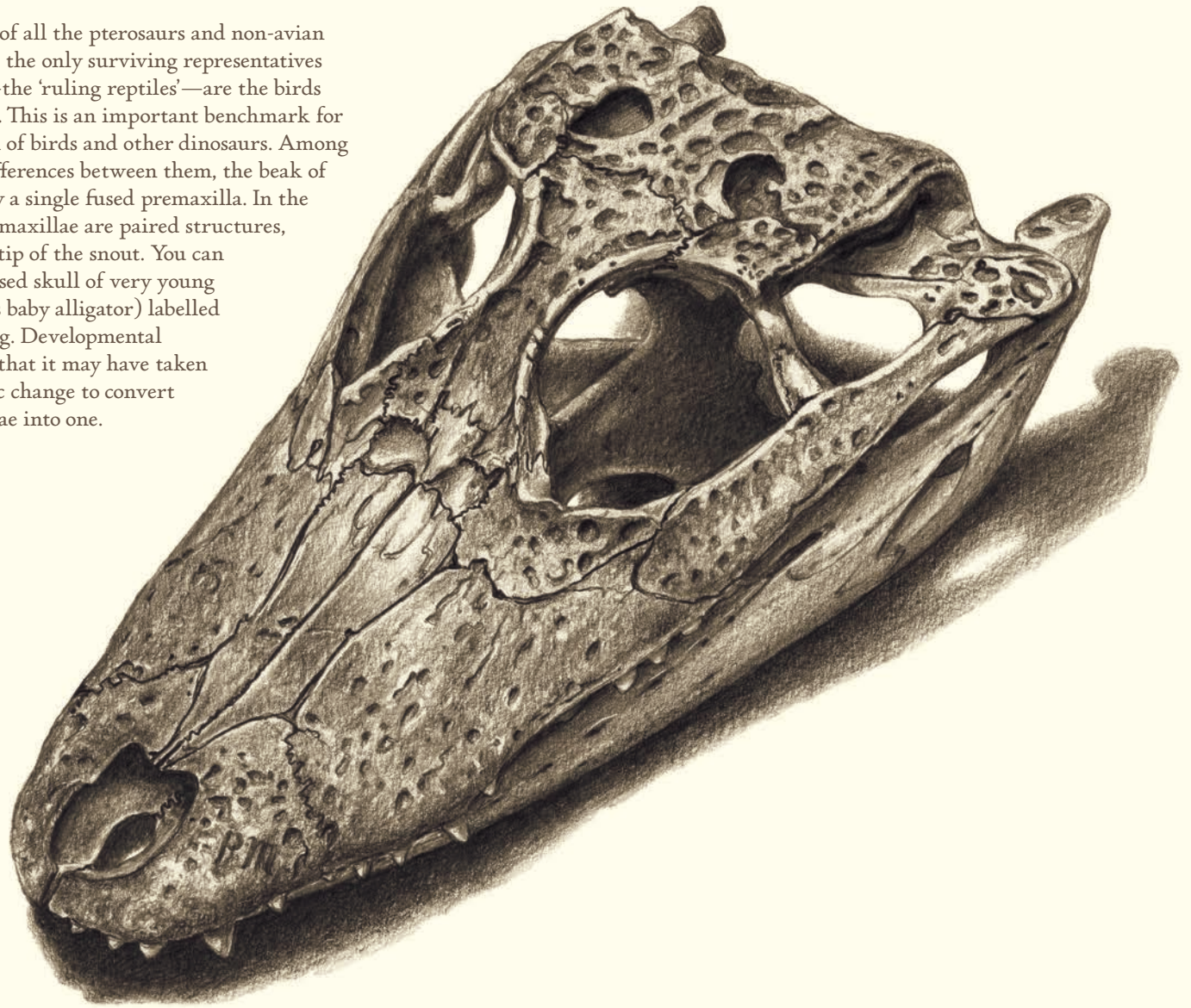
Unfortunately, it doesn't. The endocast specimen of *Ichthyornis*, although slightly damaged on its upper surface, reveals a brain configuration little different from that of *Archaeopteryx*: a midbrain sandwiched between a minimally expanded cerebrum and cerebellum, aligned along a more or less linear plane¹⁰. However, not all brains of modern birds are flexed to the same degree; function plays a part too, and in general, waterbirds that thrust and stab with a long, dagger-like beak have a higher, more posterior neck attachment than terrestrial or arboreal species, making their brain less flexed as a result. *Ichthyornis* too was a seabird, and so the functional requirements of hunting aquatic prey, albeit with toothed jaws, may have caused a reversal from a more flexed brain to a less flexed one, resembling the ancestral condition¹².

¹² Chiappe, L. M., Navalón, G., Martinelli, A. G., et al. 2022. Fossil basicranium clarifies the origin of the avian central nervous system and inner ear. *Proc. R. Soc. B.* 289(1982): 20221398.



From the neck downward, the skeleton of the Late Cretaceous seabird *Ichthyornis* could almost pass as a modern bird. Its skull, however, tells a different story. It had toothed jaws, the mandible tipped with a tiny conical bone called a 'prementary'. Only this mandible tip, along with the premaxilla of the upper jaw, were toothless, and may have constituted a small beak. Of even greater significance, *Ichthyornis* possessed a simple, unflexed brain structure very different from that of modern birds.

With the extinction of all the pterosaurs and non-avian dinosaurs after K-Pg, the only surviving representatives of the Archosauria—the ‘ruling reptiles’—are the birds and the crocodylians. This is an important benchmark for tracing the evolution of birds and other dinosaurs. Among the many obvious differences between them, the beak of birds is dominated by a single fused premaxilla. In the crocodylians, the premaxillae are paired structures, confined to the very tip of the snout. You can see them in the unfused skull of very young individuals (like this baby alligator) labelled ‘p. m.’ on this drawing. Developmental biology has revealed that it may have taken just one small genetic change to convert the paired premaxillae into one.



We still can't say with certainty whether the flexed brain of modern birds evolved once and was subsequently lost, or evolved many times convergently. Perhaps just inches away, where Late Cretaceous rock outcrops close to the surface of the earth, yet more exquisitely preserved fossil birds are patiently awaiting their resurrection, and will show us the answers.

BILLS AND BIRD BILLS

Returning to the bill, the entire tip and top of the rostrum, and much of the sides, too, are dominated in birds by a bone called the premaxilla. You've probably heard of the maxilla (plural = maxillae) which is the main component in the upper jaw of most vertebrates, including ourselves. (The same word is applied, rather misleadingly, to the non-homologous mouthparts of insects.) However, in birds the place of the maxilla is taken by the premaxilla instead, with the maxillae reduced to just insignificant narrow strips of bone in the region of the gape adjoining the jugal bar, and along a proportion of the palate. The avian premaxilla is comparatively enormous and forms the bill tip, much of the top edge of the bill and the anterior circumference of the nostril openings, with the ‘nasal’ bones occupying just the nostrils' rear edge.

The nostrils can be small and almost circular—called ‘holorhinal’—with a broad expanse of flat bone surrounding them, or large triangular open spaces—termed ‘schizorhinal’—separating the nasal bones and the ridge-like culmen of

the bill's upper surface into long slender bars. The difference between these nostril types is related to the location of the zone of flexion as the bill rotates upward. A holorhinal nostril shape usually indicates the presence of a hinge joint along the border between bill base and the frontal portion of the skull, allowing birds like parrots to raise the entire upper portion of their beak like the hinged lid of a beer stein. This is known as 'prokinesis'. Schizorhinal nostrils indicate rhynchokinesis, in which a variable portion of the bill can be raised; an especially useful adaptation for birds that probe and forage in deep mud or sand. Lots of terms have been devised for the various degrees of rhynchokinesis¹³—whether it's confined to just the bill tip or a greater length, whether there's one flexible zone or two, and whether these are long or short—but it's easier, and probably most accurate, to think of these as a seamless gradation between extremes instead of separate mechanisms. The general term for birds' ability to move their upper jaw upward by the combined movement of the interconnecting palate bones, is 'cranial kinesis'.

Another important feature of the premaxilla of birds is that they have only one. In the overwhelming majority of vertebrates, including all the non-avian dinosaurs, the premaxillae are paired structures confined to just the tip of the snout. Even in the 'beaked' turtles the premaxillae are tiny and paired. In the massively armoured skull of crocodiles—the closest living relatives of birds—the premaxillae are fused with the other skull regions in adults and are difficult to make out, but in very young crocodiles you can clearly see them at the end of their snout around the outer margin of the single nasal opening—two small bones separated by a deep suture. When the animal matures, despite the suture being almost completely closed and the two bones knitted tightly together, their developmental origin as two separate structures renders them always a pair.

In contrast, only in the earliest days of embryonic development do the premaxillae of birds take the form of two separate entities. A wave of gene action across the entire developing bill tip 'fills in' the space between them, meaning that the two sides are already solidly fused long before hatching. By blocking the proteins responsible for this secondary developmental stage, researchers have succeeded in creating chicken embryos with a crocodilian-type bifurcated face, suggesting that just a small genetic change may have been sufficient to redirect the course of evolution in the dinosaur ancestors of birds¹⁴.

Nevertheless, birds don't have the sole claim to this innovation. The beaked pterosaurs, too, convergently evolved a single premaxilla which dominates not just the bony rostrum of the bill but often forms massive bony crests which may have supported conspicuously patterned soft tissue structures. In the Early Cretaceous pterosaur *Tapejara wellnhoferi*¹⁵ the toothless premaxilla is seamlessly fused not just with the maxillae, but with the palatine bones of the palate to form a continuous structure without any indication of a joint or suture.

It would be easy to assume that the independent transformation to a single large premaxilla in birds and pterosaurs is a result of bill lengthening—the 'protracted' jaws of Linnaeus's definition—but overall bill length appears to have nothing to do with it. The Early Cretaceous euornithine *Changzuornis*¹⁶, for example, (which may have looked rather like a modern rail) had a rather long rostrum dominated not by its premaxilla but by its maxillae. Likewise, convergently, did the Malagasy enantiornithine *Falcatakyli*¹⁷, whose tiny, paired premaxillae were situated right at the tip of long, deep, toucan-like jaws. The jaws of the euornithine seabird *Ichthyornis*, too, were undisputedly protracted: long, pointed, and virtually indistinguishable from the bill of a modern gull or tern. Again the premaxilla is restricted to just the tip and the central culmen above the large schizorhinal nostril openings, with the sides of the bill being formed by the

¹³ Zusi, R. L. 1984. A functional and evolutionary analysis of rhynchokinesis in birds. *Smithsonian Contrib. Zool.* 395: 1–40.

¹⁴ Bhullar, B.-A. S., Morris, Z. S., Sefton, E. M., et al. 2015. A molecular mechanism for the origin of a key evolutionary innovation, the bird beak and palate, revealed by an integrative approach to major transitions in vertebrate history. *Evol.* 69(7): 1665–1677.

¹⁵ Eck, K., Elgin, R. A., & Frey, E. 2011. On the osteology of *Tapejara wellnhoferi* Kellner 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. *Swiss J. Palaeontology* 130: 277–296.

¹⁶ Huang J., Wang X., Hu Y., et al. 2016 A new ornithurine from the Early Cretaceous of China sheds light on the evolution of early ecological and cranial diversity in birds. *PeerJ* 4: e1765.

¹⁷ O'Connor, P. M., Turner, A. H., Groenke, J. R., et al. 2020. Late Cretaceous bird from Madagascar reveals unique development of beaks. *Nature* 588(7837): 272–276.

maxillae. A further and rather conspicuous difference between *Ichthyornis* and modern birds is the row of sharp conical teeth lining the edges of the maxillae, with a matching set along the dentaries of the mandible.

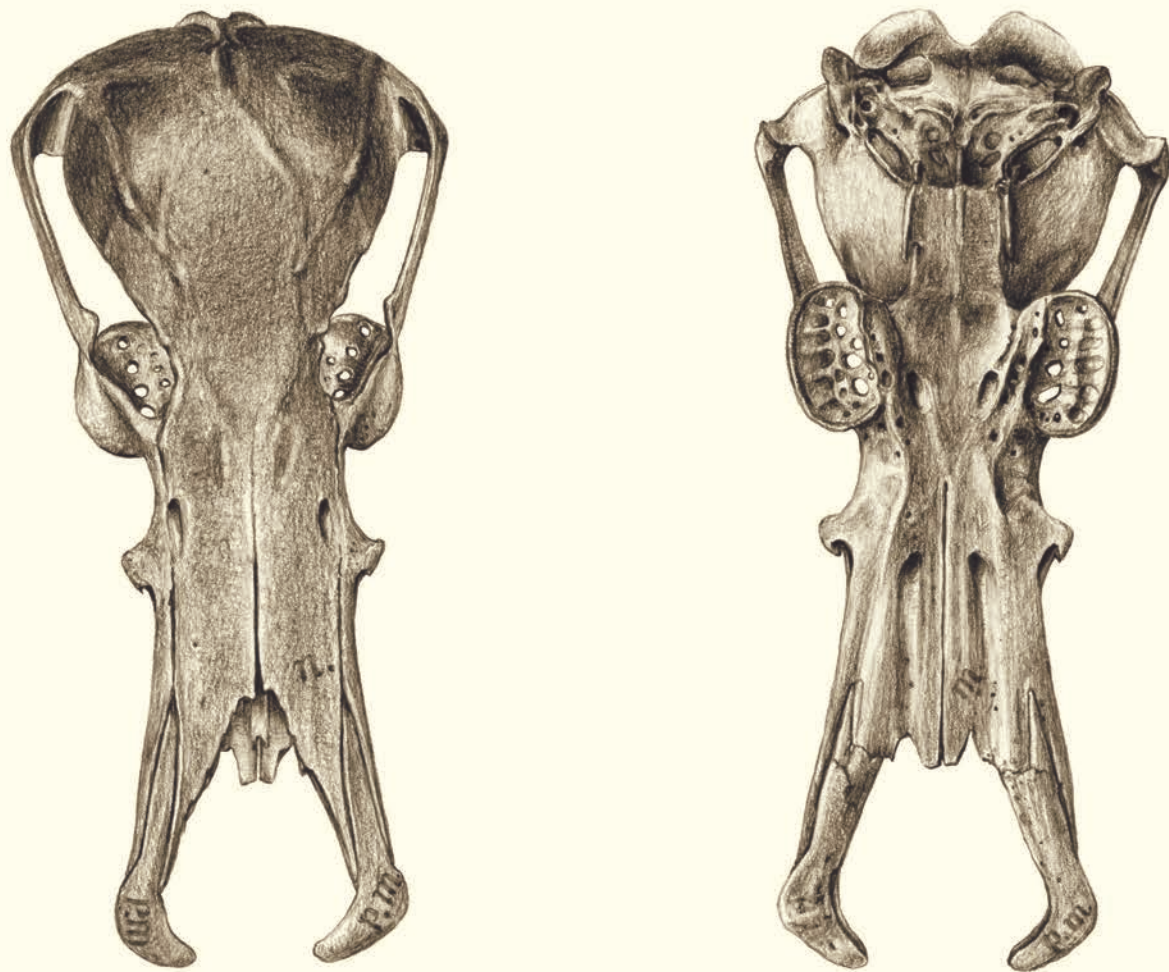
The rhamphotheca is rarely seen in fossils, even from substrates fine enough to preserve the delicate impressions of feathers, so we have no way of knowing what proportion of the jaws may have been covered, or whether the rhamphotheca may have overlain both the toothed and toothless parts of the jaws. In both *Ichthyornis* and *Hesperornis* the teeth are reduced at the tip of the upper jaw, which has led to *Ichthyornis* being described as having only a very small beak⁷, i.e., a presumably very small rhamphotheca covering just the toothless premaxilla. Other fossil taxa, however, including *Falcatakely* mentioned earlier, retained teeth at the tip of their jaws but are toothless farther back toward the face. In their case it's harder to envisage the likely distribution of leathery bill sheath with soft lips and gums.

The keratinous bill of the hadrosaurs, of the clade Ornithopoda—the 'duck-billed' dinosaurs—was formed from paired but exceedingly well-developed premaxillae, often extending to form large crests, with the maxillae along the sides of the upper jaw (along with the dentaries below) supporting a battery of supremely sophisticated cow-like molar teeth. The combination of teeth and bill presumably allowed the ornithopods to diversify the function of their jaws, using the sharp cutting edge of their beak for shearing off vegetation and their teeth for grinding. The Miocene mammal *Obdurodon* also had a combination of molar teeth and a duck-like bill. We have a very good idea of what that looked like because its single living descendant has a skull virtually identical, except that the teeth have been replaced with keratinous grinding pads¹⁸. This is, of course, the monotreme egg-laying Platypus *Ornithorhynchus anatinus*. In both the platypus and *Obdurodon* the premaxillae are elongated and are curved inward at the front edge in a shape like a bottle opener (I'd love a bottle opener made from a cast of a platypus skull!) but they're nevertheless still a pair

¹⁸ Asahara, M., Koizumi, M., Macrini, T. E., et al. 2016. Comparative cranial morphology in living and extinct platypuses: feeding behavior, electrosensation, and loss of teeth. *Sci. Adv.* 2(10): e1601329.



Birds are not alone in their possession of a single, large premaxilla. It's a feature of the beaked pterosaurs, too, and dominates not just the bony rostrum of the bill, but often forms massive bony crests. In the Early Cretaceous pterosaur *Tapejara wellnhoferi* the toothless premaxilla is seamlessly fused not just with the maxillae, but with the palatine bones of the palate to form a continuous structure without any indication of a joint or suture. IMCF 1061. Iwaki Museum of Coal Mining & Fossils, Japan.



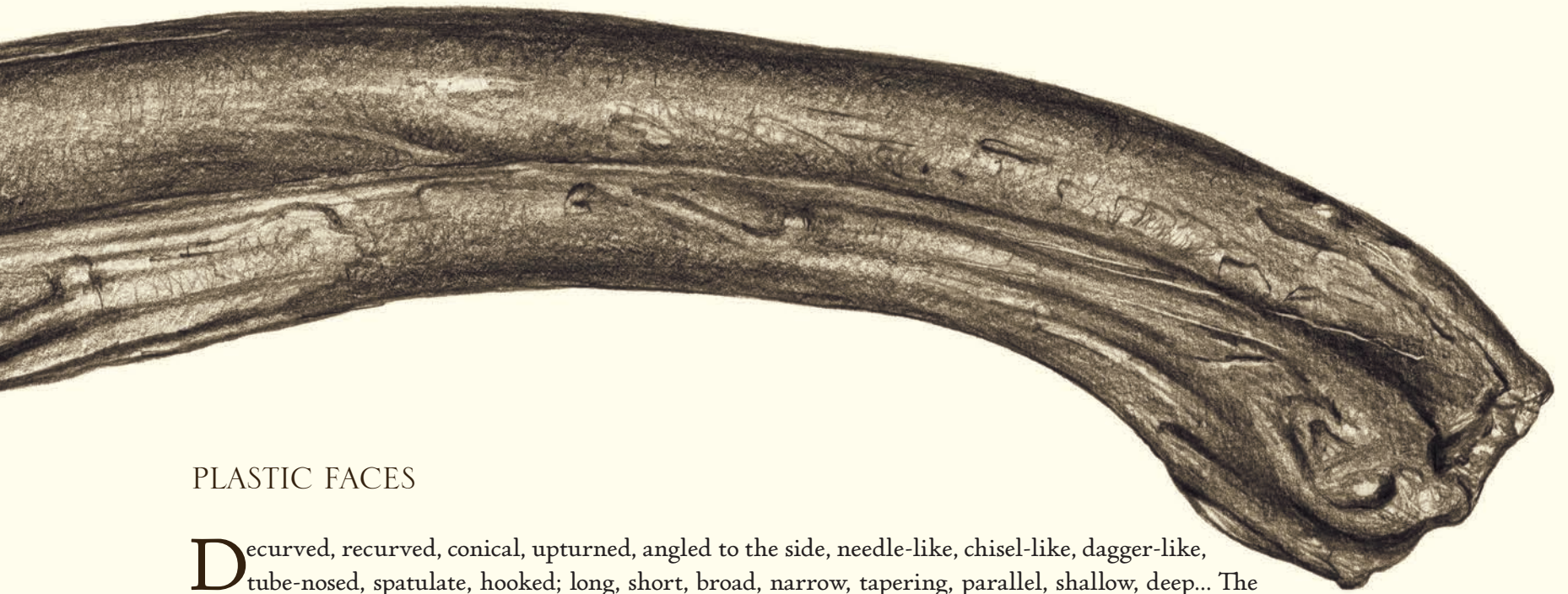
Although it's a feature of both birds and pterosaurs, an enlarged premaxilla isn't a required characteristic for the possession of a beak. In the monotreme egg-laying Platypus *Ornithorhynchus anatinus* the premaxillae are elongated, and are curved inward at the front edge, but they're nevertheless still a pair, and don't replace the other bony elements as they do in birds. You can see them labelled 'p.m.' on this drawing, along with 'n' for the nasals, and 'm' for the maxilla. The perforated oval structures on the underside of the skull hold keratinous grinding pads which have replaced the molars in modern platypuses.

and don't replace the other bony elements as they do in birds. Beaks of various kinds have evolved independently in multiple vertebrate lineages: in platypuses and birds, in hadrosaurs and ceratopsians, pterosaurs and turtles; though their outward similarity is no more than analogous, demonstrating the many different ways of 'doing' a bill. However, this raises the question of exactly what a bill is, and why the bill of birds is so uniquely special.

Although the *Navaornis* skull has a modern, toothless beak and shares a startling number of similarities with modern birds, the 'post-cranial' anatomy (everything except the skull) of Enantiornithes—the 'opposite birds'—was markedly different. In contrast, the body and limbs of *Ichthyornis* and other Mesozoic Euornithes, the 'true birds', were virtually identical with those of their modern relatives. Euornithes and Enantiornithes lived side by side for about 64 million years until the K-Pg mass extinction event obliterated all the Enantiornithes and many of the Euornithes too, including *Ichthyornis*. All the toothed birds were wiped out, never to return.

The keratinous bill of the hadrosaurs, of the clade Ornithopoda—the ‘duck-billed’ dinosaurs—was formed from paired, but exceedingly well-developed, premaxillae, often extended into large crests. The maxillae along the sides of the upper jaw (along with the dentaries below) supported a battery of supremely sophisticated cow-like molar teeth. The combination of teeth and bill probably allowed them to use the sharp cutting edge of their beak for shearing off vegetation, and their teeth for grinding. This is *Parasaurolophus*, at the Witmer Lab, Ohio University.





PLASTIC FACES

Decurved, recurved, conical, upturned, angled to the side, needle-like, chisel-like, dagger-like, tube-nosed, spatulate, hooked; long, short, broad, narrow, tapering, parallel, shallow, deep... The astounding diversity of bill forms and their almost endless potential for novel combinations is, perhaps even more than flight itself, the secret of the birds' success, allowing them to probe, sweep, sift, stab, rip, nip, trawl, crush, grind, spear, hammer, and pick in a plethora of different ways. Where competition for available resources is strongest, the bill reaches its peak of adaptability. Much more than just the requisite tool for this or that foodstuff, the versatile, adaptable, plastic, and rapidly evolving bill is the product of, and the driving force behind, the behavioural diversity of the 11,000 or so bird species alive today—along with the multitudes which came before. 'Niche partitioning' is the name we give to the resulting diversification, allowing similar organisms to share the same geographical range with the minimum of competition through the evolution of subtle differences in foraging style and morphology. The finches in the family Fringillidae are an excellent example. At opposite extremes in the European faction are the massive-billed nut-cracking hawfinch, and the delicately thin-billed goldfinches—eaters of thistle seeds. The bullfinches' stubby bill, too, is deceptively delicate and best suited to eating buds and fruit. Medium-sized seeds suit the medium-sized conical bill of chaffinches, while the overlapping tips of crossbill jaws are highly specialised tools for extracting the seeds of pine cones. There are many more examples of niche partitioning throughout this book, and most are a result of differing bill shapes.

The most iconic example of bill shape evolution is in the Galapagos, or 'Darwin's' finches—not finches at all but tanagers of the family Thraupidae¹⁹ most closely related to the modern grassquits (genus *Asemospiza*)²⁰. Their mutual ancestor somehow dispersed to the geologically young volcanic archipelago, 600 miles off the coast of Ecuador, by being blown off course or by hitching a ride on floating vegetation. In the absence of existing avifauna, the lineage quickly radiated to fill the available niches, attaining a range of morphological and behavioural diversity surpassing even the European finches. They include massive-billed nut-crackers called ground finches that are convergently similar to hawfinches, cactus finches—long-billed nectar-feeders from cactus flowers, fine-billed insectivores, and vampire finches with a penchant for fresh blood. Their rapid diversification famously supports Charles Darwin's theory of evolution by natural selection—but the malleable bill and skull of Galapagos finches had yet more surprises to offer.

Although the Galapagos Islands straddle the equator, giving them consistently uniform weather year-round, the longer-term conditions are periodically disrupted by the El Niño and La Niña climate cycles, resulting in balmy periods of high rainfall alternating with severe drought. The result is a rhythmic tightening and relaxation of natural

¹⁹ Burns, K. J., Hackett, S. J., & Klein, N. K. 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evol.* 56(6): 1240–1252.

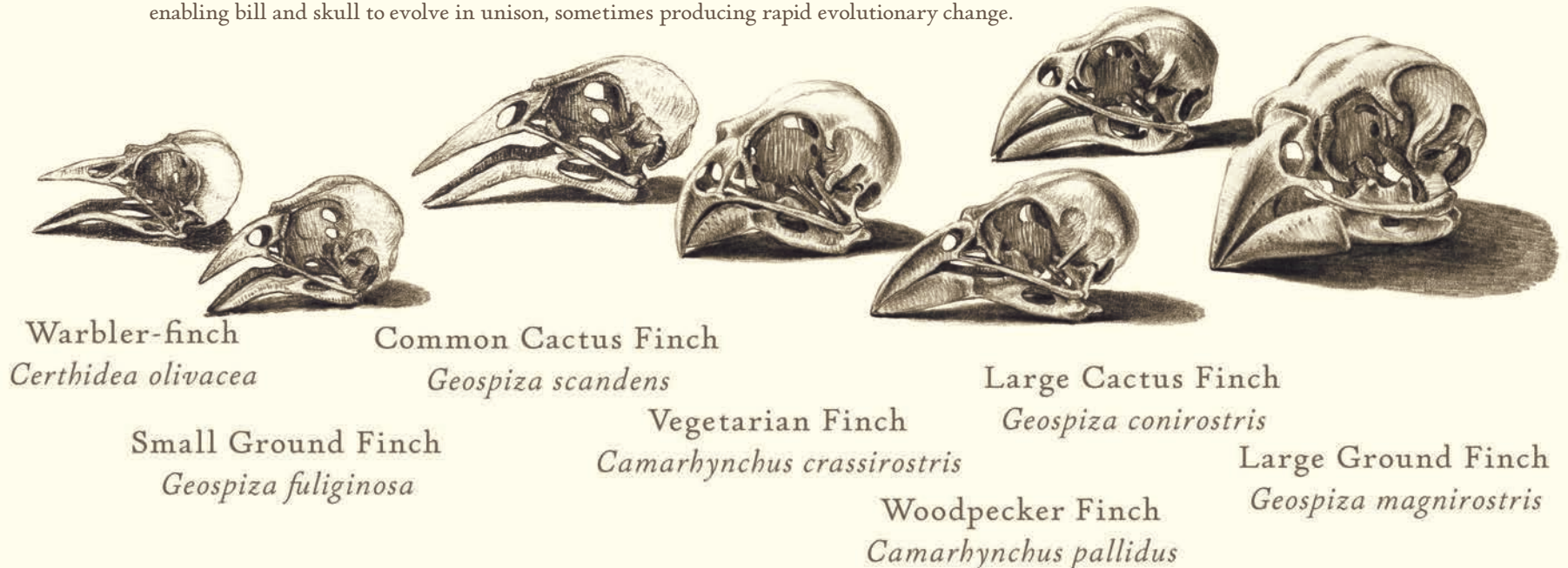
²⁰ Sato, A., O'hUigin, C., Figueroa, F., et al. 2001. Phylogenetic and biogeographic origins of Darwin's finches. *Proc. Nat. Acad. Sci. USA* 98(21): 11352–11357.

selection pressure, reflected in the fluctuating size and shape of subsequent generations of finch beaks—sometimes smaller, sometimes larger, sometimes longer, sometimes shorter.

As competition between individuals decreases during the verdant years when food is abundant, birds with less extreme bill shapes are able to survive and raise offspring. But when conditions change, those individuals able to exploit the more challenging food sources—to crack the hardest nuts and probe the deepest flowers—will have a selective advantage, passing their hereditary traits for these qualities down to the next generation²¹. The bill shapes are steadily evolving, but in a series of peaks and troughs. These fine-tuned fluctuations give us an unsurpassed opportunity to observe natural selection in action, not as a slow process spanning millions of years through an examination of the fossil record, but in real time, from living birds and fresh embryos.

The shapes are controlled by complex molecular activity expressed first on the cartilaginous nasal zone of the face during the early developmental stages, and then, in later development, on the single enlarged premaxilla, which

The textbook example of adaptive radiation is the diversity in bill shape between the Galapagos (Darwin's) finches, diverging to exploit the range of ecological niches available on the newly formed volcanic archipelago. The evolvability of the bill in this group is, nevertheless, closely integrated with the skull, potentially restricting the bill's plasticity but enabling bill and skull to evolve in unison, sometimes producing rapid evolutionary change.



constitutes the major part of the upper jaw, independently regulating the three axes of height, width, and length.²²

Earlier in this chapter I described the mosaic of features—some derived, others ancestral—evolving at different rates in different taxa along the lineage towards modern birds. There was the Early Cretaceous *Confuciusornis*, the first non-neornithine dinosaur known to possess an entirely toothless and very birdlike beak dominated by a single premaxilla. It combined this with a birdlike pygostyle—the fused terminal vertebrae on its very short tail. But the parts in between, including the remainder of its skull, were decidedly dinosaurian; non-avian dinosaurian, that is. Contemporary with *Confuciusornis* was *Sapeornis*, which boasted a similar birdlike tail and also enormous wings, but retained teeth only at the front of its jaws, in the premaxilla. And also *Jeholornis*, with a long reptilian tail and a toothless premaxilla—the

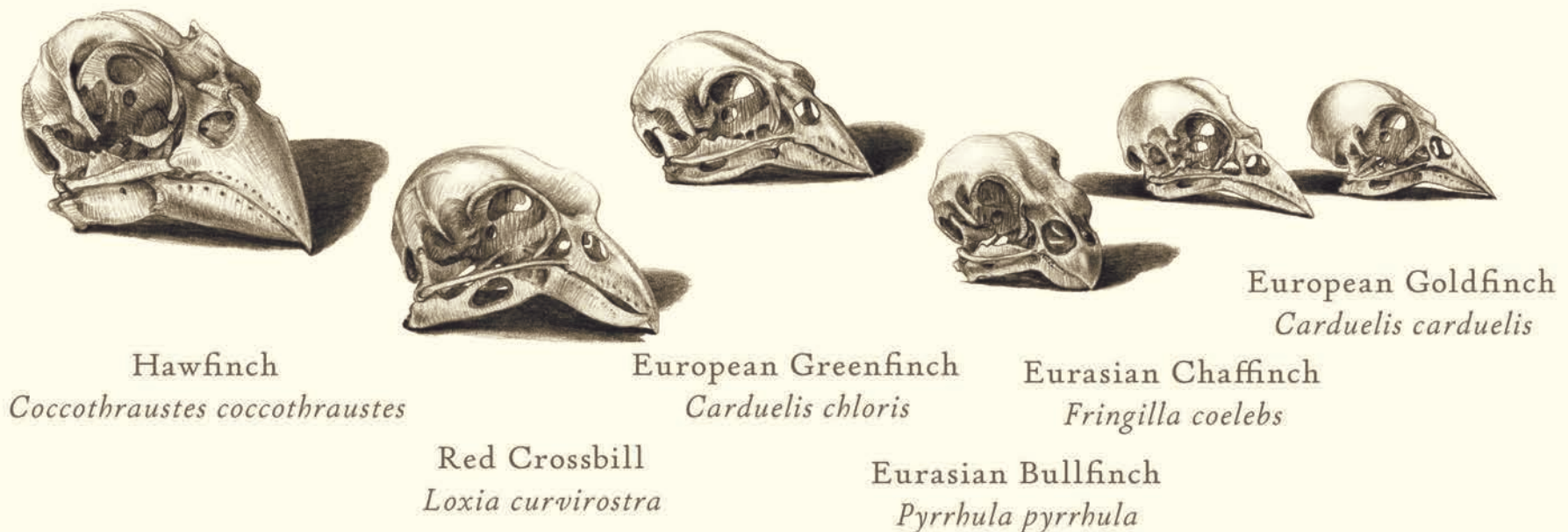
²¹ Grant, B. R. & Grant, P. R. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296(5568): 707–711.

²² R. Mallarino, R., Grant, P. R., Grant, B. R., et al. 2011. Two developmental modules establish 3D beak-shape variation in Darwin's finches. *Proc. Natl. Acad. Sci. USA* 108(10): 4057–4062.

teeth, where present in the upper jaw, were in the maxillae, halfway along the sides. These conflicting patterns suggest that different skeletal regions evolve at different rates. Looking for evidence of this in the bones of modern birds has, however, produced conflicting results. Broad studies encompassing a wide range of avian taxa suggest that the bill and face form a distinct module separate from and more readily ‘evolvable’ than the remainder of the skull²³—rather like Lego pieces that can be changed around without affecting the remaining parts. This was supported by embryonic evidence suggesting a different developmental origin of the cells destined to form the skull from those of the face and bill. However, other studies focusing on smaller groups of closely related species suggest the opposite: that the beak and braincase form a tightly integrated unit, with beak and skull evolving together^{24,25}.

Think of integration like the gears in that car, where engaging one element forces the others to engage with it. These studies were on raptorial birds and parrots which are rather morphologically uniform groups. Far more surprisingly, this was also the conclusion for those icons of beak evolvability the Galapagos finches and, in the same study, also

Adaptive radiation doesn’t only happen on newly formed archipelagos. It also occurs over longer timescales, within the complex and highly competitive environment of much older ecosystems. European finches of the family Fringillidae—unrelated to the Galapagos ‘finches’ (which are actually tanagers, in the family Thraupidae)—provide a strong parallel, with a convergently similar range of bill shapes produced.



the Hawaiian honeycreepers, a less famous but even more extreme textbook example of island adaptive radiation²⁶. The classic expectation would be for the jaws to be able to evolve freely in these groups, unconstrained by any fetters imposed by the rest of the skull. Instead, the opposite is true: in these highly integrated skulls, the plasticity of the bill is severely constricted. But when it does work—when bill and braincase can be shaped together—the change is rapid

23 Felice, R. N. & Goswami, A. (2018) Developmental origins of mosaic evolution in the avian cranium. *Proc. Natl. Acad. Sci. USA* 115(22): 5550–5555.

24 Bright, J. A., Marugán-Lobón, J., Cobb, S. N., et al. 2016. The shapes of bird beaks are highly controlled by nondietary factors. *Proc. Natl. Acad. Sci. USA* 113(19): 5352–5357.

25 Bright, J. A., Marugán-Lobón, J., Cobb, S. N., et al. 2019. The multifactorial nature of beak and skull shape evolution in parrots and cockatoos (Psittaciformes). *BMC Evol. Biol.* 19: 104.

26 Navalón, G., Bright, J. A., Marugán-Lobón, J., et al. 2020. The consequences of craniofacial integration for the adaptive radiations of Darwin’s finches and Hawaiian honeycreepers. *Nature Ecol. & Evol.* 4: 270–278.

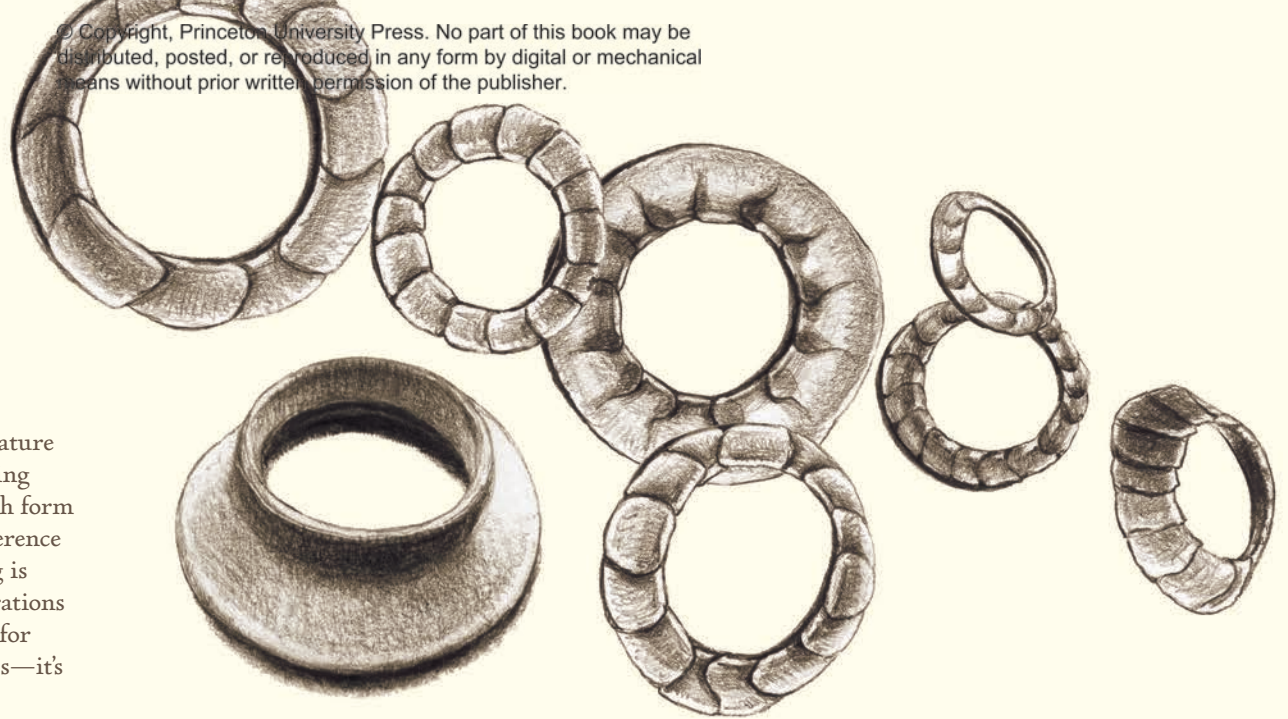
The skull of birds is dominated by their large eye orbits, which house the relatively enormous eyeballs supported by their ring of tiny interlocking bones. You can see the ear openings here too, and, behind them, the hyoid 'horns' of the tongue. Running down the neck are the oesophagus and trachea. The serrations along the bill edges are not teeth, but part of the rhamphotheca—the bill sheath. The bony 'horn' on the forehead of this Chinese goose is however a product of selective breeding under domestication.

and functionally robust: fewer roads, but faster travel; an evolutionary fast lane supremely attuned to adaptive radiation to fill new niches.

Perhaps it was this capacity for integration in the avian skeleton that allowed the Neornithes to radiate so rapidly in the early Paleogene following the K-Pg mass extinction, allowing lineages to take morphological leaps instead of the tentative steps available from modular changes. In the competitive landscape of the early Paleogene, when vacant niches were abundant but the evolutionary race to occupy them was intense, this capacity for rapid, directed change may have given birds a decisive advantage, channelling variation along a few well-defined trajectories leading swiftly to functional extremes—seed-crackers, nectar-feeders, hunters of tiny flying insects, tearers of flesh, and spearers of fish—underpinning the extraordinary early diversification of modern birds. Modularity may have later added the details as a secondary phase, the 'fine brushwork', but for explosive radiation—the big, sweeping application of colour to canvas—integration could, speculatively, have been the key to the birds' success.

WINDOWS BEHIND THE EYES

To a palaeontologist familiar with the cranial bone structure of non-avian dinosaurs, the avian qualities of the skull of *Navaornis hestiae* must appear startlingly modern. To me, only really comfortable with the bones of modern birds, its near-perfect little skull initially appeared totally and reassuringly familiar. But then I began to notice odd-shaped elements I didn't recognise. The jugal, instead of being a straight and slender bar, was chunky and ended in an upward curve. There was a displaced separate bone I didn't recognise—the post-orbital. The quadratojugal, which is closely fused with the tip of the jugal in modern birds, was a separate large three-pointed bone, and the maxilla, too, was large and three-pointed, with a branch to connect with the nasal at the top edge of the nostril¹. The effect was disconcerting, like a momentary glimpse of the wolf in the face of a familiar pet dog.



Bird eyes have retained the reptilian feature of an orbital ring—a circle of interlocking bony plates called scleral ossicles—which form a supporting ridge around the circumference of the cornea. The structure of this ring is highly variable, with different configurations of overlapping plates. In some groups—for example the frogmouths, *Podargiformes*—it's fused into a solid structure.

Seen from the side, the skull of a modern bird can be roughly divided into thirds: at either end are the beak and the braincase, separated by the eye orbits which dominate the entire middle section. I can't overstate how enormous the eyes of birds are compared with those of most other animals, even the non-avian dinosaurs. Birds have irregularly shaped eyeballs divided into two hemispheres: a small cornea—the clear 'window' to the outside world, which lets the light in—and a very large retina onto which the image is projected. The eyes are consequently considerably larger than they appear through the eyelids of the feathered bird. They're situated on either side of the skull, filling virtually its entire width and separated by a wafer-thin bony sheet called the interorbital septum. 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. Perhaps for this reason birds have retained the interlocking ring of bony plates called scleral ossicles, which form a supporting ridge around the circumference of the cornea. These are a feature of many living and extinct reptile groups, and also of bony fishes, but have been lost in some lineages, including crocodiles²⁷.

Compared with a non-avian theropod dinosaur, birds have a very 'open' skull. The orbits (except in parrots) aren't encircled with bone, and only the thin rod, the jugal bar, delineates its lower margin. In fact, the orbits are the only opening into the skull of birds, besides the nostrils of the beak. As I mentioned earlier, the jugal of birds is the equivalent of our cheekbone, properly called the zygoma, or the zygomatic arch, and in all vertebrates except birds it has a rigid attachment to the cranium. Its shape is entirely different in birds, too; just a slender rod forming a pulley between the maxilla of the beak and the quadrate.

Moving to the top of the skull, I've already talked a little about the rounded shape to the back of the braincase, and the rather ventrally positioned attachment of the neck of most birds, including the enantiornithine *Navaornis*. The cranium itself is divided into several sections corresponding with the underlying brain and other internal structures. Above the articulation of the quadrates, at the front of the cavernous ear openings, is the squamosal region. The occipital region surrounds the brainstem where the spinal cord enters the skull through a large opening called the foramen magnum (or occipital foramen); the parietal region covers the midbrain and cerebellum, and the frontal region contains the enlarged frontal lobe—shaped rather like a garlic clove—the forebrain. You don't need to remember all these terms. More significant here are the two bony processes which protrude downwards from the braincase into the space behind the eye (in galliforms these are sometimes connected at their tip). The hindmost, part of the squamosal and close to the articulation of the quadrate, is the zygomatic process. The foremost, just behind the eye orbit, is the appropriately named postorbital process and it's important to the story because, in non-avian dinosaurs, it connected indirectly with the jugal. The bone in between has disappeared altogether in modern birds, but this was called the postorbital, and you'll recall that it was present in *Navaornis hestiae*, though already very small, along with the startlingly unbirdlike jugal which curved up to meet it¹.

²⁷ Franz-Odegaard, T. A. 2020. Skeletons of the eye: an evolutionary and developmental perspective. *Anat. Rec.* 303(1): 100–109.

Bird skulls are ‘open-plan architecture’. Those massive bony bridges connecting the regions of the skull in the non-avian dinosaurs are, in birds, reduced to slender spikes. Instead of the ‘fenestrae’—open windows surrounded by bone—the walls between the windows have come down, leaving wide, open spaces. The remaining bony elements have just enough connections to allow them to slide and pivot, enabling birds to move their upper jaw independently—opening the door to their diversification.

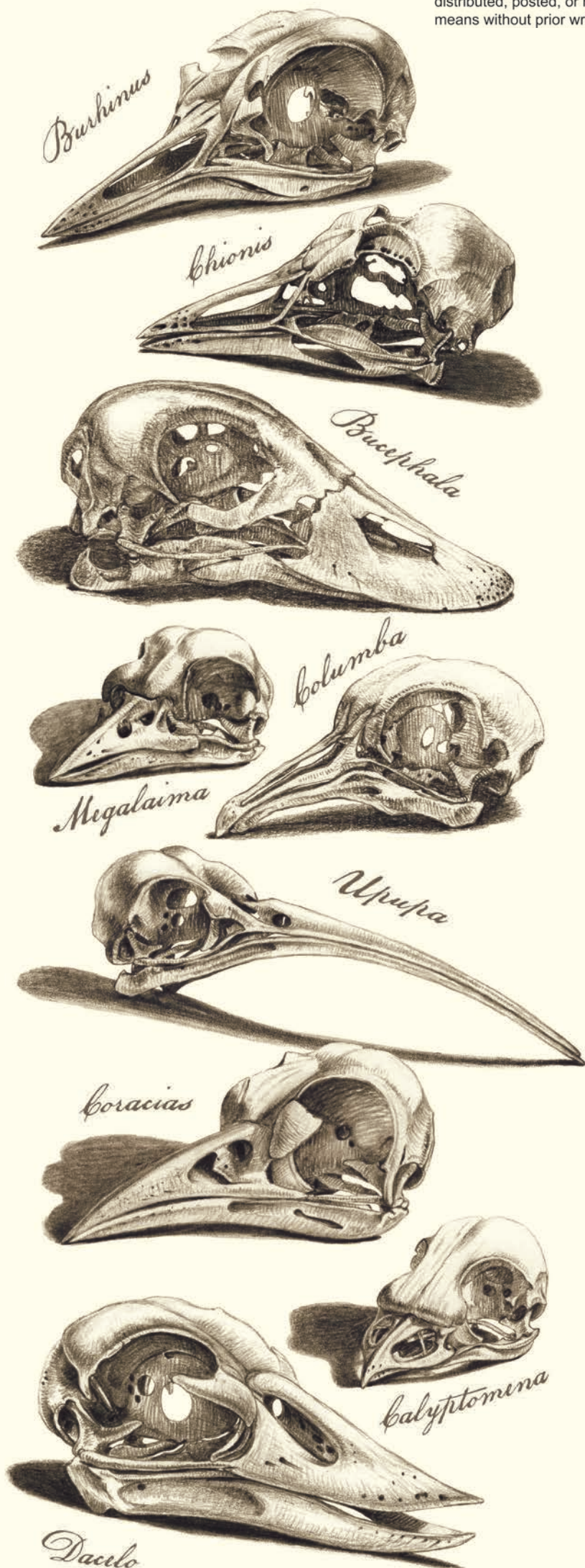
The postorbital was a three-branched bone (yes, there are lots of three-branched bones in the theropod skull). The two vertical branches, as we’ve seen, connected with the jugal and the postorbital process to form a vertical strut separating the orbit from the ‘temporal’ region behind it (think of the ‘temples’ in your own face, just behind your eyes). The third, horizontal, branch formed a bridge with the zygomatic process just mentioned in the squamosal region at the rear of the skull. This bridge bifurcated the temporal space, forming two large ‘windows’ or ‘fenestrae’, one on the dorsal surface of the skull, and the other on the side²⁸.

These aren’t just random open spaces. In life, they were filled with air sacs (you can read all about air sacs in the next chapter) and with the muscles powering the lower jaw. Their number and position are fundamental for the classification of vertebrates, marking the broad divisions between the two major clades: the Synapsida (the mammals and their mammal-like ancestors) and the Sauropsida (the reptiles which, as you’ll recall, includes birds). The synapsids have just one ‘window’ on each side, while the sauropsids have two, as just described. However, while it’s normal for zoologists to talk about the ‘synapsid skull’, you won’t hear anyone mentioning the ‘sauropsid skull’; they’ll be referred to instead as ‘diapsid’. This is because some of the very earliest reptiles from the Late Carboniferous and Early Permian had no ‘windows’ at all and were therefore termed ‘anapsids’. Anapsida gained status as a recognised third group because of another modern reptilian clade, the Testudines—the tortoises, turtles and terrapins, which also lack fenestrae—though it now seems likely that these began as diapsids and subsequently lost both openings early in their evolutionary history²⁹, making ‘Anapsida’ a redundant term. The term ‘diapsid’ has nevertheless continued.

Archosaurs are defined by the possession of an antorbital fenestra, in front of the eye, separated from the orbit by a bone called the lacrimal. This, too, was ancestrally attached to the jugal, and was reduced in the bird lineage to a small shelf of bone partially overhanging the front of the orbit as the supraorbital

²⁸ Wang, M. & Hu, H. 2017. A comparative morphological study of the jugal and quadratojugal in early birds and their dinosaurian relatives. *Anat. Rec.* 300(1): 62–75.

²⁹ Field, D. J., Gauthier, J. A., King, B. L., et al. 2014. Toward consilience in reptile phylogeny: miRNAs support an archosaur, not lepidosaur, affinity for turtles: reptile phylogeny from miRNAs. *Evol. & Develop.* 16(4): 189–196.



process. Confusingly, as the antorbital fenestra has closed up in modern crocodylians, and has opened up entirely in modern birds, neither of the two remaining archosaur groups actually possess this defining archosaur feature!

As dinosaurs, birds are diapsids too, though with the reduction and eventual disappearance of the postorbital bone, and the reduction of the lacrimal, these two large ‘postorbital fenestrae’—the ‘windows behind the eyes’—along with the antorbital fenestra, were obliterated entirely; absorbed like rock pools by a rising tide by the expanding orbit, allowing space for the eyes of birds to reach their enormous size. Most significantly their erasure freed up the jugal to be repurposed as a mobile pushing rod for cranial kinesis. The tiny zygomatic process, and the postorbital process, mentioned earlier, are all that remains to tell the tale.

...AND STRAIGHT ON ‘TIL MORNING

It’s no coincidence that baby dinosaurs begin life with a remarkably birdlike skull: large eyes, a bulbous braincase, delicate jugals and palate, and a short snout. Crocodile hatchlings share these features, in fact all ‘higher’ vertebrates do, and very sweet they look too! However, as they mature, non-avian dinosaurs undergo a major change in their skull structure: their maxillae lengthen to give a long snout, the orbit shrinks, the braincase becomes relatively smaller, and all the bones of the skull become thicker and heavily ossified. So different are they in appearance that several dinosaur ‘species’ are now thought to be juveniles of existing taxa previously known only from their adult form^{30,31}. Adults and juveniles inhabited different ecological niches, functioning as different species within an ecosystem, each with different food and foraging methods, avoiding direct competition through their own intra-species niche partitioning. Compare this with birds and there’s barely any change in skeletal structure at all from juvenile to adult³². An exception is in taxa with a bony casque in adults, like hornbills and cassowaries, in which the casque develops only as the bird matures.

Paedomorphosis is the name we give to the retention of juvenile traits into adulthood; the evolutionary process of growing up without ever fully ‘growing up’—like Peter Pan and the lost boys who wanted to remain forever young and have fun. Admittedly a bird’s life is probably not that much fun most of the time but, like Peter Pan, they can at least fly. The best-known textbook example is the Axolotl *Ambystoma mexicanum*, a salamander that matures sexually without transforming from its larval form. Somewhat closer to home, there’s a strong argument to suggest that humans, with our flat faces, naked skin and large cranium are paedomorphic great apes³³. We’re talking here only about the skull of birds. The developmental stages in this region (or most of it) are switched off or slowed down, early in the developing embryo, while the post-cranial skeleton—the neck and everything beyond it—is allowed to continue at the normal rate. Meanwhile at the front end, premaxilla development is left switched on, and even continues beyond the usual developmental time window for theropods, accounting for its large size and early fusion into a single structure³⁴. This is called peramorphic development, and together these changes to the timing of development are known as heterochrony. We tend to think of evolution as a phenomenally slow process, one tiny step at a time—“*natura non facit saltus!*” as Darwin was fond of stressing: “nature does not make leaps”³⁵. However, studying how evolutionary processes work on embryonic development—‘evolutionary developmental biology’, or ‘evo devo’ for short—shows that large evolutionary changes are often the result of shifts in developmental timing rather than solely the steady accumulation of random

30 Horner, J. R. & Goodwin, M. B. 2009. Extreme cranial ontogeny in the Upper Cretaceous dinosaur *Pachycephalosaurus*. *PLoS ONE* 4(10): e7626.

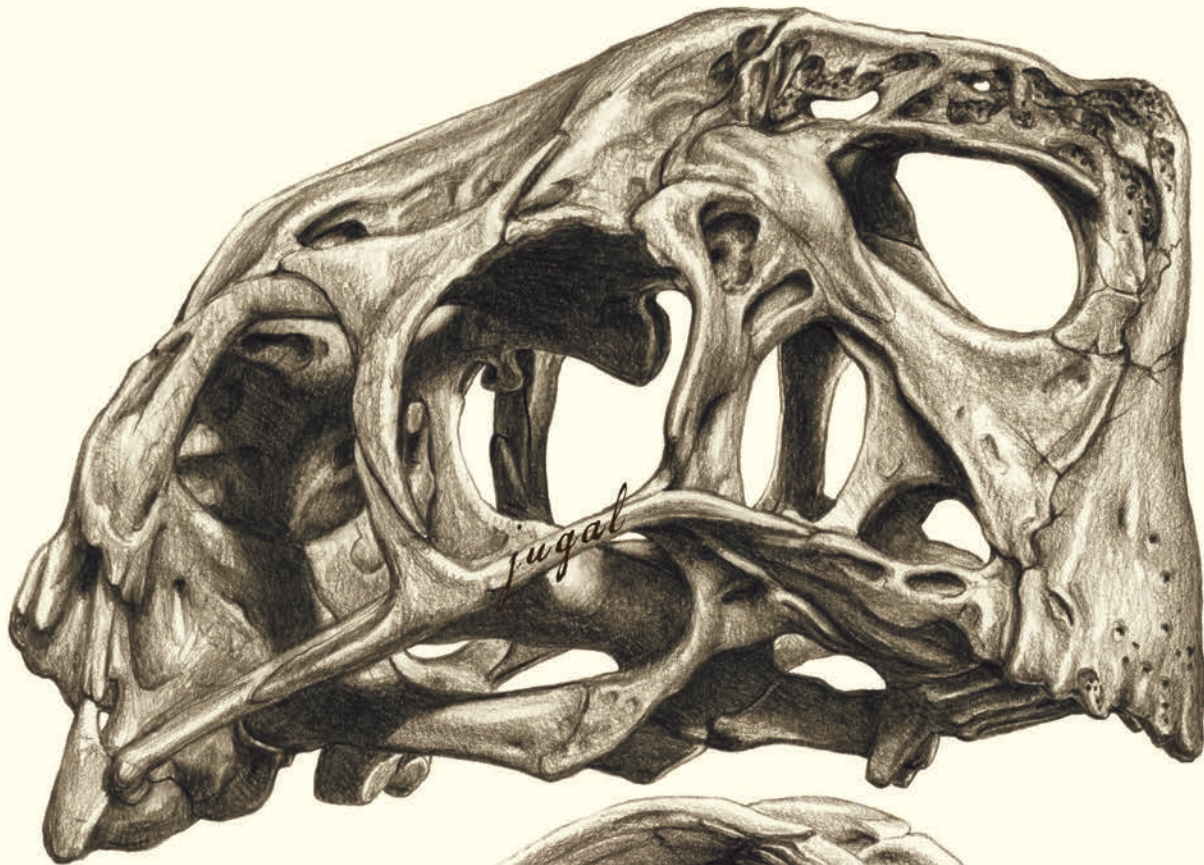
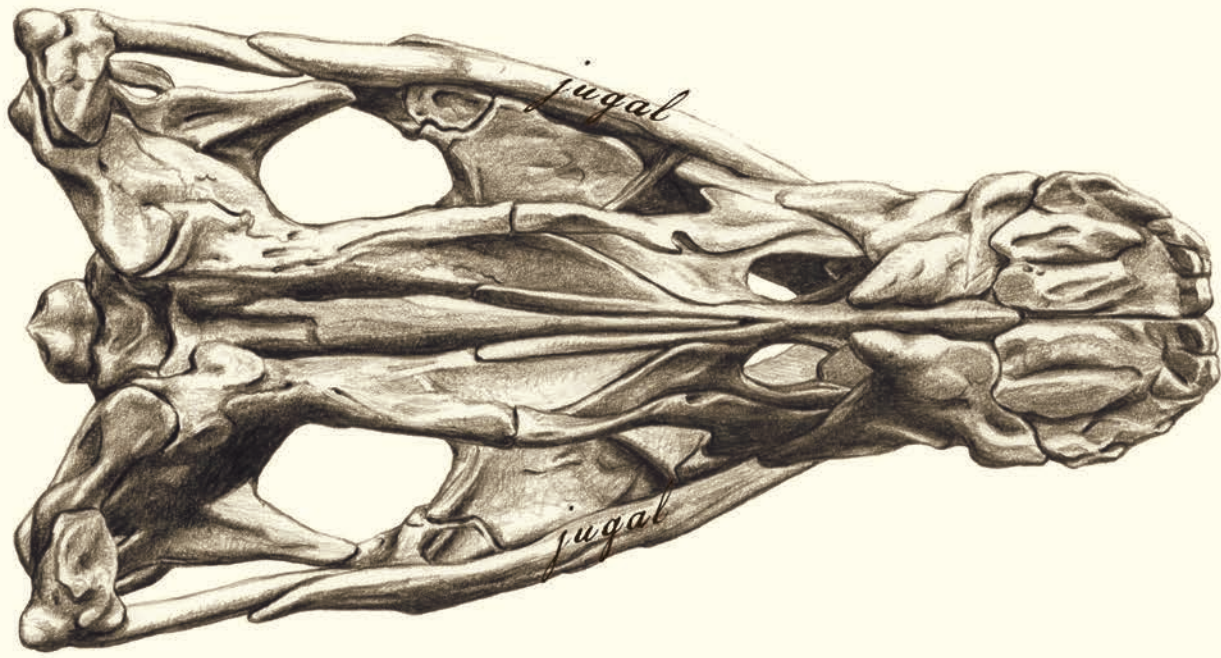
31 Peyer, K. 2006. A reconsideration of *Compsognathus* from the Upper Tithonian of Canjuers, southeastern France. *J. Verteb. Paleontology* 26(4): 879–896.

32 Bhullar, B.-A. S., Marugán-Lobón, J., Racimo, F., et al. 2012. Birds have paedomorphic dinosaur skulls. *Nature* 487(7406): 223–226.

33 Shea, B.T. 1989. Heterochrony in human evolution: the case for neoteny reconsidered. *Phys. Anthropology* 32: 69–101.

34 Plateau, O. & Foth, C. 2020. Birds have peramorphic skulls, too: anatomical network analyses reveal oppositional heterochronies in avian skull evolution. *Commun. Biol.* 3(1): 195.

35 Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. John Murray.





- ↑ All the elements of a bird skull are present in the rigidly immobile cranium of a non-avian theropod—along with much else besides. Most significantly, the horizontal bone marked ‘jugal’ on these drawings is connected by several vertical struts to the top of the skull, preventing any movement. The quadrate region, too, connecting the jugal with the rear of the
- ↙ cranium and forming the articulation surface for the lower jaw, is fixed and rigid. The gradual reduction and separation of these individual bony elements along the lineage toward birds freed the jugal and quadrate, along with the bones of the palate, allowing them to take on a new function as the machinery for cranial kinesis, enabling the avian upper jaw to be moved independently. This is the toothed skull of *Velociraptor* (above) and the beaked skull of *Citipati* (left)—with a more ‘airy’ bone structure and superficially birdlike palate, but still entirely akinetic.

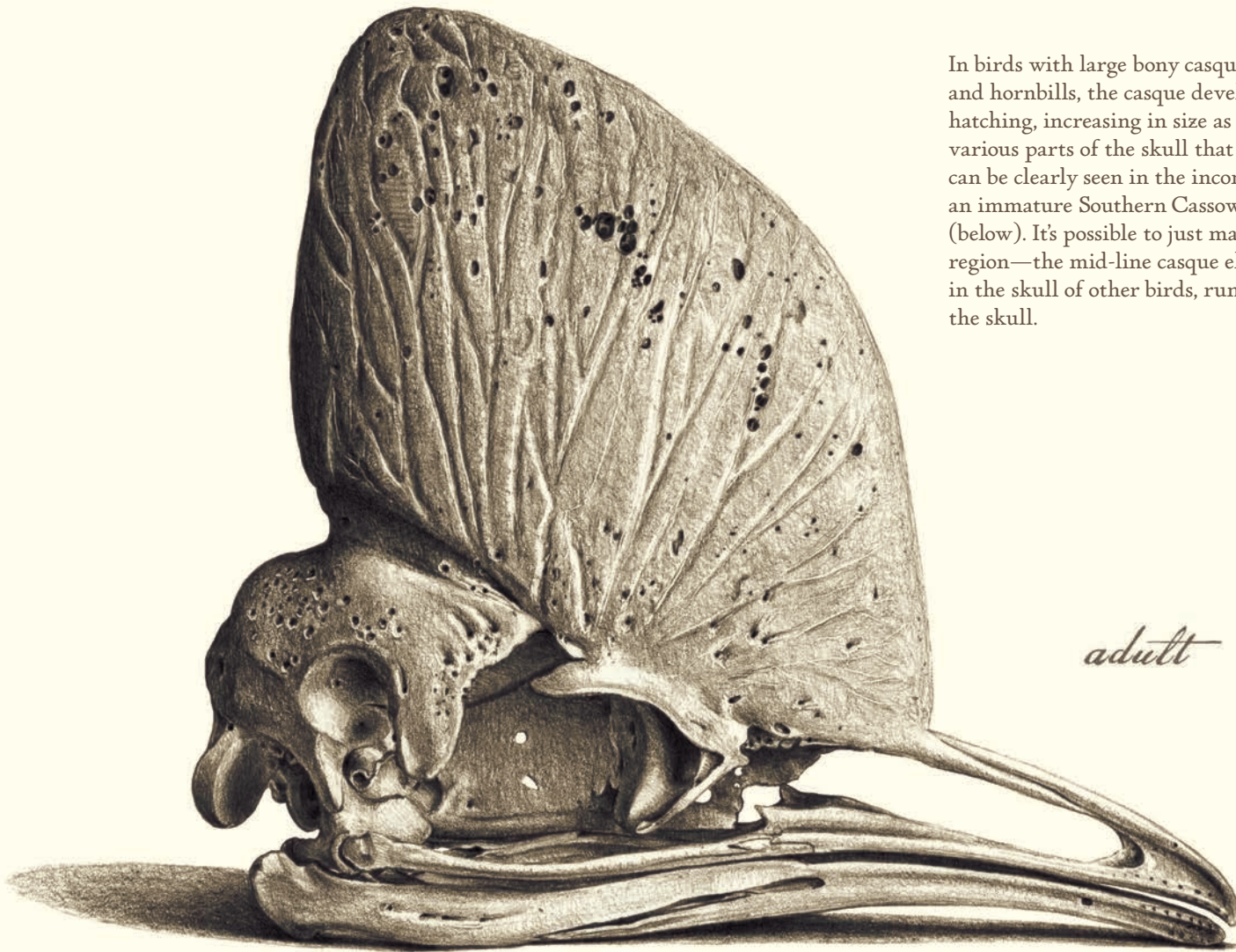
genetic mutations. Heterochrony can (comparatively) rapidly re-route evolution, like shifting a lever on a railway track, modifying existing structures and creating new combinations. Because juvenile features in juvenile non-avian theropod dinosaurs had already been fine-tuned by natural selection, prolonging these to remain throughout the animal’s lifetime was simply cashing in on a winning formula, unchaining the body plan to allow evolution in new directions.

I used the word ‘rapidly’ but of course these changes didn’t happen overnight, and it’s misleading to think of such things in terms of timescales. Viewed phylogenetically they became increasingly prevalent throughout the Avialae, the lineage which includes *Archaeopteryx* and all living birds. They coincided with a trend for reduction in overall body size and, most significantly, with the repurposing of the forelimbs as an aerofoil for flight. Without the dexterity of the digits of the wing, the new avialans relied increasingly on their mouth for foraging and for the maintenance of their plumage. As the digits were reduced so the premaxilla lengthened into a precision instrument endowed with neuroreceptors to refine their sense of touch³⁶. The neck, too, increased in length and flexibility along the Maniraptora, allowing the ancestors of birds an increasing degree of head movement and the ability to oil their plumage with secretions from the ‘uropygial’ or ‘preen’ gland situated above their tail. Their eyes expanded as the postorbital bone and its associated elements withdrew, allowing vision to become the dominant sense in birds, and the larger skull:body size ratio allowed the evolution of a larger and more complex brain able to process the superabundance of sensory information³⁷.

³⁶ O’Connor, J. K., Clark, A. D., Kuo, P. -C., et al. 2025. Avian features of *Archaeopteryx* feeding apparatus reflect elevated demands of flight. *The Innovation* 6: 101086.

³⁷ Bhullar, B.-A. S., Morris, Z. S., Sefton, E. M., et al. 2015. A molecular mechanism for the origin of a key evolutionary innovation, the bird beak and palate, revealed by an integrative approach to major transitions in vertebrate history. *Evolution* 69: 1665–1677.

In birds with large bony casques, like cassowaries and hornbills, the casque develops only after hatching, increasing in size as the bird matures. The various parts of the skull that comprise the casque can be clearly seen in the incompletely fused skull of an immature Southern Cassowary *Casuarius casuarius* (below). It's possible to just make out an additional region—the mid-line casque element—not present in the skull of other birds, running along the top of the skull.



Among the most dramatic changes was the loss of teeth. Birds are utterly toothless, yet many of their ancestors, from *Archaeopteryx* right up to the latest Cretaceous euornithines like *Ichthyornis*, bore rows of sharp, peg-like teeth. Growing teeth takes considerable embryonic time and energy^{38,39} so by dispensing with them altogether, birds could shorten their incubation period. For example, a non-avian dinosaur such as *Protoceratops* (with eggs about the size of a mallard's) needed nearly three months to hatch its eggs, whereas a mallard egg hatches in less than one month. In even larger dinosaurs incubation times stretched to almost half a year; far longer than any modern bird of equivalent egg size^{40,41}. Faster hatching means less time spent as vulnerable eggs exposed to predators or environmental hazards. It also means that successive broods can be raised in a single nesting season and, in the event of a clutch being lost in the latter stages of incubation, the eggs can potentially be replaced. It allows, too, the colonisation of polar regions where summers are short and reproduction can be swiftly followed by moult and migration.

And yet toothlessness may not have started as an adaptation at all. If the avian skull is essentially a frozen juvenile theropod skull, then the absence of teeth may have been nothing more than a developmental side effect of that paedomorphic trajectory. Many reptiles show delayed tooth eruption in hatchlings, or produce only simple, reduced teeth early in life. If birds inherited and amplified this juvenile pattern, then edentulism—the lack of teeth—may simply have arisen as serendipitous collateral damage⁴². Birds didn't lose their teeth in a single stroke; they lost them by degrees, through developmental truncation and later genetic hardwiring. The blueprint for tooth generation is still present in the genome of birds⁴³, though the ability to produce the materials for it, the enamel and dentine, was permanently inactivated in their common ancestor, never to return⁴⁴.

"Second star on the right, and straight on 'til morning." These were Peter Pan's directions to Neverland, the place where you could live your lifespan in perpetual childhood without growing up. And straight on 'til morning, through the terrible extinction crisis and its aftermath and out the other side, to the Eocene—named for Eos, the goddess of the dawn—was exactly where the little dinosaurs emerged, perpetually young, to enjoy the new phase of their global domination as birds.

NEW JAW, OLD JAW

At first sight edentulism looks like an evolutionary compromise. As teeth are such effective tools for cutting, tearing, and processing food, why give them up? One popular idea is that losing teeth lightened the head, which would have made flight more efficient. However, comparisons between toothed jaws and the keratin-sheathed bill of birds show that the actual weight difference is negligible⁴⁵. The real advantages lie in the versatility of a toothless bill, which gives birds a structure that evolution could experiment with quickly and repeatedly, generating the extraordinary variety of feeding adaptations we see today.

38 Louchart, A. & Viriot, L. 2011. From snout to beak: the loss of teeth in birds. *Trends in Ecol. & Evol.* 26(12): 663–673.

39 Yang, T.-R. & Sander, P. M. 2018. The origin of the bird's beak: new evidence from dinosaur incubation periods. *Biol. Lett.* 14: 5.

40 Erickson, G. M., Zelenitsky, D. K., Kay, D. I., et al. 2017. Dinosaur incubation periods directly determined from growth-line counts in embryonic teeth show reptilian-grade development. *Proc. Natl. Acad. Sci. USA* 114(3): 540–545.

41 Deeming, D. C. (ed.) 2002. *Avian Incubation: Behaviour, Environment, and Evolution*. Oxford University Press.

42 Brocklehurst, N. & Field, D. J. 2021. Macroevolutionary dynamics of dentition in Mesozoic birds reveal no long-term selection towards tooth loss. *iScience* 24(11): 103301.

43 Harris, M. P., Hasso, S. M., Ferguson, M. W. J., et al. 2006. The development of archosaurian first-generation teeth in a chicken mutant. *Curr. Biol.* 16: 371–377.

44 Meredith, R. W., Zhang, G., Gilbert, M. T. P., et al. 2014. Evidence for a single loss of mineralized teeth in the common avian ancestor. *Science* 346: 1254390.

45 Zhou, Y.-C., Sullivan, C., & Zhang, F.-C. 2019. Negligible effect of tooth reduction on body mass in Mesozoic birds. *Vertebrata Palasiatica* 57(1): 38–50.

The keratinous rhamphotheca is lumped with the claw sheaths and other appendages as ‘soft tissues’, even though it can be exceedingly hard! Nevertheless, it’s not made of bone and seldom fossilises. For this reason it’s easy to underestimate its importance: a mistake, because the horny or leathery bill sheath multiplies the bill’s existing versatility into a massive toolkit of additional forms—a cutting notch, serrations for holding fish or detaching fruit, a sophisticated filter for micro-organisms, a grinding surface, an enclosed tube to surround and protect the nostril openings, even a laterally flattened blade to slice through water like a ploughshare, snapping shut the moment contact is made. It grows continuously, like our own keratinous fingernails do, wearing down throughout life to subtly adapt the external bill shape to whatever local conditions prevail.

These ‘extras’ combine with perfectly smooth bill edges on the underlying bony skull, rather like adding a specialist drill bit to a universal chuck. Every barbed- or serrated-billed bird you can think of—mergansers, barbets, toucans, geese, and so on—all have perfectly smooth edges to their bony beak. Only two bird groups, both of them extinct, have ever possessed bill edges that are not smooth. One was the ‘moa-nalo’ (their name means ‘lost fowl’)—flightless goose-like ducks of the Holocene of Hawaii. The other was the pelagornithids, the predominant seabirds of the Cenozoic world for over 57 million years and without a doubt the most iconic—and enigmatic—of all bird groups. Even after nearly two centuries of study their affinities remain elusive. As well as being remarkable for the immense size and wingspan of some taxa, their bony bill was unique in having its edges formed into tooth-like projections of different lengths. No vestige of a rhamphotheca so far exists in the fossil record so we have no way of knowing with certainty the appearance of this beak in life, or what it might have been used for.

Despite the thickness of the rhamphotheca the bill of birds is nevertheless a highly sensitive tactile organ. The little holes you can see in the underlying bone, especially around the tip and along the bill edges, are the neurovascular canals, and they’re particularly numerous in groups which rely on tactile foraging for out-of-sight invertebrate prey. They’re especially advanced in kiwi, which are nocturnal foragers convergently similar to insectivorous mammals⁴⁶. Kiwi nostrils are situated at the very tip of the bill, but more than simply smelling prey, this sensitive organ is able to detect subtle vibrations in the soil. They listen for movement, too, and have exceptionally acute hearing. Even the bristles (modified feathers) surrounding their bill are tactile, so it’s no loss to a kiwi that their eyes are mere pinheads (metaphorically speaking) and that their vision is reduced to just a few feet.

In their sensory bill tip and foraging technique, kiwi are also very similar to long-billed shorebirds, particularly those which probe in the soft mud and leaf detritus of woodlands and inland marshes: the snipes and woodcocks.

Shorebirds, however, belong to the Neognathae, a major division in birds based on the structure of their palate. It means ‘new jaw’, while kiwi belong to the Palaeognathae, with their ‘old jaw’. Of over 11,000 bird species in the world today (the number is always approximate and fluid depending on the lumping or splitting of geographical races) only sixty, at the very bottom of the avian phylogenetic tree, are palaeognaths, meaning that they represent a minuscule 0.54% of all crown group birds. But what an iconic assemblage of birds they are! In a later chapter I’ll describe in detail the flightless ratites—living and extinct—and the reluctantly volant tinamous, and the astounding story of their dispersal across the globe. Here, however, I need to introduce not the birds but their allegedly ‘old’ jaw.

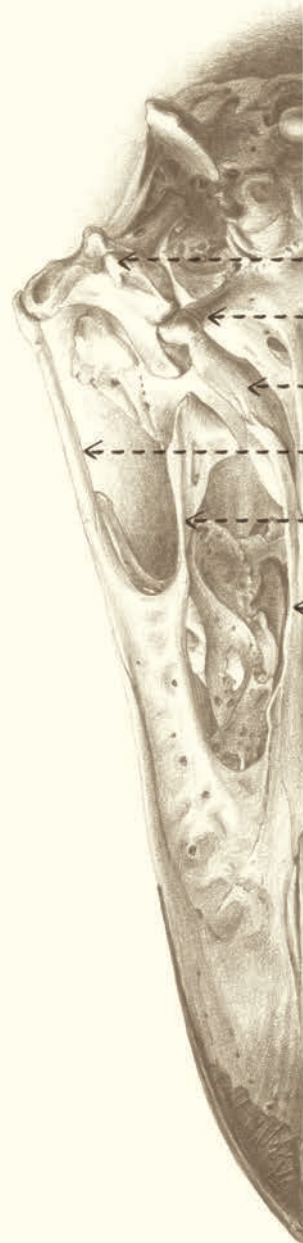
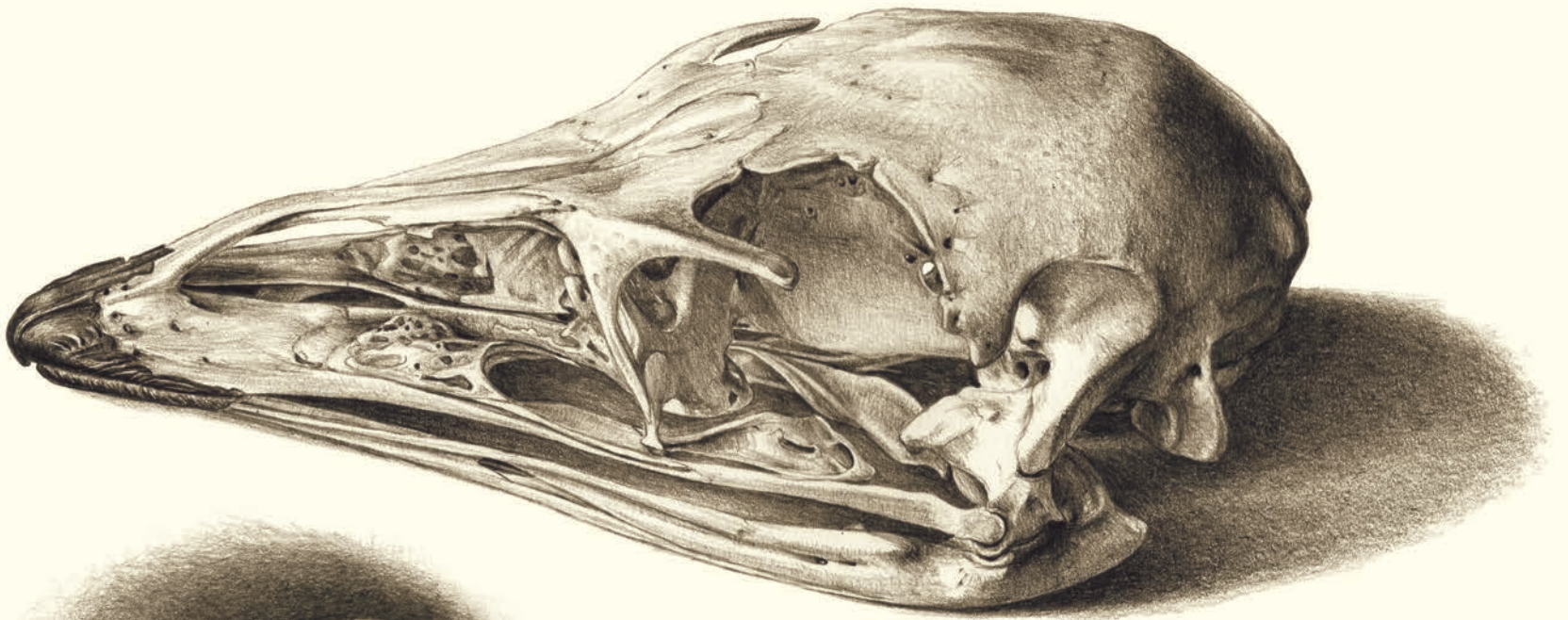
I’ve set the scene by describing the gradual transformation of the rigidly immobile skull into moveable machinery. How the quadrates became independent and the finger-like projections of the jugal and postorbital bone relinquished their hold and separated. How the quadratojugal, too, broke its attachment with the skull and merged seamlessly with the jugal tip, like the end of a cotton bud, and how the lacrimal receded, severing the last of the jugal’s bonds and enabling it to be reinvented in piston-form, from a mobile articulation with the quadrate.

⁴⁶ Cunningham, S. J., Corfield, J. R., Alley, M. R., et al. 2007. A new prey-detection mechanism for kiwi (*Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. *J. Anatomy* 211(4): 493–502.



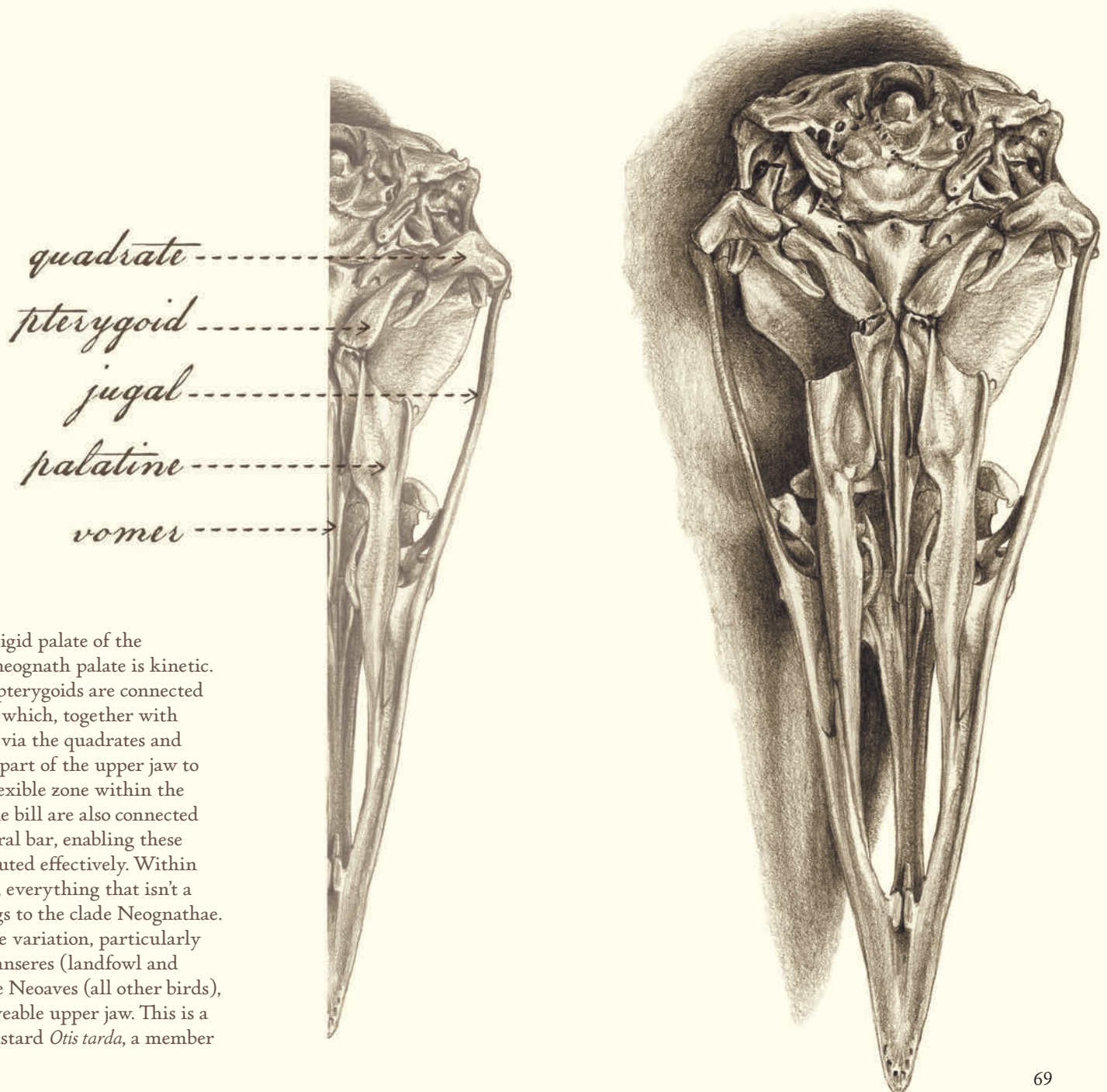
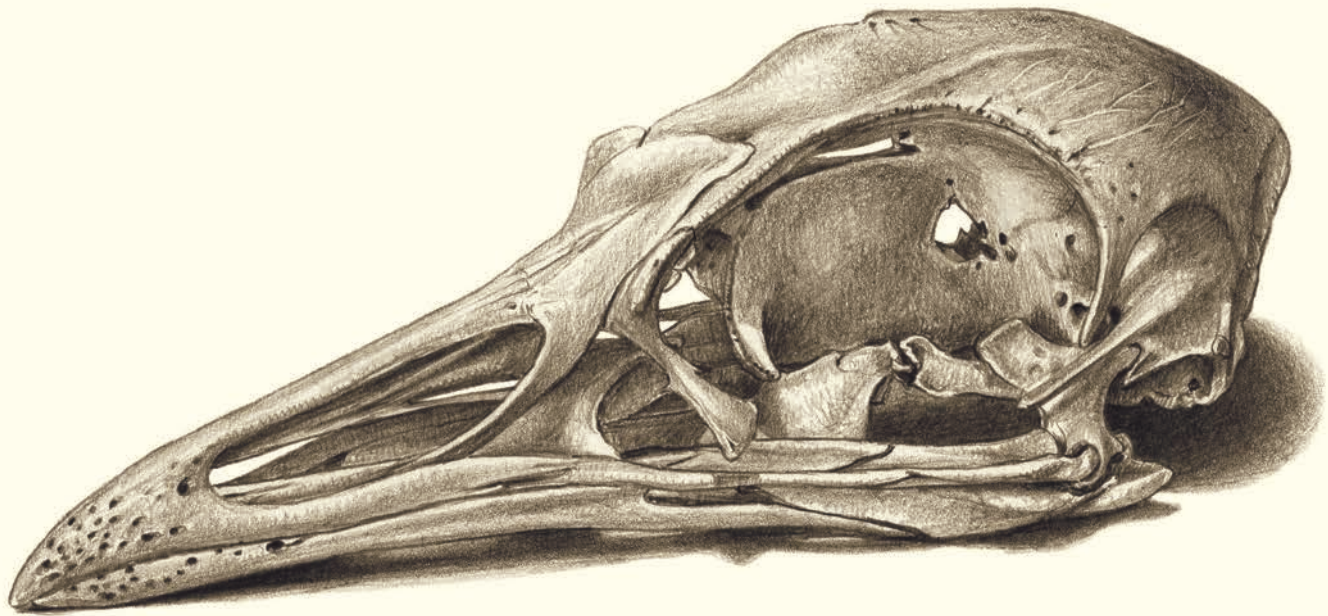
The two sides of the lower jaw are known as 'rami' (singular = ramus) and they meet at the bill tip to form an area called the gonys. Between the rami, forming the floor of the mouth, the skin is soft, flexible, and very elastic. This is called the gular region, or gular sac, and it's used by many birds, for catching, carrying, or storing food. In general, the smaller the gonys, the larger the gular sac. Nowhere is this more notable than in the pelicans. Pelicans use their gular sac as a trawling net, and have flexible zones along the rami that can be bowed outward at the sides to maximise the catch, in a manner convergent with rorqual whales.





quadrate
basipterygoid process
pterygoid
jugal
palatine
vomer

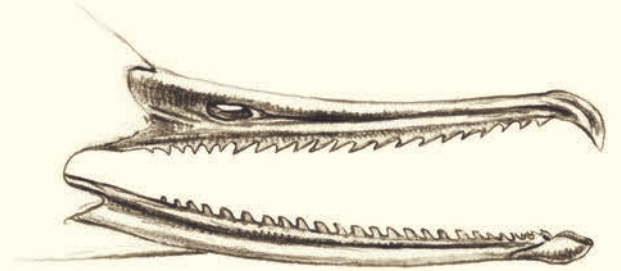
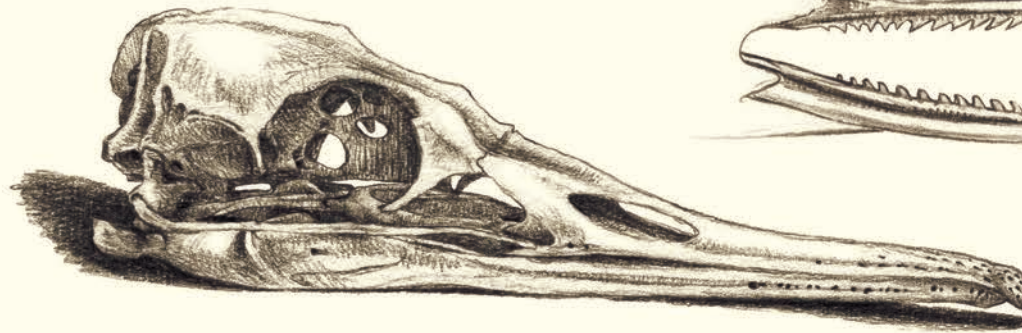
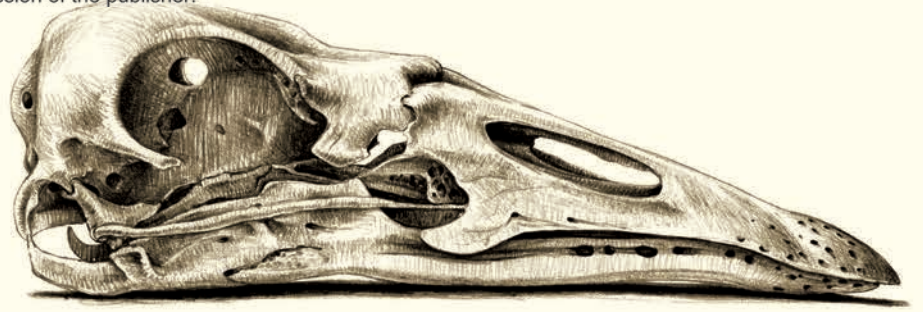
'Palaeognath' means 'ancient jaw', reflecting a configuration of the palate that was traditionally assumed to be primitive (compared with the 'new jaw' of the neognaths). All have a relatively rigid palate with the palatines and pterygoids fused and braced against the skull floor by enlarged and elongated bony struts called basipterygoid processes. The jaw sides and top are widely separated, connecting only at the bill tip. Although it's likely that this isn't the ancestral jaw type for all birds, the Palaeognathae—comprising the flightless ratites and the volant tinamous—nevertheless occupies the lowermost branch at the very foot of the phylogenetic tree of crown group birds. This is the skull of an Emu *Dromaius novaehollandiae*.



In contrast to the rigid palate of the palaeognaths, the neognath palate is kinetic. The palatines and pterygoids are connected by moveable joints which, together with forces transmitted via the quadrates and jugals, allow all or part of the upper jaw to lift at a hinge or flexible zone within the bill. The sides of the bill are also connected to the top by a lateral bar, enabling these forces to be distributed effectively. Within crown group birds, everything that isn't a palaeognath belongs to the clade Neognathae. There's considerable variation, particularly between the Galloanseres (landfowl and waterfowl) and the Neoaves (all other birds), but all share a moveable upper jaw. This is a skull of a Great Bustard *Otis tarda*, a member of Neoaves.

Swan Goose

Anser cygnoides



Red-breasted Merganser
Mergus serrator

Small-billed Moa-nalo

Ptaiochen pau

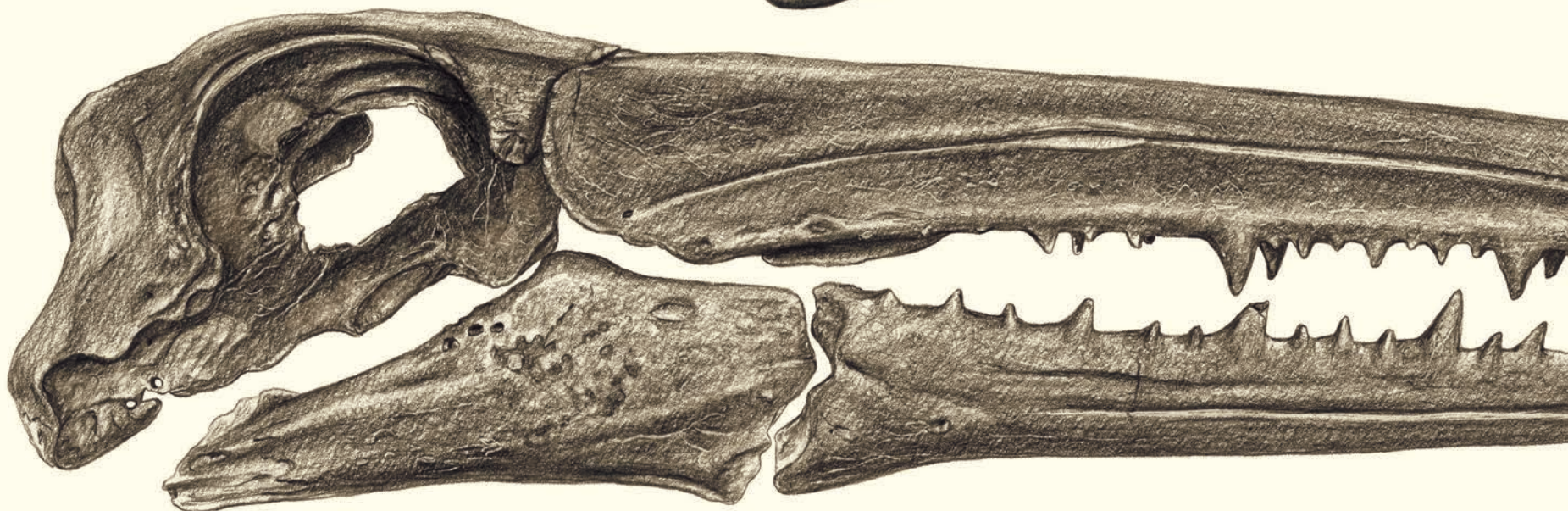
USNM 384776

Smithsonian, USA



An undescribed bony-toothed seabird
(pelagornithid). MUSM 1622.

Museo de Historia Natural de San Marcos, Peru.



(continued...)

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