Don't call it a seagull!

by

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ABSTRACT

Many people assume there's only one kind of "seagull." On the contrary, the world is home to dozens of gull species spanning an array of shapes, sizes, plumage patterns, behaviors, and lifestyles (and some of those gulls aren't affiliated with the sea at all). The pattern of similarities and differences between species poses an interesting taxonomic challenge: Can we interpret that pattern to reconstruct evolutionary history and determine where each species fits on the gull family tree? Up through the twentieth century, our efforts to retrace evolution relied on comparisons of superficial traits—but as we discovered along the way, such traits can be misleading. In the past couple of decades we have developed a much more reliable window into the evolutionary past: rather than comparing outward characteristics, we have begun comparing genes. Modern taxonomy has taught us much about the gulls and helped us better understand the planet-wide ecological network that we all belong to.

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The gulls at Jodrey Pier

Introduction:

Identity crisis

In New England, winter is for gull-watching. I stood on Jodrey State Fish Pier in the fog and drizzle of a late Friday morning in January, inside a roiling cloud of gray and white birds. A stocky fisherman in orange foul-weather gear had just thrown a bucketful of old bait into the water in front of me. Pungent scent wafted up, mixing with the salt air. The gulls perched on pilings, paddled on the water, and whirled in arcs over the floating debris. They were calling stridently, scuffling over fish chunks, releasing streams of white droplets as they jockeyed for position on the wing.

I was in Gloucester, Massachusetts, but the scene could have been from any waterfront on the New England coast. To the casual observer, it probably looked like just another bunch of seagulls—hundreds of indistinguishable birds.

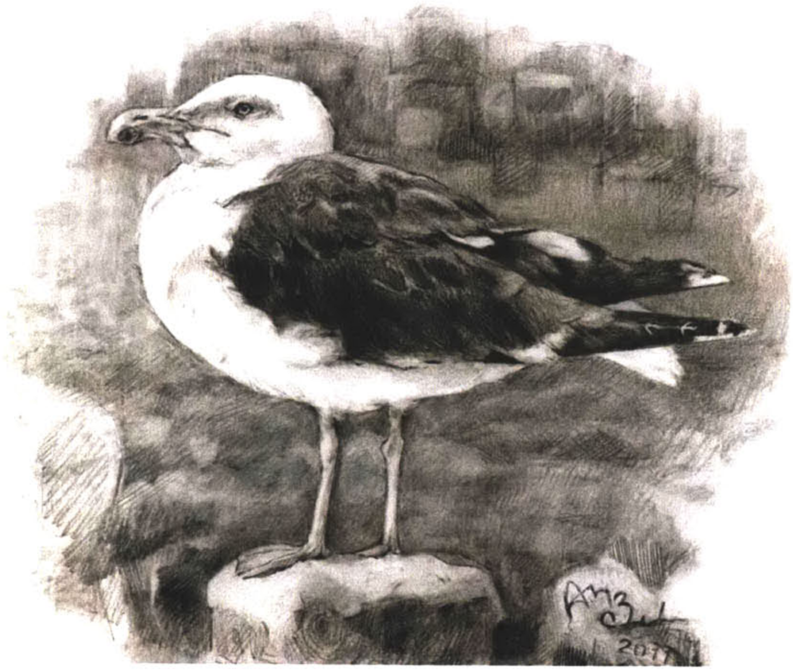
I scrutinized the swirling flock. Yes, it *was* full of Herring Gulls, the kind of bird that looks like everyone's idea of a seagull. There were gray-and-white adults, sporting pale pink legs and a yellow bill tipped with a red dot. Mixed in here and there were brown-mottled young Herring Gulls at varying stages of development. But I knew there must be more to the flock than that, and I kept looking.

The black wings were the first thing to jump out: a Great Black-backed Gull gulping down a piece of fish, bigger than the gulls around it, looking like a bully on the playground. As I scanned the crowd, I realized that some of the brownish immature gulls were just a little larger, paler, and more checkered-looking than the rest. They were young Black-backeds rather than young Herring Gulls.

Next I saw what looked like a Herring Gull in miniature: a Ring-billed Gull, well-known haunter of fast food parking lots and garbage dumps. Size can be hard to judge on a flying bird, but the Ring-billed was set apart just by the contrast of its darting, buoyant flight against the steadier wingbeats of the bigger gulls. As for the black ring on its bill, or its yellow feet, well, I knew better than to try and pick those out from a distance.

Herring Gulls, Great Black-backed Gulls, and Ring-billed Gulls are all common here year-round. But winter is special, because it's when other gull species migrate down from the Arctic. Birders love it. Their summer warblers, vireos, and thrushes are long gone, so any bird that comes *to* New England (to escape an even fiercer winter) is extra exciting. It doesn't hurt that gulls are especially fun to watch. They're smart, pushy, and acrobatic. They're at home on land, in the water, and in the air. And they can be unexpectedly beautiful. Their pristine breeding plumage typically gets a little speckled in the wintertime, but their flight is among the most graceful and athletic of all birds at any time of year.

It took a few minutes, but I finally spotted some of our visitors from the Arctic. A couple of Iceland Gulls were circling on the outskirts of the flock, shyer, paler, and more delicate than Herring Gulls. And there, standing on a submerged plank across the way, was a young



Great Black-backed Gull

Slaty-backed Gull

Glaucous Gull, as big as a Great Black-backed but very pale all over. That brings the flock up to five species.

Just a bunch of seagulls? I should say not.

Next to me on the pier, another birder was surveying the flock with a far more discerning eye than my own. Jeremiah Trimble, a lanky, sandy-haired gull fanatic in his early thirties, has been a birder ever since he was a kid growing up on Cape Cod. For the past ten years he has also been the Curatorial Associate of the Ornithology Department at the Harvard Museum of Comparative Zoology. Every weekend in the winter, Trimble embarks on the fifty-minute drive from Cambridge to Gloucester to make the rounds at all of the best gull-watching spots—Jodrey Pier, Niles Pond, Eastern Point, the Elks Lodge.

Trimble especially hopes for vagrant birds that have been blown far off course while migrating. That's another reason for watching gulls in the winter: the tantalizing possibility of seeing a real rarity. Just last week, he got photographs of a Slaty-backed Gull, a bird normally found between Japan and Alaska. The same individual, or one that looks identical in photos, was originally spotted a few days before that at a dump in Maine—the very first record of a Slaty-backed Gull in the state. (It wasn't a first for Massachusetts, but it was still the talk of the Massbirds listserve for days.)

The average bystander would notice nothing exceptional about a Slaty-backed Gull. To me, it might have passed for a Great Black-backed Gull or even an extra-dark Herring Gull. But for someone like Trimble, its subtly different plumage—the sooty smudge around its eye, the white "string-of-pearls" spots on its black wingtips as it stretched its wings—stood out like a neon sign. Even though the gull was surrounded by other birds, he picked it out immediately as a third-year Slaty-backed.

That's right: Trimble not only knows what the adults of the different species look like, both in breeding season and in winter, but he knows the different plumages for first-year birds, second-year birds, and third-year birds. He can identify transition plumages while birds are molting. He can even tell when two gull species seem to have hybridized and produced offspring with roughly intermediate characteristics.

Birders like Trimble are hooked on identification. Some of them see it as an intellectual challenge, a puzzle to be solved like the Sunday crossword. Some particularly enjoy the thrill of the chase, the camaraderie of like-minded people, the excuse to be outside. But on a fundamental level, birders are simply acting on an impulse that's familiar to everyone: we all want to know who's who. We want names and groups to hold onto, so we can begin to have relationships with our fellow inhabitants of earth.

My botany professor in college once confided to me how deeply she loves recognizing plants everywhere she goes. "It's like seeing friends!" she said. When you recognize the identity of another living being, you become more connected to it and the world you both live in. I think that's why, underneath everything else, humans are so drawn to identification. That's why we go through the world persistently asking *who are you?*

There are different ways of answering that question. For some people, it's enough to be able to tell a bird from a fish. For birders, it's often about pinpointing identity as finely as possible, down to species or even subspecies. And for the science-minded, there's a whole other layer to the question: *What makes you who you are?*

Part 1:

The surface

Maybe you're familiar with the evolutionary story of Darwin's finches, a group of small birds in the Galápagos. Each finch species eats a specific type of food. One species hunts insects, for instance, while another eats big seeds off the ground. To go along with their special diets, the finches have evolved differently-shaped beaks: a small, sharp beak for catching bugs; a set of heavy-duty pliers for cracking seeds. As a result, those finch species are easy to tell apart.

Gulls, on the other hand, tend to be jacks-of-all-trades. They procure all kinds of food in all kinds of ways, whether it's hunting for bugs or fish or eggs, or scavenging, or stealing your sandwich. When it comes to athletic abilities, they're triple threats: they can swim and walk as well as fly. They live and nest in an array of different habitats, often by the coast. Since most of them spend their lives doing more or less the same things in similar places, gulls tend to conform to a stereotype—large bodies, white and gray feathers, stout bills, webbed feet, long wings, saucy attitudes. It's hard to blame people for just calling them all seagulls.

But if you look more closely at the fifty-plus gull species scattered across the far reaches of the earth, you find many that break the mold. To start with, some gulls aren't affiliated with the sea at all. The Gray Gull nests in the Atacama Desert of Chile. The Andean Gull lives high in the Andes, four or five thousand meters above sea level. Franklin's Gull of the North American prairies may spend its whole life in the interior of the continent, where lakes and rivers are the closest thing it has to an ocean. And terrestrial gulls aren't the only ones that stand out. The Sooty Gull is so dark it's almost black. The Little Gull is the size of a dove. The Ivory Gull is pure white and endowed with extra-developed claws for clinging to ice in the Arctic. The Dolphin Gull from the tip of South America has a fire-engine-red beak, and during the breeding season its diet consists largely of sea lion turds. No wonder birders cringe when they hear the word "seagull." Lumping together so much diversity into one inaccurately named category is an affront to the principles of identification.

One of the world's most extraordinary gull species breeds in the Galápagos. The Swallow-tailed Gull is the only fully nocturnal member of the gull family. It fishes for squid in the dark, and during the day stands guard at its rocky cliffside nest, emitting a bone-chilling scream at anyone who approaches. It's a lovely, dainty bird with a forked tail, a black head, and unusually bulbous eyes. Unlike other gulls which breed annually, it nests once every nine months—staggered, so that there are always Swallow-tailed Gulls on the Galápagos Islands,

Dolphin Gulls

Swallow-tailed Gull

no matter the time of year. It comes to land only while nesting and spends the rest of its life on the open ocean, a characteristic it shares with only two other gull species, the Black-legged and Red-legged Kittiwakes. Biologists are still researching these phenomena, trying to figure out the reasons for the Swallow-tailed Gull's lifestyle.

Such remarkable traits—the nocturnal behavior of the Swallow-tailed Gull, the claws of the Ivory Gull, the desert nests of the Gray Gull—are all the more intriguing in contrast to the overarching similarities within this family of generalists. Those patterns of similarities and differences hint at a complex story that began millions of years ago, a story of ecological interactions and evolution over time, a story that lies at the core of the birds' identities.

That story tells of one prehistoric bird, the ancestor of all gulls, whose lineage split into two, and then split again and again. It tells how the landscapes of the Arctic and the Galápagos molded the Ivory Gull and the Swallow-tailed Gull into the unique birds we see today. It tells why the gulls at Jodrey Pier look so similar, and what makes them different.

For centuries, taxonomists have been grouping different species into genera, genera into families, and so on up to the broadest divisions of life. To come up with those groupings, they consider each species as a product of history, of ancestral genes being shaped by ancestral conditions. They dig for the true identity of the gulls; they delve into the evolutionary past.

Yet reconstructing history is no simple matter. Fossils are an obvious place to start, but gulls, like other birds, have left a pathetic fossil legacy. Their bones are hollow and too easily destroyed. Although parts of gull skeletons have been unearthed in different spots across the world, making sense of them is like trying to put together a thousand-piece puzzle after you've lost, say, 998 pieces.

In the absence of a reliable fossil record, evolutionary reconstruction has traditionally been based on which species look alike. It's human nature to analyze similarities and differences, trying to categorize and figure out relationships. If you've ever been to someone else's family reunion, you know the impulse. While hovering around the hors d'oeuvres table, you scan the room, instinctively grouping siblings who have the same nose or the same hair color. Similarly, if two gull species share the same kind of beak or plumage pattern or body type or mating behavior, it might be because they inherited it from a common ancestor.

Or it might not. Bill shape, plumage color, and other characteristics depend not only on ancestry but also on the influence of the environment over evolutionary time. Every individual gull in history contended with certain conditions—hot or cold, dry or wet, dangerous or relatively safe. Gulls that weren't able to cope or compete died, failing to pass on their genes to the next generation. Gulls whose chicks grew up, and had their own chicks, passed on the characteristics that helped them survive.

On the New England coast, those favorable traits were different than in the Galápagos or the Arctic. As closely-related gulls spread out over space and the world changed over time, their traits evolved on separate tracks. At the same time, when distantly-related gulls experienced similar conditions, their traits sometimes converged.

Translating resemblances into an evolutionary story is tricky business. And yet until very recently, superficial resemblance is really all taxonomists had to go on.

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For most of human history, taxonomic efforts to classify the natural world amounted to little more than a free-for-all. One of the first nudges toward order came in the late seventeenth century, when an English naturalist named John Ray cast a critical taxonomic eye on a wide variety of organisms. In his *Synopsis Methodica Avium et Piscium*—a treatise on the taxonomy of birds and fish, published posthumously in 1713—he recognized 18 species of "gulls." Some of these were actual gulls, while others were species of terns and jaegers, which we now recognize as cousins of gulls. Others were simply large, white, ocean-faring birds called gannets, which bear a superficial resemblance to gulls but are not closely related. Ray further partitioned the gull-like birds into two groups based on similarities in their toes (for some reason, feet seemed to be one of his favorite criteria for determining the identity of an animal).

John Ray (1627-1705)

The next big step toward order came a few decades later, when the Swedish taxonomist Carl von Linné—better known by his Latin *nom de plume* "Linnaeus"—set up a now-ubiquitous system of nested groups (Kingdom, Phylum, Class, Order , Family, Genus, Species) into which he attempted to file every living thing on earth. In the 1750s, as part of his magnum opus *Systema Naturae*, Linnaeus grouped the gulls into a single genus that he called *Larus*. He declared that this genus had six species in it, and he added five more in 1766.

Like Ray, Linnaeus didn't get everything right. One of his "gulls" turned out not to be a gull at all, but what we now call a Parasitic Jaeger—a beefier, more predatory version of a gull. And needless to say, he overlooked most of the world's 50-odd gull species. But shortcomings aside, Linnaeus's efforts created order where there once was chaos, laying the foundation of modern taxonomy.

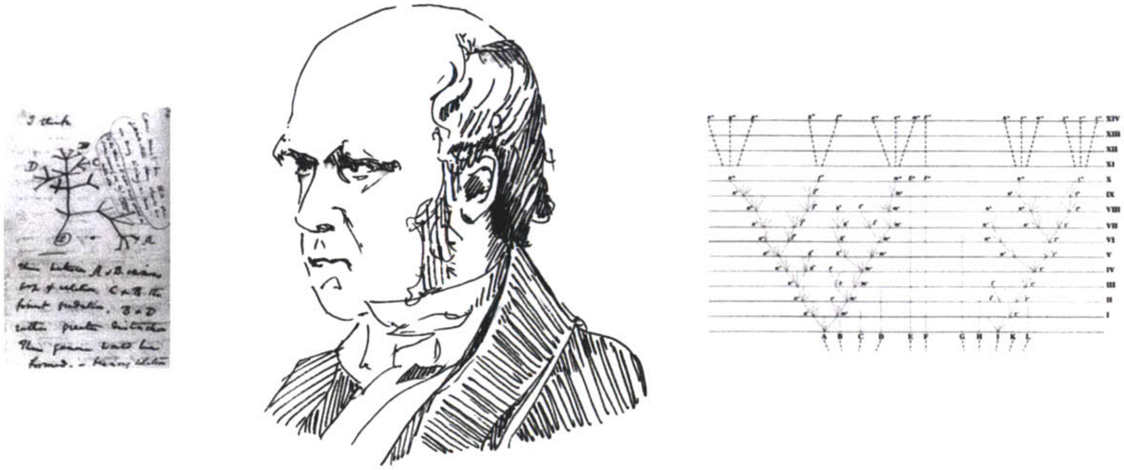
As he did for all other organisms, Linnaeus gave every gull two Latin names: for example, he bestowed the name *Larus marinus* upon our friend the Great Black-backed Gull, which is found on both sides of the Atlantic. *Larus* was the genus name, and *marinus* designated the bird as a particular species within that genus. Nowadays, a species is usually considered to be a group of individuals that can interbreed, and a genus loosely refers to a group of species with a recent common ancestor, but in the eighteenth century those definitions had not yet come into being. Linnaeus's groupings reflected his observations of the present rather than any speculations about the past.

Carl von Linné. a.k.a.
Linnaeus (1707-1778)

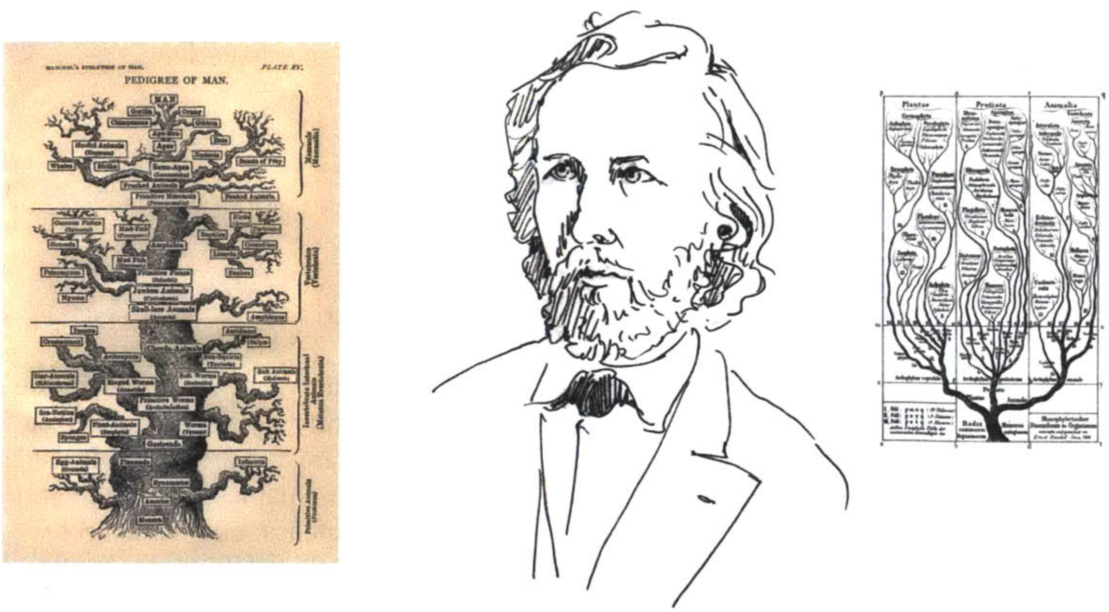
It wasn't until Darwin published *On the Origin of Species* in 1859 that people really started thinking about resemblances between species as *family* resemblances. In his treatise on evolution, Darwin used an image of a "Tree of Life" to illustrate an abstract example of the relationships between species. He drew branching lines to trace the supposed path of evolution, starting with an ancestor at the base of the tree and ending with each of the modern species at the tips of the twigs.

A contemporaneous German taxonomist named Ernst Heinrich Philipp August Haeckel grabbed this image and ran with it, developing a genealogical tree for all living things. The coiner of many well-known scientific terms, including *ecology* and *phylum*, Haeckel also came up with the word *phylogeny* to refer to the evolutionary history of organisms. The genealogical diagrams that so entranced Haeckel later became known as phylogenetic trees, or simply phylogenies.

For the first time, the identities of living species were being treated as a culmination of past events. And for the first time, each interesting body part or behavior was being evaluated as a clue for reconstructing history.



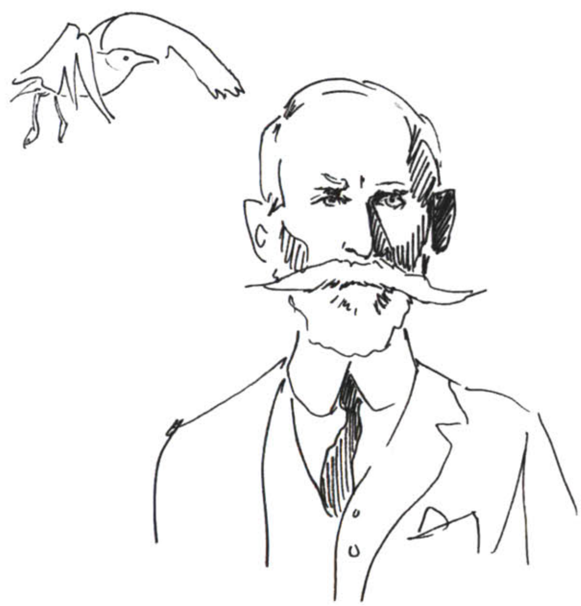
Charles Darwin (1809-1882) with his first-ever sketch of an evolutionary tree (left, 1837) and the tree diagram he published in the *Origin* (right, 1859)



Ernst Haeckel (1834-1919), who got a little carried away with the tree idea

Still, it took a while for taxonomic efforts to gel around the idea of evolution. The first time someone made a really thorough effort to put gulls in their evolutionary context was in the 1920s, when a New Yorker named Jonathan Dwight set out to construct a gull phylogeny. Dwight was a trained as a physician, but his real passion had always been birds: his college roommate at Harvard remembered him getting up at three in the morning to climb trees and collect eggs. He was in his sixties when he turned to the taxonomy of gulls.

Dwight spent countless hours in the American Museum of Natural History in Manhattan, comparing the color patterns and body structure of the different gulls. In 1925 he published a huge article, over three hundred pages long, in the museum's bulletin: *The Gulls (Laridae) of the World; Their Plumages, Moults, Variations, Relationships and Distribution*. It included 195 drawings of gull wings and tails, spread to show the patterns on the feathers, and 26 drawings of gull heads and feet. It showed table after table categorizing the different species by their sizes, their toe lengths, their bill shapes.



Jonathan Dwight (1858-1929) and friend

Dwight turned the "family resemblance" idea into a systematic endeavor. Trying to figure out how to best account for all of his measurements, he drew up a family tree that categorized seemingly related species in nested groups. Dwight's tree was spare and practical. It read from left to right instead of up and down, consisting simply of Latin names, bracketed and arranged. And it split the gull family—Laridae—into two big branches: one made up of mostly large, white-headed gulls, like the ones at Jodrey Pier, and the other made up of mostly small, dark-headed gulls. Not everything fit neatly into the two groups, but Dwight did his best.

Taxonomists like Dwight could gather some data from live animals, by observing or capturing them in the field. But it was museum collections—essentially repositories of dead animal specimens—that were the real bread and butter for taxonomists in Dwight's era. Nowadays, Jeremiah Trimble is in charge of just such a collection: the bird section of the Museum of Comparative Zoology (or MCZ) at Harvard, Dwight's alma mater. Along with collections of mammals, fish, insects, mollusks, and other creatures, the bird specimens are housed in the same complex as the better-known public displays of the Harvard Museum of Natural History, just northeast of Harvard Yard.

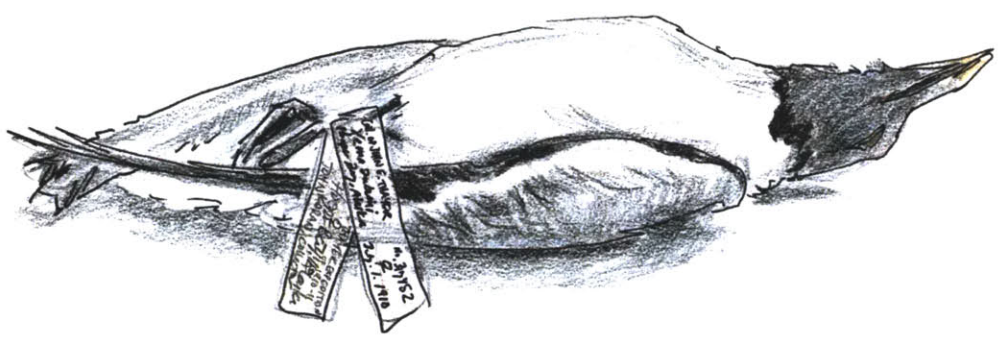
Jeremiah Trimble

It was a cold, sunny afternoon when I arrived at the MCZ and made my way up to the fifth floor. An antique radiator was clanging loudly, and sunlight poured in from the big windows on one side of the room. There was no question that I'd found the bird department. From a pedestal on the large central table, a mounted Adjutant Stork presided over the room, peering down its enormous beak at me with glassy eyes. Tucked under its long legs was a skeleton of a Great Auk, an extinct relative of puffins. On one wall, next to a pendulous nest that hung from the ceiling, were three whole shelves of bird skeletons, looking like little dinosaurs. From their beaks and general shapes I could pick out some of the more obvious IDs: a flamingo, a parrot, a toucan.

Trimble looked as at home there, slouching with a cup of coffee next to a stuffed Cinereous Vulture, as he did with a pair of binoculars on the waterfront. He and the department's curatorial assistant, Kate Eldridge, obligingly dropped what they were doing and gave me a personal tour of the bird collection. I followed them down hallways and into cavernous old rooms, learning which bird families were stored where. Some of the rooms were outfitted with new storage containers—the raptor room was like an unusually well-maintained laundromat, stark and white, its rows of storage containers reminiscent of washing machines—but others looked like they hadn't changed since the early 1900s.

The gull collection was in one of the latter. It was a high-raftered room with long rows of multi-door plywood cabinets, ten feet tall, painted a queasy pale green. Each cabinet door opened to reveal slide-out trays. Unlike the lifelike stork and vulture that greeted me at the door, most of the MCZ's bird specimens are simply stuffed skins, prepared for space

Bird skeletons at the Harvard Museum of Comparative Zoology



Sabine's Gull specimen

efficiency. Eldridge opened a cabinet at random and pulled out a few trays to show me ranks of iridescent hummingbirds lying on their backs with ID tags tied to their feet. I couldn't decide if the place reminded me more of a library or a morgue.

The gull collection was kept in seven cabinets occupying nearly an entire row. To complicate matters, the narrow aisle next to that row was crowded full of enormous wooden dressers. Eldridge and I spent half an hour shoving dressers back and forth to clear out space to open the cabinets (later I found out what was inside those dressers: the museum's eggshell collection). Apparently the gulls had not been in high demand recently.

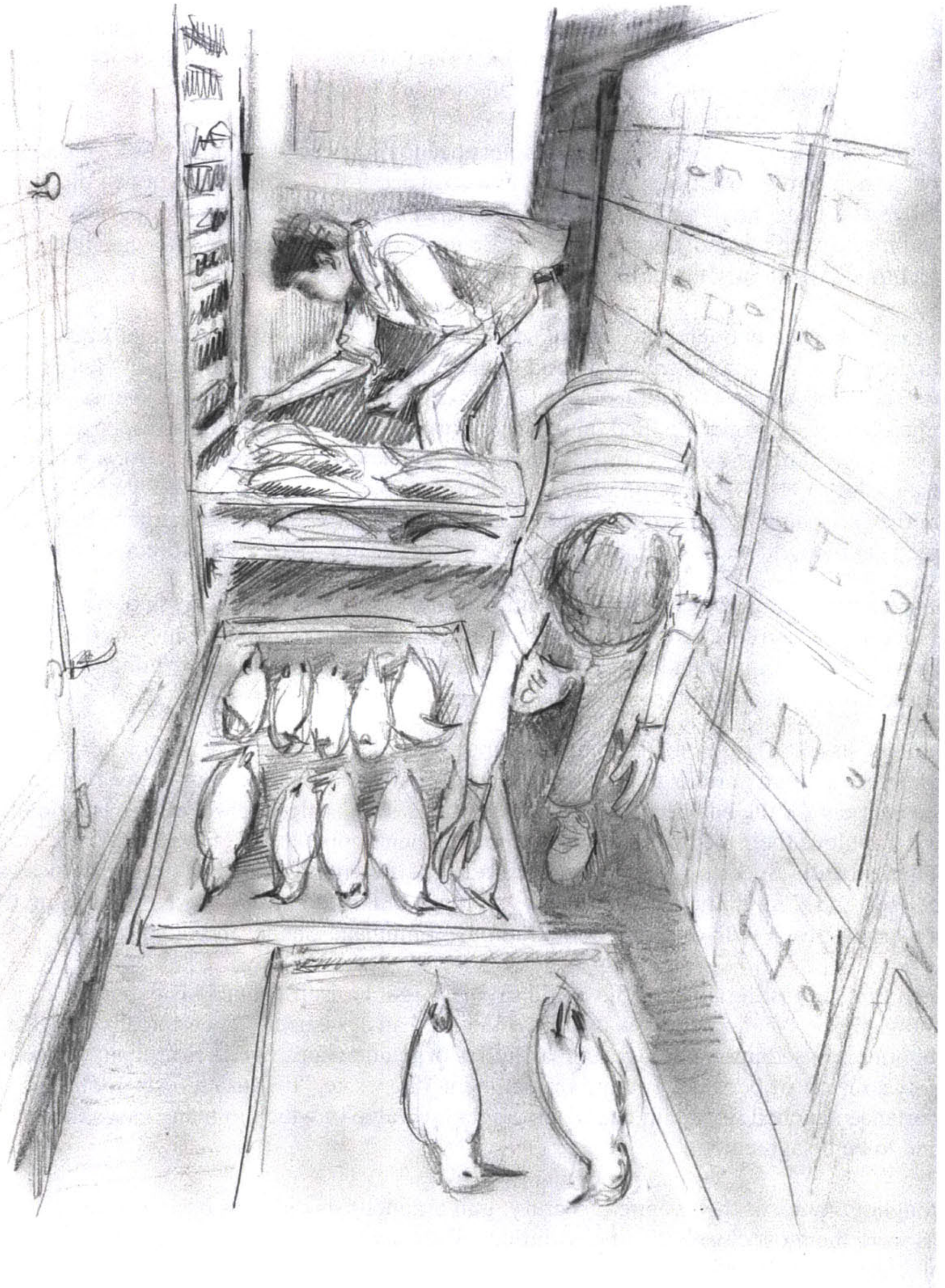
Eventually we had enough space to unlatch one of the cabinets, swing the door open, and pull out a tray. The gulls lay there stiffly and mutely, with cotton protruding from where their eyes used to be. Most of them had been shot, skinned, and stuffed by some naturalist or another, decades before. I pulled on a pair of purple rubber gloves from a dispenser and gingerly picked up a Sabine's Gull, laying it on a white cardboard pallet. "Hooper Bay, Alaska – July 1, 1910," read the yellowed tag on its foot. I also selected a Swallow-tail Gull from the Galápagos, collected around the same time. Taking the two specimens into the main room, I set them down on the table under the disconcerting gaze of the Adjutant Stork.

The specimens had flattened slightly against the surface they had been lying on for a century, and their beaks and feet had faded, but they still information to impart. They're the only two gulls with forked tails, and they both have dark heads and red eye rings. Though the two specimens had some striking similarities, Sabine's Gull was a lot smaller.

Taxonomists like Dwight made careful comparisons of such specimens. They not only considered qualitative traits like plumage color but also made meticulous measurements, using calipers for the beaks and feet, rulers for the wings, scales for weighing. But no matter how scrupulous their methods or how systematic their approach, taxonomy still came down to a judgment call. Species A and B might have had different plumage but similar shapes, while Species B and C might have had the same plumage but different shapes. Now imagine fifty more species, each with different combinations of plumage, shape, and other traits.

Which trait is most reliable? Who could say? Dwight himself opened his paper by acknowledging that taxonomy was more of an art than a science. "Theoretically, at least, taxonomy is based upon phylogenetic affinities or relationships, while practically it becomes largely a matter of personal opinion or judgment," he wrote, "because it rests upon the importance attached to certain characters about the value of which in many cases there is bound to be disagreement."

Throughout much of the twentieth century, gull taxonomists did their best to figure out which traits *were* the most closely tied to evolution. They learned that colors and patterns tend to evolve very quickly in response to selection pressures, with visible changes that are disproportionate to the overall change in genome. Gull researchers like Niko Tinbergen of Oxford tried to shift the emphasis onto traits like mating behavior, which seemed less prone to wild fluctuation over evolutionary time. In the 1950s a student of Tinbergen's, Martin



Jeremiah Trimble and Kate Eldridge sort gull specimens

Moynihan, published a phylogeny of gulls that incorporated not only their visible traits, but their vocalizations as well. Going back to Dwight's schema, Moynihan modified it by dividing the dark-headed group into further subgroups, "masked" versus "primitive" hooded gulls.

Yet with nothing else to go on but natural history data, taxonomists seemed to be doomed to forever shuffle and reshuffle the gull family tree—giving weight to one trait or another—without having any way to prove that one version was the most valid.

Part 2:

The core

Phylogenics couldn't move forward—and taxonomy, arguably, couldn't become a science—until biologists found a better way of comparing species. They needed a trait that was more exclusively tied to relatedness. A trait that changed at a predictable speed without being skewed by environmental pressures, and that depended less on our subjective judgment of what constitutes family resemblance.

In the mid-twentieth century, they found something: the molecules that make up living things. A recently-perfected technique called chromatography allowed taxonomists to analyze microscopic structures like proteins and compare those structures between different organisms. Some of the greatest advances in this new field were bird-related, thanks to the pioneering work of ornithologists and molecular biologists Charles Sibley and Jon Ahlquist of Yale University.

Sibley and Ahlquist's protein comparisons didn't uproot any of the avian family trees on their own. But they did open up a field of study that was about to take taxonomy to a new level. Proteins are more fundamental than the traits they control; they're more directly tied to relatedness and less directly influenced by the environment. But what if taxonomists could use the most fundamental molecule of all—the nucleic acid that had been recently identified as the blueprint of proteins and the medium of heredity? What if they could compare DNA?

DNA contains information that contributes to every aspect of an organism. The subtlest of changes in a gene sequence can cause drastic changes in outward appearance, because outward traits result from complex interactions between different parts of the genome. Even if two sister species look very different, their DNA will retain high similarity—particularly the segments that don't code for outward colors and shapes (since those are the traits that tend to change quickest as a result of environmental pressures).

"I recall discussions dating back to 1964 in which we yearned for a single genetic measurement, yielding clusters of related species, groups of related genera, and so on," wrote Ahlquist in a memoir. He and Sibley devised a molecular method to compare genes across different organisms: DNA-DNA hybridization, which involved taking strands of DNA from two organisms and throwing them together. The tighter the strands bound with each other, the more similar they were. Ahlquist wrote: "Our first DNA data were so clear, so unambiguous, and so promising that any lingering doubts quickly disappeared. Here was a technique that provided simple numbers, reproducibility, reciprocity, and a range of resolution that encompassed all living birds." The foundations of a new field had been built: molecular phylogenetics, the gold standard of modern taxonomy.

Still, it was a few more decades before molecular phylogenetics took hold. Complications cropped up with the initial techniques, which were scrapped in favor of a new approach: comparing the sequences of single genes. And even after the methods were ironed out, some taxonomists were reluctant to abandon the skills they had honed over their careers in favor of a new, much more expensive way of collecting data. As late as 1998, Philip Chu of the Carnegie Museum of Natural History in Pittsburg did a gull phylogeny that was simply a refinement of the old approach, with no molecular work involved. Chu is one of the few modern taxonomists who still, to this day, bases phylogenies on anatomical comparisons. (He does recognize the value of comparing DNA, but says he prefers to keep working with the visible, tangible organism).

For his gull phylogeny Chu compared minute measurements of the bones, feathers, and skin, and ended up reshuffling the previous groupings of the gulls. He called one big group the Larines: Dwight's "white-headed" group paired with Moynihan's "primitive" group. He called his other big group the Sternines, or tern-like gulls: Moynihan's "masked" group plus several loner species. At the turn of the century, that was the best understanding we had of gull relationships.

Finally, in the year 2000, gull taxonomy caught up with modern taxonomic methods. An evolutionary biologist (and birder) named Pierre-André Crochet, of the Center of Functional and Evolutionary Ecology in Paris, published a molecular phylogeny that encompassed most of the world's gull species. Five years later, Crochet's colleague Jean-Marc Pons took the reins and added in the remaining species, resulting in a complete phylogeny of the gulls. Meanwhile, other teams of researchers around the world were determining how the gull family fits within the "order" of Charadriiformes, which contains shorebirds, terns, jaegers, and puffins. Still more researchers were figuring out where Charadriiformes fall within the entire "class" of Aves—all birds—and so on down to the base of the tree of life.

For each of these studies, the starting point was getting the DNA. My own attempt to witness that process took me back to the chemical-scented aisles of the MCZ gull collection. But this time I wasn't here to measure dead birds, à la Jonathan Dwight. I was here to watch dead birds being plucked.

"Look for some all-white gulls," Trimble said, opening a cabinet or two and scanning up and down for Ivory Gulls. He had a general sense of where they were, though of course he could have easily looked it up. The entire bird collection is arranged in taxonomic order, albeit an obsolete one based on an influential publication from the 1960s that Trimble and Eldridge call "the Peters" (published by James Lee Peters, a former curator of the MCZ). This system may be hopelessly outdated, but the vast size of the collection makes it impossible to switch systems every time someone comes up with a new taxonomy.

Jean-Marc Pons, Pierre-André Crochet,
and some of their study subjects

It took Trimble and Eldridge only a minute or two to locate their species of interest. The all-white gulls were lying on three trays near the bottom of the far-right cabinet. Eldridge knelt down pulled open a drawer, examining the yellowed tags tied to the birds' feet. "Greenland... Labrador... Labrador... Siberia...," she muttered, sorting the birds like a librarian who'd encountered a disorderly shelf. She selected certain birds and laid them out on a cardboard pallet on the floor, squeezed between the gull cabinets and the eggshell dressers. We brought them into the next room and put them on the big central table. I watched Eldridge carefully grasp a chest feather with tweezers and give it a gentle tug. Then I got to give it a try myself. Occasionally the delicate feather shafts broke, but it was best to remove the full feather, including perhaps a bit of skin from around the base.

Eventually eight feathers (more or less) from each gull went into little ziploc bags, to be mailed off to a biologist who was testing trends in heavy metals. This same procedure can be used when researchers want to look at DNA. Lying dormant in the base of the feather is viable DNA that can be extracted in a lab. An even better way to get DNA is by cutting a tiny wedge out of the bottom of the bird's foot. Such "destructive sampling" techniques are the main thing the MCZ bird collection is used for nowadays.

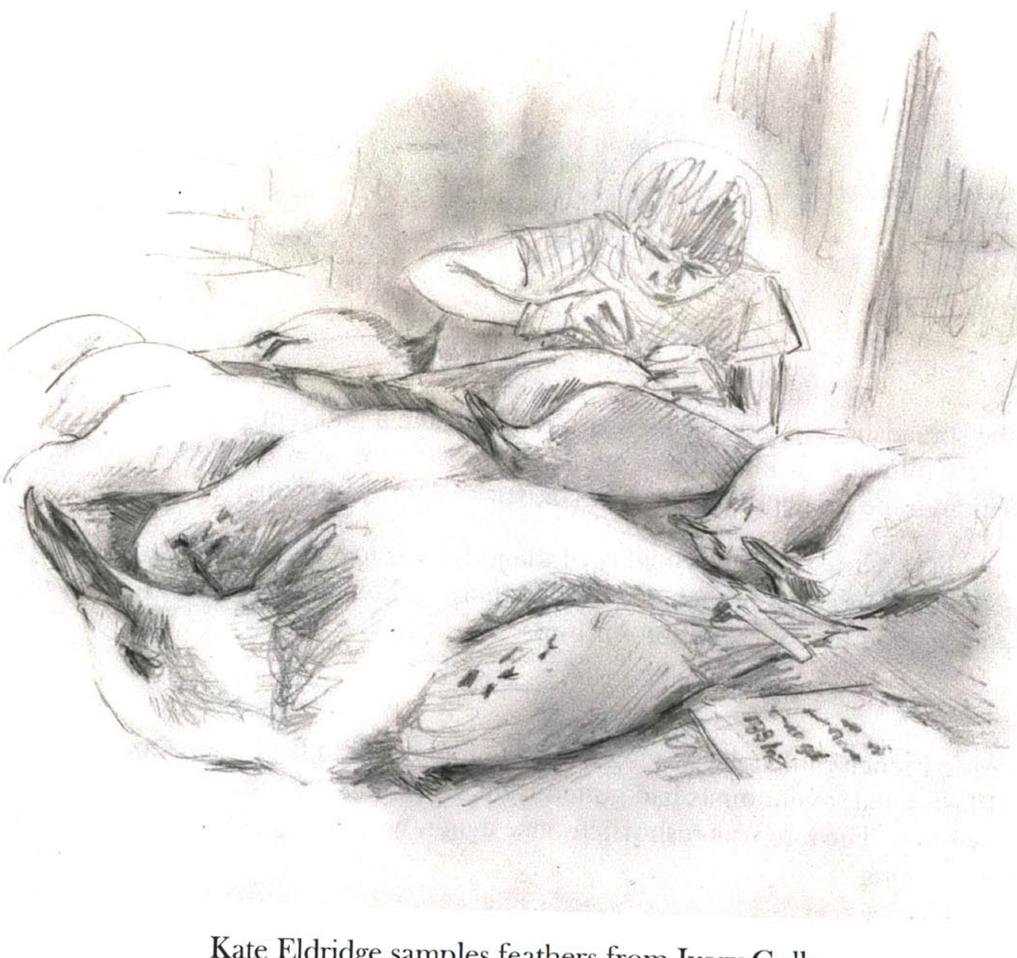
Crochet and Pons got much of their DNA from this kind of sampling. The methods section of Crochet's phylogeny reads: "Samples were plucked feathers, muscles or blood in buffer or ethanol, skin or feathers from long-dead bodies, dried plucked feathers, dried blood on paper, or...skin from the underside of the foot." The researchers also collected feathers and muscles from thirty species in the field, sampling multiple individuals when possible. Crochet himself took samples from two Slender-billed Gulls and over thirty Yellow-legged Gulls in Camargue, France.

From their tissue samples, Crochet and Pons isolated mitochondrial DNA—genes found not on the chromosomes in the cell nucleus, but inside the mitochondria, where respiration takes place. Mitochondrial DNA is particularly useful for fine-scale taxonomy because it has a faster rate of evolution than nuclear DNA, yielding a similar amount of information with a much shorter sequence.

The researchers chose a short segment of cytochrome b, which codes for a protein involved in respiration and is the most commonly used gene for phylogenies. They also chose two sections of the so-called control region, the only large region of avian mitochondrial DNA that doesn't code for proteins. If they'd had more time and money, they would probably have used more genes: the more genes, the less likely that the results would be skewed by a gene that has evolved more slowly or quickly than the rest of the genome.

Pons sent me the file of mitochondrial gene sequences from each member of the gull family. I opened it to find a multicolored spreadsheet full of green Cs, yellow Gs, red As, and blue Ts, representing the four nitrogen bases of DNA (cytosine, guanine, adenine, and thymine). Each gull species had its own line, and there were nine hundred and forty seven columns, one for each base pair. I surprised myself by feeling a sudden sense of awe, a sense that I had stumbled upon a very private, essential part of an organism. I felt as though I were seeing the true core of the birds' identity, or at least a little piece of it.

Ivory Gull specimen



Kate Eldridge samples feathers from Ivory Gulls

Much of the spreadsheet was solid columns of colors: where one species had a C, the others did too. But in spots, the columns were interrupted by blips of another color: where most species had Ts, for instance, one species had an A instead. GGCAC, read one bit of the Relict Gull's sequence. GTCAC, said the same bit of Olrog's Gull, while Pallas's Gull read GGTTC. The species with the fewest differences were the most closely related. The species with the greatest differences would be the most distantly separated on the family tree.

To generate their family tree, the French group simply had to feed that spreadsheet of colorful letters into a computer program. I managed to recreate that process with the help of Allison Shultz, a Harvard grad student studying avian evolutionary biology, whose office is just down the hall from the gull collection at the MCZ. Shultz is currently finishing up a phylogeny of the tanagers, a large family of smallish Neotropical birds. She showed me how to use some of the tools of her trade, including a program called RAxML and a web portal called CIPRES.

Allison Shultz

We input the spreadsheet of gene sequences and out came a gull family tree, in a process that took only a few minutes. It looked essentially identical to the ones the French group had published (though the branchings with low statistical significance toggled a bit).

The final step in constructing a phylogeny of the gulls was to estimate how many thousands or millions of years ago each branch occurred, which the French group did by calibrating their data with an accepted rate of evolution for birds.

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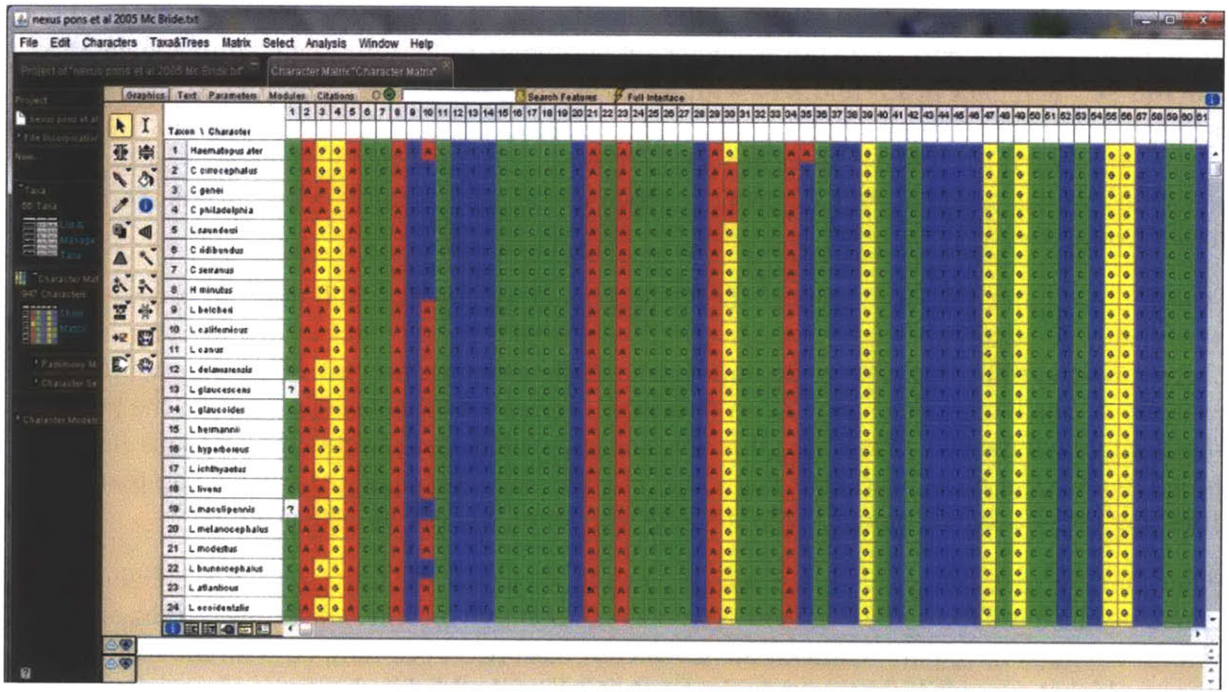
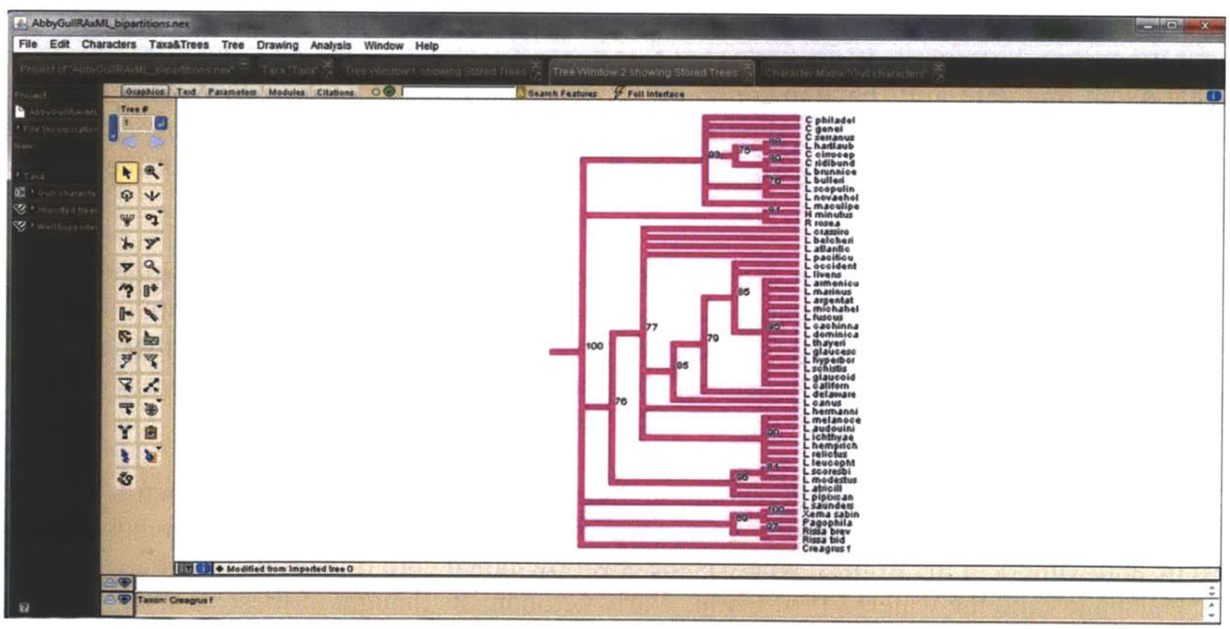
The pioneering French molecular phylogeneticists found all kinds of interesting things: things that the old-fashioned taxonomists had gotten right, and things that they had gotten completely wrong. The tree was reshuffled once again, with new groups and subgroups, new patterns of branching.

It turned out that plumage coloration had really thrown early taxonomists for a loop. They had tended to place white-headed gulls in one group and dark-headed gulls in another group. They reasoned that the two lineages had probably branched off from each other early on, each



Gull mitochondrial gene sequences, courtesy of Pons et al.



The gull tree I generated from those gene sequences giving rise to descendants who inherited their head color. But the new phylogeny showed that head color is not to be trusted. For instance, one group of 11 closely-related gull species contains six with dark heads and five with white heads. Based on the relationships between each of those species, there must have been at least three times in that group's history when head color shifted from black to white. The French group suggested that these 11 gulls be placed in a genus called *Chroicocephalus*, which in Latin essentially means "head of some color or other."

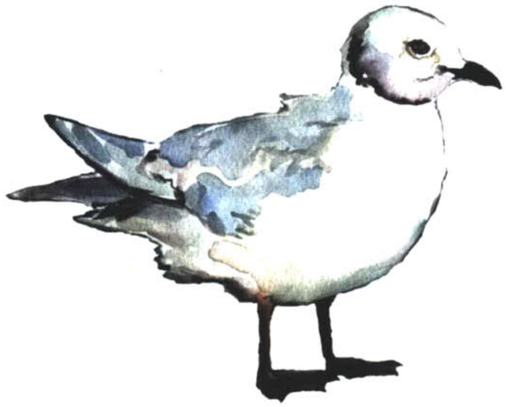
Two of those gulls, the Brown-Headed Gull and the Gray-Hooded Gull, have gray or brownish heads that look, to me, like transitional stages between black and white. I asked Crochet whether they may be in the middle of a millennia-long process of turning white. That certainly seems like a possibility, he said, though we cannot be sure they aren't in the process of turning black instead. Ross's Gull is another interesting case—rather than a black head fading in or out, it has a headband that looks like the lower boundary of a black cap that's shrinking away. Again, though, who's to say it's not on its way in, instead?

Other plumage patterns proved misleading as well. Consider the Lava Gull of the Galápagos, named because it's the same dark gray color as the craggy volcanic coastlines it lives on. Since most gulls have pale feathers, the Lava Gull has often been lumped with the handful of other gulls that are similarly swarthy: the Sooty Gull of the Middle East, the Heermann's Gull of the west coast, and White-eyed Gull of the Red Sea. Crochet showed that those four gulls actually belong to three different main branches of the gull tree: they're each more closely related to pale gulls than to each other.

If the four dark gulls didn't share one dark ancestor, something else must be responsible for their similar appearance. The Lava Gull's color could be an adaptation to help it blend in with its surroundings while it's nesting, but that doesn't account for the other three species. What do all four dark gulls have in common? For one thing, they all live in tropical climes, subject to high levels of sunlight. Having lots of dark melanin pigment could be an adaptation for protecting feathers from being bleached by the blazing sunlight, which can wear them out prematurely.

These four species seem to have independently evolved dark plumage, rather than inheriting it from a common ancestor. This is an example of what's called convergent evolution, in which different lineages with contrasting traits evolve to be increasingly similar because they're subject to similar conditions. Whether that constraint is actually feather bleaching, as suggested, is another question that needs to be tested.

I'd seen some results of convergent evolution during my first visit to the MCZ, when I compared the similar-looking Sabine's and Swallow-tailed Gulls. Sabine's Gull breeds in the Arctic and winters in the tropics, whereas the Swallow-tailed Gull divides its time between the Galápagos and the waters off of Chile. Early taxonomists thought of these as sister species, based on their forked tails, black heads, and other resemblances. But the French phylogeny disproved this relationship. It seems that the traits they share are a result of shared conditions, not shared ancestry. In fact, the semi-tropical Sabine's Gull was shown to have a totally unexpected sister relationship with the arctic Ivory Gull.



Ross's Gull

Lava Gull

Ivory Gull

What's more, the pure white Ivory Gull is involved in a convergence of its own. Remember the two species of pale gulls that had migrated down to Jodrey Pier from the Arctic? Arctic gulls depend heavily on fishing, and light plumage may make them less easily seen and evaded by their prey. The Ivory Gull appears to have simultaneously converged with other pale arctic gulls and diverged from its own sister species as a result of their different habitats.

The old-fashioned taxonomists knew a thing or two, and they weren't ignorant of convergent and divergent evolution. Dwight, Moynihan, and their contemporaries had noted that some white-headed gull species behaved suspiciously like black-headed gulls without a black head, and vice versa. They had attempted to weight other characteristics that might be less changeable, like behavior, or bone characteristics, or even juvenile plumage (which at least isn't subject to sexual selection like adult plumage is).

The new phylogeny showed that some cases in the early taxonomists had been remarkably successful, given their limitations. For instance, pre-molecular taxonomists had suspected the Ross's Gull and the Little Gull to be closely related. The two are not superficially that similar: the Little Gull has a black head and a white belly; Ross's Gull has a black stripe on the back of its head and a pink-tinged belly. Yet based on a few obscure factors, like the fact that both species exhibited a "reduced skull ossification" that no other gulls shared, taxonomists had made the sophisticated assessment that these were sister species. The phylogeny proved them right.

Before the molecular phylogeny, though, there was simply no way to be sure whether similar traits were the result of relatedness or convergent evolution. As Crochet said to me over the phone, "If there's one thing we have learned about avian evolution in the last ten or twenty years, it's that there are no accurate morphological features."

Part 3:

The whole

Even where the early taxonomists made faulty interpretations, their data is still valuable. With a solid molecular framework, the same natural history information that misled previous phylogeny efforts—like carefully analyzed plumage patterns and bill sizes and behavior—suddenly becomes an essential addition to the story.

Without a doubt, molecular phylogeneticists can reach the innermost core of identity in a way that was inaccessible to the earlier taxonomists. Yet they have also distanced themselves from their subjects: they work in sterile labs and offices, and their results are encoded in symbols and mathematical relationships. They end up with outlines of Latin names branching off from each other in a particular order, and estimates of how many thousands of years ago each of those events happened—diagrams with little context. To figure out what might have happened at each of those branch points, we need to return to the natural history data, to the physical characteristics of gulls and their environments.

Black-billed Gull of New Zealand, currently listed
as Endangered on the IUCN Red List

That's why Dwight's research continues to be relevant, as does ongoing research by biologists and ecologists around the world. The very disparities between apparent relatedness and actual relatedness give us great insight into how natural selection molds the traits of living things. When species share traits but turn out to be unrelated, we know there has been something interesting going on between those traits and the outside world.

But how can we systematically analyze this interplay between apparent relatedness and actual relatedness? One way is by mapping natural history information right onto the phylogenetic tree: an "ancestral state reconstruction." The idea is that by assessing the traits of modern gulls, we can infer the traits of their ancestors. It seemed fairly simple, so I decided to try it out myself.

Crochet's group had already performed this process with head color, so I started with that trait to see if I could come up with the same results. I went through all 53 gull species, drawing a blank circle next to the ones with white heads and a shaded circle next to the ones with black heads. For example, the Red-billed Gull, the Black-billed Gull, and the Silver Gull are three white-headed species from Australia and New Zealand that fall into their own little taxonomic trio. Each of them got a blank circle to stand for their white heads. The next step was to guess the head color of their common ancestor: black or white?

If the ancestor had a black head, it would have had to switch multiple times to white. More likely, it started out white and didn't have to switch at all. So I drew another blank circle at the node that branches out into those three gulls.

Next, I looked at the other eight species that were clumped around that white-headed threesome on the family tree. A twist: most of them actually had black heads. The shaded circles in this larger branch ended up outnumbering the blank circles, suggesting that the common ancestor of the bigger group was black-headed. I worked my way outward and upward to the base of the tree, where I was able to determine—as the French group had—that the ancestor of all gulls probably had a black head as well.

The French team had stopped after head color, but I could think of all kinds of other traits to map onto the tree: location, diet, behavior, juvenile plumage, voice, leg color, and so on. Having limited time, I was willing to try any trait that someone else had already gone to the trouble of measuring. I requested a copy of Dwight's book-sized paper from the library. I also borrowed *The Handbook of the Birds of the World, Volume Three (Hoatzin to Auks)*, part of a vast multivolume work that has lots of information about all kinds of birds around the globe.

On a spreadsheet I gave each species its own row, and I made a bunch of columns for the traits. In the *head color* column I typed in a "0" or a "1" to designate a white or black head. In my *hemisphere* column I marked a "0" for "mostly northern" and a "1" for "mostly southern." I made designations for bill color, bill shape, leg color, body size. My *diet* column was perhaps one of the more unconventional: I decided to mark a "0" to designate gulls that "hunt animals (like fish) that could hypothetically see them coming," a "1" for those that "sometimes or sort of" hunt such animals, and a "2" for those that rely completely on scavenging and other ways of finding food. I figured it might inform the discussion of whether white heads are better for camouflaging gulls to sneak up on prey.

This seemingly straightforward process gave me a new appreciation for the patience and obsessiveness that Dwight and his ilk must have had when they compiled traits for their phylogenies. I was borrowing most of my data from other people, rather than painstakingly measuring it for myself. Yet it was still maddening to go through all 53 species again and again for one trait after another, trying to categorize traits that didn't want to fit into neat categories, and eventually abandoning traits (like juvenile plumage) that were proving too tricky. I tried to remind myself that 53 species isn't bad compared to some ancestral state reconstructions—for example, there are hundreds of tanagers in the group Allison Shultz studies.

A handy program called Mesquite did the rest of the work for me, taking mere seconds to map each trait onto a separate copy of the phylogenetic tree. The zeros and ones and twos showed up as different colors, and at each node in the tree I could see a color representing what the ancestor of each nested group was probably like. According to my reconstruction, the ancestor of all gulls not only had a black head, but it was small and dark-eyed with a dark bill. And it had red legs! It lived in the northern hemisphere and depended only somewhat on fish. I could track the hypothetical evolutionary progress of its descendants over time, reading colors across the tree from the base to the branch tips.

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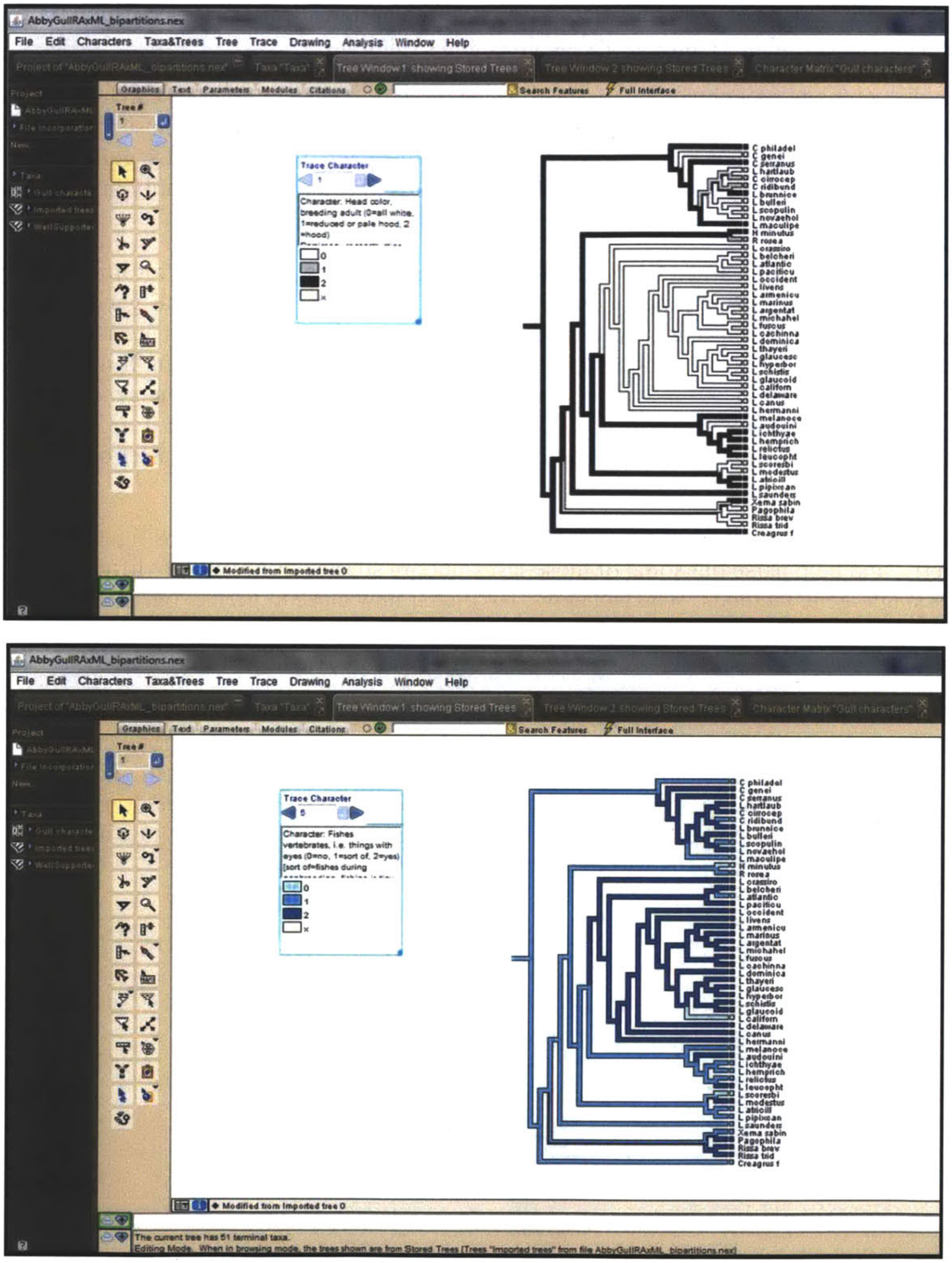
Ancestral state reconstructions can give us an idea what happened in the past, but they are never more than a sort of historical fiction. To start with, they're limited by the accuracy of the phylogeny. Some of the branches of the gull tree are still weaker than we'd like. If the tree misrepresents the order in which a group of species split off from each other, it will misrepresent the most likely ancestral state.

And even with a perfect phylogeny, everything about an ancestral state reconstruction is based on probability. If three out of four sister species have black heads, their ancestor *probably* had a black head, but that's no guarantee that it didn't actually have a white head. Normally taxonomists assume that the simplest tree is the best one, but with traits like plumage color switching around so much, assumptions like that may very well be wrong. We'll never be sure what happened a million years ago, no matter how hard we try.

Even so, there's merit in speculating about what the gulls of the past looked like, how they acted, how they split off into new species, and how they spread from region to region over millions of years. For one thing, it makes us think of gulls as belonging to the earth as much as we do. For another, ancestral state reconstructions—and other techniques that merge natural history data with molecular phylogenies—are very useful as a springboard for further research. As I looked at my colorful tree diagrams, I could see some intriguing patterns: for instance, almost every time diet shifted to heavy fishing, head color switched from black to white. This kind of observation helps biologists make and test hypotheses about plumage evolution—like whether darker plumage really does impede gulls when they're fishing.



Ancestral state reconstructions: When gulls switched to white heads (white lines, top image) they tended to also switch to a diet heavier in fish (dark blue lines, bottom image)

Researchers can also compare the rates at which different traits evolved, to see which traits were most instrumental in the species' ecology and evolution.

Since the complete gull phylogeny was published in 2005, a slew of other researchers have used it as a framework for their comparative and biogeographical studies. Those studies have addressed subjects as diverse as blood parasites, animal vision, viruses that use gulls as vectors, head lice that match dark- or light-headed birds in color, homosexuality in birds, and climate change.

Despite all that we've learned from the French phylogeny, there's still room for improvement. The next opportunity for advancing our grasp of gull taxonomy is through full-genome comparisons. Though currently expensive and time-consuming, such studies are the last word in determining evolutionary relationships. (Once they become the norm, even Philip Chu says he'll consider giving up on his anatomical comparisons.) By looking at all the genes, we won't have to wade through masses of DNA to pinpoint the exact same gene from multiple organisms, or worry about our results being skewed by a gene that evolved faster or slower than the rest.

The good news: Genomic studies will assure us that we have the relationships figured out properly, and help parse out some of those last stubborn species that refuse to differentiate under single-gene methods. The bad news: No matter how close to perfect our methods get, we will never reach a point where we have every organism on earth neatly categorized into species.

At the MCZ, the room with the Adjutant Stork has a door on one wall with a nameplate that reads "Ernst Mayr." The famous evolutionary biologist and ornithologist passed away a few years ago, but he was once the director of the museum and he had an office in the ornithology department. It was Mayr who came up with the now-accepted idea that speciation is not usually gradual, but happens quickly, followed by long periods of time with little change. One of his main study subjects was the gull family.

Ernst Mayr (1904-2005)

As it happens, at this snapshot in time, we're catching some of the gulls at an unusual moment: smack in the middle of a speciation event. When Jeremiah Trimble identifies a hybrid gull at Jodrey Pier—a cross between a Herring Gull and a Glaucous, for example—he's looking at a bird that's blurring the boundaries between species, challenging the species concept.

The Herring Gull of the New England coast is one of 14 large, mostly-white species that all have a very recent common ancestor—so recent that they haven't managed to fully extricate themselves from each other. Four of the five species we saw on Jodrey Pier are part of this complex (and the fifth—the Ring-Billed Gull—is a close relative). They occasionally hybridize and backcross with each other, producing the mixed-breed offspring that Trimble strives to identify on the waterfront. Some of these species could potentially remerge with each other in another several thousand years, or they could diverge enough to completely split apart and stop hybridizing. It depends on chance and the environment.

A member of the 14-species
herring gull complex

The herring gull complex is one of the parts of the gull family tree that would benefit most from a genome-wide study, in terms of our ability to tease apart the subtle patterns of relatedness within a group of species that have only recently diverged. But even in the best-case scenario, the gulls will never fit into a neat package. Speciation is messy. We can argue about whether something is a separate species or a subspecies, but in the end there's no concrete line between them. Instead of a simple "family tree" with one root and an increasing number of branches, we have some branches merging back into other branches, sharing genes with other species.

This happens all across the entire tree of life, to varying degrees (it's relatively uncommon in animals, for instance, but many plants are masters of hybridization). Even our idea of one common ancestor of all living things has been called into question in the past decade or so. It seems that life sprang from an ancestral community of cells—more like a thicket than a single-rooted tree. It's a bit of a mess, but it's also a richer story than we conceived of before.

Humans have struggled for centuries to make sense of the complex identity recorded in the bodies of living creatures, and we've made much scientific progress. But perhaps our greatest achievement has had less to do with concrete, accurate results and more to do with the process of searching for answers. We have watched gulls in their habitats and on their nests; we have made painstaking measurements; we have studied the secret code that's fundamental to their identity. We have acknowledged gulls as fellow inhabitants of the world who spent millions of years evolving alongside our own hominid ancestors. They have become part of *our* identity.

Epilogue

Another day, another gull-watching adventure. This time I'm on Mount Desert Island in Maine, staying with my brother in the town of Bar Harbor on the coldest weekend of the year. I wake up late. Putting on three pairs of pants, several layers of shirts, and two winter coats, I head outside with my binoculars. Main Street is icy and deserted. The first sign of life I see is a Herring Gull. It wheels overhead across the grim gray sky, looks around, and disappears behind a rooftop.

That gull reminds me of an impression I've had before—that Herring Gulls are like guardians of some sort, keeping an eye on things. The New England coast in winter is their domain. The cold and wind drive everyone else inside, or to warmer climes, but the gulls keep on going about their business, day in and day out. I make my way down Bridge Street to the famous sandbar—the strip of rocks and sand, 500 yards long, that connects little Bar Island to the town of Bar Harbor, surfacing at low tide and disappearing at high tide. Every summer a few tourists get stuck on Bar Island, trapped by the rising tide, and occasionally someone will thoughtlessly park a vehicle on the bar and then go for a walk, coming back to see only the antennas sticking out over the waves.

On this frigid winter day there are no tourists, no people at all. Just the gulls. I only see Herring Gulls, in fact—and if there are any Iceland Gulls or Glaucous/Great Black-Backed hybrids out there, I'm too cold to worry about picking them out. The gulls are scattered across the bar, huddled on the gravelly sand, wading in the shallows of the rising tide, hovering in the air and dropping mussels onto the rocks to crack them open. They are braced against the brutal northwest wind, and a driving snow has begun.

Up and down, up and down: gulls carry mussels high and then drop them, swooping down to try again until the shells finally crack. The wind is too loud for me to hear the sounds of shell against stone.

In this desolate place the gulls are rhythmically going about their lives, just as their ancestors have been doing for centuries upon centuries. I like to think about the scene as a snapshot in the long story of gull evolution, a story that will continue for who knows how many millions of years after I'm gone. I like to think, too, of all of the other gull species living their different lives across the world, all variations on a theme of gullhood, and yet unique, each with their own tale to tell.

Yes, I like to think about these things, but the bar is shrinking away under the waves and I can only stay in that wind for so long. I leave the gulls behind to carry on their lives, tracked only by the rhythm of the tides. I'll catch up with them again another day.

Bibliography

Interviews and correspondence:

Baker, Allan (Senior Curator of Ornithology, Royal Ontario Museum, Toronto). Phone interview: November 1, 2011. Email correspondence: October 4, 2011.

Bevier, Louis (Research Scientist, Colby College, ME). Email correspondence: January 14, 2012.

Chu, Philip (Associate Professor, St. John's University, MN). Phone conversation: April 4, 2012.

Crochet, Pierre-André (Research Fellow, Centre d'Ecologie Fonctionnelle et Evolutive, France). Phone interview: January 31, 2012. Email correspondence: November 4, 2011; March 9, 2012.

Cruz, Sebastian (PhD candidate, Max Planck Institute for Ornithology, Migration, and Immuno-Ecology, Germany). Phone interview: September 26, 2011.

Edwards, Joan (Professor of Biology, Williams College, MA). Personal conversation: Spring 2006.

Eldridge, Kate (Curatorial Assistant, Harvard Museum of Comparative Zoology, MA). In-person interviews. January 18, 2012; March 22, 2012.

Ellis, Julie (Research Assistant Professor, Tufts University, MA). Email correspondence: November 7, 2011.

Pons, Jean-Marc (Professor, Institut de Sciences Molécuaires de Marseilles). Email correspondence: March 20, 2012.

Shultz, Allison (PhD candidate, Harvard University). In-person interviews: November 7, 2011; April 10, 2012. Email correspondence: January 16, 2012.

Trimble, Jeremiah (Collections Manager, Harvard Museum of Comparative Zoology, MA). In-person interviews: January 18, 2012; January 27, 2012; March 22, 2012.

Journal articles, books, and online sources:

Ahlquist, J. (1999) Charles G. Sibley: A Commentary on 30 Years of Collaboration. *The Auk*, V. 116, No. 3: 856-860. The American Ornithologist's Union. Retrieved January 28, 2012 from: http://elibrary.unm.edu/sora/Auk/v116n03/p0856-p0860.pdf.

Avibase bird checklist of Sweden. Retrieved January 25, 2011 from: http://avibase.bsc-eoc.org/checklist.jsp?region=SE&list=howardmoore.

Baker, A., Pereira, S., Paton, T. (2007) Phylogenetic relationship and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biology Letters* 3, 205-210.

Baker, A., Tavares, E., Elbourne, R. (2009) Countering criticisms of single mitochondrial DNA gene barcoding in birds. *Molecular Ecology Resources* 9 (Suppl. 1), 257-268. Retrieved January 28, 2012 from: http://onlinelibrary.wiley.com/doi/10.1111/j.1755-0998.2009.02650.x/pdf.

Bevier, L. (January 21, 2012) Email to Maine-birds listserv.

Birdlife International Data Zone, Gulls and terns. Retrieved November 4, 2011 from: http://www.birdlife.org/datazone/speciessearchresults.php?reg=&cty=&cri=&fam=61&gen=0&spc=&cmn=&hab=&thr=&bt=&rec=N&vag=N&hdnAction=ADV_SEARCH&SearchTerms=.

Burger, J., Gochfeld, M. (1996) Family Laridae. In del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), *Handbook of the Birds of the World, Volume 3 (Hoatzin to Auks)*, 572-623. Barcelona: Lynx Edicions.

Bush, S., Kim, D., Reed, M., Clayton, D. (2010) Evolution of Cryptic Coloration in Ectoparasites. *The American Naturalists* 176 (4), 529-535.

Chu, P. (1998) A Phylogeny of the Gulls (Aves: Larinae) Inferred from: Osteological and Integumentary Characters. *Cladistics* 14, 1-43.

Crochet, P., Bonhomme, F., Lebreton, J. (2000) Molecular phylogeny and plumage evolution in gulls (Larini). *Journal of Evolutionary Biology* 13, 47-57.

Dwight, J. (1925) The Gulls (*Laridae*) of the World; Their Plumages, Moults, Variations, Relationships and Distribution. *Bulletin of the American Museum of Natural History* 52, 63-401. New York: American Museum of Natural History.

Fleming, J. (1930) In Memoriam: Jonathan Dwight. *The Auk*, Vol. 47, No. 1. The American Ornithologist's Union. Retrieved January 28, 2012 from: http://elibrary.unm.edu/sora/Auk/v047n01/p0001-p0006.pdf.

Hailman, J. (1964) The Galápagos Swallow-tailed Gull is Nocturnal. *The Wilson Bulletin* 76 (4), 347-354.

Håstad, O., Partridge, J., Ödeen, A. (2009) Ultraviolet photopigment sensitivity and ocular media transmittance in gulls, with an evolutionary perspective. *Journal of Comparative Physiology A* 195, 585-590.

Iwaniuk, A., Heesy, C., Hall, M. (2010) Morphometrics of the eyes and orbits of the nocturnal Swallow-tailed Gull (*Creagrus furcatus*). *Canadian Journal of Zoology* 88, 855-865.

Liebers-Helbig, D., Sternkopf, V., Helbig, A., de Knijff, P. (2010) The Herring Gull Complex (*Larus argentatus – fuscus – cachinnans*) as a Model Group for Recent Holarctic Vertebrate Radiations. *Evolution in Action*, 351-371.

Macaulay Library, archive of gull audio and video recordings, The Cornell Laboratory of Ornithology. Retrieved January 5, 2012 from: http://macaulaylibrary.org/browse/taxa/laridae.

Maddison, W., Maddison, D. (2007) Mesquite: a modular system for evolutionary analysis. Version 2.0 Retrieved March 27, 2012 from: http://mesquiteproject.org.

Massbird listserv archive. Retrieved January 21, 2012 from: http://birdingonthe.net/mailinglists/MASS.html.

McFarlane, G., Blomberg, S., Vasey, P. (2010) Homosexual behavior in birds; frequency of expression is related to parental care disparity between the sexes. *Animal Behaviour* 80, 375-390.

Miller, M., Pfeiffer, W., Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop*, New Orleans, 1-8.

Nudds, R., Oswald, S. (2007) An interspecific test of Allen's Rule: evolutionary implications for endothermic species. *Evolution* 61 (12), 2839-2848.

Paton, T., Baker, A. (2006) Sequences from 14 mitochondrial genes provide a well-supported phylogeny of the Charadriiform birds congruent with the nuclear RAG-1 tree. *Molecular Phylogenetics and Evolution* 39, 657-667.

Pons, J., Hassanin, A., Crochet, P. (2005) Phylogenetic relationships within the *Laridae* (Charadriiformes: *Aves*) inferred from mitochondrial markers. *Molecular Phylogenetics and Evolution* 37, 686-699.

Quillfeldt, P., Arriero, E., Martínez, J., Masello, J., Merino, S. (2011) Prevalence of blood parasites in seabirds - a review. *Frontiers in Zoology* 8 (26), 1-10.

Ragan, M. (2009) Trees and networks before and after Darwin. *Biology Direct* 4 (43). Retrieved April 6, 2012 from: http://www.biology-direct.com/content/4/1/43.

Raven, C. (1942) *John Ray: Naturalist*. Cambridge, England: Cambridge University Press. Retrieved on January 25, 2012 from: http://books.google.com/books?id=ETusSTe5O8YC&printsec=frontcover&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false.

Ray, J. (1713) *Synopsis Methodica Avium et Piscium*. London: Impensis Gulielmi Innys. Retrieved April 12, 2012, from: http://books.google.com/books?id=f5Mf5MtffVsC&printsec=frontcover&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false.

Sandvik, H., Erikstad A. (2008) Seabird life histories and climatic fluctuations: a phylogenetic-comparative time series analysis of North Atlantic seabirds. *Ecography* 31, 73-83.

Seitz, L. (January 11, 2012) Email to Maine-birds listserv.

Snow, D. (1984) Evolution and adaptations of Galapagos sea-birds. *Biological Journal of the Linnean Society* 21, 137-155.

Stamatakis, A. (2006) RAxML-VI-HPC: Maximum Likelihood-based Phylogenetic Analyses with Thousands of Taxa and Mixed Models. *Bioinformatics* 22 (21), 2688-2690.

Tinbergen, N. (1958) *Curious Naturalists*. London: Country Life. Retrieved May 1, 2012, from: http://books.google.com/books?id=qRql5FjHwLUC&printsec=frontcover&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false.

Wille, M., Robertson, G., Whitney, H., Bishop, M., Runstadler, J. (2011) Extensive Geographic Mosaicism in Avian Influenza Viruses from Gulls in the Northern Hemisphere. *PLoS ONE* 6(6): e20664. doi:10.1371/journal.pone.0020664

Yorio, P., Bertellotti, M., Quintana, F. (1995) Preference for covered nest sites and breeding success in Kelp Gulls *Larus Dominicanus*. *Marine Ornithology* 23, 121-128. Retrieved February 10, 2012 from: http://www.marineornithology.org/PDF/23_2/23_2_4.pdf.

Yorio, P., Boersma, P., Swann, S. (1996) Breeding biology of the Dolphin Gull at Punta Tombo, Argentina. *The Condor* 98, 208-215.