Images of the medical school anatomy lab are impossible to forget. Imagine walking into a room where you will spend several months taking a human body apart layer by layer, organ by organ, all as a way to learn tens of thousands of new names and body structures.

In the months before I did my first human dissection, I readied myself by trying to envision what I would see, how I would react, and what I would feel. It turned out that my imagined world in no way prepared me for the experience. The moment when we removed the sheet and saw the body for the first time wasn’t nearly as stressful as I’d expected. We were to dissect the chest, so we exposed it while leaving the head, arms, and legs wrapped in preservative-drenched gauze. The tissues did not look very human. Having been treated with a number of preservatives, the body didn’t bleed when cut, and the skin and internal organs had the consistency of rubber. I began to think that the cadaver looked more like a doll than a human. A few weeks went by as we exposed the organs of the chest and abdomen. I came
to think that I was quite the pro; having already seen most of the internal organs, I had developed a cocky self-confidence about the whole experience. I did my initial dissections, made my cuts, and learned the anatomy of most of the major organs. It was all very mechanical, detached, and scientific.

This comfortable illusion was rudely shattered when I uncovered the hand. As I unwrapped the gauze from the fingers—as I saw the joints, fingertips, and fingernails for the first time—I uncovered emotions that had been concealed during the previous few weeks. This was no doll or mannequin; this had once been a living person, who used that hand to carry and caress. Suddenly, this mechanical exercise, dissection, became deeply and emotionally personal. Until that moment, I was blind to my connection to the cadaver. I had already exposed the stomach, the gallbladder, and other organs; but what sane person forms a human connection at the sight of a gallbladder?

What is it about a hand that seems quintessentially human? The answer must, at some level, be that the hand is a visible connection between us; it is a signature for who we are and what we can attain. Our ability to grasp, to build, and to make our thoughts real lies inside this complex of bones, nerves, and vessels.

The immediate thing that strikes you when you see the inside of the hand is its compactness. The ball of your thumb, the thenar eminence, contains four different muscles. Twiddle your thumb and tilt your hand: ten
different muscles and at least six different bones work in unison. Inside the wrist are at least eight small bones that move against one another. Bend your wrist, and you are using a number of muscles that begin in your forearm, extending into tendons as they travel down your arm to end at your hand. Even the simplest motion involves a complex interplay among many parts packed in a small space.

The relationship between complexity and humanity within our hands has long fascinated scientists. In 1822, the eminent Scottish surgeon Sir Charles Bell wrote the classic book on the anatomy of hands. The title says it all: *The Hand, Its Mechanism and Vital Endowments as Evincing Design*. To Bell, the structure of the hand was “perfect” because it was complex and ideally arranged for the way we live. In his eye, this designed perfection could only have a divine origin.

The great anatomist Sir Richard Owen was one of the scientific leaders in this search for divine order within bodies. He was fortunate to be an anatomist in the mid-1800s, when there were still entirely new kinds of animals to discover living in the distant reaches of the earth. As more and more parts of the world were explored by westerners, all sorts of exotic creatures made their way back to laboratories and museums. Owen described the first gorilla, brought back from expeditions to central Africa. He coined the name “dinosaur” for a new kind of fossil creature discovered in rocks in England. His study of these bizarre new creatures gave him special insights: he
began to see important patterns in the seeming chaos of life’s diversity.

Owen discovered that our arms and legs, our hands and feet, fit into a larger scheme. He saw what anatomists before him had long known, that there is a pattern to the skeleton of a human arm: one bone in the upper arm, two bones in the forearm, a bunch of nine little bones at the wrists, then a series of five rods that make the fingers. The pattern of bones in the human leg is much the same: one bone, two bones, lotsa blobs, and five toes. In comparing this pattern with the diversity of skeletons in the world, Owen made a remarkable discovery.

Owen’s genius was not that he focused on what made the various skeletons different. What he found, and later promoted in a series of lectures and volumes, were exceptional similarities among creatures as different as frogs and people. All creatures with limbs, whether those limbs are wings, flippers, or hands, have a common design. One bone, the humerus in the arm or the femur in the leg, articulates with two bones, which attach to a series of small blobs, which connect with the fingers or toes. This pattern underlies the architecture of all limbs. Want to make a bat wing? Make the fingers really long. Make a horse? Elongate the middle fingers and toes and reduce and lose the outer ones. How about a frog leg? Elongate the bones of the leg and fuse several of them together. The differences between creatures lie in differences in the shapes and sizes of the bones and the numbers of blobs, fingers, and toes. Despite
radical changes in what limbs do and what they look like, this underlying blueprint is always present.

The common plan for all limbs: one bone, followed by two bones, then little blobs, then fingers or toes.

For Owen, seeing a design in the limbs was only the beginning: when he looked at skulls and backbones, indeed when he considered the entire architecture of the body, he
found the same thing. There is a fundamental design in the skeleton of all animals. Frogs, bats, humans, and lizards are all just variations on a theme. That theme, to Owen, was the plan of the Creator.

Shortly after Owen announced this observation in his classic monograph *On the Nature of Limbs*, Charles Darwin supplied an elegant explanation for it. The reason the wing of a bat and the arm of a human share a common skeletal pattern is because they shared a common ancestor. The same reasoning applies to human arms and bird wings, human legs and frog legs—everything that has limbs. There is a major difference between Owen’s theory and that of Darwin: Darwin’s theory allows us to make very precise predictions. Following Darwin, we would expect to find that Owen’s blueprint has a history that will be revealed in creatures with no limbs at all. Where, then, do we look for the history of the limb pattern? We look to fish and their fin skeletons.

**SEEING THE FISH**

In Owen and Darwin’s day, the gulf between fins and limbs seemed impossibly wide. Fish fins don’t have any obvious similarities to limbs. On the outside, most fish fins are largely made up of fin webbing. Our limbs have nothing like this, nor do the limbs of any other creature alive today. The comparisons do not get any easier when you remove the fin
webbing to see the skeleton inside. In most fish, there is nothing that can be compared to Owen’s one bone–two bones–lotsa blobs–digits pattern. All limbs have a single long bone at their base: the humerus in the upper arm and the femur in the upper leg. In fish, the whole skeleton looks utterly different. The base of a typical fin has four or more bones inside.

In the mid-1800s, anatomists began to learn of mysterious living fish from the southern continents. One of the first was discovered by German anatomists working in South America. It looked like a normal fish, with fins and scales, but behind its throat were large vascular sacs: lungs. Yet the creature had scales and fins. So confused were the discoverers that they named the creature *Lepidosiren paradoxa*, “paradoxically scaled amphibian.” Other fish with lungs, aptly named lungfish, were soon found in Africa and Australia. African explorers brought one to Owen. Scientists such as Thomas Huxley and the anatomist Carl Gegenbaur found lungfish to be essentially a cross between an amphibian and a fish. Locals found them delicious.

A seemingly trivial pattern in the fins of these fish had a profound impact on science. The fins of lungfish have at their base a single bone that attaches to the shoulder. To anatomists, the comparison was obvious. Our upper arm has a single bone, and that single bone, the humerus, attaches to our shoulder. In the lungfish, we have a fish with a humerus. And, curiously, it is not just any fish; it is a fish that also has lungs. Coincidence?
As a handful of these living species became known in the 1800s, clues started to come from another source. As you might guess, these insights came from ancient fish.

One of the first of these fossils came from the shores of the Gaspé Peninsula in Quebec, in rocks about 380 million years old. The fish was given a tongue-twister name, *Eusthenopteron*. *Eusthenopteron* had a surprising mix of features seen in amphibians and fish. Of Owen’s one bone–two bones–lotsa blobs–digits plan of limbs, *Eusthenopteron* had the one bone–two bones part, but in a fin. Some fish, then, had structures like those in a limb. Owen’s archetype was not a divine and eternal part of all life. It had a history, and that history was to be found in Devonian age rocks, rocks that are between 390 million and 360 million years old. This profound insight defined a whole new research program with a whole new research agenda: somewhere in the Devonian rocks we should find the origin of fingers and toes.

In the 1920s, the rocks provided more surprises. A young Swedish paleontologist, Gunnar Save-Soderbergh, was given the extraordinary opportunity to explore the east coast of Greenland for fossils. The region was terra incognita, but Save-Soderbergh recognized that it featured enormous deposits of Devonian rocks. He was one of the exceptional field paleontologists of all time, who throughout his short career uncovered remarkable fossils with both a bold exploring spirit and a precise attention to detail. (Unfortunately, he was to die tragically of
tuberculosis at a young age, soon after the stunning success of his field expeditions.) In expeditions between 1929 and 1934, Save-Soderbergh’s team discovered what, at the time, was labeled a major missing link. Newspapers around the world trumpeted his discovery; editorials analyzed its importance; cartoons lampooned it. The fossils in question were true mosaics: they had fish-like heads and tails, yet they also had fully formed limbs (with fingers and toes), and vertebrae that were extraordinarily amphibian-like. After Save-Soderbergh died, the fossils were described by his colleague Erik Jarvik, who named one of the new species *Ichthyostega soderberghi* in honor of his friend.
The fins of most fish—for example, a zebrafish (top)—have large amounts of fin webbing and many bones at the base. Lungfish captured people’s interest because like us they have a single bone at the base of the appendage. *Eusthenopteron* (middle) showed how fossils begin to fill the gap; it has bones that compare to our upper arm and forearm. *Acanthostega* (bottom) shares *Eusthenopteron*’s pattern of arm bones with the addition of fully formed digits.
For our story, *Ichthyostega* is a bit of a letdown. True, it is a remarkable intermediate in most aspects of its head and back, but it says very little about the origin of limbs because, like any amphibian, it already has fingers and toes. Another creature, one that received little notice when Save-Soderbergh announced it, was to provide real insights decades later. This second limbed animal was to remain an enigma until 1988, when a paleontological colleague of mine, Jenny Clack, who we introduced in the first chapter, returned to Save-Soderbergh’s sites and found more of its fossils. The creature, called *Acanthostega gunnari* back in the 1920s on the basis of Save-Soderbergh’s fragments, now revealed full limbs, with fingers and toes. But it also carried a real surprise: Jenny found that the limb was shaped like a flipper, almost like that of a seal. This suggested to her that the earliest limbs arose to help animals swim, not walk. That insight was a significant advance, but a problem remained: *Acanthostega* had fully formed digits, with a real wrist and no fin webbing. *Acanthostega* had a limb, albeit a very primitive one. The search for the origins of hands and feet, wrists and ankles had to go still deeper in time. This is where matters stood until 1995.

**FINDING FISH FINGERS AND WRISTS**

In 1995, Ted Daeschler and I had just returned to his house
in Philadelphia after driving all through central Pennsylvania in an effort to find new roadcuts. We had found a lovely cut on Route 15 north of Williamsport, where PennDOT had created a giant cliff in sandstones about 365 million years old. The agency had dynamited the cliff and left piles of boulders alongside the highway. This was perfect fossil-hunting ground for us, and we stopped to crawl over the boulders, many of them roughly the size of a small microwave oven. Some had fish scales scattered throughout, so we decided to bring a few back home to Philadelphia. Upon our return to Ted’s house, his four-year-old daughter, Daisy, came running out to see her dad and asked what we had found.

In showing Daisy one of the boulders, we suddenly realized that sticking out of it was a sliver of fin belonging to a large fish. We had completely missed it in the field. And, as we were to learn, this was no ordinary fish fin: it clearly had lots of bones inside. People in the lab spent about a month removing the fin from the boulder—and there, exposed for the first time, was a fish with Owen’s pattern. Closest to the body was one bone. This one bone attached to two bones. Extending away from the fin were about eight rods. This looked for all the world like a fish with fingers.

Our fin had a full set of webbing, scales, and even a fish-like shoulder, but deep inside were bones that corresponded to much of the “standard” limb. Unfortunately, we had only an isolated fin. What we needed was to find a place where whole bodies of creatures could
be recovered intact. A single isolated fin could never help us answer the real questions: What did the creature use its fins for, and did the fish fins have bones and joints that worked like ours? The answer would come only from whole skeletons.

Our tantalizing fin. Sadly, we found only this isolated specimen. Stipple diagram used with the permission of Scott Rawlins, Arcadia University. Photo by the author.
For that find, we had to search almost ten years. And I wasn’t the first to recognize what we were looking at. The first were two professional fossil preparators, Fred Mullison and Bob Masek. Preparators use dental tools to scratch at the rocks we find in the field and thereby expose the fossils inside. It can take months, if not years, for a preparator to turn a big fossil-filled boulder like ours into a beautiful, research-quality specimen.

During the 2004 expedition, we had collected three chunks of rock, each about the size of a piece of carry-on luggage, from the Devonian of Ellesmere Island. Each contained a flat-headed animal: the one I found in ice at the bottom of the quarry, Steve’s specimen, and a third specimen we discovered in the final week of the expedition. In the field we had removed each head, leaving enough rock intact around it to explore in the lab for the rest of the body. Then the rocks were wrapped in plaster for the trip home. Opening these kinds of plaster coverings in the lab is much like encountering a time capsule. Bits and pieces of our life on the Arctic tundra are there, as are the field notes and scribbles we make on the specimen. Even the smell of the tundra comes wafting out of these packages as we crack the plaster open.

Fred in Philadelphia and Bob in Chicago were scratching on different boulders at the same general time. From one of these Arctic blocks, Bob had pulled out a particular small bone in a big fin of the Fish (we hadn’t named it Tiktaalik yet). What made this cube-shaped blob of bone different
from any other fin bone was a joint at the end that had spaces for four other bones. That is, the blob looked scarily like a wrist bone—but the fins in the block that Bob was preparing were too jumbled to tell for sure. The next piece of evidence came from Philadelphia a week later. Fred, a magician with his dental tools, uncovered a whole fin in his block. At the right place, just at the end of the forearm bones, the fin had that bone. And that bone attached to four more beyond. We were staring at the origin of a piece of our own bodies inside this 375-million-year-old fish. We had a fish with a wrist.

The bones of the front fin of Tiktaalik—a fish with a wrist.

Over the next months, we were able to see much of the rest of the appendage. It was part fin, part limb. Our fish had fin webbing, but inside was a primitive version of Owen’s one bone–two bones–lotsa blobs–digits arrangement. Just as Darwin’s theory predicted: at the right time, at the right place, we had found intermediates between two apparently
different kinds of animals.

Finding the fin was only the beginning of the discovery. The real fun for Ted, Farish, and me came from understanding what the fin did and how it worked, and in guessing why a wrist joint arose in the first place. Solutions to these puzzles are found in the structure of the bones and joints themselves.

When we took the fin of *Tiktaalik* apart, we found something truly remarkable: all the joint surfaces were extremely well preserved. *Tiktaalik* has a shoulder, elbow, and wrist composed of the same bones as an upper arm, forearm, and wrist in a human. When we study the structure of these joints to assess how one bone moves against another, we see that *Tiktaalik* was specialized for a rather extraordinary function: it was capable of doing push-ups.

When we do push-ups, our hands lie flush against the ground, our elbows are bent, and we use our chest muscles to move up and down. *Tiktaalik*’s body was capable of all of this. The elbow was capable of bending like ours, and the wrist was able to bend to make the fish’s “palm” lie flat against the ground. As for chest muscles, *Tiktaalik* likely had them in abundance. When we look at the shoulder and the underside of the arm bone at the point where they would have connected, we find massive crests and scars where the large pectoral muscles would have attached. *Tiktaalik* was able to “drop and give us twenty.”
A full-scale model of Tiktaalik’s body (top) and a drawing of its fin (bottom). This is a fin in which the shoulder, elbow, and proto-wrist were capable of performing a type of push-up.

Why would a fish ever want to do a push-up? It helps to consider the rest of the animal. With a flat head, eyes on top, and ribs, Tiktaalik was likely built to navigate the bottom and shallows of streams or ponds, and even to flop around on the mudflats along the banks. Fins capable of supporting the body would have been very helpful indeed for a fish that needed to maneuver in all these environments. This interpretation also fits with the geology of the site where we found the fossils of Tiktaalik. The structure of the rock layers and the pattern of the grains in
the rocks themselves have the characteristic signature of a deposit that was originally formed by a shallow stream surrounded by large seasonal mudflats.

But why live in these environments at all? What possessed fish to get out of the water or live in the margins? Think of this: virtually every fish swimming in these 375-million-year-old streams was a predator of some kind. Some were up to sixteen feet long, almost twice the size of the largest *Tiktaalik*. The most common fish species we find alongside *Tiktaalik* is seven feet long and has a head as wide as a basketball. The teeth are barbs the size of railroad spikes. Would you want to swim in these ancient streams?

It is no exaggeration to say that this was a fish-eat-fish world. The strategies to succeed in this setting were pretty obvious: get big, get armor, or get out of the water. It looks as if our distant ancestors avoided the fight.

But this conflict avoidance meant something much deeper to us. We can trace many of the structures of our own limbs to the fins of these fish. Bend your wrist back and forth. Open and close your hand. When you do this, you are using joints that first appeared in the fins of fish like *Tiktaalik*. Earlier, these joints did not exist. Later, we find them in limbs.

Proceed from *Tiktaalik* to amphibians all the way to mammals, and one thing becomes abundantly clear: the earliest creature to have the bones of our upper arm, our forearm, even our wrist and palm, also had scales and fin webbing. That creature was a fish.
What do we make of the one bone–two bones–lotsa blobs–digits plan that Owen attributed to a Creator? Some fish, for example the lungfish, have the one bone at the base. Other fish, for example *Eusthenopteron*, have the one bone–two bones arrangement. Then there are creatures like *Tiktaalik*, with one bone–two bones–lotsa blobs. There isn’t just a single fish inside of our limbs; there is a whole aquarium. Owen’s blueprint was assembled in fish.

*Tiktaalik* might be able to do a push-up, but it could never throw a baseball, play the piano, or walk on two legs. It is a long way from *Tiktaalik* to humanity. The important, and often surprising, fact is that most of the major bones humans use to walk, throw, or grasp first appear in animals tens to hundreds of millions of years before. The first bits of our upper arm and leg are in 380-million-year-old fish like *Eusthenopteron*. *Tiktaalik* reveals the early stages in the evolution of our wrist, palm, and finger area. The first true fingers and toes are seen in 365-million-year-old amphibians like *Acanthostega*. Finally, the full complement of wrist and ankle bones found in a human hand or foot is seen in reptiles more than 250 million years old. The basic skeleton of our hands and feet emerged over hundreds of millions of years, first in fish and later in amphibians and reptiles.

But what are the major changes that enable us to use our hands or walk on two legs? How do these shifts come about? Let’s look at two simple examples from limbs for some answers.
We humans, like many other mammals, can rotate our thumb relative to our elbow. This simple function is very important for the use of our hands in everyday life. Imagine trying to eat, write, or throw a ball without being able to rotate your hand relative to your elbow. We can do this because one forearm bone, the radius, rotates along a pivot point at the elbow joint. The structure of the joint at the elbow is wonderfully designed for this function. At the end of our upper-arm bone, the humerus, lies a ball. The tip of the radius, which attaches here, forms a beautiful little socket that fits on the ball. This ball-and-socket joint allows the rotation of our hand, called pronation and supination.

Where do we see the beginnings of this ability? In creatures like Tiktaalik. In Tiktaalik, the end of the humerus forms an elongated bump onto which a cup-shaped joint on the radius fits. When Tiktaalik bent its elbow, the end of its radius would rotate, or pronate, relative to the elbow. Refinements of this ability are seen in amphibians and reptiles, where the end of the humerus becomes a true ball, much like our own.

Looking now at the hind limb, we find a key feature that gives us the capacity to walk, one we share with other mammals. Unlike fish and amphibians, our knees and elbows face in opposite directions. This feature is critical: think of trying to walk with your kneecap facing backward. A very different situation exists in fish like Eusthenopteron, where the equivalents of the knee and elbow face largely in the same direction. We start development with little limbs
oriented much like those in *Eusthenopteron*, with elbows and knees facing in the same direction. As we grow in the womb, our knees and elbows rotate to give us the state of affairs we see in humans today.

Our bipedal pattern of walking uses the movements of our hips, knees, ankles, and foot bones to propel us forward in an upright stance unlike the sprawled posture of creatures like *Tiktaalik*. One big difference is the position of our hips. Our legs do not project sideways like those of a crocodile, amphibian, or fish; rather, they project underneath our bodies. This change in posture came about by changes to the hip joint, pelvis, and upper leg: our pelvis became bowl shaped, our hip socket became deep, our femur gained its distinctive neck, the feature that enables it to project under the body rather than to the side.

Do the facts of our ancient history mean that humans are not special or unique among living creatures? Of course not. In fact, knowing something about the deep origins of humanity only adds to the remarkable fact of our existence: all of our extraordinary capabilities arose from basic components that evolved in ancient fish and other creatures. From common parts came a very unique construction. We are not separate from the rest of the living world; we are part of it down to our bones and, as we will see shortly, even our genes.

In retrospect, the moment when I first saw the wrist of a fish was as meaningful as the first time I unwrapped the fingers of the cadaver back in the human anatomy lab. Both
times I was uncovering a deep connection between my humanity and another being.