ACROSS *the* BRIDGE

Understanding the Origin of the Vertebrates

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Contents

CHAPTER 1

What Is a Vertebrate?

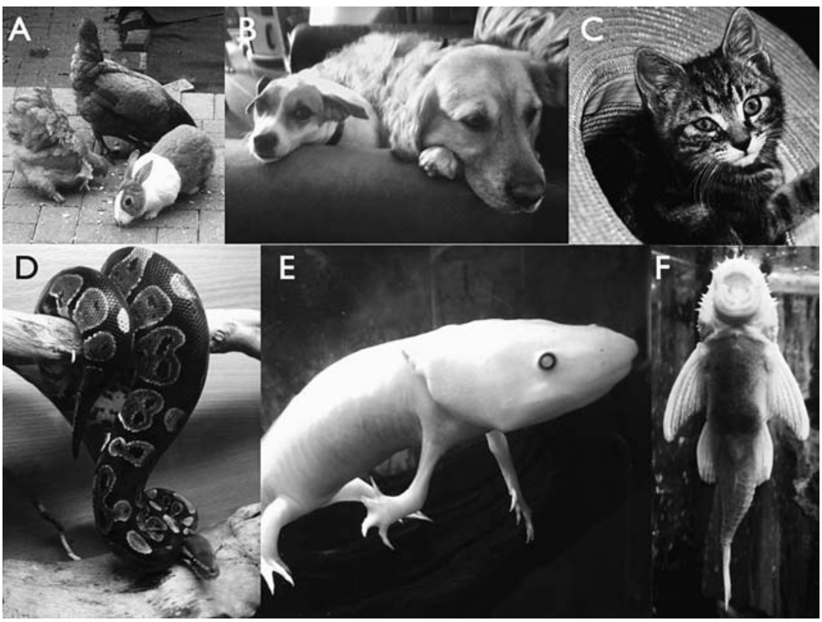
1.1 VERTEBRATES IN CONTEXT

Most familiar animals are vertebrates—that is, animals with backbones. We are vertebrates, as are most of our domestic animals, such as cows, horses, poultry, sheep, and pigs. The numerous animals housed at various times chez Gee—dogs, cats, chickens, rabbits, guinea pigs, hamsters, snakes, axolotls, and fish, not forgetting the frogs that crowd our garden pond each spring, are vertebrates.

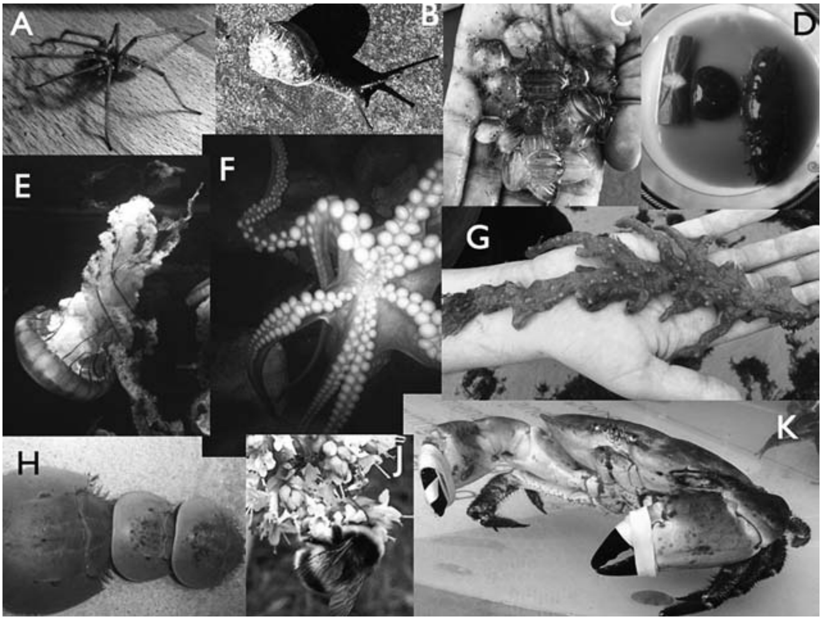
Most of the animals you will meet in a zoo, from lions to lorikeets, geckos to giraffes, are also vertebrates, so much so that non-vertebrates are usually confined to a single building labeled something like "creepy crawlies." The invertebrates, though, comprise a wider and more diverse domain than that. With a proper zoological perspective, vertebrates represent one rather small branch of a riotously various and diverse array of animal life. To understand vertebrates and how they evolved, one has to have a good overview of the entirety of animal life.[1]

Perhaps the most important invertebrates, at least in terms of numbers of species, are the insects. Many of these will be familiar to the most wildlife-averse urbanite, even if they are only flies and cockroaches (see fig. 1.2). Bees, ants, wasps, butterflies, moths, beetles, dragonflies, and grasshoppers are all familiar insects. Most known animal species are, in fact, insects. And yet insects form just one branch on the much more extensive tree of arthropods, or jointed-legged animals. Besides insects, this includes spiders, scorpions, ticks, mites, crabs, lobsters, centipedes, millipedes, barnacles, and other, less familiar creatures such as pycnogonids (sea spiders) and xiphosurans (horseshoe crabs).

Other invertebrates include mollusks such as clams, squid, slugs, and snails; as well as a diverse range of worms, jellyfishes, starfishes, sponges, and so on, to name just the more familiar among a still wider array of animals. Many of these are small, rare, or obscure, and known mainly to professional zoologists, or those students who, like me, liked to explore the dusty end of the textbook in search of unpronounceable exotica.



1.1 A selection of vertebrates. A: rabbit *Oryctolagus cuniculus* (mammal) and chickens *Gallus gallus* (birds); B: dogs *Canis familiaris* (mammals); C: cat *Felis domesticus* (mammal); D: royal python *Python regius* (reptile); E: axolotl *Ambystoma mexicanum* (amphibian); F: plecostoma, possibly *Pterygoplichthys* sp. (fish). Photographs by the author, from the author's menagerie.



1.2 A small selection of invertebrates. A: a house spider (arthropod); B: land snail (mollusk); C: a handful of sea gooseberries, *Pleurobrachia* (ctenophores); D: a sea cucumber (echinoderm): the rightmost object on the plate; E: jellyfish (cnidarian); F: octopus (mollusk); G: a colony of sea chervil, *Alcyonidium* (bryozoan); H: horseshoe crabs, *Limulus* (arthropod); J: bumble bee (arthropod); K: edible crab (arthropod). Photographs by the author.

Amateur microscopists will have seen the rotifers (wheel animalcules) and tardigrades (water bears) that swarm in water or crawl out of damp moss. Sharp-eyed beachcombers will have encountered sponges, tunicates, and bryozoa (moss animals). But it's a fair bet that most people will never have seen, or even heard of, priapulids, pogonophorans, placozoans, or phoronids, and those are just the ones I could immediately think of beginning with the letter *p*.[2] Yet each represents a "phylum," that is, a distinct and distinctive kind of animal life.

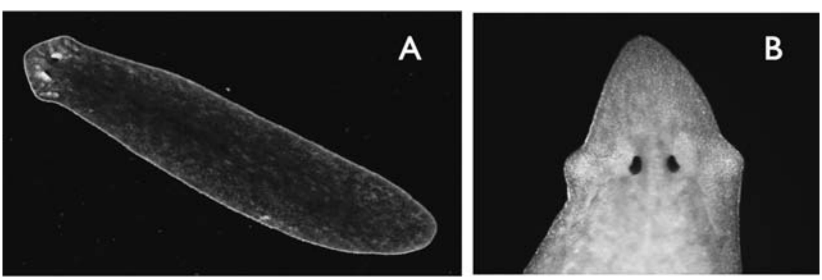
1.2 WHAT MAKES A VERTEBRATE?

Despite this diversity, vertebrates seem to stand apart. They are so different from other animals that recognizing a vertebrate seems almost instinctive. Could it be because we ourselves are vertebrates, and so recognize our kin, even if only from a distance? This is undoubtedly a reason, yet even when one discounts our very understandable prejudice, vertebrates do seem qualitatively different from other animals.

The presence of a distinct head is a vertebrate feature, and the characteristic vertebrate arrangement of a "face" with two eyes, set side-by-side, and a mouth beneath, might explain the almost universal feeling of kinship with all vertebrates, whereas the arrangements seen in other animals—whether a panoply of eyes, tentacles, or spiny mouthparts, or a front end that is featureless or eyeless—seem alien to us and might be greeted with horror. The emoticon of a smiley face ☺ typifies the vertebrate arrangement and has universal appeal, whereas people have to learn to love many-eyed spiders and eyeless worms. This is, in fact, proven in the breach. Tiny flatworms called planarians,[3] found in streams and ponds, are very different in their construction from vertebrates, and yet some have two large eyes at the front that make them seem curiously appealing, if not actually cuddly. You can see a couple of examples in fig. 1.3.

It's worth listing some of the many ways in which vertebrates differ from other animals. I'll go into these in much more detail later in the book, but for now it's worth rehearsing them, to get to grips with that feeling we have that there is a substantial gap between vertebrates and other animals, a chasm we need to bridge if we are to understand vertebrate origins.

I've already alluded to the presence of a head, and, in particular, a face. A head is a concentration, at one end of an animal, of entry points for air, food, and sensory information. A head, in such a broadly defined sense, is



1.3 The eyes of Planaria. A: *Cura* cf. *pinguis*, from Australia. The head is on the left, and the whole animal is about 4 mm long (courtesy Miquel Villa-Farre). B: a close-up of the head of another species *Dugesia sanchezi*, just to show it's not a fluke (courtesy Alejandro Sanchez Alvarado).

only to be expected in bilaterally symmetrical animals with a preferred direction of travel. Other such animals include insects and other arthropods. These, too, have heads, but they are constructed differently from the heads of vertebrates. Insect eyes are made in a completely different way from vertebrate eyes, being constructed of many repeated units (think of pixels) rather than a single, camera-like unit with a flexible lens, as found in vertebrates. Insects' ears are found on their legs, their noses on their feet; and they breathe not through their mouths, but through many tiny pores on their bodies. This suggests that the heads of insects and vertebrates evolved entirely independently, each from headless ancestors. This is supported by what we know of the evolutionary relationships of insects and vertebrates. Insects are more closely related to various more-or-less headless worms than to vertebrates. By the same token, the closest relatives of vertebrates among the invertebrates—the sea squirts, or tunicates, and the superficially fish-like amphioxus—do not appear to have distinct heads. However, I shall explain in this book, this does not mean that tunicates and the amphioxus do not have structures comparable with what we see in the vertebrate head—it is that they are not immediately obvious. Perhaps it is truer to say that these invertebrate relatives of vertebrates do not have the smiley faces we instinctively associate with the vertebrate state.

Vertebrates are built around an internal skeleton of cartilage, which in many cases is reinforced with harder tissues such as bone, dentine, and enamel. Although cartilage of various sorts is found throughout the animal kingdom,[4] bone, dentine, and enamel are tissues unique to vertebrates. The principal mineral constituent of vertebrate hard tissues is hydroxyapatite, a form of calcium phosphate. The shells and other hard tissues of invertebrates are made of a different substance, calcium carbonate.[5] The vertebrate skeleton comprises a brain case, housing the brain and sense organs such as the eyes, ears, and nose, to which might be attached skeletal supports for jaws and gill arches, and of course the backbone made of interlocking vertebrae, from which the group gets its name.

The skeleton also includes internal supports for fins and limbs, if present. During development, the backbone replaces a longitudinal stiffening rod called the notochord, which is found at some stage in the life cycle of vertebrates as well as tunicates and the amphioxus. Because of this, the vertebrates, the tunicates, and the amphioxus are united into a larger group, the chordates.

Along with the notochord, all chordates possess, at some part of their life cycle, a system of serially repeated pouches on each side of the throat region or pharynx, which in many cases pierce the body wall and open either directly to the outside, or into a protective cavity or atrium, which communicates with the outside through a smaller number of openings. In tunicates, the amphioxus, and the larvae of lampreys alone among vertebrates, these pharyngeal pores or slits form part of a unique filter-feeding system.[6] Water is taken in through the mouth and propelled, by currents generated by cilia, outward through the pharyngeal slits. Mucus secreted by the endostyle—a region of glandular cells in a longitudinal gutter on the pharyngeal floor—is carried up the cartilage-supported bars between the slits, trapping any water-borne debris before it escapes. The food-laden mucus makes its way to the roof of the pharynx where it enters the oesophagus and the digestive system. Tunicates and the amphioxus feed like this throughout life. Filter-feeding lampreys lose this arrangement at metamorphosis. The endostyle is transformed into the thyroid gland, and in adult lampreys and all other vertebrates, the pharyngeal slits are transformed into supports for gills used to extract oxygen from water and, in fishes, to excrete excess salt. In most tetrapods (that is, land-living vertebrates) the pharyngeal slits never form at all and the elements that otherwise would have made up their bony or cartilaginous supports become incorporated into the inner ear, the jaw, or the hyoid skeleton that supports the tongue.

Pharyngeal slits are found in animals other than chordates, notably marine animals called hemichordates,[7] even though these creatures do not appear to have endostyles, notochords, or other structures found in chordates. Hemichordates come in two forms: enteropneusts (acorn worms) and pterobranchs, neither of which will be familiar to anyone but professional zoologists. Enteropneusts are blind, brainless, flaccid, and sometimes foul-smelling worms that live in marine sediment; pterobranchs are small, often colonial organisms, feeding through an arrangement of tentacles called a lophophore.[8]

Some extinct echinoderms—a group of animals that today includes starfishes, sea urchins, and sea cucumbers—appeared to have had pharyngeal slits, although no extant echinoderm does so.[9] Hemichordates and echinoderms together form a group called the Ambulacraria, and ambulacrarians and chordates together form a larger animal group called the deuterostomes.

The notochord of chordates provides support and purchase for muscles and other tissues such as nerves and blood vessels, arranged in a series of segments called somites. Although many other animals are segmented—arthropods, as well as segmented worms or annelids—these segments are constructed entirely differently. Tunicates appear to have lost their segmentation in evolution, whereas the segmentation in amphioxus differs from vertebrate segmentation in important ways.

As the notochord develops during the life of a chordate embryo, it secretes substances that induce the development, dorsal to it (that is, along the upper surface, or back), of a hollow, longitudinal nerve cord, the basis of the vertebrate central nervous system.[10] The dorsal, hollow nerve cord is a unique feature of chordates. In all invertebrates that have a central nervous system, the nerve cord, if present, is ventral (that is, along the belly) and solid. Some invertebrates have two or more nerve cords. In some animals, paired, ventral cords are joined by cross-bridges at regular intervals like the rungs of a ladder.

The formation of the dorsal nerve cord is accompanied by the migration of cells from its lateral edges, along specified routes, to various parts of the body. These cells, collectively the neural crest,[11] are responsible for many uniquely vertebrate features such as the bones of much of the head and face; parts of the organs of special sense, notably the ears; the formation of the skin, its pigmentation, and its appendages such as scales, hair, feathers, and teeth; and other parts of the anatomy such as the spinal ganglia, the adrenal glands, the nervous system that lines the intestines, and parts of some major blood vessels. In that much of the instantly recognizable vertebrate face is formed by the neural crest, one could argue that this is the single most important defining feature of vertebrates. There are, however, traces of modest neural-crest-like activity in tunicates,[12] but none at all in the amphioxus or any other invertebrate.

Vertebrates have large brains. Nothing like the vertebrate brain is seen in either tunicates or the amphioxus, although there are traces of its ground plan in the amphioxus, tunicates, and even hemichordates, if one looks hard enough.[13] Other animals have brains, notably arthropods and mollusks, and in some cases these are elaborate structures associated with complex and even intelligent behavior. One thinks of the octopus, a famously canny creature with a large and complex brain. But the brains of invertebrates are constructed differently from those of vertebrates, and are not enclosed within that other distinctively vertebrate feature—the skull.

In addition to all the features mentioned above, vertebrates have a wealth of internal features that, although less obvious, are unique to the group and serve only to widen the gap between vertebrates and other animals. These include a water management system centered on the kidneys, which has allowed vertebrates, among only a select few animal groups and uniquely among deuterostomes, to live their lives entirely away from water. The kidneys are connected to a unique system of sex organs, which are in turn connected, chemically, to a sophisticated network of internal, hormone-based signaling, complementary to that of the nervous system. Although many animals (and plants) have a degree of innate immunity to agents of disease, which can on occasion be highly discerning and sophisticated, only vertebrates have a system of acquired immunity in which the cells of the immune system can be trained to recognize and neutralize threats never before encountered. All this and lymphatic drainage, a closed blood circulation with vessels lined with a specialized tissue called endothelium, and powered by a chambered heart. Because of these internal refinements, vertebrate animals can live a life much more independently of the environments in which they are found, compared with many other animals.

At a deeper level, the genome of vertebrates seems to have been duplicated—not once, but twice—at some point in the earliest history of the group,[14] although there is some debate about whether the second duplication happened before or after the emergence of the lineage leading to the most basal extant vertebrates, that is, the jawless hagfishes and lampreys.[15] It has been thought that genome duplication allows for an increase in complexity. If two genes are produced where there was one before, each one can evolve in its own way, perhaps allowing for previously unattainable subtleties in gene regulation, morphological specification, and so on. However, what seems to happen is that many of the duplicates are lost, so the connection between gene duplication and complexity remains moot. The genomes of teleost fishes—the group of bony fishes that includes most familiar kinds, such as the cod with your fries to the guppies in your aquarium—have undergone a further duplication,[16] and although these creatures exhibit a wide range of morphology (forms as varied as sea-horses and the ocean sunfish) they are all recognizably vertebrates.

The presence in vertebrates of the head, brain, hard tissues, notochord, distinctive nervous system, neural crest, kidneys, adaptive immune system, and so on, features seen nowhere else in the animal kingdom, serves to divide vertebrates from all other animals.

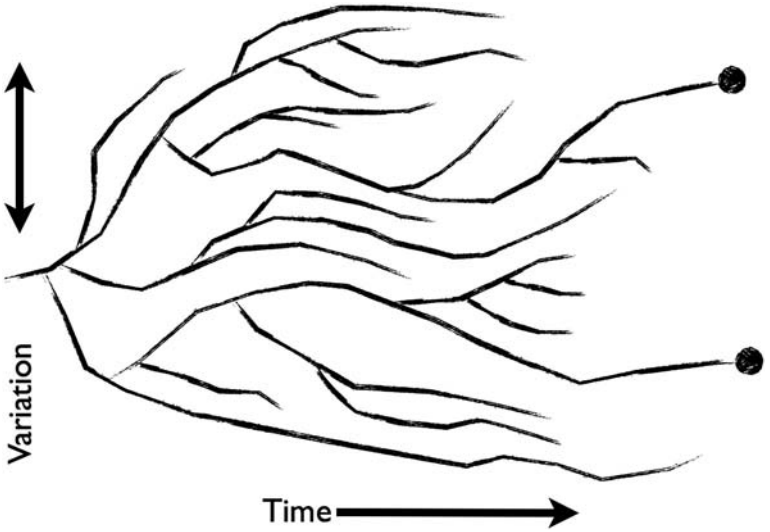
1.3 BREAKING BRANCHES

At first sight, many of the characteristic features of vertebrates appear to have evolved all at once. This explains why vertebrates appear so different from anything else in the animal world. However, it is legitimate to ask whether the apparently unique features of vertebrates evolved not simultaneously, but one at a time, and, if so, in which order; and whether some of them might be found, even if in some more modest form, among invertebrates.

These are reasonable questions, because we already know that some of the features we see in vertebrates, such as the neural crest, are to some extent presaged in tunicates; that the notochord and hollow dorsal nerve cord are also found in invertebrate chordates such as tunicates and the amphioxus; and that the pharyngeal gill slits are found in hemichordates and possibly some now-extinct echinoderms.

This allows us to reconstruct an order in which these features were acquired. Pharyngeal gill slits evolved first, in the common ancestors of all deuterostomes; with the notochord and hollow nerve cord evolving later on, in the common ancestor of all chordates. The rudiments, at least, of the neural crest appeared later still, in the common ancestry of tunicates and vertebrates. Therefore it should be possible to break down all the features we see in vertebrates and try to imagine how they might have evolved sequentially.

When new species evolve, they can be recognized as different because they have traits other species do not share. As the tree of life grows, twigs thicken into branches, branches into trunks, affirming these differences. The problem is that many of the twigs lower down the branches wither and die, removing evidence of intermediate stages, so it's hard to understand how species on one evolutionary branch come to look so different from those on another. When intermediate stages are removed, branches



1.4 Evolution and extinction in action. Reading from left to right, species diversify and separate, but as time passes, many lineages become extinct. The effect is that the few surviving lineages (marked with the black circles), each evolving in its own way, represent only a subset, and can seem so different from one another that it's hard to imagine how they are related.

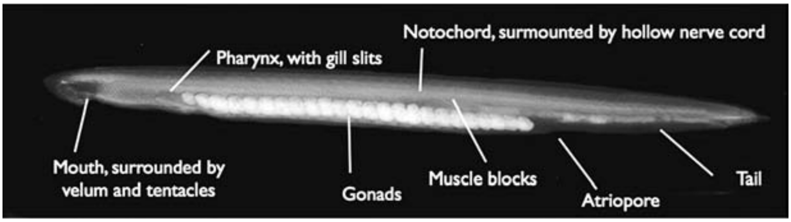
become denuded and bare, and yet seem to carry on uninterrupted. The effect will be to make the surviving species, at the ends of the branches, seem quite different from those on other branches (fig 1.4).

One could therefore recast the problem of the origin of vertebrates as what biologists call a "long branch problem." It could be that vertebrates seem so different from other animals because all the intermediate forms have disappeared. Such creatures might have had some of the traits we'd now see as quintessentially vertebrate, but not others: or showed, in one single species, a combination of traits now seen in totally separate groups. But these creatures are either undiscovered or have become extinct without trace. It would be especially interesting, for example, to find creatures that break the long branch between vertebrates and tunicates, which, despite their very different forms and lifestyles, are the closest living relatives among the invertebrates.

You might be tempted to call such a creature a "missing link," but if you are, you shouldn't.[17] The reason is that such a creature, were it ever found, has presumably not remained static, in evolutionary terms, existing for the sole purpose of our scientific enlightenment. It would have evolved from its common ancestor with vertebrates for the same length of time as vertebrates would have evolved from that same common ancestor. Furthermore, it would have accumulated unique traits all its own that might have had nothing to do with vertebrates, or any other living form. Because we cannot but interpret such a creature in the light of animals with which are already familiar, we are likely to be misled. If we came across a creature utterly unlike anything we have ever seen, how would we recognize it as an animal at all?[18]

If you need any proof of this idea in action, the tunicates themselves provide many examples. For more than a century it was thought that the amphioxus, not tunicates, was the closest relative of vertebrates. After all, it looks rather like a fish, with a clear front end and back end, and neatly arranged somites in between (fig 1.5).

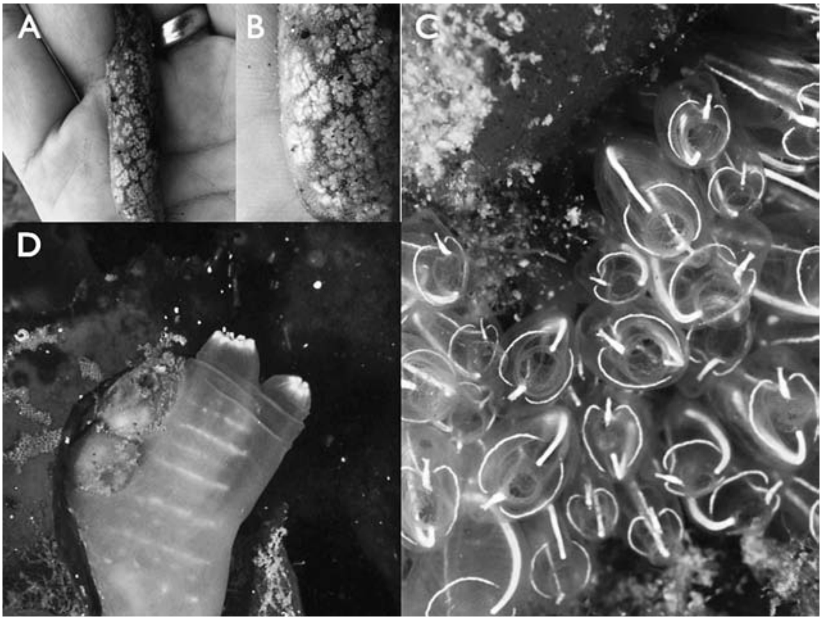
The discovery that tunicates were in fact more closely related to vertebrates[19] than the amphioxus was perhaps the most significant advance in the entire field in decades. It overturned the canonical picture of the steady acquisition of vertebrate complexity, from a tunicate-like chordate ancestor, through the development of an animal with somites, to a full-fledged vertebrate.[20] The shock, however, was visceral, because tunicates do not look much like vertebrates at all. Indeed, tunicates come in all shapes and sizes. They are solitary or colonial; they live attached to one spot throughout their lives; they move about freely; or, indeed, combinations of the above. Specimens of the colonial tunicate *Botryllus* I've found on the beach near where I live defy interpretation as anything at all. That the creature is a close relative of vertebrates seems unimaginable. Although many tunicates have notochords and dorsal, tubular nerve chords



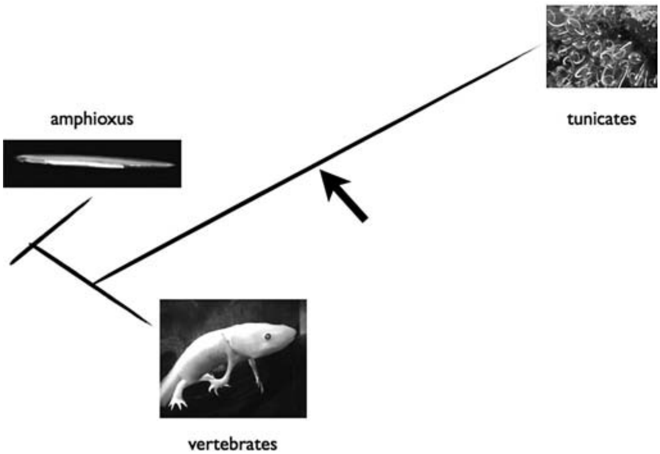
1.5 An adult amphioxus in lateral view, showing its major features. Photo courtesy of Dale Stokes.

in approved chordate fashion, most tunicates display these only fleetingly, during a brief, tadpole-like larval stage, and they are shed when the animal settles down to adult life. Although some tunicates, the larvaceans, retain this tadpole-like state into adulthood, many others have dispensed with it completely, leaving little or no sign of chordate heritage (fig. 1.6).

Clearly, tunicates have been so busily evolving away from their common ancestor with vertebrates, shedding canonically chordate features along the way, that it is now very difficult to imagine what the common ancestor of tunicates and vertebrates looked like, except that it must have looked a little like an amphioxus. However, tunicates only seem to be distant relatives because they have evolved much further from the common chordate ancestry than the amphioxus, or—in some ways—vertebrates themselves. Any and all intermediates that might have existed between tunicates and their common ancestor with vertebrates no longer exist, emphasizing the uniqueness of tunicates. Looked at from the perspective of tunicates, it is



1.6 Common tunicates from British waters. A: the colonial tunicate *Botryllus* on a piece of weed; B: close-up showing individual zooids. (Photos A and B by the author.) C: a group of the gregarious but non-colonial *Clavelina*; D: a solitary adult *Ciona*. (Photos C and D courtesy of Becky Hitchin.)



1.7 How to break a branch. In this phylogeny of chordates, the length of each branch represents a measure of relative evolutionary distance. Tunicates have evolved so far and so fast from their common ancestor of vertebrates that breaking down this evolution into steps seems hopeless. Any creatures we might find that branched off the tunicate line somewhere in the middle (bold arrow) could break that long branch, helping us to make sense of the evolution of tunicates.

they, not vertebrates, that occupy a special place in the animal kingdom (fig. 1.7).

1.4 SUMMARY

The problem with writing a book about vertebrate origins is working out where to begin. So I began at the beginning, setting the vertebrates in context as one twig in the great tree of animal life, briefly outlining the principal features that set them apart from the rest of the animal world. I showed that vertebrates join sea creatures called the amphioxus and tunicates in a more inclusive group, the chordates, united by a number of features including the notochord and the dorsal, tubular nerve cord. The chordates join hemichordates and echinoderms—collectively, the ambulacrarians—in a still more exclusive group, the deuterostomes. Perhaps the single most distinctive feature of deuterostomes is the presence of paired pharyngeal gill slits. I closed with the revolutionary discovery that tunicates, not the amphioxus, turn out to be the closest invertebrate relatives of vertebrates, even though tunicates do not look or behave very much like vertebrates. This leads us to the conclusion that the amphioxus is the most primitive chordate, and therefore that vertebrates have retained a more conservative form. The tunicates, in contrast, have explored realms of morphological space quite alien to vertebrates. Perhaps it is they, rather than vertebrates, that are special.

In the next chapter I shall introduce a little history. I shall briefly survey how scientists tried to organize animals into categories; how Darwin's ideas of evolution changed these ideas fundamentally; and how people approach classification today. This might seem like a digression, but it should give you the means necessary to understand concepts discussed further on in the book.