



Facing the World

THE EVOLUTIONARY INVENTION
OF THE ORIENTED BODY

William de France

CLEMENTINIUM EDITIONS

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Clementinium Editions

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“What an organism feeds upon is negative entropy.”

Erwin Schrödinger,
What is Life? (1944).

CONTENTS

<i>Foreword</i>	vii
<i>Prologue</i>	1
I THE QUESTION OF ENERGY	5
1 Living Means Eating the World	6
2 The Cambrian Feast	12
II THE PRECONDITIONS	18
3 A Body Without a Face	19
4 The Division of Labour	24
5 The Wheel-Shaped Body	29
6 The Third Layer	33
III THE INVENTION OF THE FRONT	38
7 Front and Back	39
8 The Tube	44

9	The Head	48
10	The Interior	52
11	The Repeated Body	56
12	Mouth First, Mouth Second	61
IV	THE THREE GREAT WAYS	67
13	The Armour	68
14	The Shell and the Tentacles	73
15	The Inner Scaffolding	78
V	OUT OF THE WATER	83
16	Walking	84
17	The Liberated Egg	89
18	The Warm Body	93
VI	THE DIRECTIONAL ANIMAL	98
19	The Forward-Looking Mind	99
20	Being an Animal with a Front	104
	APPENDICES	109
	<i>Annotated Bibliography</i>	111
	<i>Index of Names and Concepts</i>	119
	<i>Biological Glossary</i>	135

FOREWORD

This book grew out of a conversation in a garden. I was standing beside a friend, on a spring morning, looking at a snail moving slowly along the edge of a flowerpot. Half in earnest and half in jest, I told him the snail and I were relatives. This is literally true, since all animals share a common ancestor. But what came out next, and what I had never quite articulated before, was that there was something dizzying about that common ancestry. On our two branches of the family, everything since the last shared meeting had passed itself on to the next generation without a single break. Every one of the snail's ancestors, in their millions of generations since the Cambrian, had survived long enough to reproduce. Every one of my own ancestors, in their equally long line, had done the same. Not once in six hundred million years had any link in the chain failed.

The strange thing is that this is not a claim about my ancestors, or even about the snail. It is true of every living creature on Earth today. The oak at the end of the garden, the sparrow on its branch, the bacteria in the soil, the lichen on the wall, the reader of this book: each of them is the current end of a chain that has not broken in a billion years or more. To be alive at all, today, is to be the descendant of an uninterrupted succession. The mathematics of it is simple. The vertigo of it, once one has felt it, is not easily put down.

What I found myself most unable to shake, that morning in the garden, was the question of what the chain had been transmitting. Not bodies: bodies are born and decay. Not genes, exactly: genes change. The thing that has been transmitted, from one link to the next, is the form of a working animal, adjusted at each generation, sometimes modified, but sufficient at every step to keep the chain going. To ask what that form is, and how it came to be what it is, became for me, from that morning forward, a question I wanted to

try to answer at some length.

This book is that attempt. It does not try to cover the whole tree of life. It takes the particular branch on which the reader and I are sitting, the branch of the bilateral animals, and it asks: how did this branch come to have the body it has? Where did the front come from? The gut that runs through the body? The head that leads? The interior cavity that holds the machinery? The segmented structure that supports the muscles? The four limbs that walk on land? The warm body that operates in the cold? The brain that tries, at the far end of the chain, to understand its own origin? At each stage the book tries to give the specific answer the fossil record and developmental biology now make available, and to relate it to the one thing that, across all six hundred million years, has never stopped mattering: the energy that the animal must extract from the world to live.

The book is therefore about two things that travel together. On the surface, it is about the forms of the body. Underneath, it is about the energy budget those forms serve. Each of the twenty chapters that follow asks what a particular morphological invention is, and how it pays for itself. The two are not independent. The first could be read as the visible story, the second as the substrate that makes it possible.

A word on what the book is not. It is not a textbook of zoology. It is not a history of life in general; sponges, cnidarians, plants, and fungi appear only in comparison. It is not a history of the bilateral animals either, if one means by that a comprehensive account of all their lineages; many familiar groups are treated in a few lines, and many less familiar ones are left aside altogether. What the book attempts is a literary essay, in twenty chapters, on the particular thread of invention that runs from a flatworm on the Cambrian seafloor to the hand now holding this volume. It is written for anyone curious about biology without being a biologist, who enjoys the feeling of the particular arriving at the general, and who is willing to follow the thread where it goes.

If such a reader finds, at the end of the book, the vertigo I felt that morning in the garden, I will have done what I set out to do.

One last thing. The snail, after our conversation, went on about its business. It is probably still there, or one of its descendants is, leaving its silver trail along the edge of the flowerpot. The conversation continues with the reader instead.

PROLOGUE

Burgess Pass, British Columbia, 31 August 1909

Late summer in the Canadian Rockies, the long days of the expedition beginning to shorten. Charles Doolittle Walcott, Secretary of the Smithsonian Institution, is riding down a ridge with his wife Helena and three of their children. They are returning from a summer's fieldwork in the mountains, collecting fossils along the formations that sweep up from the plains toward the continental divide. The weather has turned, and snow will soon close the high passes. On the ridge between Mount Field and Wapta Peak, at something over seven thousand feet of elevation, Walcott halts the pack train beside a dark slab of shale that has fallen from the cliffs above.

He splits it with a hammer. Inside, pressed into the black rock as if into a page, are the bodies of creatures he has never seen.

They are small, mostly a few centimetres long, a few of them reaching a hand's breadth. Their outlines are preserved with an exactness he knows at once to be extraordinary. Walcott has collected fossils all his life. In ordinary conditions, what survives of an ancient animal is its hard parts: the shell of a brachiopod, the carapace of a trilobite, the bones of a vertebrate. Soft bodies disappear within weeks of death. Here, in the slab between his hands, are creatures whose entire anatomy has been preserved. He can see their gut contents. He can see the filaments of their gills. He can see the paired eyes of one and the five eyes of another.

He does not yet know the age. It will take the stratigraphers further work, over the following years, to establish that the formation dates from the middle Cambrian, five hundred and eight million years ago. What Walcott does know, within the first hour, is that he has

found a site unlike any previously recorded on Earth. He returns in 1910 to open a systematic quarry on the ridge. Over eight summers, until 1917, he and his family extract more than sixty-five thousand specimens. He describes them in a long series of papers. He assigns most of them, with the taxonomic conservatism of his generation, to groups already known: an arthropod here, a worm there, a sponge, a crustacean.

For more than fifty years the Burgess specimens rest in the drawers of the Smithsonian as unusually well-preserved examples of familiar animal plans. Then, in the late 1960s, a group of English palaeontologists begins to re-examine them. Harry Whittington at Cambridge, together with his students Derek Briggs and Simon Conway Morris, dismantles and redescribes one creature after another. What emerges over the following fifteen years is a conclusion that Walcott himself had not drawn. The Burgess fossils are not, for the most part, ordinary members of the animal phyla still alive today. Many of them are stranger. Opabinia has five eyes on stalks and a soft, grasping proboscis; it fits into no living group. Anomalocaris, the largest predator of its ecosystem, is a metre-long segmented swimmer with a pair of armoured appendages beneath a circular, plate-ringed mouth; it, too, has no close living relatives. Hallucigenia, at first reconstructed upside down because no one could believe the animal's true orientation, is a worm-like creature walking on seven pairs of clawed legs, its back bristling with seven pairs of rigid spines. The list goes on. A significant fraction of the Cambrian fauna, it turns out, belongs to body plans that no longer exist.

This finding, published by Whittington and his students across the 1970s and then narrated for the general reader by Stephen Jay Gould in Wonderful Life (1989), changed the shape of the question that had been asked about animal evolution. Until then, the dominant assumption had been that the living phyla represented, in essence, the exhaustive inventory of animal possibility. The Burgess fauna showed that the inventory had once been larger, and that what we call animal form today is a subset of what has existed.

The phyla we know are survivors of a wider Cambrian experiment. Some of the experiment failed, by chance or by selection, and left no descendants at all. Others left descendants that look nothing like themselves. The diversity of animal form, for the first time, became visible as a history rather than as a given.

From that recognition a further question began to take shape, which is the question this book attempts to answer. If animal forms are inventions, made once, in a particular order, under particular conditions, then we are entitled to ask why they are the forms they are. Why does an animal have a front? Why are most animals built along a single axis, with a mouth at one end and a gut that passes through them to the other? Why do the eyes, the sensors, the brain, gather themselves at that leading end? These features seem so obvious, and so nearly universal in the animals we encounter, that we tend to forget they are features at all. But the Burgess slab reminds us that they are. They were invented. There were moments, traceable in the rock, when they did not yet exist. And there are lineages, still alive today, in which they never arose. An adult sponge has no front. A jellyfish has none. A flatworm has the beginnings of one. A fruit fly, a fish, a human being: each is built around an axis along which one end of the body meets the world before the other.

The thesis of this book is that this axis, and the body plan that goes with it, is not a geometric accident but an answer to a problem. The problem is ancient. It is the problem all animals share, the problem that sets animals apart from the rest of life on Earth: animals do not make their own food. They must find it and take it in. Plants capture sunlight where they stand. Fungi dissolve the matter around them. Animals alone must search, pursue, seize, and ingest. The whole of animal biology, from the first cell specialisation to the vertebrate brain, can be read as a long exploration of this single constraint. How can a body extract more energy from the world, extract it faster, and use it more efficiently?

Bilaterality, this book will argue, is the invention that opened the widest path through this problem. An animal built around a

front-to-back axis can move toward what it needs. It can concentrate its senses in the direction it goes. It can organise its digestion as a pipeline rather than as a sack. It can specialise its tissues along its length. An animal built without that axis is limited to waiting. Sponges and jellyfish wait; they are magnificent at it, and they have been doing it for six hundred million years. But the line that led from a flatworm on the Cambrian seafloor to the creatures that later colonised the land, the air, and the company of one another, is the line that came to face the world. The Burgess slab caught that invention at the moment when it was beginning to radiate through every niche the Earth then offered.

The chapters that follow tell how this happened. They describe the conditions that had to be met before a directional body became possible: the oxygenation of the oceans, the specialisation of cells, the invention of a third embryonic layer. They follow the cascade that bilaterality set off once it arrived: the through-gut, the head, the coelom, the segmented body. They trace the three great strategies the descendants of the first bilaterian adopted for building themselves: the armour of the arthropods, the shell of the molluscs, the inner skeleton of the chordates. They describe how one of those strategies, hundreds of millions of years after its origin, left the water, became endothermic, and grew a brain large enough to ask what it was.

Throughout, a second thread runs beneath the first. Every morphological invention this book describes is, at its base, an energetic solution. The biology is visible; the thermodynamics is not, or not yet. But once the reader has seen the shark eating the seal, the worm advancing on a rock, the octopus opening a jar, it becomes harder and harder to avoid the recognition that what is really being made, in each of these cases, is a new way of converting the world into oneself.

This book is, in the end, an attempt to say what kind of creatures we are by saying what kind of problem animals have been working on for six hundred million years, and what the body we inherit evolved to address.

PART I

THE QUESTION OF ENERGY

I

LIVING MEANS EATING THE WORLD

A great white shark rises beneath a seal in a stretch of dark green water off the coast of South Africa. The seal is diving from a rock where it has been resting. For an instant, the two bodies are on the same vertical line, one ascending and the other descending. Then the shark's mouth closes and the surface of the water breaks in a plume of white spray and blood. The scene lasts a second. It has been filmed thousands of times by now, by patient crews on pitching boats, and sold to television audiences as an illustration of nature's violence. The violence is real. What is also real, and more to the point for the argument of this book, is that for the shark to keep existing, the seal must be converted into shark. The seal's tissues must be broken down, its proteins disassembled, its fats oxidised, its calcium repurposed. The seal must, in a sense that does no violence to the biology, become the shark.

All animal life rests on this fact. An animal is, by one of the sharpest definitions biology has given itself, a creature that does not make its own food. The plant, rooted in the ground, catches the energy of the sun by its leaves and builds its own body from it, molecule by molecule. The fungus, invisible for most of its life, dissolves what lies around it with acids secreted by its threads and absorbs the results. The animal does neither. It must find its food. It must approach it, seize it, tear it, swallow it, and break it down. Every morning, in every ocean and every forest, an enormous mobilisation begins at first light, in which animals of every size set out to encounter and incorporate other pieces of the world.

This is the primary peculiarity of animal life. The fundamental

characteristic, at the root of the branch of life to which we belong, is to go looking.

Consider the daily energy budget of a human being. An adult of average size burns about two thousand kilocalories a day simply to stay alive and modestly active. Of that, about a fifth, some four hundred kilocalories, goes to the brain, a tissue that represents two per cent of body mass and consumes twenty per cent of the energy. The rest is distributed among the heart, the liver, the muscles, the digestion itself (which costs its own share to run), the kidneys, and the maintenance of body temperature. A human body that receives less than this, over any stretch of time, loses mass. A human body that receives none of it, for a long enough stretch of time, dies.

Now shift the scale. A shrew, one of the smallest of the mammals, weighs a few grams and runs at a metabolic rate far higher, per unit of body mass, than ours. It burns about ten times as much energy per gram as we do. It is a warm animal inside a tiny body that loses heat extremely fast, and to compensate, it must eat almost constantly. A shrew will die if it cannot feed for more than a few hours. Its heart beats six hundred times a minute. At the other end of the scale, a jellyfish drifting in the surface waters of a temperate sea burns, per gram, perhaps a tenth of what we do. It has almost no warm tissue, almost no muscular activity beyond slow pulses, and it eats infrequently. It lives on a budget so modest that, in some species, it can persist for months with very little input. Each of these creatures occupies a different place on a single spectrum of energetic intensity. Each has, over evolutionary time, balanced a budget.

Nothing in biology escapes this budgetary constraint, because nothing in biology can. An animal whose budget is not balanced does not live. The phrase is more than a metaphor. If the energy extracted, day by day, is less than the energy spent, the body consumes itself and eventually stops. Selection takes no account of intentions; only the balance of inputs and outputs matters. The animals alive today are the descendants of lineages that, without

interruption, balanced their budgets for every generation of the last six hundred million years.

What kind of object is an animal, seen from this vantage? A physicist, looking at it from outside the particular history of biology, would be tempted to call it a dissipative structure. A dissipative structure is a pattern that maintains itself by the continuous flow of energy passing through it. The flame of a candle is a dissipative structure; so is a hurricane; so, in their different ways, are a cell, a tree, and a shark. Each takes in energy in a concentrated form (the wax, the warm ocean, the seal) and releases it in a dispersed form (heat, spent air, waste). The structure is stable not because nothing is happening but because the flow is maintained. Stop the flow, and the structure falls apart.

Presented this way, the second law of thermodynamics, the general statement that isolated systems tend toward disorder, is not violated by the existence of life. It is, on the contrary, the engine of life. Life is a local eddy in the general current of disorder. It imports order, in the form of molecules rich in energy and low in entropy, and exports disorder, in the form of heat dispersed into the environment. The order it keeps inside itself is bought at the price of a larger disorder released outside. Seen from the point of view of the whole system, the universe becomes less ordered every time a shark eats a seal. The shark is betting, not against the second law, but on a small local reversal that the second law permits, as long as something else, somewhere, produces more disorder.

For the biologist, the same question also breaks down into practical terms. The energy question, for an animal, breaks into three distinct problems, each of which sets a different evolutionary challenge.

The first problem is extraction. How does the animal obtain food at all? The food is out there, contained in other bodies, and the animal must find it, reach it, and seize it. An animal that filters water for particles has solved extraction passively, by letting the sea bring food to it. An animal that chases its prey has

solved it actively, by going to find the food. The history of animal morphology, from the sponge to the shark, is a long exploration of the strategies of extraction. Each strategy has its costs and its yields, and the ratio between them, more than any aesthetic principle, decides what survives.

The second problem is processing. Once the food has been extracted, it must be turned into energy the body can use. Raw food is not energy; it is a complicated package of molecules in which energy is locked in chemical bonds. To release the energy, the body must digest the food, absorb the products, and deliver them to the cells that will burn them. Every step of this sequence is a place where efficiency can rise or fall. A digestive system that processes food poorly returns less energy to the animal than the same food would return elsewhere. A circulatory system that distributes the results poorly starves the cells far from the gut. Over the long run, the quality of processing is as decisive as the quality of extraction, and it accounts, as later chapters of this book will suggest, for some of the oldest and most fundamental inventions of animal morphology.

The third problem is expenditure. Once the animal has extracted food and processed it into usable energy, the question remains of how to spend the energy. Spending is not a trivial problem. An animal that spends its budget extravagantly, on brain tissue for instance, or on maintaining a high internal temperature, gains certain capabilities at a certain cost. It can think faster; it can act in cold environments; it can sustain longer activity. But it must then extract more food to pay for what it has committed itself to. An animal that spends minimally can survive on very little, but it can do less. There is no universally best strategy, and the history of life has produced essentially every combination of strategies that the constraint admits.

The chapters that follow will argue that every major morphological invention of the animal kingdom addresses at least one of these three problems. Bilaterality, to which several chapters

are devoted, is above all an invention about extraction: it allows an animal to move toward its food rather than wait for it. The coelom and the mesoderm, inventions of the same epoch, are about processing: they make possible the complex internal machinery, from circulation to digestion, that turns extracted food into delivered energy. Endothermy, the capacity to maintain a warm internal temperature, is about expenditure: it pays an enormous cost in energy to buy a return in constancy of action. These three fronts, visible in the plan of the book, are nothing other than the three fronts on which the budget of every animal is always being negotiated.

The creatures encountered in this first chapter will recur throughout the book. The shark is the figure of the animal as active predator, a body built for extraction, its morphology essentially a muscle organised around a mouth. The jellyfish is the figure of the animal as minimal budget, still extraordinarily successful after six hundred million years of doing almost nothing. The shrew is the figure of the animal committed to a high expenditure strategy, a life lived at full speed, paid for by constant effort. The human is the figure of the animal that carries the most expensive of all animal organs, the large and metabolically demanding brain, pressed to the limit of what the body can support. Each is a different answer to the same underlying question. Each is a different combination of solutions on the three fronts.

But this way of seeing animal life, as a long exploration of how to balance the energetic equation, leaves unanswered the question of why the exploration happened at all. The Earth has had life, of some kind, for nearly four billion years. It has had animal life of any serious complexity only for the last six hundred million. For most of the planet's biography, the energetic game that this book describes was not even available. The fuel for it, the free oxygen on which all aerobic metabolism depends, was absent from the atmosphere in the quantities it would require. An animal of any significant size, with muscles to move and a brain to run and a

body to keep warm, is a late device on Earth. The conditions that made it possible converged at a specific threshold and released, at the other side of that threshold, the diversity we still live within.

That threshold, and the feast that followed its crossing, are the subject of the next chapter.

2

THE CAMBRIAN FEAST

A shallow sea, five hundred and twenty million years ago, somewhere in the tropics of a world whose continents bear no resemblance to any modern map. The light comes down through clear water to a floor of fine mud. Drifting over the mud, or crawling across it, or swimming a little above it, are creatures that belong, together, to one of the densest assemblies of novel life ever to have existed. A metre-long segmented swimmer sweeps past, a pair of armoured, grasping appendages beneath a circular mouth; this is *Anomalocaris*, the largest predator of its ecosystem. Half-buried in the sediment is a five-eyed animal with a soft, grasping trunk, *Opabinia*. Clusters of trilobites hunt small prey or pick at the mud. Spiky, worm-shaped forms creep along on multiple pairs of legs. Soft bodies of many other creatures, preserved in the mud by the accident of an undersea slide, will be found four hundred million years later, in the Rockies of British Columbia and the mountains of Yunnan, and will give their names to Cambrian palaeontology.

For nearly fifty years after the Burgess Shale was first opened to serious scrutiny, the question that haunted the fossils was not *what* they were but *why they were there at all*. What had happened in that particular interval of geological time, brief by the standards of the Earth's biography, that produced such a sudden proliferation of forms? For three billion years before, since the first microbes formed in the young oceans, life had been microscopic, or nearly so. Molecular clocks place the origin of sponges around seven hundred million years ago, soft-bodied creatures not much more complicated than animated sheets. Cnidarians, the jellyfish and their relatives, followed. For the hundred or two hundred million

years before the Cambrian, shallow seas were populated by animals of which most were sessile, radially symmetric, modest in size, slow in their movements, limited in what they could do, and dependent on filter-feeding. Then, in the space of perhaps twenty million years, at the opening of the Cambrian period five hundred and thirty-nine million years ago, most of the major animal body plans that we know today appear in the fossil record. Almost nothing that came after, in half a billion years, is qualitatively new. What we call the diversity of animal life was, to a first approximation, in place by the middle of the Cambrian.

The temptation, in the nineteenth century, had been to treat this fact as evidence against deep evolutionary continuity: animal life appeared suddenly, as if decreed. Darwin himself, writing in 1859, acknowledged the apparent suddenness as a serious difficulty for his theory, which required long, gradual lineages. The difficulty was, for a long time, unresolved. It began to resolve itself in the second half of the twentieth century, as the geological record was better understood and the chemistry of the ancient atmosphere reconstructed. The answer that has come out of this reconstruction is not philosophical but thermodynamic. The Cambrian explosion, before it is an explosion of forms, is an explosion of energy.

For most of its existence, the Earth's atmosphere contained little free oxygen. The early atmosphere, formed from volcanic outgassing, was rich in carbon dioxide, methane, and water vapour. Oxygen, a highly reactive gas, was absent. Free oxygen first appeared, around two and a half billion years ago, as a by-product of the new biochemical invention of photosynthesis, developed by some of the bacteria that then ruled the planet. The oxygen they released reacted at once with the iron dissolved in the seas, which precipitated as vast banded iron formations still visible in Australia and South Africa. Only after the oceans had rusted did free oxygen begin to accumulate in the atmosphere. This first rise is called the Great Oxidation Event; it brought atmospheric oxygen to perhaps

a few per cent of its modern level, where it stayed for a long and eventless billion years.

The critical change, for the purposes of animal life, came much later. Beginning around eight hundred million years ago, and continuing through the Neoproterozoic era into the opening of the Cambrian, a second rise took oxygen from that first plateau to something approaching the concentration we breathe today. The causes are still debated: a combination, probably, of tectonic movements that buried organic carbon (removing it from the atmospheric cycle), of glaciations that rearranged the oceans, of changes in the biosphere itself. What is agreed is that, toward the end of this interval, a threshold was crossed. Free oxygen in the atmosphere and, more importantly, in the dissolved form in which marine animals can actually use it, reached concentrations that had not previously been available on Earth.

Why does this change everything? Why should oxygen, rather than any other gas, unlock a new regime of animal life?

The answer lies in the arithmetic of cellular metabolism. A living cell obtains its energy by breaking down molecules of fuel, most often sugars, into simpler products and capturing the energy released in the process. If the fuel is broken down without oxygen, by the process called fermentation or anaerobic metabolism, the cell can extract only a small fraction of the chemical energy that the sugar contains. The end products (ethanol, lactic acid) still hold much of the energy, and the cell leaves it in them. If the fuel is broken down with oxygen, by aerobic respiration, the process goes all the way to carbon dioxide and water, and nearly all of the chemical energy is captured. In the accounting of a biochemistry textbook, a molecule of glucose fermented anaerobically yields two units of useful energy; the same molecule, oxidised aerobically, yields roughly thirty. For the same amount of food, the aerobic cell obtains nearly an order of magnitude more useful energy than the anaerobic cell. It is the difference between burning wood and burning petrol.

The cellular machinery for aerobic respiration existed long before the Cambrian. It sits today in every animal cell in a small organelle called a mitochondrion, inherited from a bacterial symbiont that was absorbed into an ancestral cell more than a billion years ago. The trick was already learned; the fuel was not available. Before the Neoproterozoic rise of oxygen, aerobic respiration was possible only locally, in the small volumes where oxygen happened to be available. A large animal, with muscles to drive and a nervous system to run, could not be supported by anaerobic metabolism alone: the yield is too low. Something had to change outside the cells, in the atmosphere and in the oceans, for the cellular machinery to be fed the fuel it could burn at full capacity. That change came in the hundred million years or so leading up to the Cambrian.

Once oxygen became abundant, the race began. Energy, previously rationed, was now available in quantities that made new ways of life possible. Being larger paid, because a larger predator could overpower smaller ones, and a larger prey could endure a wound. Being faster paid, because a faster hunter caught more and a faster prey escaped more often. Being able to see paid, because early detection is cheap energy compared with late detection. Being able to think paid, because a predator that anticipates its prey expends less than one that blunders through the water. Each of these capabilities cost additional energy to build and to maintain. Each, in the oxygen-rich seas of the early Cambrian, could now be paid for. The explosion we see in the fossil record is the result of lineages discovering, more or less simultaneously, that they could afford what had previously been unaffordable.

One point must be made against a common simplification of this picture. The Cambrian did not replace the earlier plans with newer, better ones. It added new plans to the old. Sponges were there; sponges are still there, on reefs, in deep water, ancient filterers on a modest budget. Cnidarians were there; cnidarians are still there, drifting in the open sea as jellyfish, building reefs as corals,

clinging to rocks as anemones. The creatures of the Cambrian explosion (the trilobites, the anomalocarids, the priapulids, and all the others from whose descendants the arthropods, the molluscs, and the chordates would eventually emerge) joined a cast that did not scatter. The diversity of animal life today is not a pyramid crowned by one invention; it is a fan, spread wide, of coexisting strategies from several different eras, each playing its own game. To describe the Cambrian as the birth of modern animals is, in this sense, misleading: what was born in the Cambrian was a new kind of animal, fast, directional, high-budget, that took its place beside older kinds that had, and still have, their own reasons to persist.

The creatures of the Cambrian, read from the vantage that will guide the rest of the book, are experiments in how to spend a newly available energetic budget. *Anomalocaris*, at a metre long, was spending a great deal. To propel its segmented body through the water, to close its armoured appendages on a trilobite, to watch the sea through compound eyes mounted on stalks, the animal had to sustain a metabolism that would have been impossible a few tens of millions of years earlier. *Opabinia*'s five eyes, on their moving stalks, are an unusually pure experiment in investment in sensory capacity; whatever it did with all those eyes, it was the sort of investment an animal can only make when the oxygen is there to run the neurons. The trilobites, whose hard carapace preserves them more often than the soft-bodied forms, were themselves, for their time, unusually quick and mobile. Each of these creatures, and each of the lineages they belonged to, was an experiment in the new arithmetic of a breathable sea.

For the remaining chapters of the book to make sense, one more thing must be said. The Cambrian explosion, remarkable as it is, did not invent its lineages from nothing. It could not have. No explosion of biological forms at that scale is possible without a prior accumulation of tools, deployed and tested, waiting to be assembled. The kinds of cells that build a trilobite, the kinds of

tissues that make its muscles contract, the kinds of embryological processes that produce its segmented body: none of these were invented in the twenty million years of the explosion itself. They had been invented, one by one, during the preceding hundreds of millions of years, at a slower rhythm, by organisms less spectacular in the fossil record and often not preserved at all. The Cambrian, in this sense, was the moment at which a long-prepared kit was suddenly assembled at high speed. The chapters that follow describe the kit.

*PART II**THE PRECONDITIONS*

3

A BODY WITHOUT A FACE

In 1883, in the aquarium of the Zoological Institute of Graz, the biologist Franz Eilhard Schulze found, creeping along the glass of a seawater tank, an organism so strange that he was not immediately sure what it was. A flat oval of cells, a millimetre across at most, moved by extending one margin and drawing itself toward it. It had no visible organs. It had no head, no mouth, no gut, no nervous tissue, no muscles in any recognisable sense. Under the microscope it showed only two layers of cells above a narrow middle, and within each layer the cells were of only a few types. Schulze described it briefly and gave it a name, *Trichoplax adhaerens*, the adhesive hairy plate, and left to later biologists the question of what, exactly, this creature was.

More than a century of further examination has not fully answered the question, though it has placed *Trichoplax* more firmly in the tree of animal life. The organism belongs to a phylum of its own, the Placozoa, a group with, as of the most recent revisions, just a handful of described species. It feeds by settling over a patch of algae or bacteria and secreting, onto the substrate directly below its ventral surface, enzymes that digest the food externally; the digested products are then absorbed back through the cells of its lower side. It has no specialised tissues of the kind that distinguish most other animals. It lacks neurons in the usual sense, though the cells of its upper layer communicate chemically. It reproduces, under the conditions of the aquarium, by fission: an adult individual pinches itself in two and the two halves go their separate ways.

If one wanted a concise demonstration that “animal” is a

threshold rather than a given, it would be difficult to improve upon *Trichoplax*. It is alive. It is multicellular. It moves. It eats. And yet if one asked, of this flat plate, where is its front, where is its head, what direction is it facing, the questions have no clear answer. There is an upper surface, which does not eat, and a lower surface, which does. Beyond that distinction, the animal has no orientation. No direction is privileged for it. The world comes to it equally from every side.

Trichoplax is an extreme case, a living reminder of how little, at the limit, an animal needs to be. But the more instructive creatures, for the understanding of animal life before the emergence of the directional body, are the sponges. The sponges (phylum Porifera, “the pore-bearers”) are a far larger and far more widely distributed group. They have occupied shallow and deep seas since at least the late Precambrian, perhaps earlier; molecular-clock estimates place their origin somewhere between seven hundred and nine hundred million years ago. They have also occupied a distinctive architectural niche, which they have held, essentially unchanged, for all of that time.

A sponge, seen from the outside, resembles a vase, a cushion, a branching shrub, or a thin crust on a rock. Seen from the inside, it is a more interesting object. Its body is perforated by a fine network of channels. Sea water, drawn in through many small pores on the surface (the *ostia* from which the phylum takes its name), flows through these channels and exits through a smaller number of larger openings (the *oscula*). Along the walls of the channels are arranged cells of a remarkable kind, the choanocytes, or collar cells, each bearing a long whip-like flagellum surrounded by a collar of fine microvilli. The flagella beat in coordinated waves, and together they drive the flow of water through the entire network. As the water passes, the collars filter out the bacteria and other fine particles that provide the sponge with its food. A large sponge may move several thousand litres of water a day through its channels. Its feeding is entirely internal; its motion, zero.

The sponge is oriented, in a limited sense, with respect to gravity and the substrate: one side is anchored, the other exposed. It is not oriented with respect to the water, or the food, or any direction in the ecological world in which it lives. The water brings food from every side. The sponge does not need to face any particular direction, because no direction, for it, is preferred. In the terms introduced in the previous chapter, the sponge has solved the problem of extraction passively, by persuading the environment to do the work. It filters; it does not hunt.

There are things a sponge cannot do. It cannot approach. It cannot pursue. It cannot flee. It cannot distinguish one direction of the world from another. It cannot, except in the slow response of the body as a whole to local damage, produce anything like what an animal with a nervous system would call a reaction. What one might call the experience of the sponge, if one wanted to speak poetically, is a state without tense, without agency, without a direction in which the future lies. Every direction is equally the future. None is privileged. Nothing approaches; nothing is approached.

It would be misleading, however, to present this mode of existence as a defective or unfinished form of animal life. The sponges are not failures of the directional body; they are successes of a different body altogether. They have persisted, in essentially their present architecture, since before the Cambrian. They survived each of the mass extinctions that swept across the Earth in the intervening half-billion years, often while more agile and more sophisticated lineages went under. They occupy habitats, from coastal shallows to the abyssal plain, in which other animals cannot live. Some of them, the glass sponges of the deep ocean, have been shown to reach individual ages of several thousand years. They are champions, in other words, of a particular strategy: architectural economy, robust simplicity, and longevity. The costs of being directional (a nervous system to run, muscles to maintain, sensory organs to keep calibrated, a whole internal machinery that

demands food) are costs the sponge lineage never incurred, and not incurring them bought it a kind of evolutionary patience that the faster lineages have had no reason to match.

ENERGETIC READING. The sponge is the most minimalist of all the energetic strategies that the animal kingdom has tried. It lets the water do the work. It spends little because it acts almost not at all, and it has balanced its budget, successfully, for hundreds of millions of years on this near-zero level of expenditure. Sobriety of this depth has its own reward: a length of evolutionary persistence that the more active lineages, with their higher budgets and their correspondingly higher risks, have not matched. But sobriety also has a ceiling. One does not build a brain, a jaw, an eye on a tiny budget. To do more than filter, to chase prey rather than wait for it, to see a predator before it arrives, to think at all, an animal would have to spend more, and therefore to extract more. The rest of the animal kingdom is, in the most economical description, the story of lineages that made this bet and lived with the consequences.

Something was, however, already moving. Even within the world of non-directional animals, one can trace the first tentative steps toward the differentiated body. *Trichoplax* itself has a handful of distinct cell types, each specialised for a particular task. Sponges, although they are often described as lacking true tissues, have at least six or seven cell types, each doing work the others cannot: the choanocytes drive the water and capture food, the porocytes form the pores, the archaeocytes differentiate as needed, the pinacocytes line the surface. None of this is a tissue in the full sense, but it is a division of labour at the cellular level; it is the first, cautious step away from the uniform cell mass.

That step, once taken, would never be taken back. For an animal to do more than wait, its cells had to become different from one another. They had to specialise. And specialisation, as the next chapter will show, is the hinge on which all subsequent

morphological complexity turns.

4

THE DIVISION OF LABOUR

Under the microscope, a neuron is a cell drawn out into filaments. At one end of its body, a tree of short, branching extensions, the dendrites, receives signals from the neurons around it. From the other end, a single long fibre, the axon, extends for a distance that in some cases, in large animals, exceeds a metre. The axon ends in its own fine branching, where it passes its signal to the next cell in the chain. Everything about the neuron's shape is subordinated to a single function: the propagation of an electrical and chemical message from one place to another. The neuron cannot divide. In most animals, it cannot be replaced if it dies. It cannot digest food; it cannot contract; it cannot sense light, or pressure, or temperature, except through the specialisations of its receiving membrane. It has given up everything that a generic cell can do, in exchange for being able to do one thing with exceptional reliability and speed.

The neuron is an extreme example of a principle that runs through the whole of animal biology. The principle is that a mass of identical cells can do, at most, one thing at a time, and only what any of its cells alone can do. To build an animal capable of sensing, contracting, digesting, reproducing, defending itself, and coordinating its behaviour, the cells must be different from one another. They must specialise.

The fact that they can specialise is, in itself, strange. The cells of an animal are, with few exceptions, genetically identical. The cell that will become a neuron and the cell that will become a muscle fibre inherit the same genome from the same fertilised egg. They will in the end switch on different subsets of the same set of