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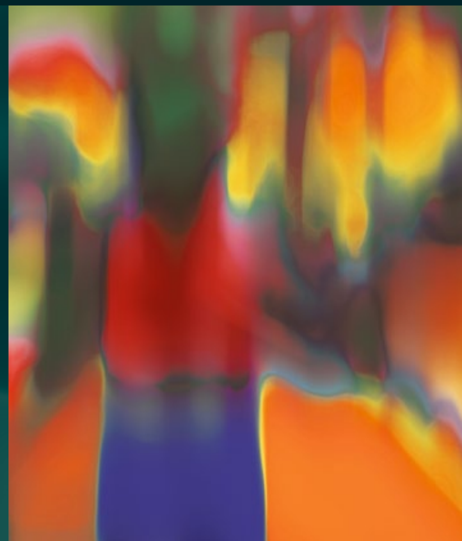

Sonya Bahar

THE ESSENTIAL TENSION

Competition, Cooperation and Multilevel Selection in Evolution

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The Essential Tension

Competition, Cooperation and Multilevel Selection in Evolution

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for

Frank Moss

1934–2011

& for C & D

Acknowledgements

There are many people I could acknowledge, but I don't want this to sound like the Oscars, so I will limit myself to the essential thanks that are due to the wonderful Maria Bellantone, for urging me to write this book and for her infinite patience in waiting for the manuscript to finally be completed.

Contents

Introduction

I…suggest that something like 'convergent thinking' is just as essential to scientific advance as is divergent. Since these two modes of thought are inevitably in conflict, it will follow that the ability to support a tension that can occasionally become unbearable is one of the prime requirements for the very best sort of scientific research.

Thomas S. Kuhn

Je juge cette longue querelle de la tradition et de l'invention, de l'Ordre et de l'Aventure.

Guillaume Apollinaire

I MUST begin with an apology to Thomas Kuhn. The title of this book has been borrowed – lifted, liberated, stolen, as you prefer – though my editor assures me that titles cannot be copyrighted and that I commit no actionable offense – from the title essay of a volume of Thomas Kuhn's writings subtitled *Selected Studies in Scientific Tradition and Change*. The essay was initially delivered as a lecture at a 1959 University of Utah conference on, of all things, the "identification of scientific talent." Kuhn was already well known as a self-described "ex-physicist now working in the history of science," though the publication of his masterpiece, *The Structure of Scientific Revolutions*, still lay 3 years in the future. Invited to speak at a conference – run by educational psychologists – on the key characteristics of the creative personality and how to identify such a personality early in the educational process, Kuhn addressed a core issue in scientific education, in terms that clearly show his evolving thought on the themes of creativity, "normal science," and scientific revolutions. Is iconoclasm, he asked, the only characteristic needed for a successful and creative scientist? Kuhn argued that a thorough grounding in tradition is as important to scientific advance as the ability to strike out into the unknown. He said:

> Normal research, even the best of it, is a highly convergent activity based firmly upon a settled consensus acquired from scientific education and reinforced by subsequent life in the profession. Typically, to be sure, this convergent or consensus-bound research ulti-

> mately results in revolution. Then, traditional techniques and beliefs are abandoned and replaced by new ones. But revolutionary shifts of a scientific tradition are relatively rare, and extended periods of convergent research are the necessary preliminary to them.

As a result, "the successful scientist must simultaneously display the characteristics of [both] the traditionalist and of the iconoclast" (Kuhn 1977, p. 227).[1]

Kuhn suggested that major scientific advances take place only following the achievement of consensus, when a field has left behind its "natural history stage," filled with a myriad of conflicting results and interpretations. This sequence is necessary because the convergent thought required to build consensus inevitably leads, Kuhn argued, to a period of conservative, incremental research which might at first appear routine, even boring, but is in fact bursting with the seeds of fruitful contradictions. "Work within a well-defined and deeply ingrained tradition seems more productive of tradition-shattering novelties than work in which no similarly convergent standards are involved," Kuhn said. "How can this be so? I think it is because no other sort of work is nearly so well suited to isolate for continuing and concentrated attention those loci of trouble or causes of crisis on whose recognition the most fundamental advances in basic science depend" (Kuhn 1977, p. 234).

When I set out to write a work on the complementary drives that lead to collective behavior in biological systems and how these drives can be illuminated through the lens of physics, I struggled to find a better phrase to represent this delicate balance than "the essential tension". The phrase became the book's provisional title, and, for better or worse, it stuck. Indeed, the tension Kuhn discussed in his 1959 essay has thematic parallels with the tension that will be explored in the following chapters. Kuhn discussed the balance of convergent and divergent thought. This conceptual structure is mirrored in the balance between short-range and long-range forces that leads to clustering of entities in a real or theoretical space and also in the balance between the aspects of nonlinear systems that render them unpredictable, yet constrained, in phase space. Kuhn suggested that an "essential tension" could exist within the mind of a single scientist as well as within a scientific community; the relation between individual and group dynamics will be a recurring theme in the chapters below. Kuhn's model of long periods of "normal science" building up to periods of rapid transition echoes Niles Eldredge and Stephen Jay Gould's mantra that "stasis is data" in their analysis of the fossil record. Indeed, their model of punctuated equilibrium itself reflects the Kuhnian dynamic of consensus followed by revolution.

In short, I swiped the title, it got stuck to my hand, and I couldn't get rid of it.

*** *** ***

[1]A note on reference formatting: within the text, citations from books will be given using the author's last name, date of publication or book title, and the page number (e.g., Lannister 1992, p. 205), and articles will be cited using the name of the author(s) or the first author, followed by the year of publication (e.g., Snow et al. 2016; Targaryen and Stark 2016).

Thomas Kuhn analyzed the tension between different styles of thought. In contrast, the tension I will discuss in the present work is a delicate balance between orthogonal and complementary – but not opposing – drives in natural systems. I will trace the development of scientists' understanding of these drives in their various forms, especially as they relate to collective behavior in biological systems and to evolutionary dynamics. These themes all involve the formation of groups of (mostly living) things and lead to the question of how a bunch of individual things comes together to form a group that can be said to exist as a unique entity in its own right. This question has arisen for social scientists investigating crowd behavior and the division of labor in human society, for evolutionary biologists struggling to define what constitutes a species, and for biological physicists investigating the forces that lead fish to swarm and birds to flock. And all these problems are driven by some aspect of the "essential tension" that is the subject of this book. *Short-range birth processes must be offset by global death processes* in order for clusters to form in a reaction-diffusion model (Young et al. 2001). *Balance between competition and cooperation* is critical for the formation of social groups and may hold the key to the process by which a group of organisms begins to function as a collective entity. The *balance between "stretching" of trajectories* in a chaotic attractor as they experience separation at an exponential rate and *"folding"* as the attractor's infinite leaves wrap back on themselves to remain contained in a bounded region of phase space is an essential property of nonlinear dynamical systems. The process of evolution itself is driven by a balance between the noise of random variability and the dual constraints of historical contingency and adaptation to the environment.

In the following pages, I will explore how these themes recur again and again in the study of collective biological systems – groups, swarms, and species. I will also explore how fundamental principles from the physics of complex systems can assist in the struggle to unravel these deep problems. One final tension will emerge from this discussion – a tension between levels of selection, between the individual and the group, and between the needs of the single organism and the species. I will investigate how this delicate balance is driven by the other tensions we have explored and how it relates to fundamental controversies in modern evolutionary theory, such as the role of group selection. Finally, I will propose that the tension between the levels at which natural selection acts is not only essential but that, in fact, it is an inevitable result of the noisy interaction between biological objects at different scales.

One last point needs to be made before we get underway. The concepts that exist in tension here are complementary, not contradictory. They are not dichotomies. *Form* in biology (driven partly by physical constraints and partly by historical contingency) is not antithetical to *function* (driven primarily by adaptation and partly by what Gould and Vrba call "exaptation", the usefulness of a biological character in a role it was not initially selected for). It cannot be too strongly emphasized that concept pairs such as these are *orthogonal*, not *opposing*, axes. Tracing the degree to which each component of such a pair influences a given natural phenomenon becomes, then, a sort of intellectual principal component analysis. In sum, this book will be more than a plea for pluralism. It will be one long argument that pluralism is *essential*.

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Part I
The History of an Idea

Chapter 1
Crowds

> *Puisque ces mystères nous dépassent, feignons d'en être les organisateurs.*
>
> Jean Cocteau

THE MATHEMATICIAN is tossing fitfully in his bed, talking in his sleep. He was up late talking with his friend the philosopher, and now he is dreaming. Mademoiselle de l'Espinasse watches him, worried. In the morning she calls in Doctor Bourdeu for a consultation. She has noted down her friend's ravings and, looking for reassurance, reads them to the doctor. *"Have you ever seen a swarm of bees leaving their hive? … Have you seen them fly away and form at the tip of a branch a long cluster of little winged creatures, all clinging to each other by their feet? This cluster is a being, an individual, a kind of living creature."* To Mlle. de l'Espinasse's dismay, instead of trying to help the delirious patient, Doctor Bourdeu takes the ball and runs with it. *"Do you want to change the cluster of bees into one individual animal?"* he asks (Fig. 1.1). *"Soften the feet with which they cling to one another, that is to say make them continuous instead of contiguous. Obviously there is a marked difference between this new condition of the cluster and the preceding one, and what can this difference be if not that it is now a whole, one and the same animal, whereas before it was a collection of animals? All our organs… are only distinct animals kept by the law of continuity in a state of general sympathy, unity, identity."* (Diderot, *D'Alembert's Dream*, pp. 168–170).

* * *

The idea of an ensemble of individuals coming together to form a qualitatively different collective entity was not new when Denis Diderot explored it in *D'Alembert's Dream*, a dialogue that touched on ideas so radically new and dangerous that the manuscript was only circulated among a select group of friends during Diderot's lifetime. But the idea, as expressed by earlier thinkers, was more metaphor than theory. In the hands of Diderot, the notion of the emergence of a new collective organism crossed the threshold from analogy to hypothesis.

S. Bahar, *The Essential Tension*, The Frontiers Collection,
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Fig. 1.1 An engraving of a beekeeper tending his apiary (Lyon, France, 1560). Public domain

With the exception of the poem *Moretum*, attributed to Virgil, from which the phrase *e pluribus unum* derives in the context of the assembly of a salad, early notions of an emergent collectivity come from descriptions of human crowds. Many people assemble, and behave together like a single beast. Plato, who described the crowd as "a large and powerful animal", describes in the *Republic* what happens "when they crowd together into the seats in the assembly, or law courts or theatre, or get together in camp or any other popular meeting places and, with a great deal of noise and a great lack of moderation, shout and clap their approval and disapproval of whatever is proposed, or done, till the rocks and the whole place re-echo, and re-double the noise of their boos and their applause. Can a young man be unmoved by all this? He gets carried away and soon finds himself behaving like the crowd and becoming one of them." (McClelland 1989, pp. 38–39) From the perspective of modern physics, this description – all too real in 2016 as it was in classical Greece – corresponds to local, microscopic interactions between elements of a large ensemble.

The crowd continued to fascinate philosophers in the years following Plato, not least due to its strange manner of emerging as a separate entity from hundreds of individuals. In *Federalist No. 55*, James Madison[1] suggested that

> [s]ixty or seventy men may be more properly trusted with a given degree of power than six or seven. But it does not follow that six or seven hundred would be proportionally a better depositary [of the public interests]. And if we carry on the supposition to six or seven thousand, the whole reasoning ought to be reversed. The truth is, that in all cases a certain number at least seems to be necessary to secure the benefits of free consultation and

[1] Or possibly Alexander Hamilton; the authorship of this one of the Federalist papers remains uncertain, according to some scholars.

> discussion, and to guard against too easy a combination for improper purposes; as, on the other hand, the number ought at most to be kept within a certain limit, in order to avoid the confusion and intemperance of a multitude. In all very numerous assemblies, of whatever character composed, passion never fails to wrest the scepter from reason. Had every Athenian citizen been a Socrates, every Athenian assembly would still have been a mob.

Analyses such as that of Madison, though written in a totally different context (in this case, arguments over the total number of members in the House of Representatives), presage studies of the role of population density in triggering behavioral transitions in flocks and swarms, a topic we will return to in Chap. 8. However, the *inner* dynamics of crowd structure remained relatively unparsed by eighteenth and nineteenth century commentators, who focused on the role of the crowd in the larger flow of history. The Gordon riots in 1780[2] were described by Edward Gibbon in typical elite-versus-rabble style. "Forty-thousand Puritans, such as they might be in the time of Cromwell[,] have started out of their graves, the tumult has been dreadful…that scum which has boiled up to the surface of this huge cauldron [of the City of London]…the month of June, 1780 will ever be marked by a dark and diabolical fanaticism." (McClelland 1989, p. 113)

In his classic history of the French revolution (Fig. 1.2), Thomas Carlyle continued what J. S. McClelland calls a "pre-psychological account of the leaderless crowd". In McClelland's reading, Carlyle painted the crowd as a pure force of history, a collective whirlwind created by fate, by providence, a sort of pre-Marxist sweep of history itself. The crowd was a key protagonist in Carlyle's history, but it did not have an internal structure to be dissected: it simply *was*. In McClelland's analysis, other scholars of the French revolution such as Jules Michelet portrayed the crowd as equally inscrutable, but in a nationalist rather than a metaphysical (or meta-historical) sense: the crowd was "the people", "the nation".

Like Gibbon, Hippolyte Taine's view of the crowd was influenced by his own personal politics: fearfully watching the events of the Paris Commune unfold in 1871 from a sabbatical in Oxford, he saw the crowd as a mob of beasts rather than a collection of Rousseau's noble savages. Taine wrote: "Take women [who] are hungry and men who have been drinking; place a thousand of these together and let them excite each other with their exclamations, their anxieties, and the contagious reaction of their ever-increasing emotions; it will not be long before you find them a crowd of dangerous maniacs." (McClelland 1989, p. 129) Like Plato's, this description centered on the local forces within a group that lead to collective behavior. But Taine's purpose was not to explore the internal structure that binds together elements of a crowd: he was more concerned with describing how the crowd triggers regression to "the animal in us". It is a view driven by Tennyson's simplified Darwinism, red in tooth and claw, exacerbated by an aristocratic (and, by the late nineteenth century, even bourgeois) fear of the working class. Taine appealed to metaphors of society as an organism, in which "the body politic stops functioning properly because the belly tries to usurp the function of the brain...a wild beast,

[2] It was during these riots that the phrase "King Mob" was used for the first time, scrawled on the walls of Newgate Prison.

Fig. 1.2 The women of Paris march on Versailles, 1789. Public domain

incompletely domesticated, goes wild again." (McClelland 1989, pp. 134–35) But Taine used these metaphors for emotional effect, not as the starting point of an analysis.

Approaching the turn of the last century, crowd theorists such as Scipio Sighele and Gabriel Tarde struck out in a variety of new directions. They approached the idea of a crowd in a criminological context, but resisted Cesare Lombroso's simplistic identification of criminality (and, by implication, collective behavior of the crowd) with atavism. Sighele argued that, in McClelland's wording, the collective behavior of crowds was

> … genuinely new in a way that no other collective phenomenon is. In the ordinary evolutionary sense, it has no past and no future. This is true phylogenetically and onogenetically. There is no crowd out of which the crowd comes, and there is no crowd-individual before the individual becomes a member of the crowd. When the crowd disperses, crowd-individuals become their ordinary workaday selves. The crowd is in this sense outside ordinary time. (McClelland 1989, p. 164)

The crowd is also different in kind, and is more than simply a sum of its parts. Sighele asked under what circumstances humans' moral and intellectual qualities would be more than simply additive, writing that crowds often behave far better, or far worse, than their constituent individuals would alone. These thoughts suggested the question of how to define a "true individual" in a social group, or in nature itself. In their correspondence, Sighele and Tarde speculated about whether the definition of individuality should be parsed down to the level of the cell, or even to the level of the atom (McClelland 1989, p. 173). McClelland dismisses ideas of this sort as flights of fancy. He notes that Walter Bagehot, in *Physics and Politics* (1872) "makes great leaps from reflections on the evolution of the human body to reflections on the development of human societies as if there were nothing between them… [suggesting] what look like wild analogies to us, analogies between combinations of cells and human groups, or between animal societies and human societies" (McClelland 1989, p. 158). But – as we shall explore over the next few hundred pages together – such crude analogies provide a blunt instrument by which we can begin to excavate the structure of the world. Moreover, these "wild analogies" echo actual, mechanistic, materialist questions asked no less by scholars of Tarde and Sighele's era than by scientists today. Alfred Espinas was not just tossing off wild analogies when he wrote in his 1878 work *Les Sociétés Animales* that

> In fact, we are composed of millions of little entities whose interactions have been compared by the most illustrious physiologists to the work of laborers in a vast factory, to the inhabitants of an immense city, the arteries being like the roads and canals that carry nourishment to different regions, while the nerves resemble telegraphic wires that transmit information and impulses from the parts to the center and from the center to the parts. (Espinas 1878, p. 214, my translation; see also the paraphrased text by McClelland 1989, p. 168)

It was perhaps such metaphors that inspired crowd theorists to inquire – yes, metaphorically – whether the body of a crowd, or indeed any collective, could assemble itself in the absence of a head. Espinas held that a division was essential between the leader and the led; thus, a flock of birds did not constitute a real "society" (McClelland 1989, p. 160). Gabriel Tarde agreed, writing "every mob, like every family, has a head and obeys him scrupulously" (McClelland 1989, p. 185). With perhaps a bit of special pleading, Tarde argued that there are no leaderless crowds: when all else fails, whoever throws the first stone is the leader.[3] Even Freud constructed a theory of the crowd nucleated by a leader. In his view, described in *Group Psychology* (1921), individuals in the crowd projected their own ego-ideal onto the crowd leader. The crowd members then become identified with each other at the ego level, because of the common projection (or, in Freud's terminology, introjection) of their ego-ideal (McClelland 1989, pp. 241–242).

In searching for a mechanism by which a leader could enchant a crowd, some late-Victorian scholars turned to the then-popular phenomenon of hypnotism. Gabriel Tarde took it a step further, suggesting that hypnotism is merely one example of the type of persuasion that society usually exerts on its members, and analyzed social interactions in terms of imitation ("sociability is suggestibility"). Espinas spoke of a "mutual heating-up" between an orator and the audience, a phenomenon we in the United States have witnessed quite clearly in our 2016 election. Many of these interactions can occur between members of a crowd as well as between the crowd members and a leader, so these mechanisms in themselves do not provide an argument that leaderless crowds are an impossibility.

By the end of the nineteenth century, Gustave Le Bon had published a work purporting to show how leaders could manipulate crowds in a popular book largely considered to have been plagiarized from the work of Sighele and Tarde. "The

[3] Tarde's investigations were not limited to crowds, but to all of society; he suggested that there is a continuum from a loosely affiliated crowd to what he called a "corporation", a well-defined, durable, organized social structure. The crowd-corporation transition has an important structural resonance with another idea we will explore later: the transition from MLS1 to MLS2 selection.

secret of Le Bon's success," writes McClelland, "was to use science to frighten the public, and then to claim that what science could understand it could also control." (McClelland 1989, p. 196).

Much later, Elias Canetti, writing in *Crowds and Power* (1960), saw the identification between crowd members as far more important than the interaction between the leader and the crowd. He understood crowds as a mass of individuals looking for release from external pressures (the "stings of command"), and from the emotional burdens of separation, through mutual connection ("discharge"). This process could be catalyzed by a demagogue (an example of what Canetti called a "crowd crystal") but was not dependent on him. The demagogue might directly affect a small proportion of individuals in the crowd, who would then spread the excitement horizontally.

* * *

Like the crowd theorists described above, Emile Durkheim (Fig. 1.3) investigated the forces that hold groups of individuals together. In *The Division of Labour in Society* (1893), Durkheim traced the mutual excitations in a crowd to the way like-minded individuals reinforce each other's ideas. Every strong, intense state of

Fig. 1.3 Émile Durkheim. Public domain

consciousness, he argued, is perceived as a strong source of life, since we identify with our feelings.

> It is therefore inevitable that we should react vigorously against the cause of what threatens a lowering of the consciousness…Among the most outstanding causes that produce this effect must be ranged the representation we have of an opposing state…This is why a conviction opposed to our own cannot manifest itself before us without disturbing us. It is because at the same time as it penetrates into us, being antagonistic to all that it encounters, it provokes a veritable disorder. (Durkheim 1997, p. 53)

Hence, right-wingers in the United States rarely watch MSNBC. Likewise, Durkheim continues,

> just as opposing states of consciousness are mutually enfeebling to one another, identical states of consciousness, intermingling with one another, strengthen one another…If someone expresses to us an idea that was one we already had, the representation we evoke of it is added to our own idea; it superimposes itself upon it, intermingles with it, and transmits to it its own vitality…This is why, in large gatherings of people, an emotion can assume such violence. It is because the strength with which it is produced in each individual consciousness is reciprocated in every other consciousness. (Durkheim 1997, p. 55)

Durkheim is describing essentially a resonance effect; in this analysis, shared emotions are *not* simply additive. The interactions Durkheim described can be visualized as parallel

$$\uparrow\uparrow$$

and antiparallel

$$\uparrow\downarrow$$

spin states where the parallel state has lower energy. Reinforcing, parallel interactions generate what Durkheim called *mechanical solidarity*. This is the solidarity of the crowd, the solidarity of the like-minded, which is always weakened by the presence of an anomaly. If Durkheim had ended his analysis here, he would simply have been another member of the crowd of crowd theorists. But he dug much deeper, searching for an explanation of how societies progress along a continuum from fleeting, amorphous crowd to structured society. There is, Durkheim suggested, another type of solidarity, which he called *organic*, because it "resembles that observed in the higher animals. In fact each organ has its own special characteristics and autonomy, yet the greater the unity of the organism the more marked the individuation of the parts." (Durkheim 1997, p. 85).

Organic solidarity derives from the division of labor. Aggregates whose members depend on each other to perform different essential tasks are tied together with qualitatively different bonds than aggregates whose members are connected merely by similarity. Clearly, division of labor exists in human society, as it does among different cell types in multicellular organisms. Durkheim's argument for how division of labor arises in society parallels models of cellular differentiation and, as we shall see in later chapters, of the origin of multiple levels of selection in evolution.

Durkheim began his argument by sketching the development of modular, or segmentary, structures in human societies such as families and clans. These societies "are formed from the replication of aggregates that are like one another, analogous to the rings of annelida worms." (Durkheim 1997, p. 127) Each group might take over a certain role in society, such as herding a particular species of cattle, or performing religious or ceremonial functions. At this point, one type of structure (*social role*) has been superimposed upon another (*social aggregate*). All that remains is for the increasing specialization to overflow the boundaries of the original social aggregate and erode the original structure. "Generally it may be said," Durkheim wrote, "that classes and castes have probably no other origin or nature: they spring from the mixing of the professional organization, which is just emerging, with a pre-existing familial organization." (Durkheim 1997, p. 133) But it is not just mixing: the new structure climbs out of the old one, and sits on it. Explicitly commenting that "the same law governs biological development", Durkheim wrote: "in organic as in social evolution, the division of labour begins by using the framework of segmentary organization, but only eventually to free itself and to develop in an autonomous way." (Durkheim 1997, pp. 139–141) He emphasized that this development happens without any centralized control. The process continues, driven by a positive feedback loop: the old segmentary structure breaks down, rendering "the social substance free to enter upon new combinations" (Durkheim 1997, p. 200). This leads to flow, migration and realignment of human populations, which results in an increase in the division of labor.[4] But just as the bald fact of genetic modularity provides only the raw material, and not the driving force, for nature's experimentation with different numbers of legs and wings, the foregoing does not fully explain *what drives specialization in the first place*. To address this key question, Durkheim invoked an explicitly Darwinian argument.

> If labour becomes increasingly divided as societies become more voluminous and concentrated, it is not because the external circumstances are more varied, it is [rather] because the struggle for existence becomes more strenuous. Darwin very aptly remarked that two organisms vie with each other the more keenly the more alike they are…The situation is totally different if the individuals coexisting together are of different species or varieties. As they do not feed in the same way or lead the same kind of life, they do not impede one another…If therefore one represents these different functions in the form of a cluster of

[4] Herbert Spencer had proposed that the simple spread of human populations led to specialization of social roles according to the local environment in which people lived: those who live near the sea make their living as fishermen, etc. (This process can be compared to niche specialization in evolution.) Durkheim argued that this certainly occurs, but not to a sufficient extent to explain the degree of actual division of labor present in human society.

> branches springing from a common root, the struggle is least between the extreme points, whilst it increases steadily as it approaches the centre. This is the case not only within each town but over society as a whole. (Durkheim 1997, pp. 208–210)

These divergent societal functions are drawn together through mutual need, resulting in organic solidarity. This evolution is dependent on the prior existence of an initially cohesive, though undifferentiated, group.

> In physiology the division of labour is itself subject to this law: it never occurs save with the polycellular masses that are already endowed with a certain cohesion…this integration supposes another sort that it replaces. For social units to be able to differentiate from one another, they must first be attracted or grouped together through the similarities that they display. This process of formation is observed, not only at the origins, but at every stage of evolution. (Durkheim 1997, p. 219)

The development of differentiation from a simple aggregate is indeed a well-worn evolutionary pathway which we will encounter later in these pages, for example, in our exploration of the evolution of the volvocine algae in Chap. 11.

Once established, "*the division of labour unites at the same time as it sets at odds; it causes the activities that it differentiates to converge; it brings closer those that it separates*." (Durkheim 1997, p. 217, my italics) This is our first glimpse of the essential tension, that delicate balance between things at once drawn together and pulled apart – a structure that endlessly mirrors itself from the ideas of one century to those of another, and from one field of science to another.

Durkheim has been critiqued for a rather selective reading of Darwin's work. Sociologist William Catton (1998, 2002) suggested that Durkheim's assumption that mutualism develops in order to minimize competition is unrealistic in many biological contexts. First, the assumption is roughly equivalent to sympatric speciation (the divergence of co-localized populations), which occurs far less frequently in nature than allopatric speciation (the divergence of populations already separated by some environmental barrier). Second, there is the issue of causality. Darwin himself, Catton argued, never presented population divergence as a *means of* abating competition. Rather, enhanced competition *led to* divergence of populations and extinction of intermediate forms. This does not negate Durkheim's argument, for it is easy to envision a scenario in which someone who works with tin and iron is outcompeted by specialists in each individual metal. Clearly, also, causal factors in sociological evolution are not identical to those at work in the process of speciation. Nonetheless, Catton's critique points to an important issue. Many biological mutualisms, he pointed out, originate in exploitative relationships from which the participants are unable to separate. Here, the ultimate cooperative benefit may be a side-consequence rather than a direct adaptation. Stephen Jay Gould and Elisabeth Vrba called such unintended side-consequences *exaptations*. As Gould noted, Catton explicitly referred to this concept in one of his analyses of Durkheim (Gould 2002, p. 1239). "An adaptation has a function," Catton wrote. "An exaptation has an effect. Once that effect becomes important in the life of an organic type (in its new environment), natural selection may 'improve' the exapted trait, eventually making it an adaptation, and converting the effect into a true function." (Catton 1998) It is entirely likely that many aspects of the division of labor may have arisen as unintended consequences of an initial population divergence, and only later had the added benefit of abating competition, a function for which they were not originally selected. We will revisit the idea of exaptations in later chapters, and we will find that they play a crucial role in mediating the tension and balance between the levels at which natural selection operates.

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Chapter 2
Classification

Only connect.

E. M. Forster

IN THE previous chapter, we explored the problem of how one thing emerges from many. A related intellectual problem, how a multitude of things can be grouped into one, has also preoccupied scholars for many centuries. This is the problem of *classification*. Historically, arguments over classification did not explicitly contain the dynamical axes of differentiation/convergence that we have seen in the work of Durkheim. The tension between differentiation and convergence in biological classification arose only later, in the context of actual evolutionary theory, as we will see in the following chapter. For now, let us explore the conundrum of classification as it occurred before the late eighteenth century, in two interlocking problems: *how to categorize*, and *how to draw boundaries*. The problem addressed by the crowd theorists was a *bottom-up* problem: how individuals form a group. In contrast, classification of animals and plants was the decidedly *top-down* problem of how (and even if) one should draw boundaries. Crowd theory contained the seeds of the essential tension in the question of how groups can be stabilized by counter-balancing forces operating at different levels. In the top-down problem of classification, it is hard to find any hint of a balance between push and pull – things being drawn into a group and yet held separate by orthogonal forces.[1] Instead, we find only a sharp knife slicing from above at the Great Chain of Being.

The history of the Great Chain of Being is masterfully traced in A. O. Lovejoy's groundbreaking 1936 book of the same name; Lovejoy's work virtually inaugurated the study of the history of ideas. The Chain of Being is, in essence, a picture of the world, conceived as a hierarchy extending up toward the "divine". Lovejoy located the origin of the Great Chain in the creation myth in Plato's dialogue *Timaeus*. Here, the world of imperfect beings is formed from a deity's inner abundance, the overflow

[1] It is possible that the tension was easier to discern in crowd theory because the opposing forces of push and pull act at the same scales of time and space, while in problem of (biological) classification they do not. Moreover, an understanding of this uneasy balance of forces in biological classification, and the different scales at which they act, requires a vision of classification as extending in time – which was developed only comparatively recently.

S. Bahar, *The Essential Tension*, The Frontiers Collection,
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of a "best soul" defined by the attributes of goodness and self-sufficiency. Executing what Lovejoy kindly terms a "bold logical inversion", Plato stated that whatever is good must diffuse itself (*omne bonum est diffusivum sui*, in the Medieval Latin formulation used by Thomas Aquinas and the Scholastic philosophers who followed him).

And thus good overflowed, creating a host of imperfect things. How many imperfect things? All of them. For, as Lovejoy put it, "the 'best soul' could begrudge existence to nothing that could possibly possess it and 'desired that all things should be as like himself as they could be.'" (Lovejoy 1964, p. 50). Since "nothing incomplete is beautiful", the created universe must be complete. All things that are possible must become actual. Lovejoy named this the *principle of plenitude* (*lex completio*). According to this "strange and pregnant theorem", Lovejoy wrote, "no genuine potentiality of being can remain unfulfilled, … the extent and abundance of creation must be as great as the possibility of existence and commensurate with the productive capacity of a 'perfect' and inexhaustible Source, and … the world is the better, the more things it contains." (Lovejoy 1964, p. 52)[2]

Unlike Plato, Aristotle did not insist upon a world stuffed to the gills with all things, writing that "it is not necessary that everything that is possible should exist in actuality…it is possible for that which has a potency not to realize it." (Lovejoy 1964, p. 55) Instead, Aristotle emphasized a concept that is a consequence (though not a guarantee) of plenitude: *continuity*. The passage from inanimate to animate, as well as from one class of living creatures to another, is so gradual "that their continuity renders the boundary between them indistinguishable" (Lovejoy 1964, p. 56). Lovejoy called this idea the *principle of continuity* (*lex continui*).

The idea of the Great Chain of Being has clear implications for the problem of biological classification (Fig. 2.1). If one accepts that the chain is continuous, is it even possible to define any segment of the chain as a group in its own right? And if so, how? Any segment is to be composed of individual, infinitesimal links on the chain. But how is one to know where to make the cut? As Socrates suggested[3] in

[2] This *filled* world is one of all necessity, and no contingency, even for the deity. This caused religious objections to the principle of plenitude, since it could be interpreted as denying the deity free will. Compare this to the sparsely populated, highly contingent world Thoreau pondered in *Walden* (writing in 1854, five years before Darwin published the *Origin of Species*) when he asked "Why do precisely these objects which we behold make a world? Why has man just these species of animals for his neighbors; as if nothing but a mouse could have filled this crevice?" (Thoreau 1982, p. 273)

[3] The actual quote involves a suggestion to divide things "by classes, where the natural joints are, and not trying to break any part, after the manner of a bad carver". I thank my colleague Dan Lehocky for bringing the original quote to my attention. Lehocky notes out that the idea of an "essential tension" may indeed go back to the pre-Socratic philosophers, as for example in Heraclitus's approach to the one-many problem. Heraclitus addressed the problem of division and classification with his famous metaphor of never being able to step into the same river twice. How can something constantly changing remain the same? The same problem arises in parsing a human being's identity: is the self you were as a child the same as the self you are at this moment? Heraclitus suggested that a solution to the problem of constant change lies in an inherent structure in the world that derives from a balance of opposites: the river is made both by the struggle between

Fig. 2.1 The Great Chain of Being, from a 1579 work by Diego de Valades. Public domain

Plato's *Phaedrus*, one must "cut nature at its joints". But if the *scala naturae* is continuous, are there any joints at which to make a section? This is a broad philosophical problem, but it became an increasingly practical one, as we shall see, during the development of seventeenth- and eighteenth-century natural history. A related problem is whether a classification is an actual "thing": does a species have an essence, in the Platonic sense, or is it simply an arbitrary and convenient name for a grouping of individuals[4]? And is a species defined by the collective properties of its members, or are the members of a species so designated because they partake of some universal characteristics that are part of the species essence? Various thinkers took more or less nuanced positions on these questions. John Locke, for example, declared that "the boundaries of species, whereby men sort them, are made by man". (Lovejoy 1964, p. 229). He did hold that species exist in an essential sense, but also that a true understanding of how to parse the components of nature was inaccessible to human knowledge. "In all the visible corporeal world," Locke wrote,

> there are no chasms or gaps. All quite down from us the descent is by easy steps, and a continued series that in each remove differ very little one from the other. There are fishes that have wings and are not strangers to the airy region; and there are some birds that are inhabitants of the water, whose blood is as cold as fishes…There are animals so near of kin to both birds and beasts that they are in the middle between both. Amphibious animals link the terrestrial and aquatic together…and the animal and vegetable kingdoms are so nearly joined, that if you will take the lowest of one and the highest of the other, there will scarce be perceived any great difference between them. (quoted by Lovejoy 1964, p. 184)

Locke further asserted that this structure was part of the "magnificent harmony of the universe", and that "the species of creatures…by gentle degrees, ascend upwards" toward the "infinite perfection" of the universal architect.

Simply extrapolated to the realm of natural history, the idea of a continuous chain of being could lead to the conclusion that separate species did not, indeed *could* not, exist, either in essence or in practicality, and that, therefore, classification was an enterprise doomed from the start. Thus Buffon, who strongly opposed Linnaean classification, wrote in his *Histoire Naturelle* (1749) that

> [t]here will be found a great number of intermediate species and objects belonging half in one class and half in another. Objects of this sort, to which it is impossible to assign a place, necessarily render it vain to attempt to find a universal system…In general, the more one increases the number of one's divisions in the case of the products of Nature, the nearer one comes to the truth; since in reality only individuals exist in Nature. (quoted by Lovejoy 1964, p. 229; Wilkins 2009, p. 75)

Others echoed the same sentiment, but allowed that the establishment of a tentative system of classification was nonetheless of practical use for the naturalist (and for

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the flow of the water and the pressure of the banks on either side. This also echoes Anaximander's idea of balance and moderation between elements in the universe. Anaximander represented this as a sort of metaphorical form of cosmic justice, writing that things "make reparation to one another for their injustice according to the ordinance of time", as summer succeeds winter. Note, however, that the principles that exist in an "essential tension", as explored in the present work, are *complementary* rather than *opposing*.

[4] This philosophical position is known as species nominalism.

the physician, looking to distinguish herbal cures from poisons!). Bonnet wrote in his *Contemplation de la Nature* (1764) that "[i]f there are no cleavages in Nature, it is evident that our classifications are not hers. Those which we form are purely nominal, and we should regard them as means relative to our needs and to the limitation of our knowledge." (Lovejoy 1964, p. 231; Wilkins 2009, p. 84).

The application of the laws of continuity and plenitude to nature in the seventeenth and eighteenth centuries had an immediate positive result: it spurred observational research, as naturalists struggled to "fill in the gaps". But those laws also posed two clear philosophical problems. The first arose simply from observations of the world. Some data actually did suggest a lack of continuity, and sharp, uncrossable boundaries between species. Indeed, influenced by such observations, Buffon ultimately abdicated his contention that "individuals alone exist in Nature". Convinced by the sterility of hybrid species, he reversed himself totally, claiming in his later writings that "Les espèces sont les seuls êtres de la Nature" and that "an individual, of whatever species, is nothing in the universe"[5] (Lovejoy 1964, p. 230). The second problem arose from a drive that is perhaps as much aesthetic and psychological as it is scientific: the need to order and classify.

An example from recent biological studies serves to highlight the immense conceptual difficulty of defining an individual. One of the most dramatic examples of the porous definitional boundary between group and individual is provided by *Populus tremuloides*, the quaking aspen (Fig. 2.2). The aspen brings home the complexity of defining an individual, and how knowledge of that individual's history may be key to establishing its identity. The quaking aspen, widespread across the northern and western United States and in Canada, varies dramatically in its life cycle according to environmental conditions. Capable of sexual reproduction, seed viability has been measured at greater than 90% (Mitton and Grant 1996). However, seedlings often have trouble germinating in arid environments. A second survival strategy enables aspens to circumvent this difficulty: they are also capable of asexual reproduction, sending out lateral roots in a process called suckering. These lateral roots then send up stems called *ramets*. As discussed in Chap. 13, these could be considered as the "parts" within the "whole" of a *genet*, defined as the "totality of plant tissue that comes from a fertilized zygote" (Okasha 2006, p. 45).

Sustained by a massive underground root system, aspen clones are able to repopulate a forest after most other species, such as conifers, have been decimated by fire, avalanche, or mudslide. As Mitton and Grant (1996) explain, "[p]ersistent root systems allow aspen to colonize, occupy, and even prefer disturbed sites, justifying their general characterization as a successional species. After a fire has removed the conifers, the ramets that sprout from a healthy, mature root system may grow vertically by as much as a meter in a single summer season…The root system of aspen grows so aggressively that adjacent stems can be spaced more than 30 m apart."

The dominance of a clonal aspen grove within an ecosystem is temporary. As other species grow back into a fire-devastated area, conifer competitors may eventually overtake the aspen clone. Nonetheless, giant aspen forests formed from single

[5] This stance also led Buffon to conclude that species are fixed and unchangeable.

Fig. 2.2 A forest of a single tree: Pando, a quaking aspen clone, in autumn. Photograph by J. Zapell. http://www.fs.usda.gov/photogallery/fishlake/home/gallery/?cid=3823&position=Promo, Public Domain, https://commons.wikimedia.org/w/index.php?curid=27865175

clones do persist. The most dramatic of these is a male clone consisting of nearly 50,000 trunks, dubbed "Pando" (from the Latin, *I spread*) by Grant and colleagues. Growing near Utah's Wasatch Mountain Range, Pando – including its root system – is estimated to weigh six million kilograms, making it the most massive known living organism. Its age is difficult to determine, but an upper limit of a million years has been suggested.

Dishearteningly, aspen clones' need for rejuvenation by fire has set Pando's survival at odds with modern society's desire to prevent forest fires. As Grant (1993) explains,

> The quaking aspen gained its name because of the way the tree's leaves tremble in even the slightest breeze. French Canadian woodsmen in the 1600s believed that the trees quaked in fear because the cross Jesus was crucified on was made of aspen. Now giant aspen clones like Pando have a new reason to tremble: human incursions. Several private homes have recently been built within one section of Pando, and another section has been turned into a campground, complete with parking spaces, picnic tables, and toilets. Paved roads, driveways, and power and water lines built to serve these developments dissect this spectacularly beautiful aspen stand. The presence of people has led the U.S. Forest Service to suppress wildfires, and yet Pando's remarkable size and longevity are largely a consequence of the cleansing, rejuvenating power of wildfires. Ironically, ending wildfires could well mean the end of Pando.

Different aspen clones growing in proximity to one another may be distinguishable simply by their physical characteristics. The angle branches make with a ramet's