FOREWORD

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I. INTRODUCTION

Julian Huxley's *The Individual in the Animal Kingdom* is a book about the major transitions in evolution (MTEs), *avant la lettre*. When it was published in 1912, the modern evolutionary synthesis had not occurred, the central dogma of molecular biology was unknown, and the experimental methods we now take for granted were impossible to fathom. Biology has clearly come a long way since the early twentieth century, so some might infer they will find little of value in this monograph. The standard response would be that standing on the shoulders of past giants is the only way to see into the distant scientific horizon, but Newton's aphorism only holds true if the footings we are perched upon are sound. Sifting through the historical literature, it becomes apparent that many works are, in fact, best forgotten. However, intellectual archaeology can sometimes help to uncover long-lost gems with unique vantage points that modern biologists can use to advance their research. In our view, *The Individual in the Animal Kingdom* is one of these treasures.

A close reading of enduring works from the past often confirms that their insights have been incorporated into the contemporary literature in a refined and expanded form. This is cumulative scientific progress at its finest. Revisiting

The Individual in the Animal Kingdom, one gets the impression that research on the MTEs has charted a less desirable course. Huxley's hypotheses are so strikingly clear and original that our present-day understanding of the MTEs appears to represent modest, incremental progress. Indeed, one could argue that the field has actually regressed in some respects due to a neglect of rigorous, falsifiable theorizing and subsequent empirical testing. The current state of affairs is partly attributable to the lack of attention *The Individual in the Animal Kingdom* has received. Our goal in overseeing this reissue is to give this groundbreaking work a second hearing. Despite the fact that it is now over one hundred years old, and despite Huxley himself being just twenty-five years old when it was pressed (figure F.1), the book remains highly relevant to contemporary research on the MTEs. The primary aim of our introduction is to demonstrate this point in order to encourage biologists to read the body of the text in its original form. An exhaustive historical contextualization of the book that purports to be free from evaluative judgments will have to wait for another day.

Current thinking[1,2] is that the MTEs—understood as a series of events where formerly independent entities joined forces to form a more organizationally complex whole—were first described by John Maynard Smith and Eörs Szathmáry in their 1995 book,[3] *The Major Transitions in Evolution*, and a *Nature* paper published in the same year.[4] In a semantic sense, this is correct because the *term* "major evolutionary transition" had not previously been used in this specific context. However, the *fact* that life has increased in organizational complexity over time—the central tenet of the modern MTE framework—had been appreciated for well over a century. More specifically, many of the ideas currently circulating in the literature were

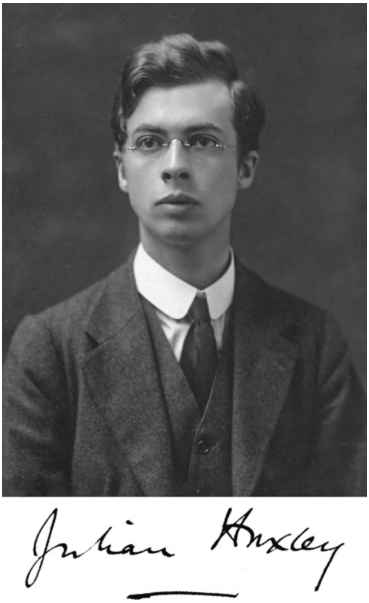

Figure F.1
Photograph courtesy of Woodson Research Center, Fondren Library, Rice University. Signature provided by and used with the permission of Cold Spring Harbor Laboratory Archives, NY.

first incisively formulated by Huxley in *The Individual in the Animal Kingdom*. Yet, it is important to emphasize that even in 1912, the basic idea that organisms have evolved different levels of hierarchical complexity was not new.

For example, by the 1800s biologists were regularly highlighting parallels between multicellular "cell-states" and human societies. Much of this work was focused on how cellular order is maintained physiologically,[5,6] but more than a few researchers of this period began to explore the dangerous possibility that such systems might provide a desirable model of government for human societies. As the better-known controversies between Herbert Spencer and T. H. Huxley illustrate,[7] evolutionary biology in the late nineteenth century was highly political, and some of the mistaken ideas developed during this time eventually helped to spawn disastrous totalitarian regimes in the twentieth century. Thankfully, the scientific discourse on cells and societies eventually became more rigorous following the formalization of cell theory. During the early 1900s, researchers began to realize that the biological part–whole relationship between metazoan cells and the integrated organisms they form is not comparable to the sociopolitical dynamics that exist between free citizens and their states.[8] That being said, important parallels between "insect states" and cell states do exist, and Huxley was among the first to see these.

By noting the affinities between metazoan bodies and caste-differentiated insect colonies, Huxley was following in the footsteps of the myrmecologist William Morton Wheeler. One year before *The Individual in the Animal Kingdom* appeared, Wheeler hypothesized that the same type of common descent relationship that holds between differentiated metazoan cells and protists exists between the members of an ant colony and their solitary sister clades.[9] Elaborating on Darwin's concept of family selection as an explanation of insect neuters, he concluded that ant colonies are *organisms*, meaning their lineages have transitioned to a higher type of organization that is more hierarchically complex than obligate multicellularity. Wheeler's original "superorganism" was a carefully crafted theoretical concept that used ontogenetic considerations to identify lineages that have transitioned to a new level of social organization. Despite its sophistication, his concept failed to garner significant interest, and was eventually misappropriated when ecologists incorrectly claimed that communities and ecosystems undergo development, and subsequently exhibit organism-like harmony.[10] However, related topics such as levels-of-organization and the interactions between the component parts and larger wholes of organisms were regularly explored throughout much of the twentieth century. A substantial portion of this work was aimed at understanding causation in animal development from a physiological perspective, but later studies added an explicit evolutionary component as well.[11]

None of this historical work, including Huxley's book, was cited by Maynard Smith and Szathmáry, giving many the incorrect impression that their conceptual framework had no precedent. Their dialectic stood in contrast to Leo Buss's book *The Evolution of Individuality*,[12] which was more explicitly informed by natural history, had a wider range of taxonomic coverage, and relied on a broader, albeit sometimes eclectic, range of primary sources. Although he was more thorough in his details, Buss also failed to acknowledge Huxley's pioneering work. Part of the reason why the phenomena we now refer to as the MTEs have been "discovered" multiple times is that subsequent generations used different terms to describe these events—including "individuality," "organismality," "organizational complexity," and most recently, "major transitions" facilitated by changes in encoded genetic information—without making an effort to determine how these ideas relate to one other. Everyone seems to have assumed that they were first to coherently describe the evolution of organizational complexity, and since none of these research programs used Huxley's logic as a foundational stepping-stone, the literature has fragmented into parallel traditions that provide varying levels of insight into different features of the MTEs.

The Individual in the Animal Kingdom is written in a narrative style that was common in the early 1900s, when biology was essentially a qualitative discipline. Because of this, some of Huxley's language will be unfamiliar to modern readers (see glossary), and the text may seem almost poetic at times because it lacks the rigid structural format we have become accustomed to in recent decades. Nevertheless, in terms of the actual scientific content, one is hard-pressed to identify claims that are false, and this is what truly matters. It would be absurd to ignore the works of Shakespeare or Chaucer because they deviate from the rules of the *Chicago Manual of Style*, but we often appear more than willing to do something similar when an older work of science does not strictly conform to modern semantic conventions. There is no doubt that Huxley's book takes more effort to read and digest than a contemporary journal article that consists of boilerplate declarative sentences interspersed with summary figures and uninterpreted p-values. However, we believe that biologists—along with a much wider circle of academics—who take the time to read the rather modest number of pages that comprise *The Individual in the Animal Kingdom* will find it to be a rewarding experience.

Throughout his book, Huxley strives for theoretical precision and conceptual coherence. Paragraph by paragraph, page by page, he is pulling his readers toward a very specific set of conclusions. Huxley begins by carefully defining what he means by "individuality" and then applies the concept to a wide array of terrestrial and aquatic organisms that span multiple kingdoms. For each of the taxa examined, he reviews the basic biology of example species and then indicates what level of organizational complexity the lineages have achieved. Huxley was a skilled naturalist who was not content with producing a mere descriptive taxonomy of individuality. From the start, he argues that transitions in hierarchical organization must have been *adaptive*, and develops testable inferences about the ultimate and proximate causes that facilitated these events. Huxley's overarching system of concepts, and the wide-ranging logical principles that he applied to all known levels of hierarchical complexity were so far ahead of their time that they continue to stand tall in the company of modern work on the MTEs.

In contrast to *The Individual in the Animal Kingdom*, Maynard Smith and Szathmáry's book offers almost no hypotheses about the necessary conditions that precede the origin of an MTE. The lack of emphasis on ultimate selective forces and their enabling proximate mechanisms that began with their descriptive framework continues to characterize a substantial portion of current MTE research. Instead of formulating falsifiable hypotheses that seek to explain *why* transitions in organizational complexity take place, many biologists remain content to note *that* they have occurred. To make matters worse, the term "major transition" is now used in an array of contexts that have little or nothing to do with hierarchical changes in organization. Once the MTE-concept *sensu* Maynard Smith and Szathmáry had acquired a certain degree of professional cachet, researchers began using it to describe almost every imaginable type of change that was deemed to be evolutionarily important, or simply worthy of study. The precedent for this promiscuous usage was arguably set by Maynard Smith and Szathmáry themselves. As others have correctly pointed out,[13] the criteria they used to identify the MTEs were vaguely defined, and as a result the events they considered to be major transitions were a highly heterogenous menagerie from the outset.

One of the refreshing features of Huxley's approach is his implicit emphasis of the fact that MTEs promote what we would now call adaptive radiations. Conceiving things in this way enabled him to carve the natural world along joints that had long been obvious to naturalists. It appears that Huxley's primary goals were to: (i) formulate a generalized predictive theory of progress in organizational complexity, and (ii) demonstrate that natural selection has produced both quantitative and discontinuous MTE-like changes via common principles that apply across *all* levels of hierarchical organization. As Niels Bohr demonstrated with his correspondence principle, the best scientific theories tend to integrate phenomena that occur at different scales in nature. Just as Bohr was able to show that quantum discontinuities do not contradict continuum mechanics in the macroscopic world, Huxley managed to reconcile the gradual evolutionary change produced by natural selection with the seemingly conflicting fact that MTEs constitute dichotomous breaks in organizational complexity. We know of no published studies that undermine his highly parsimonious logic. If such rebuttals truly do not exist, Huxley's 1912 book deserves to be ranked among the most important works in organismal evolutionary theory published after the *Origin of Species*.

II. INDIVIDUALITY AND ORGANISMALITY

Huxley's definition of individuality explicitly considers part–whole relationships and is linked to, but not synonymous with, the complementary concept of organismality. An entity can be regarded as an individual when observation reveals that it is not a component of a larger integrated whole with its own unique ontogeny. Parts have no ability to survive or reproduce on their own, and therefore are not individuals in and of themselves. Their existence is dependent upon the context of the more inclusive unit they belong to, and this is what prevents them from qualifying as biological individuals. All organisms are individuals, but organisms always come in grades (a discrete hierarchical measure), while individuality can also vary in degree (a continuous intralevel measure) within these grades. To give an example, an isolated cardiac cell is not an individual because it is unable to naturally persist when isolated from the rest of a body—it is merely one part of an organismal whole that belongs to a higher (multicellular) grade. Yet, other single-celled entities such as *Paramecium* protists can readily survive and reproduce on their own. They are not functional parts of anything, but autonomous, free-living organisms, albeit of a lower-level (unicellular) grade. And, autonomous *Paramecium* ciliates exhibit a higher degree of biological individuality than other protists which lack some of their more derived features.

Huxley eventually sets himself to the task of making his abstract definitions useful to working biologists, and comprehensible to the general public. He notes that "living matter always tends to group itself into . . . closed, independent systems with harmonious parts" (p. xlvi), and adds that this tells us something important about the boundaries that demarcate the various types of organizational complexity. More specifically, he proceeds by suggesting that an entity can be regarded as an individual if it: (1) is a closed system, meaning it has a gatekeeping mechanism that differentiates self (the organism) from non-self (the abiotic and biotic environment); (2) exhibits some degree of independence from these environments; and (3) can be observed to possess differentiated internal parts, which (4) interact harmoniously with one another to promote the survival of a larger whole that is capable of reproduction. All organisms exhibit these characteristic features of individuality and, at first glance, they appear to be expressed in a completely continuous manner, such that some might be more independent from their environment, or show more internal division of labor, than others. However, Huxley recognized that "even the most perfect quantitative gradation from one condition to another is no guarantee that the two conditions shall not be qualitatively different" (p. 58). In other words, not all variation in individuality is continuous. Organisms vary in the hierarchical level at which they are closed, which translates into discrete differences in the "grade of individuality" or level of organismal complexity they have attained. While the continuous degrees of individuality Huxley describes address progression and secondary reduction of morphological complexity, behavioral repertoires, etc., the discontinuous differences in grade he identifies will be our primary focus because they are *evolutionarily irreversible*, and have a direct connection to the modern MTE framework.

The idea that organisms—be it cells, multicellular individuals, or organismal colonies—are closed, hierarchically arranged systems is integral to Huxley's analysis. At any given level, closure requires the evolution of physical structures, or other mechanisms that perform isolating functions. Cell membranes are a canonical anatomical feature that ensures closure, and higher-level analogues include animal epithelia, and colonial gestalts. Once closure has been established, a new boundary between self and nonself is created, and what was formerly nothing more than lower-level units staying together can become a unified organism (pp. 6–8; 10–11) that has gained a novel and higher level of independence from its environment. Closure is also necessary for the evolution of an internal division of labor, understood here as functional specialization of subordinate units that needs to take place in order for grade transitions to occur. This appears to be driven by an "all in the same boat" type of principle, where cooperation is the only viable option, and functional complementarity (think rowing and bailing out water) is obviously beneficial to all. Once some members of the newly closed unit begin to acquire specialized functional roles, the logical implication is that the fitness of the higher-level individual should increase.

Huxley's theory of how the MTEs originated is parsimonious insofar as it assumes that, provided closure is secured, complementary internal specialization has the potential to arise. This is subsequently expected to promote the evolution of analogous forms of higher-level adaptive organization across all grades. The idea that MTEs have to be irreversible is another striking feature of *The Individual in the Animal Kingdom*. At several points in the text, Huxley implies that transitional events are akin to what we might now call a "one-way street," and crucially, he attributes the progressive quality of the MTEs to the fact that natural selection must sometimes have favored organisms that increased their independence from the environment (compared to their recent ancestors) by becoming closed at higher organizational levels.

Once a lineage evolves a new closure mechanism and transitions in grade, the parts of the larger organismic whole are no longer able to survive and reproduce independently, as their free-living ancestors once did. Huxley illustrates this point with a memorable witticism, noting that "if you divide a man into two by cutting off his hand, the working of . . . [the man] . . . is rendered less effective," while the functioning of the hand is "stopped for ever" (p. 8). In contrast, he clearly recognizes that the part–whole relationship is one of convenience, not necessity, when groups are merely same-generation aggregates. The parts of aggregates keep their "perfect independence as they would have if living solitary" (p. 75), making them different from organismal structures bound by clonal or family ties that keep the whole together across subsequent cohorts of cells or individuals. Huxley also points out that the macroscopic mutualisms known at the time are always aggregative, which preliminarily suggests that their capacity to transition in organismal grade is severely constrained (pp. 95–96).

III. THE MAJOR TRANSITIONS IN EVOLUTION

From the opening pages of *The Individual in the Animal Kingdom*, it is evident that young Julian Huxley was an extraordinarily well-rounded academic who took inspiration from many sources, including the philosophers Friedrich Nietzsche and Henri Bergson. Perhaps most notably, he extracted the idea of "closed systems" from Bergson's literary prose, and transformed it into a robust scientific concept (pp. 6–8). Like other scholars, particularly in his generation, Huxley inevitably found various works of art, philosophy, and literature enjoyable, insightful, or even inspiring. However, *The Individual in the Animal Kingdom* is very much the work of an expert biologist that is firmly rooted in the empiricist tradition of comparative zoology. It would be absurd for scientists to dismiss Huxley's book as speculative storytelling because it contains quotes from *Through the Looking Glass* (p. 65), and similarly, there is nothing inherently problematic about using the abstract thoughts of philosophers as a springboard for formulating deeper insights into the biological world. Being widely read is a virtue, not a vice.

Following Darwin and Weismann, Huxley emphasized that if we want to understand gradual changes and discontinuous transitions in organizational complexity (figure F.2), we should avoid thinking in terms of a Great Chain of Being that treats human individuality as the pinnacle that all other lineages must be measured against. He stated without qualification that "any view of animal individuality as a whole . . . must not take man and mammals as the single starting-point whence we could logically work backwards to the rest of the organic world." Instead, he emphasized that we should treat the organizational complexity of our bodies and those of our close relatives as "an ending instead of a beginning" that is merely "one . . . among many" (p. 25).

Ultimately, one could argue it was Huxley's recognition that humans are not special biologically and his knowledge of comparative natural history that allowed him to formulate the first coherent MTE framework. His upbringing in a scientifically minded family, and training in neo-Darwinian comparative zoology at Oxford likely enabled him to see that increases in organizational complexity involving abrupt, discontinuous breaks with ancestral body plans and life histories evolved by the same principles across distantly related lineages. This emphasis on common causes appears to have helped Huxley avoid the anthropomorphic conclusion that metazoan multicellularity must necessarily be the evolutionary pinnacle of fully integrated hierarchical complexity. That is to say, he kept his mind open to the possibility that nonhuman taxa such as caste-differentiated social insects exhibit a higher level of organismal organization than primate bodies and the much looser societies they can form. However, he was keenly aware that such transitions always come at the expense of the liberty of the "persons" involved (pp. 90–91, 104, 108),

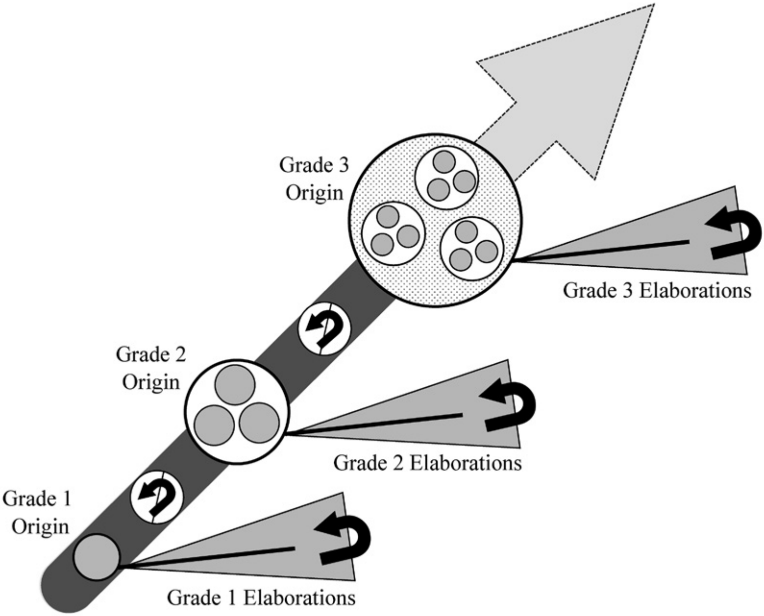

Figure F.2
Transitions in hierarchical complexity between grades are evolutionarily irreversible, but elaborations within a grade are not. A recurring theme of *The Individual in the Animal Kingdom* is that the MTEs have a hierarchically progressive quality, meaning that once a lineage has crossed into a new type of organization, its component parts can no longer survive on their own. Conversely, within any given level of organization, organisms often form facultative aggregates with other entities. In these assemblages, internal division of labor is usually weak or non-existent compared to multicellular bodies or caste-differentiated colonies. In other words, aggregates are often reversible elaborations because most individuals that belong to such collectives do not specialize to become parts. Among strictly solitary organisms, elaborations and regressions in organizational complexity are both possible. The latter are almost always a consequence of parasitic or mutualistic overspecialization (p. 100). In the figure, the trajectory along the large arrow represents irreversible transitions in organizational grade. Within each grade, lateral increases and possible decreases in complexity are illustrated by slightly tilted horizontal triangles.

implying that they should be avoided in the context of human government (p. 116).

Recent commentators on the MTEs have tended to shun the subject of evolutionary progress almost entirely, with some going so far as to suggest that organizational complexity cannot be discretely ranked.[14,15] However, Huxley was adamant that there are fundamentally distinct grades of organization in the natural world, which have evolved in a stepwise fashion from lower to higher via natural selection. His idea of progress having been both qualitative and quantitative is demonstrated by his assertion that, "in spite of many side-ventures," organisms can be "arranged in a single main series in which certain characters are manifested more clearly and more thoroughly at the top than at the bottom" (see figure F.2). Throughout the text, he compiles evidence—surprisingly solid even by current standards—which indicates that there is a directionality or arrow of organismal complexity. None of his arguments rely on untestable vitalistic or orthogenetic claims about evolutionary forces trying to achieve some sort of preordained goal state. They are based on the empirical observation that life was originally simple and increased in hierarchical complexity over time. Grade transitions, then, represent occasional events where natural selection rewards new forms of closure that facilitates higher-level division of labor and promotes increased environmental independence. In Huxley's terms, these improvements enhance an individual's "survival value," relative to its peer individuals.

Huxley identified three discrete grades of organization in the natural world: (1) unicellular protists, (2) multicellular organisms, and (3) (super)organismal colonies. The hierarchical nestedness of these grades is obvious because all grade 2 individuals are evolutionarily derived collectives of grade 1 organisms, and all grade 3 individuals are assemblies comprised of grade 2 multicellular parts. Huxley's taxonomy differs from the modern MTE framework in that it includes all unicellular organisms in the first grade. We now know that protists arose from a specific endosymbiotic fusion of prokaryote cells, and accordingly, there is unanimous agreement that the origin of the eukaryotic cell constituted a mutualistic MTE from simpler cellular ancestors. Given the technological limitations of his era, Huxley cannot be faulted for lumping all single-celled organisms into a common grade. However, his general reasoning about the evolution of hierarchical complexity is coherent enough that *The Individual in the Animal Kingdom* can easily be brought up to date by adding a prokaryote grade 0 category to his system that would set the Bacteria and Archaea apart (figure F.2) from the Eukaryota. Had Huxley known about the endosymbiotic origin of the last eukaryote common ancestor, he likely would have regarded it as a rare and welcome complement to his inference that macroscopic ectosymbioses do not induce grade-level transitions (pp. 95–96).

THE FIRST ORGANIZATIONAL GRADE

By the time *The Individual in the Animal Kingdom* was published, the basic principles of cell theory were widely accepted. Among other things, there was broad agreement that the cell is the basic compositional unit of life, and that all and only living entities are made-up of cells.[16] Huxley elaborated on established cell theory by formulating hypotheses about the origin of life (pp. 20, 24), and examining how the cellular composition of organisms has facilitated or constrained their evolution by natural selection. He argues that the formation of the first cells was a necessary precondition for life on Earth, meaning that the advent of the cell *caused* the origin of life as we know it. A century later, our increased knowledge of viruses has complicated the situation slightly, but many would still consider the first cell closure as the start of independently organized life. Although Huxley was unable to directly test his hypotheses about how life began, he used existing knowledge to make a number of plausible inferences about how the cell might have originated. It is worth emphasizing that these claims were empirically falsifiable, because vitalist theories of life were still being promoted in the early twentieth century. Huxley's tepid praise of Bergson could give the impression that he might have been sympathetic to such ideas, but there is no textual evidence for this in his 1912 book. As described above, he simply formalized Bergson's idea of biological closure, and in his hands, this has no vitalistic baggage.

According to Huxley, the early chemical constituents of life had physical properties that predisposed them to form closed cell-like structures (p. 38). These primitive cells were the first organized lifeforms, which natural selection acted on to produce more hierarchically complex, but equally closed, multicellular organisms. As Huxley put it:

> [The cell] was like Benjamin Franklin's kite, bringing lightning down from heaven, but it did more than that, for it provided a permanent resting-place on earth where individuality could stay, could gather strength and develop upwards (p. 49).

The first cells were—and all extant unicellular prokaryotes and eukaryotes continue to be—among the most successful organisms on the planet. This is partly because the basic architecture of the cell can be modified through the inclusion of structures that allow specialized functions to be performed. Huxley used the following metaphor to illustrate this point:

> Life finds in the cell the ground-plan for her first mansion—a one-roomed hut. You may change your one-roomed plan from round to square, from square to oblong, and you will not have improved it: but add a chimney and windows, and at once, though still but one room, it is something better (p. 46).

Although unicellular organisms have evolved beating cilia, photoreceptors, pseudopodia, and countless other structures that increase their fitness under specific conditions, the grade 1 body plan also has significant limitations. Almost all single-celled organisms are small, which makes them subject to a set of unique microscale challenges that haphazardly push and pull them in random directions (pp. 66–67).[17] Some unicellular organisms have evolved methods of mitigating the effects of Brownian dynamics, but these forces can never be truly defeated at smaller size ranges. Huxley therefore concludes that single-celled lifeforms are independent from their environment in only the barest possible sense. As he writes:

> [I]t is impossible to think of any single-celled animal swimming against the most sluggish river as it is to imagine a butterfly poised steady in a twenty-knot gale (p. 67).

The fact that unicellular organisms have relatively little agency relegates them to the lowest grade of individuality and limits the number of niches they can adapt to inhabit. Given these constraints, occasional tendencies towards multicellularity could obviously have been promoted by natural selection under the right environmental conditions. When selective forces transformed some protist lineages into obligately multicellular organisms, a fundamentally new type of body plan that Huxley refers to as the second grade of individuality independently arose (figure F.2) several times.

THE SECOND ORGANIZATIONAL GRADE

As Huxley described it, grade 2 transitions occur when cells begin "joining up . . . together so that each preserved a considerable measure of independence, and was yet subordinated to the good of the whole." The end result is a "type of structure, [where] the individual is built up out of a number of cells instead of one" (p. 68). Huxley's grade 2 individuals are strictly synonymous with what we would now refer to as obligately multicellular organisms. However, his views about the evolution of multicellularity did not set an immediate precedent for clear thinking that was passed down without interruption from 1912. Particularly in recent decades, researchers have consistently misunderstood multicellularity as a seamless gradient that includes both facultative aggregates of unicellular organisms, and the obligate forms of multicellularity observed in metazoans, land plants, some fungi, and some algae. The idea that there are important, empirically verifiable differences between obligate and facultative multicellularity, and between aggregative and adhesive multicellularity, used to be canonical.[18] However, these fundamental distinctions have only recently resurfaced[19]—an interesting case of a field returning to its roots after embracing alternative notions that proved unproductive.

Although multicellularity can be adaptive, the fact that so many protist species currently exist suggests that transitions to grade 2 must have been difficult, and hence rarely occurred. This being so, one could wonder why unicellular organisms have not employed other strategies to inhabit new niches, such as increasing their size by multiple orders of magnitude, while remaining within the first grade. Huxley realized that size increases of this type are generally impossible because the skewed surface area to volume ratio of excessively large cells precludes provisioning via diffusion. Once more, he employs a compelling metaphor to make his point:

> If the English Nation, with population advancing by leaps . . . were not able to build harbours and provide dock labourers as quick as she bred man, all the wheat in Canada . . . would not keep her from starvation for the simple reason that it could not get in. . . . [F]or each four-fold increase of transport workers there is a sixteen-fold increase within of the mouths to be fed (pp. 41–42).

Given the problems with surface area to volume scaling mentioned in this passage, it should come as no surprise that small clumps of cells sometimes emerged, and have been rewarded by natural selection. Huxley summarized the steps involved in this process as follows:

> Suppose that instead of separating from each other after each division, the cells remain connected. The result will be a colony of cells each one like all its fellows. If division of labour sets in later among the cells, they are rendered mutually dependent, and the colony is transformed into a true individual, which is obviously a higher order than the cell. It has attained what may be termed the second grade of individuality (pp. 46–47).

Two parts of this passage are of particular interest. First, Huxley appears to indicate that irreversible transitions to multicellularity are explicitly facilitated by adhesive properties of clonal cells, a contention that took a century to be formally confirmed by comparative data.[20,21] Second, he emphasizes that the advent of division of labor necessarily increased mutual dependence. Indeed, only in organisms that exhibit grade 2 organization are the component parts so interdependent that somatic cells are unable to escape the body and survive independently as solitary protists. As Huxley notes, reductions in complexity due to overspecialization in parasitic or mutualistic niches may occur, but these have never returned a multicellular eukaryote to a protist.

Contemporary research has tended to leave the irreversibility of MTE events unexplored, partly due to a general reluctance to see any sort of progressiveness in evolution, even when it comes to something as straightforward as the compositional structure of organisms. Claims such as "Multicellular organisms are composed of *simpler* cellular parts" or the assertion that "Metazoans are *more complex* than choanoflagellates" are scientific statements about hierarchical composition, not value judgments. As John Tyler Bonner described the situation, nearly everyone agrees that the first organisms were unicellular, and species such as our own are either the most complex, or somewhere near to this. Yet, "it is considered bad form to take this as any kind of progression," presumably because there is some sort of "subconscious desire among us to be democratic even about our position in the great scale of being."[22] Huxley lacked the blind spot identified by Bonner and this significantly enhanced his theorizing. He recognized that we often have legitimate reasons to speak of higher and lower or simple and complex in biological contexts, and he had no qualms acknowledging that some types of evolutionary change can be considered lasting advances in organizational integration. Clearly, however, such rankings are only unambiguously justified when making comparisons between phylogenetic crown groups that completed an MTE, and their sister lineages that did not.

THE THIRD ORGANIZATIONAL GRADE

The gradual emergence of classification systems that confused mere multicellular aggregations with true grade 2 organisms seems to have been part of a wider trend that accelerated with the sociobiology movement.[23] Continuing a theme that had been prominent in the Chicago School of community ecology for decades, behavioral and evolutionary researchers began to downplay the importance of obligate co-dependence in the classification of clones and families by advocating the use of all-inclusive group definitions. This effectively obscured the progressive features of the irreversible MTEs Huxley identified. Continuum-style thinking had become deeply entrenched by the time Maynard Smith and Szathmáry published their book,[24] and as a consequence few protested when they lumped facultatively and obligately cooperative phenomena into categories such as "multicellular" and "society," as if these terms were well-defined taxonomical designations.[25] Retrospectively, it is apparent that the categorical boundaries between social grades that Huxley recognized—which had been generally accepted throughout most of the twentieth century—were erased without any justification. This is not a matter of semantics, or a trivial definitional quibble. The vaguely defined sociobiological concepts Maynard Smith and Szathmáry adopted have obscured the fundamental differences between true, irreversible MTEs and facultative aggregations of grade 1 or grade 2 organisms that do not constitute a lasting advance in organizational complexity.

Groups of cells or multicellular individuals that come together to form aggregates are normally able to leave and live a solitary existence. Obligately multicellular organisms with an internal germ–soma division of labor cannot do this—their cells are forced to stay together because they are completely dependent upon the larger bodily collective. As both Wheeler[26] and Huxley realized, there is a close parallel between the developmental history of permanently multicellular organisms and colonial social insects with permanently differentiated castes. Like metazoan bodies, these colonies are tightly integrated units—albeit of a higher grade—and this mutual dependence makes it impossible for individual animals to function independently of the collective. Wilson's[27] continuum concept of eusociality masked this deep germline–soma analogy, and encouraged the formation of misleading apples-to-oranges comparisons because it did not recognize the fundamental distinctions between obligate social systems with a higher-level ontogeny, and facultative aggregates that do not develop in any meaningful sense of the term. In the end, Maynard Smith and Szathmáry's adoption of all-inclusive sociobiological gradient thinking made their account of the core features of grade 3 organisms less incisive than Huxley's.

Thankfully, there is a way to escape this confusion. The signal in the data quickly reemerges when we classify cellular collectives such as *Dictyostelium* fruiting bodies with mere temporary division of labor as aggregates of grade 1 organisms. The same transparency also re-emerges when we follow the lead of Huxley and Wheeler when dealing with the functional classification of the social insects.[28] To grasp how insect social systems differ from one another, and to understand the ways in which they are analogous to multicellular organisms, it is necessary to: (i) abandon the broad-brush continuum categories, and give serious consideration to the importance of (ii) closure and (iii) permanent, non-facultative division of labor.

Huxley followed Wheeler in acknowledging that ant colonies are grade 3 individuals and thus superorganismal (p. 108). In their comparative thinking, grade 3 organisms first formed closed colonies of core families, and then started to evolve increasing specialization of their component individuals, leading to the same mutual codependence that is the hallmark of germline and soma cells in grade 2 organisms. The key issue is that irreversible MTEs emerge when all colony members commit to either the germline or soma for life. Huxley drove this point home forcefully when he asked, "What is the meaning of a lonely bee and its actions when it comes back to find its hive destroyed?" (p. 7). Ultimately, the entity that replicates in grade 3 individuals is a specific colony lifecycle with a predictable higher-level ontogeny and replacement procedures of individual members, just like a solitary grade 2 organism reproduces a bodily lifecycle with a predictable development and turnover of somatic cells. At grade 3 MTE origins, closure at colony founding via a mated queen was a necessary condition of colony-level reproduction, just like zygote closure is for somatic body reproduction. However, in addition, natural selection must also forge an irreversible dichotomous break with the ancestral mode of reproducing by transforming formerly independent cell copies or offspring into soma (see "hierarchy" in the glossary).

In addition to recognizing that several insect lineages evolved organismal colonies, Huxley was aware that certain pelagic siphonophores have also transitioned to grade 3 organization, but was quick to add that other modular lineages of marine invertebrates have not done so, despite having some division of labor. The fact that he was able to generalize across taxa is impressive, and what made this possible was his commitment to a simple pair of theoretical principles: (i) MTEs only originated in ancestors with permanently closed social systems, and (ii) internal division of labor must be irreversibly advanced in order to qualify as a diagnostic MTE feature. Writing on the second idea, Huxley was clearly aware that division of labor in superorganisms can involve both germline (queen–worker) segregation and intra-somatic (e.g., worker–soldier) differentiation. He also grasped that the latter type of internal specialization was only known from ants and termites, and—in modular form—from cnidarians such as Portuguese man o' war.

Huxley's description of the basic biology of siphonophores is worth quoting at some length because it highlights how fundamental the concept of universal mutual dependence (or mutual parasitism for reciprocal efficiency benefits, as he writes on p. 103) was to his thinking about the MTEs between grades of individuality:

> In the majority of the Siphonophora, the persons of the colony have mostly only a historical individuality: some of them are sometimes so much modified and reduced that it has baffled all the zoologists to decide whether they are homologous with individuals or with mere appendages of individuals: and in function each is devoted so little to itself, so wholly to serving some particular need of the whole, that if one were separated from the rest, it would appear a perfectly useless and meaningless body to an investigator who did not know the whole to which it belonged. (p. 91)

The obligate, complex division of labor observed in siphonophores is particularly interesting because it illustrates that grade 3 transitions can occur in lineages that lack a complex central nervous system. At several points in *The Individual in the Animal Kingdom*, Huxley emphasizes that human brains are special, but advanced cognitive capacities are clearly neither necessary, nor sufficient for transitioning to the third organizational grade. This is vividly illustrated by the observation that brainless cnidarians have become grade 3 organisms, while our own societies remain, biologically speaking, within the second grade (pp. 108–109). In Appendix A (pp. 121–122), however, Huxley appears to add a puzzling wrinkle to the story by suggesting that human societies and some mutualisms *have* transitioned to the third organizational grade, albeit with a few caveats. The very brief tabulated entries appear to contradict claims made earlier in the text, where he argues in more detail that these systems have made only minor progress in this direction. Regardless, the crucial takeaway remains that Huxley was clearly aware that most offspring in ant and honeybee societies are developmentally somaticised into colony-parts, and that this system of biological organization would not be desirable for human social groups (p. 116).

IV. HISTORICAL REFLECTIONS AND FUTURE DIRECTIONS

Looking back at the scientific literature from the twentieth century, there are multiple examples of contributions that failed to receive adequate attention because they appeared in obscure journals or were the work of lesser-known practitioners. This is unfortunate, but also understandable given the sheer volume of research that was produced. In contrast, *The Individual in the Animal Kingdom*'s anonymity among contemporary biologists makes almost no sense at all. How did we manage to lose track of a Cambridge University Press monograph dedicated to a widely studied subject that was composed by one of the most revered scientists of the twentieth century? As we have shown, Huxley's book was not forgotten because it is filled with empirically inaccurate claims or dated theories that are no longer tenable in light of modern scientific knowledge. Although *The Individual in the Animal Kingdom*'s rapid descent into obscurity remains puzzling, three factors may help to explain how it slipped through the cracks.

First, most biologists are focused on emerging experimental methods and specific model organisms, which means that they often pay less attention to the work produced by those who came before them than physicists and chemists do. The fact that this trend has accelerated in recent decades is one of the most regrettable aspects of present-day biological research. Although modern technologies such as high-throughput genomic sequencing and their associated analysis pipelines have led to countless advances, it is important to remember that these are merely *tools*. Theories are the true bedrock of science, and in biology, the theory of evolution by natural selection continues to reign supreme. Synthetic theories and concepts function as a cross-generational matrix that keeps each science together over time. They are able to perform this function because they can remain valid, and hence relevant, no matter whether they were tested using techniques from the 1970s, 1990s, or 2010s. When our methods become the message, and the theoretical foundations of the field are ignored, the work of previous academic generations is inevitably lost, meaning we have no chance to build on their work or learn from their mistakes. In this light, the lack of attention *The Individual in the Animal Kingdom* has garnered over the years has almost certainly impacted the historical development of organismal biology. In particular, one could ask whether Wilson's *Sociobiology* and Maynard Smith and Szathmáry's *Major Transitions in Evolution* would have been written differently if earlier researchers had systematically tested and elaborated upon Huxley's framework.

Second, the trajectory of Huxley's career also seems to have played a role in the demise of his first book. Following the publication of *The Individual in the Animal Kingdom*, he embarked on a restless path through life, and was seldom settled academically. After a few years at Rice University, the University of Oxford, and King's College London, he effectively left academia in 1927 to focus on public dissemination and synthesis of existing knowledge. Yet, he never lost his passion for practical science and natural history, and remained a figure of towering influence, particularly in Oxford, UK, where his students and mentees obtained professorial positions.[29] Many believe that Huxley's crowning achievement was his well-known book *Evolution: The Modern Synthesis*,[30] but he also produced papers and monographs devoted to field observations of birds and invertebrates, experimental work on amphibian metamorphosis, and general essays on evolutionary theory and organismal scaling relationships, to name just a few. Interestingly, Huxley seldom cited *The Individual in the Animal Kingdom* in these works, even when a perfectly reasonable opportunity to do so presented itself. Given his later interest in *Drosophila* genetics—he dedicated his 1942 book to Thomas Hunt Morgan, calling him a "many-sided leader in biology's advance"[31]—it appears that he may have eventually come to regard *The Individual in the Animal Kingdom* as a product of youthful fancy that was somehow incompatible with newly arrived fashions, including the purportedly harder reductionist biology of the day.

Third, science is in an almost constant state of flux, but the rate and kind of innovation varies from decade to decade. In biology, the first half of the twentieth century was a particularly innovative period. Molecular biology, developmental genetics, and the modern evolutionary synthesis all began during this time, and these advances played a pivotal role in getting the field to where it stands today. However, in retrospect it is clear that the zeitgeist of the mid-twentieth century also led to the abandonment of perfectly good practices that were previously the stock and trade of the profession. In developmental biology, the entire tradition of comparative embryology was jettisoned almost overnight, and although it was more erratic and gradual, "old-fashioned" comparative natural history also declined. These approaches are prominently featured in *The Individual in the Animal Kingdom*, so many of Huxley's successors might have simply moved on to newer methods that appeared to promise more rapid career advancement.

One hundred ten years later, there is little question that, despite their obvious importance, the breakthroughs of the early twentieth century did not eliminate the need for careful observations, comparative phylogenetic inferences, and clear conceptual thinking within a broad frame of reference. Indeed, one could argue that these are some of biology's most essential methods that are always needed, and will never be replaced. Aside from the many empirical insights it contains, reading Huxley's 1912 book is worthwhile because it reveals that modern biological advances can sometimes lead the field down blind conceptual alleys. This is seldom apparent if we are only considering our immediate professional surroundings, or the recent history of a field. To understand whether a current direction of research is desirably incisive, it is often necessary to seek input from unbiased outside observers. No one is better suited to this task than our own academic forebears. However, when their wisdom is passed down through third-party summaries, the coherent insights they left behind may become distorted by misunderstandings, academic prejudice, and other forms of memetic drift. For this reason, it is important that we continue to read books such as *The Individual in the Animal Kingdom* in their original form. The giants of biology's past are still here to help shape the future of the field, but this can only happen if we pay the courtesy of reading their work.

⋆

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