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REVIEW

Speciation, natural selection, and networks: three historians versus theoretical population geneticists

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Abstract

In 1913, the geneticist William Bateson called for a halt in studies of genetic phenomena until evolutionary fundamentals had been sufficiently addressed at the molecular level. Nevertheless, in the 1960s, the theoretical population geneticists celebrated a "modern synthesis" of the teachings of Mendel and Darwin, with an exclusive role for natural selection in speciation. This was supported, albeit with minor reservations, by historians Mark Adams and William Provine, who taught it to generations of students. In subsequent decades, doubts were raised by molecular biologists and, despite the deep influence of various mentors, Adams and Provine noted serious anomalies and began to question traditional "just-so-stories." They were joined in challenging the genetic orthodoxy by a scientist-historian, Donald Forsdyke, who suggested that a "collective variation" postulated by Darwin's young research associate, George Romanes, and a mysterious "residue" postulated by Bateson, might relate to differences in short runs of DNA bases (oligonucleotides). The dispute between a small network of historians and a large network of geneticists can be understood in the context of national politics. Contrasts are drawn between democracies, where capturing the narrative makes reversal difficult, and dictatorships, where overthrow of a supportive dictator can result in rapid reversal.

Keywords Bateson's residue · Biometricians · Chargaff's parity rules · Eclipse of Darwinism · Macroevolution · Modern synthesis · Romanes' collective variation

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Introduction

In 2022, we celebrated the bicentennial of the birth of Gregor Mendel who discovered what we now know as genes. Although a major advance, Mendel's work had little impact on contemporary research until it was "rediscovered" thirty-five years later in 1900. Even then, Mendel's advocate, William Bateson, was fiercely opposed by mathematical biologists ("the biometricians") who were widely respected for their important contributions to statistics, but understand neither the Mendelian complexities, nor the subtleties of Bateson's interpretations (Forsdyke 1999, 2010).

After a six-year battle (1900–1906), most biometricians were cured by Bateson of their aversion to Mendel and accepted the name—"genetics"—for the new science. However, they and their followers, who came to be known as theoretical population geneticists, paid little attention to Bateson's eugenic caveats and his views on speciation (Cock and Forsdyke 2022).[1] Their brands of eugenics have been denounced in recent times, and structures that celebrate their work have been removed or denamed (Aylward 2021; Bodmer et al. 2021). However, it is their work on speciation that is the present concern, a concern which some less-noticed publications of two historians of science—Mark B. Adams (1944-) and William Provine (1942–2015)—may now assist. Having initially been influenced by mentors attracted by the teachings of the population geneticists, their studies later converged with those of the present author—a scientist historian. Together, we challenge the century-long dominance of the population geneticists. They have ignored occasional defectors (Gould 1980; Nei and Nozawa 2011), and now debate among themselves "potential artifacts," "confounding factors," and "departures from assumptions of neutrality" (Charlesworth and Charlesworth 2017), concede errors (Johri et al. 2021, 2022), and display poor historiographic understanding (Forsdyke 2021a).

For each historian of science, an important point was meeting with the Russian expatriate Theodosius Dobzhansky (1900–1975), whose *Genetics and the Origin of Species* was "perhaps the most influential single book on evolutionary biology during the period from 1937 through the 1950s" (Provine 1986, p. 327), and "undoubtedly played an important role in establishing 'population genetics' as the core evolutionary discipline" (Adams 2021a, p. 207). Dobzhansky's collaboration as a field naturalist with the mathematical population geneticist Sewall Wright, was highly productive regarding the careers of both. However, when challenged, Dobzhansky admitted that for their joint papers he had not attempted to understand Wright's mathematical reasoning (Provine 1986, p. 346). And Adams was shocked when he asked Dobzhansky about his mentor (Filipchenko) who had not thought that macroevolution was a mere expansion of microevolution.[2] The reply was a shrug: "He bet on the wrong horse" (Adams 2021a, p. 224):

> I was startled, having never (in my innocence) thought of science as a "horse race" or a "betting" matter. That comment changed my perception. This was not a scientist who had been certain of his own approach, but rather someone who realized it might have gone either way, and chose the option that, if it turned out to be right, would both justify and empower his newly coined specialty, "population genetics."

Meanwhile, puzzled philosophers had been sitting in the wings. By flooding the media with their works, the population geneticists seem to have so engaged them that few had time, either to study the science itself, or to mine the early history. When introducing a new book, the philosopher Richard Delisle (2021, p. 1) noted:

> The co-optation of historians and philosophers under the rhetorical discourses of a limited number of influential evolutionists has, apparently, played a key role in the persistence of a static and uncritical historiography. This Introduction calls for a new and more consistent paradigm that would make sense of the overall development of evolutionary biology, one based on a realignment of the alliance between all partners pursuing research in this area.

At this late hour, a consortium of current leaders in the field of population genetics (Johri et al. 2021, 2022) has conceded that "the ability to fit the parameters of one's preferred model to data does not alone represent proof of biological reality." It is their hope that fellow practitioners, having been alerted by this "simple truism," will avoid various pitfalls that may trap the unwary. However, apart from concerns on synonymous site neutrality (Kern and Hahn 2018), calls

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[1] I began writing this paper after completing (September 2021) the second edition of our Bateson biography (Cock and Forsdyke 2022), which provides detailed background. After my posting of a preprint on the Social Sciences Research Network in June 2022, the 200th anniversary of Mendel's birth was celebrated in July with an outpouring of papers in high profile journals. Their contents support the conclusion (see end of this paper) that superceding the traditional narrative (if indeed our case merits it) will take some time. This might first occur in a democracy rather than in a dictatorship, but we cannot be sure.

[2] Konashev (2023) notes: According to Filipchenko, in the simplest case, one elementary species (race) will differ from other elementary species in "only one elementary property." In this case, the question of the origin of species he wrote, "is replaced with a question of the origin of the lowest classification groups within one species, and if between them all a distinction consists in the presence of one property, then we come, eventually, to the question of there being a new property or group of new properties. Once we discover it, we will thereby also find out the source of evolution".

to reconsider evolutionary fundamentals are not mentioned. The consortium appeals for "interdisciplinarity [help] … in order to connect genotype to phenotype."

In four parts, I here attempt to realign "the alliance between all partners" by presenting a less "static and uncritical historiography." Indeed, following ancient precepts (Forsdyke 2017a), this is a history of historiographies. Under the heading "macroevolution" the first part names major protagonists, describes what they were arguing about, and considers Bateson's call in 1913 for a halt to studies of genetic phenomena until such a time that evolutionary fundamentals had been sufficiently addressed at the molecular level.

Under the heading "biometrics" the second part considers the essential takeover of the narrative by the theoretical population geneticists, which occurred independently and in-parallel with fundamental advances in the understanding of the biochemistry of life. Following the early turn-of-the-century activities of the biometricians, this occurred in two waves. The first was declared to be "*the* modern synthesis"—largely theoretical. The second, leading to present times, has increasingly attempted, but failed, to make biochemical ("reductionist") advances part of its corpus.

The third part considers the "epiphanies" of Adams and, less so, of Provine, and the convergence of their studies with those of the present author. Like the philosophers, the historians were for a while coopted by influential population geneticists and/or their followers. However, eventually they turned to the possibility of the above-mentioned "new and more consistent paradigm that would make sense of the overall development of evolutionary biology."

Finally, the fourth part considers the interrelationships of politics and science that allowed certain networks of researchers to gain momentum, not "in alliance with," but at the expense of, others—a situation documented for twentieth century immunology research (Eichmann 2008; Forsdyke 2012). Contrasts are drawn between democracies, where capturing the narrative makes reversal difficult, and dictatorships, where overthrow of a supportive dictator can result in rapid reversal. The degree to which this has impeded scientific advance is assessed in terms of various ways science operates, any one of which may slow or accelerate (become rate limiting), depending on circumstances.

Macroevolution

The Google N-gram program for books gives 1901 for the first appearance of the term "macroevolution." Yuri Filipchenko (1882–1930) employed it in the 1920s (Adams 2021b). If macroevolution were easy to understand, there would be little dispute, and this paper would not have been written. However, for over a century, its subtle complexities have puzzled many highly competent researchers—including some featured here—and have required lengthy texts to disentangle (Forsdyke 2001, 2016; Cock and Forsdyke 2022). Despite the difficulties, this paper begins with an orienting overview that may help readers, whatever their backgrounds, understand how a large network of theoretical population geneticists and a small, loosely organized, network of historians, independently saw the issues. Irrespective of which network is closest to a true understanding, the main purpose here is to clarify some evolutionary debates rather than to instruct, either on scientific subtleties (assigned to footnotes and references), or on competitive resource allocation mechanisms (Forsdyke 2022a) that may underlie the debates (see later).

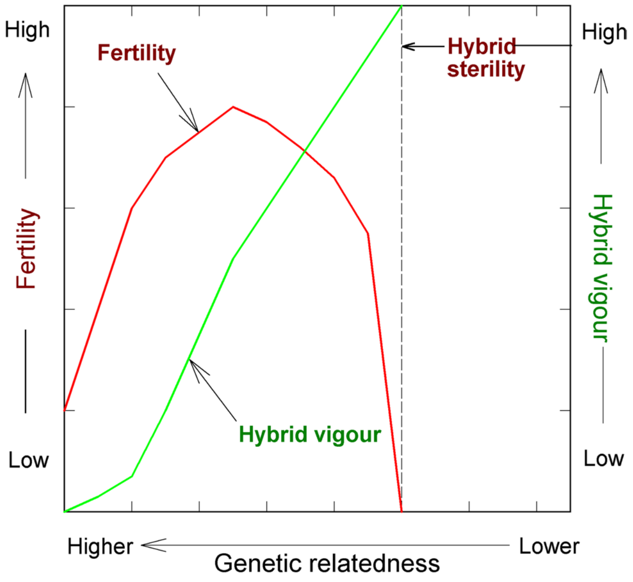

Fig. 1 Varying relationships between the degree of genetic relatedness between two organisms, the vigor of the hybrids they produce when crossed, and the fertility of those hybrids. (Reproduced from Forsdyke 2001)

Inbreeding and outbreeding

Classifications above the level of a single species (i.e., genus, family, order, etc.) are within the domain of what may be termed "macroevolution." Here, we are primarily concerned with changes *within* a species that can lead to the divergence of its lineage into two species—namely, the passage from microevolution to macroevolution without extending beyond species to higher taxonomies.

In the modern era, consideration of changes within a species includes differences in its genomic (usually DNA) sequences (i.e., changes within its *genotype*). However, in Darwin's day, changes (deemed "variations") were registered as differences in appearance or function (changes in *phenotype*). Crosses between closely related organisms (inbreeding) were generally observed to produce offspring ("hybrids") that were less well adapted than their parents. Crosses between more distantly related organisms (outbreeding) generally produced more vigorous offspring ("hybrid vigor"). Although definitions of "species" were then vague, there is now general agreement that if a cross fails either to produce hybrid offspring, or offspring are sterile (hybrid sterility), then the parents belong to independent population units—species—that are deemed to be "reproductively isolated" from each other.

Hybrid vigor is seen as reflecting an enhanced ability to compensate for, or repair, defects in parental genomes (Winge 1917, pp. 220–238; Bernstein and Bernstein 1991, pp. 235–288). Thus, the *wider* an outcross, the more vigorous are offspring, and the more likely they are to be favored by natural selection. But outbreeding has its limits (Fig. 1). As parental differences increase (i.e., their genetic relatedness declines), eventually their two sets of DNAs become so incompatible that, although a vigorous offspring may be produced, its fertility (number of fit offspring it can produce) declines, eventually to zero (hybrid sterility). This was nicely stated by Winge (1917, pp. 239–253; Forsdyke 2001, pp. 83–85), who identified "two critical stages" following the fertilization step that produces a hybrid organism:

> Once the hybrid has passed the *first test,* which decides whether it is capable of independent vital action at all [hybrid viability], it develops with often surprising luxuriance [hybrid vigour], until the inadequacy of the sexual products [resulting from defective chromosomal meiotic interactions] puts an end to its further propagation [hybrid sterility], and the biotype produced dies with the individual [line ends when the sterile individual dies].

The sterility can be *partner-specific* in that, if a different, more genetically related, parental partner is chosen, healthy vigorous offspring may be produced. Thus, when the offspring produced are sterile (i.e., the lineage discontinues), then an individual parent is reproductively isolated from *certain* individuals in the species population, *but not from others*. There is no longer free intercrossing between all species members. There are different lineages. The stage is set for a speciation event where responses to natural selection will not be reversed by crosses with the other lineage (i.e., no blending inheritance). The primary macroevolutionary problem is to determine what is disturbed when two parental genomes have such extreme differences.

Differences in kind or degree

We are here concerned with distinguishing different macroevolutionary viewpoints on the continuation of a species lineage. There are well established circumstances under which Darwinian natural selection can suffice *both* for *intraspecies* microevolution and for *interspecies* macroevolution, especially if interbreeding groups within a species first become reproductively isolated from each other geographically (allopatry). In this case, aided by their prior allopatric isolation, natural selection can suffice *both* for non-diverging within-species microevolution and for the divergence of one species into two (macroevolution).

This difference in *degree*, not in kind, can also apply even when the interbreeding groups share a geographic range (sympatry). Here, natural selection can operate, either prior to the fertilization that produces a hybrid zygote (prezygotic reproductive isolation) or after the fertilization (*one form* of postzygotic reproductive isolation; "hybrid incompatibility"). The latter is often referred to as a Dobzhansky-Muller incompatibility (Valiskova et al. 2022) which, like prezygotic isolation, depends on the nature of parental *genes*.

An alternative macroevolutionary viewpoint is that the processes of microevolution and macroevolution differ more in *kind* than in degree. While parents themselves may be fertile—so that a child is produced when they cross—that child may be infertile, because the paternal and maternal contributions to its genome (DNA) cannot work together during its gonadal cell divisions (meiosis) that would normally produce viable gametes. This hybrid sterility discontinues the lineage (*another form* of postzygotic isolation) so achieving reproductive isolation as effectively as processes involving natural selection. The paternal and maternal lines are set to separate, without having required an immediate participation of natural selection—thus, it is a difference *in kind* and does not depend on differences between genes.

Following Darwin's death in 1882, his young research associate George Romanes (1848–1894) postulated a mysterious "collective variation" within gonads. Contrasting with variations generated by conventional Darwinian *natural selection* involving interactions *external* to organisms, he envisaged a process of "*physiological selection*" that involved interactions *internal* to organisms (Romanes 1897, pp. 41–61; Krementsov 1994). Without citing Romanes, the term "physiological selection" was employed twelve times in a short paper by Dobzhansky (1940).

However, an understanding of Romanes's achievement was not evident in the literature until a graduate student at Princeton University, John E. Lesch, published his 1972 course assignment (Lesch 1975), which had won a History of Science Society prize. Although the subject did not further engage him, he had identified a key problem that would need biochemical analyses to answer:

> In order for physiological selection to work, a relatively large number of individuals within the parent species would have to vary simultaneously and in a manner to be fertile with one another but infertile with [other members of] the parent species. But this com-

> bination of circumstances appeared highly improbable and would require direct proof.

Lesch here notes that Romanes had engaged in what has become known as “population thinking” (Mayr 1982, pp. 45–47; Ariew 2022), in that a bell-curve distribution was envisaged (Romanes 1887, p. 76):

> I am guilty of no inconsistency when thus arguing for a "collective variation" on the part of the reproductive system, after having urged the difficulty against natural selection which arises from free intercrossing – i.e., the difficulty of supposing that a sufficient number of variations of the same kind should always be forthcoming simultaneously to enable natural selection to overcome the influence of free intercrossing. For, as previously explained, this objection is only valid in the case of "accidental," "sporadic," or "spontaneous" variations, which, *ex hypothesis*, are relatively few in number. The objection does not apply to "collective variations," which, being due either to common cause or to general variability of size, etc., about a mean, affect a number of individuals simultaneously.[3]

Romanes, like his contemporaries, was aware that personal features such as height and intelligence followed a bell-curve distribution that could influence procreation. Tall people tend to marry tall people and short people tend to marry short people. Likewise with levels of intelligence. However, such breeding differences are insufficient to initiate speciation since they do not prevent crossing. Thus, intermediate tall-short height-blends and high-low intelligence-blends, result. Whereas height is a *general* body characteristic, intelligence is seen as an *organ* characteristic (the brain). Romanes saw no reason why another organ, the gonad, could not also vary in some unknown function. Perhaps, in that case, the function could in some way either promote or prevent crossing. Thus, there could be an internal *something* associated with gonads that could vary in a way that was not immediately detectable. Romanes (1897, p. 43) stressed that the "independent variability" of this something occurred gradually:

> Starting from complete fertility within the limits of a single parent species, the infertility between derivative or divergent species, *at whatever stage in their evolution this began to occur*, must usually at first have been well-nigh imperceptible, and thenceforth have proceeded to increase stage by stage.

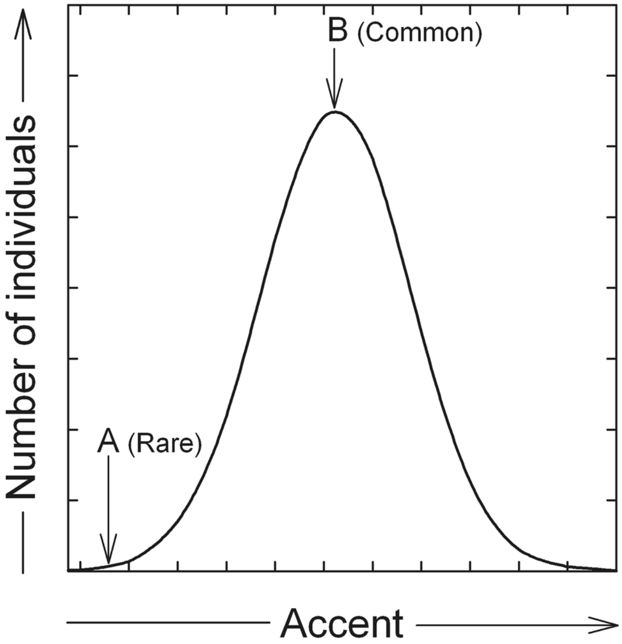

Fig. 2 Distribution of an entity—"accent"—that varies *continuously* within a population (species). In a spoken language this could be the extent to which H's are "dropped" (omitted from words). In the DNA "language," this could be GC%. The common type (B) is the population norm. At the left and right extremes (e.g., A at left), there are few individuals. For mating, given random mixing, an A-type individual is more likely to meet a B-type than either a fellow A-type or a type from the other rare extreme. Here, Fig. 1 scenario plays out on the ascending limb. The mating of two near-identical extreme A-types would produce some fertile offspring and the A-type would remain in the population (where future natural selection of individuals with A-type characters could continue). However, mating with an A partner located higher on the curve (more like B) would bring hybrid vigor into play. There would be more offspring and, in the absence of countervailing factors, the blending would decrease the A-type proportion in the population. Then, higher on the curve, as the A partner became even more like B, hybrid sterility with associated reproductive isolation (prevention of future blending) could emerge, so further decreasing the A-type proportion (Reproduced from Forsdyke 2016)

Not appreciated by his contemporaries or many who followed, Romanes's population bell-curve distribution implied that on each side of the curve, members of a population could be "physiological complements" to each other. These would register as fertile when mutually crossed. On the other hand, crosses between members that happened to be widely separated on the curve would register as sterile.

Figure 2 shows a bell-curve where members of a population are distributed according to their accent, perhaps the degree to which they "dropped their Hs" in Shaw's play *Pygmalion* (better known as the stage version—*My Fair Lady*). Those on the A-side of the curve would share, as a collective variation from the norm, English so-called upper-class accents and this would lead to their reproductive compatibility. On the other side of the curve, members

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[3] Contrasting with most characters that Mendel studied where there were two alternatives (e.g., either tall or short pea plants), most observable characters are contributed by a variety of genes that blend in different associations to generate a kaleidoscopic range of alternatives, whose relative frequencies among individuals can be displayed as bell-curves.

of the population shared, as a collective variation from the norm, English lower-class (cockney) accents that likewise would lead to their reproductive compatibility. The population norm (B) would contain various accent blends. Shaw experimented by shifting the accent of one of those on the cockney side to resemble those on the A-side of the curve. It worked! As will be discussed later, for accent one can substitute something called "GC%."[4]

The meiotic division of chromosomes within gonadal germ cells had not been described when Romanes (1886) presented his physiological selection hypothesis at the Linnean Society as an *alternative* to natural selection. The elder Darwinians—Wallace, Huxley and Thiselton-Dyer—were enraged. However, at least two of his younger contemporaries—William Bateson (1861–1926) and Joseph Cunningham (1859–1935)—strongly approved (Cock and Forsdyke 2022). Furthermore, as discussed later, Romanes found strong allies in a US evolutionist, the Reverend John Gulick (Gulick 1932, pp. 402–456), and a German expert on hybrids, Wilhelm Focke (1834–1922).[5]

Bateson and certain European botanists—Hugo de Vries, Carl Correns and Erich von Tschermak—became aware of Mendel around 1900, but it was Bateson who set the pace in bringing Mendel to world attention and suggesting a name for what he deemed to be a new science—"genetics."[6] Most of Bateson's novel and relatively unambiguous coinages—homozygote, heterozygote, allelomorph, epistasis, homeotic, meristic—have survived, except that "allelomorph" has been abbreviated to “allele”. However, his writings on an internal factor related to the divergence into species—“the residue” (Bateson and Saunders 1902; Bateson 1909, pp. 72–73)—either were not read, or were misunderstood, and the term faded from view (Forsdyke 2010; Cock and Forsdyke 2022).

Bateson's halt—reductionism

Based at St. John's College, Cambridge, where his father had been the Master, Bateson had opportunity to discuss macroevolutionary problems with physicists and chemists, and this is reflected in his writings (Cock and Forsdyke 2022). Furthermore, in the 1890s, he began corresponding with a medically qualified "physiological chemist" (as biochemists were then known), Frederick Gowland Hopkins (1861–1947). Then based in London, Hopkins became the first to hold the Cambridge chair in biochemistry (1914). By this time, a strong relationship between genetics and biochemistry was evident, and Bateson (1913; p. 86) foresaw in his *Problems in Genetics* "that before any solution is attained, our knowledge of unorganized matter must first be increased." So, regarding genetics: "For a long time we may have to halt."[7]

In short, Bateson wanted to molecularize genetics. He favored a reductionist—bottom up—approach. He recognized the importance of being able to interpret genetic phenomena, such as the linkage of characters in offspring, in molecular terms, but he did not himself feel capable of engaging in research at that level. Among those he mentored, Murial Wheldale turned to studying the biochemistry of plant pigments. The polymathic John Burden Sanderson Haldane (“JBS”) joined the Cambridge Biochemistry Department in the 1920s and made important contributions (Forsdyke 2022b) but became better known for his

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[4] GC% can be viewed as the accent of the DNA language. Given single letter abbreviations, the four main bases in DNA are A, C, G and T. The base composition of a segment of DNA can be expressed as the percentage of each base in that segment (A%, C%, G%, T%). Chargaff first parity "rule" is that for *double-stranded* (helical duplex) DNA, A% = T% and G% = C%. Certain bases are related. Thus, when comparing samples, as A% increases so does T%, and when G% increases so does C%. Since the total base concentration in a sample is constant (100%), it follows that when (A + T)% increases, (G + C)% decreases. So base composition can be approximated using just one of these—abbreviated to "GC%" (Forsdyke and Mortimer 2000; Forsdyke 2016).

[5] Romanes was aware of the work of Mendel. In an Encyclopaedia Britannica article, he listed Mendel among authors who had contributed to the study of hybridism. These included Focke who "has just published an elaborate and valuable work on hybridism in plants … giving a tabular series of all the known vegetable hybrids, and treating the entire subject in a very comprehensive manner" (Romanes 1882). There followed long correspondence with Focke (Romanes 1897, pp. 175–176; Schwartz 2010, p. 71). He believed Romanes' experiments comparing hybrids between geographically isolated forms that had been artificially brought together (i.e., rendered sympatric, Catchpool 1884), with hybrids naturally formed in sympatry, would “solve the whole mystery” (Romanes 1896, pp. 101, 314; Schwartz 2010, p. 601). Romanes was also conducting Mendelian-style breeding experiments (brother-sister matings), which were cut-short by his death in 1894 at age 46 and evidence on their existence long remained unnoticed (Olby 1966; Cock and Forsdyke 2022, p. 169). A letter (May 18th 1894) in the Wellcome Collection (London) provides essential evidence for those who wish to pursue the matter. Romanes was then primarily involved on two fronts. Countering the attacks of the establishment Darwinists on his own physiological selection hypothesis, and experimentally examining Darwin’s postulates on the mobility of the “gemmules” that were part of the latter’s pangenesis hypothesis. Romanes’ negative results on this were not formally published.

[6] The chronologies and extents to which various authors “rediscovered” Mendel’s work has been much discussed (Cock and Forsdyke 2022; Radick 2023) but does not concern us here. The Tschermak brothers supported Bateson over Weldon and were among those who came to acknowledge “special traits” that were distinct from “racial or mendeling traits” (Simunek et al. 2017).

[7] The subsequent era of "molecular biology" led to the classical helical duplex structure of DNA and, beginning in the 1970s, detailed studies of its *sequences* (Grantham 1980). These led further to the *alternative structures* that could be adopted by DNA duplexes, so influencing the nucleic interactions required for the genome shuffling and error-correction effects brought about by recombination (Forsdyke 1996).

mathematical contributions to population genetics (see below).

Following Bateson's advice, some geneticists may have turned to biochemistry, a route that physicists such as Delbruck were to follow in the 1930s (see below). While continuing his genetic studies, Herman J. Muller (1890–1967)—one of the triad of fruit fly geneticists associated with Thomas Hunt Morgan—engaged in theoretical biochemistry. He suggested that the pairing of genes as parts of chromosomes undergoing meiotic synapsis within gonads might provide clues to gene structure and replication (Muller 1922):

> It is evident that the very same forces which cause the genes to grow should also cause like genes to attract each other, ... If the two phenomena are thus dependent on a common principle in the make-up of the gene, progress made in the study of one of them should help in the solution of the other.

But Muller, like the theoretical population geneticists, did not halt. While readily adopting Bateson's coinages—homozygote, etc.,—they overlooked the most fundamental of his ideas, the "residue," as they did Romanes's "collective variation," and Grantham's "genome hypothesis" (see below), Likewise, making the mathematics easier, they embraced the “neutral” ideas of Kimura (1979; see later), instead of those of Akiyoshi Wada, his biochemical compatriot (Wada et al. 1976; Forsdyke 2016, pp. 193–206; Kern and Hahn 2018). Apart from his view that genetic code redundancy would assist the recombinational isolation of different genes (“homostabilization”) through differences in base composition, Wada pressed unsuccessfully for a Japanese "genome project," which would have anticipated by many years that of the USA (Ito 2005).

The population geneticists also overlooked comparative microscopic studies of chromosomes dividing in the gonads of various species (see below) that led Michael White in his *Modes of Speciation* (1978) to declare:

> The 'modern synthesis' of the 1940s is now 30 years old, and some attempts to revise it have not taken into account sufficiently the vast increases in knowledge that have occurred in recent years. The result is that … students of biology are presented with a stereotyped dogma that leaves them with the impression that all the basic problems have been solved. The main aim of this book has been to … point … out how much still needs to be discovered before we can confidently construct the 'new synthesis' of evolutionary theory some 25 or 30 years from now – a synthesis that may indeed be the *final* one in this field of knowledge. … This book is hence only the forerunner of the definitive work on … speciation that should be written, about the year 2000.

Grantham's genome hypothesis

The twentieth century saw great progress in conventional biochemistry (e.g., vitamins, hormones, enzymes, metabolic pathways). With the aid of biophysicists (e.g., Max Delbruck, Francis Crick) biochemistry morphed into "molecular biology" (Strauss 2017) and researchers such as Carl Woese (1928–2012)—a biophysicist who had worked with the General Electric Company—saw promise in the comparative analysis of nucleic acid sequences to identify species and their evolutionary relationships (Fox et al. 1977).

The Californian chemical engineer and ex-WWII bomber pilot, Richard Grantham (1922–2009), went further. In the 1970s, he began to ask the kind of questions that today's population geneticists—apparently unaware of his work—still pose (Johri et al. 2021, 2022): "Whether, and if so how, accurate evolutionary inferences can be extracted from DNA sequences sampled from a population?" Long before establishment of the GenBank database of sequences, which now houses thousands of sequences from numerous biological species, Grantham began to prepare his own archive at the Université de Lyon to house the first publicly available sequence fragments. He used these to study, in words of the population geneticists (Johri et al. 2021), "molecular variation and divergence data to infer evolutionary processes."

At the outset Grantham was skeptical regarding the neutral ideas promulgated by Kimura (1979) that were embraced by population geneticists. Noting Kimura's statement that "at the molecular level most evolutionary change and most of the variability within a species are caused not by selection but by random drift of mutant genes that are selectively equivalent," Grantham proffered "an independent view of evolution," declaring: "My evolutionary outlook derives from work with a new kind of methodology, based on nucleic acid sequences …. This work continues to indicate protein-independent molecular evolution of a non-neutral character." Grantham's macroevolutionary ideas, expressed in inchoate form as his "genome hypothesis" (Grantham 1980; Grantham et al 1980, 1986), can now be seen as directly in the line of descent from those expressed by Romanes and Bateson decades earlier (Cock and Forsdyke 2022).

Although Grantham disparaged neutral theory, in fact genome-wide mutations that changed the "accent" of the DNA language (GC%) could have a long-term non-neutral impact. A mutation deemed neutral in having no *immediate* effect on phenotype could contribute to the "collective" mutations of Romanes that had the potential to *later* facilitate the action of natural selection, once some degree of genome-dependent reproductive isolation had been attained. Thus, a "neutral mutation" immediately affecting only genotype could have a *long-term* effect on phenotype. To that extent, it would sometimes be misnamed "neutral." Indeed Romanes (1897, p. 77) had noted:

> But, in whatever measure collective variations are induced by any cause acting directly on a specific type, in that measure is the indirect action of natural selection superceded by the independent principles of what Mr. Spencer calls "direct equilibration." Of course, these principles may *co-operate* with that of natural selection; but none the less they are quite *distinct*. In short, my objection to natural selection on the score of free intercrossing only applies to cases of "accidental variations," relatively few in number; where "collective variations" [by implication, larger in number] are supplied to natural selection by other causes the objection, of course, is satisfied.

Meiosis and DNA structure

From light microscopic studies of chromosomes mispairing at meiosis, Michael White (1978) and others (King 1995) had implicated *large* differences between similar chromosomes (homologs) as leading to hybrid sterility with the potential for reproductive isolation that might empower speciation processes. The theoretical roots for mispairing were already evident in the early twentieth century works of Öjvind Winge (1917, pp. 239–253), of Crowther (1922) with Bateson (1922), and of Addison Gulick (1932, p. 498). It was Crick, with his "unpairing hypothesis," who worked it out (Forsdyke 1996). Most pictures of DNA molecules show them as double helices with two strands of DNA containing *inward-looking* bases, which pair with each other, thus joining the two strands to form a duplex. Crick proposed that parts of the strands might separate from each other and become *outward-looking*. In this circumstance, the outward-looking bases in the DNA of a maternal chromosome might pair with complementary outward-looking bases of a paternal chromosome.

Indeed, in the early 1990s Kleckner and Wiener (1993) implicated extruded stem-loop DNA structures in initiating homolog pairing. This meant that *small*, *base-level*, differences, if dispersed and of sufficient number, might negatively affect the pairing of stem-loops and disrupt meiosis. A relatively small intraspecies difference in genome-wide base composition (GC%) might serve to initiate speciation.[8] The earlier biochemical studies of base composition by Erwin Chargaff (1905–2002) and Noboru Sueoka (1929–2021) appeared consistent with this (Forsdyke 1996). Chargaff had revealed regularities in base composition (Forsdyke and Mortimer 2000). One of his four "rules" was the *species specificity* of GC% and Sueoka had correlated changes in GC% with reproductive isolation between "strains" of ciliated single cell organisms (tetrahymena) (Sueoka 1962; see later).

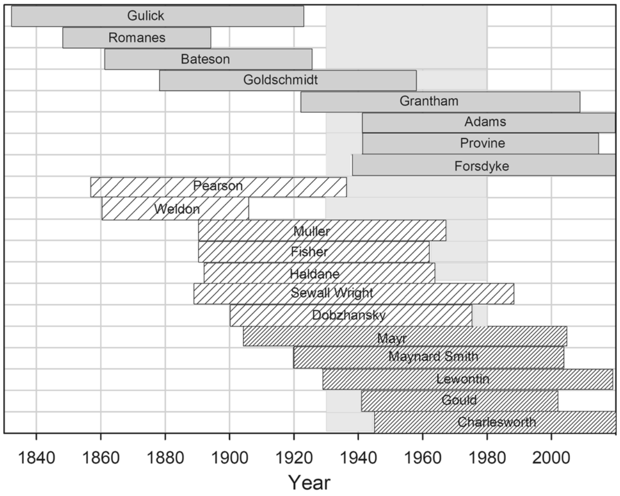

Fig. 3 Lifespans of those who, for speciation, postulated either involvement of an internal, genome-specific, character, besides natural selection (gray boxes), or a continuation of the microevolutionary primacy of natural selection (striped boxes). The pale gray background indicates the period (1930–1980) when biochemistry flowered to empower a reductionist approach. Differences in stripe intensity distinguish the early, intermediate and late biometric groups, whose important mathematical contributions aided the quantitative understanding of genetic phenomena

There is now growing recognition that the power of GC% differences is context dependent; it is not the GC%

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[8] Equivalent percentages of certain pairs of bases (Chargaff's first parity rule) assisted Watson and Crick when devising their helical model for *duplex* DNA, where two strands were wound round each other. Thus, an A on one strand would pair with a T on the opposite strand, and a G on one strand would pair with a C on the opposite strand. This pairing of complementary bases played a *structural* role. The order of the bases in each strand was such that at *every position* the duplex pairing was precise. Chargaff later found that *single* strands alone *also* possessed approximately equivalent percentages of the *same* pairs of bases (Chargaff's second parity rule). Thus, *provided* potentially pairing bases were *appropriately positioned,* single strands should be able to *locally* foldback on themselves, so adopting stem-loop configurations. It was evident that a simple property, base *order* (rather than base *composition*), should be particularly informative. Programs Forsdyke developed for single-strand structure analysis in the early 1990s demonstrated the statistical significance of base order-dependent structure forming potential. Combined with strand "kissing" ideas for recombination (Kleckner and Wiener 1993), there emerged a model for structure-dependent meiotic strand pairing, initiated by stem-loops extruded from duplex DNA helices. Stem-loop patterns were sensitive to small single base differences (DNA "accent" differences), which would impede pairing. This would impede recombination, so would have the potential to promote speciation (Forsdyke 1996). Thus, the DNAs of *different biological species* would have come to differ in their GC% values (Chargaff's GC rule).

differences themselves, but the oligonucleotides whose differences the GC% values *crudely register*. Through the reductionist line of enquiry, the "collective variations" of Romanes, the "residue" of Bateson, and the "genome hypothesis" of Grantham all reduce to something even more fundamental—relative oligonucleotide frequencies (Forsdyke 2021b).[9]

The evolutionist prime movers

As the number of people in this narrative enlarges, a temporal guide to the cast of characters, broadly labelled as "evolutionists," is appropriate. The upper part of Fig. 3 shows the lifespans of Gulick, Romanes and Bateson, who represent the first reductionist wave. Their *temporal* link (not necessarily an actual link) with Grantham is tenuously held by Richard Goldschmidt (1878–1958) who, like Bateson, was too stuck in his ways to become practically involved. After much delay, in the modern era Grantham links up with a second wave—Mark Adams, William Provine and myself (discussed later).

The lower part of the figure shows the lifespans of those who participated in what can be seen as three successive biometric waves, beginning with those who forcefully opposed Bateson. This first Pearson-Weldon wave is not easily connected with the second wave. Mendelism (genes galore!) had opened new lines of enquiry, and many believed that they had a sufficient understanding of the period from the *Origin of Species* (1859) to the first wave. The link between the second and third waves was conspicuously provided by Ernst Mayr in the USA and John Maynard Smith in the UK.

The pale gray background (Fig. 3) indicates the period (1930–1980) when biochemistry flowered, so empowering the reductionist approaches of Woese and Grantham. In the interim, the phenomenon-level studies of the population geneticists expanded and provided many important insights. However, as with the first wave, their forward movement did not proceed in parallel to complement that of the reductionists. What can be deemed as truly significant progress was often accompanied by opposition to novel reductionist insights that were either not read or, if read, were not understood. A ciliate geneticist (Nanney 1999) noted that:

> Ernst Mayr, the youngest and most autocratic of the apostles, undertook the task of elaborating and enforcing the orthodox conclusions through his long and productive career …, even after the full range of evolutionary process had been opened up through the application of molecular technology, and after the inadequate scope of the Modern Synthesis had been made manifest (Woese 1998).

And the biochemist Thoru Pederson (2013) pondered: "What did Woese see when looking at the field of evolution around 1960? He saw the swill of population genetics, a field almost crumbling to its knees at the time by mathematical obfuscation and understood by almost no one outside of the guild."

With the perspective of a philosopher, Delisle (2021) introduced a multiauthor volume with a series of consecutive historiographical labels that he saw as having been produced by population geneticists for rhetorical purposes rather than for enlightenment: Darwinism, Darwinian Revolution, Eclipse of Darwinism, Modern Synthesis, Extended Evolutionary Synthesis, Non-Darwinian Synthesis (Huxley 1942).

From their "unassailable citadel," Delisle wrote of the triumphant population geneticists who saw that "the modern synthesis needed historical roots … so Charles Darwin was placed in command of a 'Darwinian Revolution'." Then, natural selection, being "at the core of Darwin's theory," could be subsumed by the "Darwinism" label. The "no-man's land" occupied by "recalcitrant scholars" somewhere in between Darwinism and the Modern Synthesis, was called the "Eclipse of Darwinism." Following the "Modern Synthesis," there was then a branching into two "post synthetic developments," that either departed mildly ("Extended Evolutionary Synthesis") or radically ("Non-Darwinian Synthesis") from the old label.

Biometrics

The early turn-of-the-century work of the biometricians led to a growing involvement of mathematical biologists in two waves, the first leading to the highly theoretical "modern synthesis," which was followed by the second, when population geneticists seized the high ground of genetics research.

The biometricians

Delisle (2021) asked "if the 'Eclipse of Darwinism' was invented merely to fill the void between the 'Darwinian Revolution' and the 'Modern Synthesis', what was such an interstitial moment really about?" Within the "eclipse" period (1880–1920) was the first decade of the twentieth century, when the mathematically orientated, well-funded, "biometricians," led by Raphael Weldon and Karl Pearson, questioned Mendel's interpretations (Cock and Forsdyke 2022; Radick

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[9] A low GC% segment of DNA will have more sets of consecutive bases (oligonucleotides) rich in A and T (e.g., ATC, CAT, AAA, ATA, AGT). A high GC% segment will have more oligonucleotides rich in G and C (e.g., GCT, TGC, GGG, GCG, GAC). Assuming a selective advantage of differences in GC%, this raised the question as to whether a primary selection pressure acted at the GC% level, with oligonucleotide frequencies being a secondary consequence, or vice versa (Forsdyke 1995). It now seems likely that oligonucleotide levels are *primary* (Forsdyke 2021b).

2023). After the battle led by Bateson and his fellow Mendelians (1900–1906), most biometricians were cured of their doubts and accepted the name he suggested for the new science. However, while readily adopting his terminology, the biometricians overlooked the most fundamental of Bateson's ideas—the “residue.” Indeed, their attack probably diverted him from its study. An important advance was an essay in a volume commemorating both the centenary of Charles Darwin's birth and the fiftieth anniversary of the publication of his *The Origin of Species* (Bateson 1909; Forsdyke 2010). With the help of a physician, Bateson later acknowledged the possibility of a more complete chromosomal version (Crowther 1922; Bateson 1922).

Apart from their great contributions to statistics, the first wave of biometricians had little long-term influence (Cock and Forsdyke 2022). The second biometric wave was largely driven by the fruit fly studies of the Morgan group at Columbia University. These made clear that the genetic linkage of groups of characters that had puzzled the Mendelians, corresponded to chromosomes (Allen 1978).

Modern synthesis

While Adams pointed to a role for Sergei Chetverikov (see below), in the West the second biometric wave can be seen as beginning with the work of John B. S. Haldane, Ronald Fisher, and Sewall Wright in the 1920s. A fundamental unity between Mendelian genetics and Darwinian natural selection was proclaimed. This “modern synthesis,” which allowed some role for random factors (“genetic drift” most evident in small, isolated groups), was little influenced by the growing corpus of biochemical knowledge (the pale gray area in Fig. 3) and embraced the all-encompassing power of natural selection (deemed as "Darwinism"), *both* for microevolution and macroevolution. The era of the recalcitrant scholar (e.g., Bateson) was dismissed as a sad time when Darwinism was "eclipsed" (Huxley 1942; Meulendijks 2021).

Often lumped together, the three leading population geneticists were actually very different. Haldane was an independent polymath. However, Fisher occasionally turned to one of Darwin's sons for biological support and later to the Oxford biologist Edmund Ford (1901–1988). Sewall Wright developed a close working relationship with Dobzhansky who, having been recommended to Morgan by Filipchenko, had an early association with the Columbia fruit fly group (Allen 1978).

The numerous celebrations marking the 1959 centennial of Darwin's *Origin of Species* (Smocovitis 1999) can be taken as ending this "classical" era of population genetics. The complacent publication arising from that held at Cold Spring Harbor in the USA entitled "Genetics and Twentieth Century Darwinism" was summarized by Jan Witkowsky (2002):

> The published volume is notable … for the paucity of complicated equations compared with previous Symposia covering population genetics – neither Sewall Wright nor Richard Lewontin, although present, gave papers. The meeting began with presentations by Ernst Mayr and Th. Dobzhansky, each giving masterful overviews of the intertwined histories of genetics and evolutionary studies and the current state of the field. The closing remarks were given by G. Ledyard Stebbins, the eminent plant evolutionist. He pointed out that this diverse group of scientists had reached agreement on concepts "remarkably similar to those which Darwin himself held"; that is to say, the twentieth-century integration of genetics and evolutionary studies had led to a strengthening of the fundamental tenets of Darwinian evolution, a very satisfactory conclusion to a meeting to celebrate Darwin.

Theoretical population genetics

While Mayr had chided the "classical population geneticists" for their preoccupation with individual genes ("bean bag genetics"), those of the third wave were more conversant with biological phenomena involving genic interactions that could be considered mathematically. Lewontin (2003) provided some retrospective insight into the credo of the "newer population geneticists":

> Sometimes theoretical structures are nothing but calculating devises constructed from a complete and unproblematic knowledge of the underlying mechanical details. The purpose of such a calculating device is to predict how differences in inputs into the system will be reflected in output. The classic example in biology is theoretical population and evolutionary genetics. All the relevant elementary processes are already known. These include all the mechanisms of inheritance, the phenomena of mutation, of migration, of the effect of limited population size, and of the operation of natural selection through differential survivorship and fertility. Theoretical evolutionary genetics assembles all these phenomena into a formal mathematical structure that predicts changes in the genetic composition of populations and species over time as a function of the numerical values of these elementary processes. In contrast, sometimes theories are meant to help us 'understand' a process whose outcome has been observed but whose dynamic details are not known from experiment or observation. The theory provides a formal structure into which, it is supposed, the actual mechanical details will fit if we ever get to know them.

Judged from their writings, the population geneticists paid little attention to the early history (Gulick, Romanes, Bateson). Goldschmidt was ridiculed because of a brief dalliance with “hopeful monsters” (Goldschmidt 1940, pp. 390–393). The DNA studies of Chargaff, Sueoka and Grantham, the chromosome studies of White and King, and the microbial breeding studies of Nanney (see below) are scarcely evident in their writings. Among the many topics addressed (e.g., epigenics, eugenics, game theory, sex chromosome dosage compensation), speciation was more of a side-issue, since it seemed to merely require an extension of microevolutionary thinking. Many of their students, whatever their interests, were happy to accept this modern biometric wisdom. Among these in the 1960s were two embryonic biohistorians—Mark Boyer Adams and William B. Provine. Their deep probings, which included long, often taped, interviews with the major protagonists, fueled their earlier doubts that were to progress to their forcefully drawing attention to the possibility of a more limited role for natural selection in the initiation of species divergence.

The evolutionists

Adams's account

Growing up in Ann Arbor, Adams was inspired to study Russian history by Professor Andrei Lobanov Rostovsky, who had escaped from Russia ahead of the Bolsheviks and happened to be his next-door neighbor. While at high school, Adams took an extra-curricular course in Russian at the University of Michigan. At Harvard, he filled his major requirements in “History and Science” with Russian history and biology, taking courses given by George Wald and Edward O. Wilson. In the summer of 1968, he was part of a 3-month trip to South America (“The Harvard Darwin Expedition”) that was organized by a fellow student, Frank Sulloway, and sponsored by Wilson. This retraced Darwin's Beagle voyage while deeply studying Darwin's writings.

Meanwhile, as a first-year graduate student in the History of Science Department, he was admitted to a graduate seminar on evolution given jointly by Ernst Mayr and paleontologist George Gaylord Simpson. As a final paper topic, for an historian with his Russian training Mayr recommended studying Chetverikov. That research led to two papers, published while he was still a graduate student (Adams 1968, 1970), both of which acknowledged Mayr's input. In turn, Mayr, who did not read Russian, seems to have interpreted Adams's papers non-confrontationally, briefly citing them in a major history text (Mayr 1982), and often alluding to their reliably covering the “Russian” side of “the synthesis.”

At that time Adams mentioned neither Romanes nor Bateson. Mayr (1942, p. 237) had given the name “founder principle” to the peripatric speciation studies of Gulick (1872) and the first paper (Adams 1968) noted: “Chetverikov borrowed certain features of the theory proposed by Rev. John T. Gulick which suggested that non-adaptive evolution could occur as a result of the inbreeding of a few isolated individuals.” Furthermore, Mayr's "beanbag" distinction was acknowledged (Adams 1968):

> Ernst Mayr has distinguished "classical population genetics" which presented evolutionary change as essentially an input or output of genes [counting beans], from the "newer population genetics" in which a gene can have a constellation of selective values, depending on its genetic and environmental backgrounds. If we accept this distinction, it is clear that conceptually and experimentally the Russian School [in the 1920s] had laid the basis for the "newer population genetics" even while the "classical" was being enunciated.

The second paper (Adams 1970) engaged more fully with population genetics, ascribing early ideas on isolation to Moritz Wagner, and distinguishing followers of "the naturalist tradition" from statisticians:

> The biomedical camp, in which I would include such figures as Karl Pearson and W. F. R. Weldon, tended to treat natural selection as a statistical process acting on continuous variation, and their investigations fall as much in the discipline of statistics as of biology. Although this theoretical approach gained great currency at the turn of the century, there was a concurrent tradition of evolutionary explanation which had developed among Continental Darwinians, exemplified by Moritz Wagner's theory of speciation by "isolation." This type of theoretical biology tended to rely much more heavily on studies of the processes occurring in natural populations. Most turn-of-the-century taxonomists, systematists, "ecologists," and zoologists did not rely on statistical models and can be seen as members of the naturalist tradition.

Adams's "concurrent tradition of evolutionary explanation" included that of Chetverikov, who "felt compelled to explain divergent speciation without any recourse to selection. He knew the literature stemming from J. T. Gulick's nineteenth-century work on Hawaiian land snails and found it to be a convincing demonstration of speciation in the absence of selection." In a 1926 paper (for translation see Chetverikov 1961) the Russian evolutionist had cited both Gulick (1872) *and* Romanes (1886). However, Gulick's view of isolation had a geographical component (peripatric) that was more consistent with the geographical (allopatric) thinking of Chetverikov (and also Mayr). Nevertheless, many important points made by Romanes are to be found in Chetverikov's classic work.

While in these early papers Adams did not mention Bateson, he did mention "the Mendelians" and, perhaps under the influence of Mayr (who opposed Bateson; see later), he mentioned Bateson's rival, Edward Poulton. Since, like Mayr, few of his historian readers could read the Russian literature, they probably interpreted Adams as being in line with "the traditional narrative," as indeed he was at that time. His final doctoral dissertation was entitled "Genetics and the Soviet Scientific Community, 1948–1965."

Adams joined the new History and Sociology of Science Department at the University of Pennsylvania in 1970. He retained a warm relationship with Mayr, who facilitated his taped interviews with Dobzhansky in 1973 (Adams 2021b). As indicated in the Introduction (above), these interviews initiated growing doubts that were slowly explored in subsequent, little-cited, papers over the next two decades. An enlightenment was arrived at in 1988—deemed an "epiphany"—which was shared in many invited lectures both in the United States and on an international circuit that included France, where a short paper was published in French (Adams 1990).

With encouragement from the editor of *Isis* (Ronald Numbers), a longer English version was prepared for submission. Meanwhile, Adams was seeking a publisher for *The Evolution of Theodosius Dobzhansky,* which contained essays of contributions to a conference he had cochaired in Leningrad in September 1990. The editing was no light task and by the time it was published (Adams 1994), *Isis* had changed its editorship and had lost interest in Adams's paper.

Given many other pressures (e.g., histories of science fiction and eugenics, and biographies of Soviet scientists), Adams put the paper aside but circulated it privately to interested parties. Encouraged by several readers of his "samizdat," the work was eventually published, essentially unchanged from the 1990s version (Adams 2021a, b).[10] It related how he had long been wondering “about the origins of this triumphalist history,” as expounded by the population geneticists, their students, and their students' students. For "this traditional history of population genetics is the one I learned and the one I taught for more than two decades. During the same period, however, my own research on Russian and European genetics and evolutionary theory began to raise some unsettling questions." Thus, Adams regretted: "Alas, my own work has convinced me that much of this traditional view of the history of population genetics and its role in the evolutionary synthesis is fundamentally mistaken." He summed up in one paragraph the possibility that differences in *kind*, not in degree, could be of fundamental importance (Adams 2021a):

> In order to get from genetics (and population genetics) to evolution, one must see a link between the origin and character of intraspecific varieties and the origin and character of species and higher systematic categories (genus, family, order, etc.); and to do this, it is necessary to consider the variation within species (intraspecific) and the variation between species (interspecific) as qualitatively the same. If intraspecific variation and interspecific variation differ not in kind, but only in degree, then it is possible, by extension, to envision selection as the creator of new species. But if varieties are fundamentally different from species – if the fundamental character of intraspecific and interspecific variation is essentially different – then the effect of selection on a population cannot explain evolution. The species is the only link between the phenomena of the “selectionist” (breeder) and those of the “evolutionist,” who traditionally deals with such larger problems as the sudden origin of radically new forms (vertebrates, or terrestrial vertebrates, for example), “progressive” evolution, and the appearance and elaboration in the fossil record of new structural plans and new systems of respiration, circulation, and mentality.

Pondering why so many had adopted the former opinion, he suggested a need to counter the creationists might have made truth-seeking seem less important than the need to present a united front:

> Perhaps in the United States, the battle to establish the validity of evolution in the face of creationist religious opposition solidified the identification between the general theory and those experimental researches that could demonstrate, and thereby “prove,” that theory “as a fact.” This situation may well have encouraged individual scientists to downplay their reservations about the macroevolutionary question in order to protect evolutionary biology as a whole: uncertainties about mechanism may have seemed less pressing when the validity of evolution itself was under attack, especially when those uncertainties were being deployed by the creationists to disprove evolution.

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[10] Adams, Mark B. 1990. "LITTLE EVOLUTION, BIG EVOLUTION. Rethinking the History of Population Genetics." This 34-page typescript, received by the author in 2003, began with an unlabeled introduction, which in the 2021 version is labelled "Did Population Genetics Save Darwinism?" Section headings follow as in the 2021 version, except that the latter has an added section on "Julian Huxley's 'Modern Synthesis'." Furthermore, a section labelled "Simpson and Macroevolution" is retitled "Paleontology and 'Macroevolution'" in the 2021 version. The paper concludes with notes (numbered 1–41) containing comments and pre-1991 references.

Also pressing was the pragmatic need to counter the molecular biologists who were competing for access to the funding "honeypot" that had emerged after WWII (see later).

The paper of Adams mentioned Bateson only in the context of his battle with the biometricians over Mendelism. There was no mention of Gulick or Romanes, whose writings had informed Chetverikov. For these, we must go to Provine.

Provine's account

Provine's *The Origins of Theoretical Population Genetics* (1971) was written at the University of Chicago, where Provine had initially majored in Mathematics (1962).[11] Lewontin (Zoology Department) was a major influence not only on Provine, but also on other graduate students such as Joseph Felsenstein (Zoology Department), who would turn to theoretical population genetics, and Stuart Newman (Chemistry Department), who would turn to theoretical biology (Newman 2021).

At the outset, Provine (1971) stated that difficulties with Darwin's theory "were not satisfactorily *solved* until the rise of population genetics." The italics (mine) indicate, in Provine's mind at that time, a correlation between population genetics and an *actual solution* to the theory's problems. Furthermore, Provine acknowledged a division of labor—he would be dealing primarily with evolutionists other than those in the Soviet Union; this was Adams's territory. Thus, apart from brief mention in the introduction, Dobzhansky was neither cited nor indexed. Special thanks were accorded to Sewall Wright, whom he had interviewed, and to William Coleman (1934–1988), who had made available a prepublication copy of a paper on William Bateson (Coleman 1970) and had provided access to materials obtained from Bateson's relatives, which are now in various archives (Cock and Forsdyke 2022).

Despite initial enthusiasm, Provine concluded the book diffidently, noting that "acceptance by scientists of a new idea is sometimes more dependent upon its a priori acceptability than upon its scientific proof." Furthermore: "With the gap between theoretical models and available observational data so large, population genetics began and continues with a theoretical structure containing obvious internal inconsistencies."

There were then moves by Provine's mentor, Lewontin, to Harvard University (1973), and by Provine to Cornell University. From here, Provine developed a working relationship with Ernst Mayr (Smocovitis 2017) and continued his interviews with Sewall Wright. The mathematical modeling approach and the textbook of Dobzhansky (1937), which went into successive editions, were supported (Provine 1978). The textbook's important contribution to the "modern synthesis"—a term proposed by a less-mathematical evolutionist (Huxley 1942)—was essentially unquestioned. Thus, at this time, Provine was well embedded in the population genetics camp: "If the mathematical models of Chetverikov, Fisher, Haldane and Wright had influenced only Dobzhansky, the effect would have been significant. But the effect was much more pervasive because of the enormous influence exerted by Dobzhansky upon others" (Provine 1978, p. 180).

A major achievement was a biography of Sewall Wright (Provine 1986). It extended his 1971 text with the added benefit of interviews with Dobzhansky. Furthermore, in the interim, there had emerged Lesch's insightful study of the works of Romanes and Gulick. Thus, the Wright biography, dedicated to Mayr and Lewontin, was able to cover the *entire* post-Darwin range of evolutionary thinking. However, there was a caveat in Chapter 7, which dealt specifically with the pre-1925 work:

> To understand, for example, the conflict that developed between Wright and Fisher …, further background in some aspects of evolutionary biology before 1925 is necessary. … Evolutionary biology in the period 1859-1925 is extraordinarily complex so I will focus only upon those few strands that are essential for understanding Wright's work and its impact.

This was as close as Provine got to frankly admitting, despite Lesch's paper, that he had not paid as much attention to this period as he had to later periods, which were his main topic. He went on:

> Are there any nonadaptive characters? If so, what mechanisms of evolution can explain their origin in natural populations? … A large number of competing hypotheses were vigorously debated in the period 1859-1925. No convincing primary hypothesis or hypotheses emerged, except that geographical isolation, clearly insufficient as a complete explanation, was believed to play an important role. … This chapter [chapter 7] is only the briefest of introductions.

Lesch (1975) had mentioned Romanes' *Darwin, and After Darwin* trilogy that had been published in 1892, 1895 and 1897, drawing special attention to the last:

> Romanes' last words on the problems of isolation and physiological selection appeared posthumously in 1897 as Part III of Darwin, and after Darwin, …. Although necessarily incomplete, the discussion contains much previously unpublished material.

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[11] Adams recalls (personal communication; 2021) that William Provine had told him that his 1968 and 1970 papers on Chetverikov caused him to change the title of his dissertation (and book) from *The Origins of Population Genetics* to *The Origins of Theoretical Population Genetics*.

Provine noted the existence of the trilogy but mentioned that Wright had told him he had only read the first two volumes. Despite much discussion by contemporaries (Dewar and Finn 1909), the posthumous 1897 masterpiece had not been read by Wright. Perhaps this had discouraged Provine from reading it.

Meanwhile, Provine's doubts were growing. He expanded on these in a 1987 symposium celebrating Julian Huxley and "the modern synthesis" (Provine 1992): "As a historian, I am immediately suspicious when anyone describes his or her views as the 'new' or 'modern' way of seeing things, to be sharply distinguished from the 'old' inferior ways." Provine then bluntly declared "that the modern synthesis in evolution is scarcely a synthesis at all and should be renamed the evolutionary constriction"—and he cited Stephen Jay Gould's employment of a similar term ("hardening"; see below). Indeed, "What was new in this conception of evolution was not the individual variables, … but the idea that evolution depended on relatively so few of them."

In 2001 the University of Chicago Press reissued Provine's celebrated 1971 book. Whereas the strong influence of his University of Chicago mentor, Lewontin, was acknowledged for the first edition, Provine's mature and independent viewpoint emerged in the second, but only at the end. Thus, the title was extended to include "with a new afterword". Otherwise, the original 1971 text, including the index, was *unrevised*. So, it was only the "afterword" (9 pages including new references) that was new. This began with a historical retrospective (Provine 2001, pp. 197–205):

> My views on the historical origins of theoretical population genetics have changed little since the publication of this book in 1971. On the topics of theoretical population genetics and evolutionary biology and their interrelations, however, my views have changed dramatically. These changes have energized my interests in evolutionary biology and its history, and I briefly present them here, in a spirit of discussion rather than of certainty. … The book reflects the perspectives I obtained from Richard C. Lewontin (the primary influence) …. My views were typical for a graduate student in the Chicago zoology department in the mid-1960s.

There then followed a heated discourse that revealed his growing alignment with the views long expounded by Adams (see above) and those I had recently communicated to him (see below). There was first a section on "my views in 1959–1970" that presented ten "insights" that included beliefs in the great power of natural selection and that "macroevolution was a conceptually simple extension of microevolution." This was followed by a section on "review of these 10 certain insights in 2001" that indicated how much his opinions had changed in a direction that some biochemists and chromosomal cytologists had long been considering. In short, he had begun to catch up with what had happened during the period marked out by the pale gray background in Fig. 3. Regarding his earlier 1971 text:

> To me, evolutionary biology had come together into a powerful synthetic view, under which I wrote the manuscript of this book. I didn't even bother to explain the importance of theoretical population genetics to this synthesis. It was so obvious that saying so was unnecessary.

It was now conceded (Provine 2001) that "a major problem concerns natural selection at different levels of the evolutionary process. … Thus, at the DNA level, explaining any random sequence invokes selectively neutral or nearly neutral factors as the null hypothesis, an amazing turnabout since the late 1960s. I now argue that each level (phenotypic, protein, and DNA sequence) marches to different drummers." Indeed, "The DNA sequence level has ubiquitous variation that is not turned into proteins. The lovely unity of protein and DNA sequence levels is gone." Alas, "the idea that macroevolution was a simple extension of microevolution has left evolutionary biology. Instead, how microevolution becomes macroevolution is now a subject of great scientific interest instead of a process described by empty assertion." For Adams, the deemed enlightenment had been an "epiphany." For Provine, there was an unravelling element:

> The evolutionary synthesis came unraveled for me during the period since 1980. Historically, my examination of this period … showed that it was not a synthesis, but rather a systematic diminution of the factors in evolution, and I now call it the 'evolutionary constriction' …. The unity of evolutionary biology inherent in the 'synthesis' has been replaced by a much more interesting and fascinating complex of different levels marching to different drummers.

A section labelled "upshot for theoretical population genetics and evolution" concluded:

> In 1970 I could see the origins of theoretical population genetics as being an unalloyed good for evolutionary biology, and thus obviously a great subject for an historian. Now I see these same theoretical models of the early 1930s, still widely used today, as an impediment to understanding evolutionary biology, and their amazing persistence in textbooks and classrooms as a great topic for other historians.

To remedy, Provine recommended the works of various authors (e.g., Nils Roll-Hansen's translations of Wilhelm Johannsen) and concluded by recalling Chapter 7 of his own masterpiece (Provine 1986). This featured the nineteenth-century peripatric speciation studies of Gulick, and the non-geographical isolation speculations of Romanes.

However, even after the publication in 2001 of the second edition of Provine's book on the origins of population genetics, many post-2001 papers of others continued to cite only his 1971 first edition, so much of which he had disavowed (Charlesworth et al. 2017; Joshi et al. 2021; Sarkar 2021; Beatty 2021). It is possible that such authorities were consulted by publishers when approached by Provine for his last book. Alas, he had to self-publish (Provine 2014). For two decades, he had been troubled with a brain tumor and died in 2015.

Forsdyke's account

Whereas Adams and Provine, with little field or laboratory experience, regarded themselves as "historians of science," I formally entered history after three decades of laboratory studies in a biochemistry department, so might more aptly be considered a "scientist historian." I was one of a generation that had flocked to graduate studies at Cambridge University in the 1960s, where some key participants in the 1950s DNA revolution were still working and teaching. In 1968 I was hired to teach molecular biology at Queen's University in Kingston, Canada. In the early 1990s, my bioinformatic analyses of DNA sequences were guided by new work on meiosis in yeast (Kleckner and Wiener 1993) and by the observations of Vinay Prabhu (1993) on symmetries in nucleic acid sequences that had extended the work of Chargaff (see below). Guided by the “unpairing hypothesis” of Francis Crick (1971), this led to novel interpretations that seemed to provide a simple explanation for how new species might arise (Forsdyke 1996). Stripped of its molecular details, in outline my explanation seemed simple enough to have been arrived at by Darwin, or by one of the many people around him. Hence began what I called my "search for a Victorian" as is related in Forsdyke (2001, p. 204):

> A disparaging remark by Huxley that Romanes had got it "so hopelessly wrong" … caused me to ignore his work initially. Provine's 1971 book did not mention Romanes. Eventually, however, I arrived at chapter 7 of Provine's 1986 book on Sewall Wright. Here … Romanes was described as "Darwin's protégé," which is, I suppose, near to what these days we would call a graduate student or "post-doc"; if anyone would have been in a position to sort things out, it would have been Romanes. Then the magic words "physiological selection" appeared. This was followed by quotations from Romanes. I knew I had found my Victorian.

I imagined Romanes to have had a privileged UK background, perhaps with education at a leading public school that led on to Cambridge University. Then, I came across a biography written by his wife (Romanes 1896), which began: "George John Romanes was born at Kingston, Canada, on May 20, 1848, the third son of the Rev. George Romanes, D.D., then Professor of Greek in the University of that place." What I subsequently learned of the history is summarized in a paper (Forsdyke 1999), in a book on speciation (Forsdyke 2001) and in my webpages.[12]

Apart from the works of the Cambridge molecular biologists and of Grantham in France, those of two US-based biochemists, Chargaff and Sueoka, were of great importance. Both giants in their fields, Chargaff over his career had enunciated what came to be known as his four "rules" governing the frequencies of the four bases in DNA.[13]

Sueoka (1961) had shown that the nature of the twenty amino acid components of proteins, which are major contributors to the "outward faces" of organisms (their "phenotype"), could be influenced, *relatively independently*, by what Chargaff had identified as the species-specific, genome-wide, regularities in frequencies of certain DNA bases (expressed as GC%; his "GC-rule"). Thus, organisms, in addition to having to respond to *external* pressures (e.g., natural selection) that might have affected base composition, also had an *internal* base composition-determining function, which could sometimes *override* external pressures. Furthermore, in breeding studies with the ciliate geneticist David Nanney (1925–2016), base composition differences were correlated with reproductive isolation differences (Sueoka 1961):

> DNA base composition is a reflection of phylogenetic relationship. Furthermore, it is evident that those strains which mate with one another (i.e., strains within the same 'variety') have similar base compositions. Thus, strains of variety 1 …, which are freely intercrossed have similar mean GC content. … If one compares the distribution of DNA molecules of *Tetrahymena* strains of different mean GC contents, … the difference in mean values is due to a rather uniform difference of GC content in individual molecules. In other words, assuming that strains of *Tetrahymena*

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[12] My webpages were initiated in 1998 when journals were just beginning to make their papers available online. Nineteenth-century journals were then not a priority, so I scanned key papers of Romanes and Gulick, and added them to my pages together with significant twentieth century ones, including those of Winge, Chargaff and Sueoka. These may be accessed by way of the Internet Archives Wayback Machine.

[13] In 2000 I presented a paper on "Chargaff's legacy" at a workshop entitled "Neutralism and Selectionism. The End of a Debate" (Forsdyke and Mortimer 2000). Here I met Sueoka and Grantham (I had been corresponding with both). In the late 1990s, I had pleasant telephone conversations with the elderly Chargaff, who lived in New York. He was delighted to see our paper and sent a photograph for display on my webpages.

> have a common phylogenetic origin, when the GC content of DNA of a particular strain changes, all the molecules undergo increases or decreases of GC pairs in similar amounts. This result is consistent with the idea that the base composition is rather uniform not only among DNA molecules of an organism, but also with respect to different part of a given molecule.

Sueoka here correlated a *genome-wide* character, base composition, with offspring production (i.e., whether mating would continue the line). This was a function of what were then distinguished *numerically* as different "varieties" (variety 1, variety 2, etc.). However, these "varieties" had already been formally designated as non-interbreeding sets of *cryptic species*. Later they came to be distinguished based on differences in isozyme assays and ribosomal RNA (rRNA) sequences, and the naming system was changed. What had initially been designated as *Tetrahymena pyriformis* was *not* a single species (Nanney 1999)!

In 1995 I clashed with Sueoka who, despite his mastery of biochemistry and the genetic input of Nanney, had modeled his results in population genetic terms (Sueoka 1962). The dispute was over the interpretation of Chargaff's second parity rule which is concerned with the equivalent numbers of certain bases,[4,8] not only in double stranded DNA, but also in single stranded DNA. While Sueoka maintained a neutral interpretation, I advocated a selectionist one (reviewed in Forsdyke 2021a). Thus, that year, two independent papers appeared in the *Journal of Molecular Evolution*. One was by Sueoka (1995) supporting his model. The other presented an opposite interpretation based on my bioinformatic results (Forsdyke 1995). Two population geneticists later reviewed the conflict in the same journal in favor of Sueoka (Gautier and Lobry 1997). While the details need not concern us here, they illustrate a major theme of the present paper—the lack of historical and biochemical understanding among population geneticists.[14]

Over subsequent decades, when assessing evolutionary forces, the population geneticists recognized a relationship between GC% values and DNA repair (a process often labelled "gene conversion" even though also affecting non-genic regions), but they appeared agnostic regarding the "long-standing mystery," namely the underlying molecular mechanisms and their underlying significance (Long et al. 2018)[15]:

> One general force that may be of relevance is DNA stability, in that G : C pairs involve three hydrogen bonds, whereas A : T pairs involve only two. An alternative explanation for near-universal pressure towards G + C content involves gene conversion, which results from the repair of heteroduplex DNA arising from recombination between two non-identical sequences and, if biased, can operate like selection at the population-genetic level. … The molecular mechanisms encouraging such universal behaviour are unknown.

Despite errors (i.e., not understanding fundamental differences between messenger RNAs and other RNA species),[14] the Gautier-Lobry paper garnered multiple citations over subsequent decades, eventually becoming the subject of an entire paper (Forsdyke 2021a). Likewise, correcting Orr (1996) also required papers (see later; Forsdyke 2011; Nei and Nozawa 2011).

Indeed, the population geneticists had long realized something was up. There was a response to Forsdyke (1999) by Mohamed Noor (academic genealogy: Filipchenko, Dobzhanky, Lewontin, Coyne, Noor) and his associates (Kliman et al. 2001). Furthermore, my speciation book

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[14] Gautier and Lobry (1997) did not appreciate that there are two classes of single-stranded RNA, the ability to correctly fold being critical for the function of only one of the classes. Thus, there is a *structure-dependent* class, members of which do not encode the information for making a protein (e.g., ribosomal RNA), and a much *less-structure dependent* class, members of which encode information for making a protein (messenger RNA; mRNA). The structure-dependent class are protected by high GC% from heat-inactivation in organisms that can survive at high temperatures (thermophiles). As an invited peer reviewer of the Gautier-Lobry paper, I advised a correction, which was not implemented. The term "less structure dependent" needs qualification. Like GC% values, the potential of duplex DNA to extrude stem-loops is a *dispersed*, genome-wide, feature of DNA, which affects both regions encoding genes and those not encoding genes. Thus, mRNAs, while encoding a protein, also have some encoded structure that mainly reflects the structure-potential of the DNA *of the genes from which they were transcribed*. A loss of structure (at high temperatures) does not impede the mRNA protein-encoding function. Thermophiles have specific adaptations, other than high GC%, for maintaining function at the DNA level.

[15] The theoretical population geneticists here note that pairing between G and C is stronger than pairing between A and T, so that, on average, GC-rich DNAs (and RNAs copied from them) would be expected to have stronger pairing of complementary strands (hence being more stable at high temperatures). In analyses of single-strand structure potential, this genome-wide *base composition* dependent stability component can be identified in a segment because it is not affected by sequence shuffling. Once removed, there remains a precise value for the *base order* dependent stability component. Given the *dispersed* and relatively uniform nature of the contribution of base composition to the structure (it is the "accent" of DNA), the base order component reveals *local* sequence adaptations that have been selected over evolutionary time ("Nature's experiments"). When scored (by convention) as negative, base order supports the stability assigned by base composition (that also scores negatively), thus indicating a locally compact structure. When scored as positive, base order opposes the stability assigned by base composition, thus indicating a locally more open structure (Forsdyke 1996; Forsdyke 2016; Zhang and Forsdyke 2021). This approach has advantages over the modeling of various potential equilibrium structures calculated from sequence ensembles by determining probabilities of individual bases being paired or unpaired (Zhang et al. 2022). Technical disputes in this area are approaching resolution (Andrews et al. 2023).

(Forsdyke 2001) was negatively reviewed by one of the prime movers (Fig. 1; Charlesworth 2003). I replied to both (Forsdyke 2004). There was no further response. The state of play has been regularly summarized in successive editions of my bioinformatics textbook (Forsdyke 2016).

As the cogency of my case grew stronger, correspondence with the historians Provine and Adams assured me that I was not alone. Correspondence with Adams began in 2003 when he sent me his "samizdat." With Provine, correspondence began in the late 1990s and continued until at least 2004. We met once at a conference. He supported my case, but not my criticisms of Mayr, whom he himself had criticized despite a strong personal attachment.[16, 17]

Networks

Personal networks can play important roles in science. Factors influencing networks' effectiveness include the extent of their control by leading figures, the societies in which they operate, and sometimes who govern those societies. In immunology, the negative influence of a past leading figure is now well documented, but societal influences were less evident (Eichmann 2008; Forsdyke 2012).[18] In genetics, societal influences have played more decisive roles and leading figures have sometimes had to accommodate to this.

Dictatorships and democracies

Adams (2001) pondered the rise to power of Trofim Lysenko (1898–1976) and his mid-twentieth century attack on the "bourgeois" science of genetics in the Soviet Union:

> What was involved in the struggle over genetics was a *disciplinary* crisis involving competing groups and the theories, practices, traditions, and paradigms they represented. In 1948, one group was given complete control of the discipline by the central authority and patron of science. Part of the resultant crisis – and one of the reasons why Lysenko's new hegemony was so successful – was Lysenko's mandated takeover of all the *institutions* where the discipline was practiced.

Russia being a dictatorship, by "central authority" Adams meant first Stalin and then Khrushchev and their corresponding enablers. Whereas democracies can often appear as lumbering headless monsters that change slowly, dictatorships with their often-monstrous heads can make rapid, albeit sometimes narrowly considered, decisions. Depose the dictator and you may rapidly depose those whom he/she has supported. Thus, when Khrushchev followed Stalin, Lysenko and his institutional network remained secure. However, when Khrushchev fell in 1964, so did Lysenko and his followers. Subterranean networks of geneticists, who had survived by rebranding their art (e.g., "radiobiology," "cybernetics,"), quickly emerged.

In the democratic West, maintenance of academic networks is more a public relations exercise, where "public intellectuals" have much clout, especially if associated with leading universities. Some of these have recently proposed to adapt "the modern synthesis," not with a "non-Darwinian synthesis" (Delisle 2021), but with an "extended evolutionary synthesis" (Laland et al. 2015). This has been criticized as a failed example of "academic nitch construction" in this "post-truth world" (Gupta et al. 2017). However, its advocates seem unperturbed. Western academic networks are difficult to topple. Administrations may come and go, but academic networks tend to remain.

Like Roll-Hanson (2005), Adams (2001) held that the Russian experience was not an exotic exception: "But, upon reflection, can anyone active in science or the academy *anywhere* doubt that networks of the sort I have described also play pervasive and analogous roles in the West?" Whereas

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[16] It is possible that Provine was unhappy with my joking comparison between Ernst Mayr and Beau Geste—the fictional last defender of a besieged desert fortress (Wren 1924). In 2001 (18th September), I sent him a copy of my speciation book (Forsdyke 2001), which acknowledged his help: “Please accept the enclosed book for your library, with many thanks for the great help your work provided. I hope the ‘tiny’ paper you mentioned in your email of 2nd July is progressing OK and look forward to a copy. I am not so pessimistic about ‘the hopeless isolating mechanisms which differ in every case of speciation’ (quoting from your email). In the book I opt for one mechanism as likely to have been usually operative in the general case. While I agree there is no ‘the’ origin in an absolute sense, some origins are more likely to have prevailed than others, and one in particular, should be receiving more attention. With best wishes for your continuing good health.”.

[17] The 13-page, single-spaced, typescript of the ‘tiny’ paper—“Speciation in Historical Perspective” —duly arrived (9th December). Later (24th February 2004) Provine sent his review of Forsdyke (2004): “JTB asked me to review your article. My comments are attached. You asked me earlier to send you my speciation paper. It also is attached, and from it you can see that we differ a lot on species and speciation. That does not detract me from recommending that JTB publish your paper. You are one inventive guy. I have now read your entire book, too, and enjoyed it very much. You and Steve Gould tend to use history to build up to your own views, but that seems appropriate for scientists.” His 5-page review concluded cautiously: “Should the thesis of this paper be borne out by extensive future research, it would be a foundation stone of speciation studies.”.

[18] The dark side of the life of Nobelist Niels K. Jerne (1911–1994) emerged after his death (Soderqvist 2003; Eichmann 2008; Forsdyke 2012) and has received some publicity (Yakura 2011). The Soderqvist-Eichmann-Forsdyke grouping cannot be viewed as a "network" in the sense implied by Adams (2001), since there was no personal communication between its members. There was no concerted pushback. Thus, the powerful Jerne network (Eichmann 2008) had free rein.

Lysenko had only to court *dictators* in Russia, organizational equivalents of Lysenko in Western *democracies* would have had to court *far more widely* to create a comparative network. The same would have been required of those who might attempt to organize counter-networks with sufficient clout to break a stranglehold. Advances in media technology in the second half of the twentieth century—culminating in the internet—should have greatly enabled such networking. However, those who had first seized the high ground proved difficult to topple. Could the power of the population geneticists, as described negatively above in a *democracy*, be equated with that of Lysenko in a *dictatorship*? And could the opposition of Adams and Provine also be described, albeit loosely, in network terms?

In the West, without sinister motives the reasoned arguments of those aligned with the population geneticists—some deemed "celebrity scientists"—had flooded the media. Accordingly, those who opposed their evolutionary views may have been sentenced to, what may be referred to as "academic exile," in that their research papers and books were less frequently accepted by editors or publishers, and their peer-reviewed grant applications were likely often rejected. On the other hand, while Lysenko's proposals to improve Soviet crop production through his proclaimed "vernalization" procedure may have begun with good intention, by the time many of his opponents were being sentenced to gulag exile and worse, he had become so entangled in politics that, even if he had understood genetics, his arguments would have been to no avail. For Lysenko there was no going back.

Organization

Supporting the views of Chargaff (1980) on the merits of small groups in challenging the status quo, Wu et al. (2018) found that: “Small teams disrupt science and technology by exploring and amplifying promising ideas from older and less-popular work. Large teams develop recent successes, by solving acknowledged problems and refining common designs.” Thus, the reservations of the small Adams-Provine-Forsdyke "network" concerning the century-long academic monopoly of the modern biometricians (1920–2020) have only surfaced in recent years (2000–2022). Without acknowledging this, a consortium of prime movers from the population geneticists' network are now conceding possible errors (Johri et al. 2021, 2022).

Nevertheless, the population geneticists—a motley group with wide interests—have made, and will continue to make, important contributions in their fields. This fact is not here questioned, nor are their integrity and good intentions. Two figures stand out as playing central organizing roles: John Maynard Smith (1920–2004) in the UK and Ernst Mayr (1904–2005) in the USA, with Stephen Jay Gould (1941– 2002), sometimes cantankerous, but eventually falling in line (Fig. 3).

Maynard Smith studied aeronautical engineering at Cambridge and after WWII became a student with Haldane who held the Weldon Chair of Biometry at University College, London. A fruit fly geneticist with wide interests, Smith is described in his network as "one of the most influential evolutionary biologists of the generation that succeeded the 'founding fathers' of population genetics, as he was fond of calling Fisher, Wright, and Haldane" (Charlesworth 2004). Smith and Haldane both had communist party affiliations (Sarkar 2021), but this does not seem to be a general network feature despite the leftward political leanings of some US network members (e.g., Gould and Lewontin). As a "public intellectual" frequently called upon to explain evolution, Smith cavalierly dismissed mutations that appeared to have no selective influence (deemed "neutral" by Kimura). They did not matter because they had no immediate effect on function (phenotype). So, Mother Nature *did not care* whether they occurred or not (Smith 1995): "In Kimura’s own words, 'the theory does not deny the role of natural selection in determining the course of adaptive evolution.' What it claims is that in addition to genetic changes caused by selection there are much more frequent changes that occur because they do not matter."

Mayr joined Harvard’s Faculty of Arts and Sciences in 1953. A German expatriate (1931) and already advanced in years, his strengths were primarily in taxonomic field and museum work. Despite his bean bag criticisms, he embraced the modern synthesis as the "second Darwinian revolution" (Junker 1996). His writings became more historical after his above-mentioned address at the centennial celebration of Darwin's *Origin of Species* that concluded with a conciliatory note (Mayr 1959):

> I have come to the end of my short historical survey of the relation between genetics and the other branches of evolutionary science. It seems evident that there is a happy symbiosis among these various fields. The naturalist has access to a vast store of observational evidence on which he bases various empirical generalizations. It is the role of the geneticist to interpret these generalizations in terms of the genetic material and to test his conclusions by experiment. I can foresee no reason for a change in this historically established pattern of co-operation. The best evidence for its success is the modern synthetic theory of evolution.

However, Mayr was often severely judgmental. He challenged contemporaries, such as Carl Woese, who could fire back, as could those familiar with Woese's work. Pederson (2013) reminisced:

> Ernst Mayr and Woese fired fusillades across one another's parapets in the form of dueling *PNAS* papers, sometimes published with such frequency as to almost resemble postal exchanges. Mayr, who died in 2005, was at this time considered by many, perhaps justifiably, to be the greatest biologist in the world. Yet, astonishingly, it seemed he never was able to grasp the penetrating power of Carl Woese's data as the inarguable footprint of three domains of life on earth.

Mayr also challenged those who could not fire back. In 1973, citing Coleman (1970), he strongly criticized the long dead William Bateson, while welcoming, albeit with more criticisms, the new volumes of Olby (1966) and Provine (1971), which he interpreted elliptically as legitimizing the early biometricians who had opposed Bateson (Mayr 1973, p. 126):

> Both authors have searched the original sources far more thoroughly than … more broadly conceived volumes …, and both of them, as non-geneticists, have given far more emphasis to the legitimacy of the viewpoints of those with whom the early geneticists had their controversies. The results are most illuminating, and no one can read these volumes without learning a great deal not only about the history of genetics but indeed of the history of biology during the periods covered.

While declaring (Mayr 1973 p. 154) that "many obscure issues still remain to be elucidated," and general "confusion affected the interpretation of virtually all genetic and evolutionary phenomena from the Darwin period to the 1940s" (Mayr 1973, p. 130), Mayr praised, what are now recognized as, the fundamental biochemical insights of Hugo de Vries (1889): "Darwin's theory of pangenes, of course, was on the whole a theory of particulate inheritance, as de Vries (1889) perceived very clearly" (Mayr 1973, p 141). Furthermore, he confessed that Goldschmidt (1940) had first guided him to seek beyond geographical isolation as a driver of speciation (Mayr 1973, p. 148). Indeed, decades later he recalled (Mayr 1997):

> When in 1936 the great evolutionist Theodosius Dobzhansky was in New York to give the Jesup Lectures, I invited him to see the beautiful series of South Sea island birds, … which demonstrate geographic speciation so beautifully. He was greatly impressed and it contributed to his decision to discuss geographic speciation at length in his famous book Genetics and the Origin of Species, published in 1937. At about the same time, I showed the same material to another great evolutionist, Richard Goldschmidt, but curiously, it did not deflect him in the slightest from his belief in saltational evolution.

However, Mayr's attacks on reductionism ("naïve physicalism") and his confusing terminologies would probably not have encouraged many readers to explore the history themselves. At one point, de Vries and Bateson were designated as "naturalists" (Mayr 1973, p. 149), whereas at another point their opponent, Weldon, was labelled similarly (Mayr 1973, p. 127). Thus, he shrugged, "labels such as 'naturalists,' 'experimentalists,' 'laboratory scientist,' and so on, must not be taken too seriously" (Mayr 1973, p. 149).

In his great text *The Growth of Biological Thought*, Mayr (1982, p. 400–401) cited the third volume of Romanes's trilogy (Romanes 1897), but mainly in the context of some terminology Romanes shared with Gulick. Their referring to organisms varying in both time and space was deemed "an insight that was largely forgotten again after 1897, until Mayr (1942) and others revived it during the evolutionary synthesis" The second volume of Romanes's trilogy (1896) had also been cited (Mayr 1973, p. 357, 701) but then only with respect to the term "neo-Darwinism" (Butler 1880, p. 282), and to aspects of Darwin's terminology deemed to have only gained "universal acceptance" in the "1930s and 1940s, as a result of the evolutionary synthesis." Thus, Mayr overlooked Romanes' important messages referred to above.

Mayr (1980) took another crack at Bateson when summarizing, in terms of five factors, his own long-held views on the state of evolutionary biology as it had developed following the publication of Darwin's *Origin of Species.* The litany was repeated elliptically, shortly thereafter (Mayr 1983):

> In the period after 1859, only five major factors were seriously considered as the causes of evolutionary change, or, as they are sometimes called, the agents of evolution. By the time of the evolutionary synthesis (by the 1940s), three of these factors had been so thoroughly discredited and falsified that they are now no longer considered seriously by evolutionists. These three factors are: inheritance of acquired characters, intrinsic directive forces (orthogenesis, etc.), and saltational evolution (de Vriesian mutations, hopeful monsters, etc.). This left only two evolutionary mechanisms as possible causes of evolutionary change (including adaptation), chance, and selection forces.

Here he was poking both at Bateson, whom he included in the saltationist category, and at Goldschmidt, whose "monster" phraseology (Goldschmidt 1940, pp. 390–393) was subject to misinterpretation. The evening primrose mutations of de Vries (*Oenothera gigas*) were deemed a special case that applied to polyploid hybrids and, although not mentioned, Mayr and Bateson were here in agreement. The failure of de Vries to agree likewise had engendered a break with Bateson that was never overcome (Cock and Forsdyke 2022).[19]

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[19] A long-held intuition of Mayr was in principle correct. In his first book he had written (Mayr 1942, p. 225): "A single mutation does not

Thus, year after year, volume after volume, Mayr triumphal certitude was spread far and wide (Mayr 1988, p. 525):

> The evolutionary synthesis is important because it taught us how such a unification may take place; not so much by any revolutionary new concepts but rather by a process of housecleaning, by the final rejection of various erroneous theories and beliefs that had been responsible for the previous dissension. Among the constructive achievements of the synthesis was the finding of a common language among the participating fields and a clarification of many aspects of evolution and its underlying concepts.

While to close associates Mayr disclosed his insecurity regarding genetics and the activities of the population biologists (Provine 2004, 2005), from the presses of his university flew a stream of titles that would have impressed his students—many of whom came to present to the world the face of US evolutionary biology. They came to assume that he had thoroughly studied and understood all aspects of the subject, including its deep history, except that of the early Russian literature (Adams 1994). Here, like Provine, Mayr referred to Dobzhansky whose 1937 text had swept the field. For better or for worse, Provine (2004) noted that Mayr's "deep influence in systematics, systematic nomenclature, evolutionary biology, history of biology, and philosophy of biology over the past 7 decades is unmatched by anyone in his generation, or probably after." However, many credited him with solving problems others had already solved (Provine 2005):

> Many of the obituaries … credit Mayr with the solving the problems of species and speciation. Mayr was a great champion of the biological species concept, but he knew that … the concept entailed focusing upon isolating factors in speciation. He had no idea how isolating factors evolved and thought of them as ad hoc factors that did not evolve through the causes of natural selection, and were not correlated with morphological differences.

Although Mayr himself was not active in left-wing politics, he was at the center of the Harvard population genetics network. He was the elaborator and subtle enforcer of its orthodox conclusions (Nanney 1999). The network included two outspoken public intellectuals, Lewontin and Gould. As noted by Sarkar (2022) the latter's popular writings in the latter half of the twentieth century were comparable with those of the earlier Haldane.

However, being in a democracy, the Harvard "network" was less centrally organized than that of Lysenko, and some policing to deal with those who might stray was necessary. The sociobiological writings of Wilson (1975), while being defended in some quarters (Dawkins 1982, pp. 18–19), were bitterly contested by his Harvard colleagues (Allen et al. 1975). Irrespective of the merits of Wilson's case, the episode served to attract media attention to Harvard as a center of evolutionary thought with an open-minded viewpoint. With some hand-waving, Lewontin (1974, p. 318) concluded his first major work—*The Genetic Basis of Evolutionary Change*—by declaring that "context and interaction are of the essence." And Gould and Lewontin (1979) claimed a "pluralistic approach" that "does not deny that change, when it occurs, may be mediated by natural selection, but it holds that constraints restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution."

A problem arose when Gould showed signs of getting too interested in the constraints and promoted a reissue of Goldschmidt (1940). Even worse, he asked "Is a new and general theory of evolution emerging?" (Gould 1980). Here, he cited the *second* volume of Romanes' trilogy, but (as with Gould's other works) not the magical third volume (Romanes 1897):

> I well remember how the synthetic theory beguiled me with its unifying power when I was a graduate student in the mid-1960's. Since then I have been watching it slowly unravel as a universal description of evolution. The molecular assault came first, followed quickly by renewed attention to unorthodox theories of speciation and by challenges at the level of macroevolution itself. I have been reluctant to admit it … but if Mayr's characterization of the synthetic theory is accurate, then that theory, as a general proposition, is effectively dead, despite its persistence as text-book orthodoxy.

Gould probably confused, more than he explained, when it came to "reductionism." The population geneticists had interpreted the reductionist era of biochemical discovery (Fig. 3) as entirely consistent with their microevolutionary extrapolations (Gould 1980):

> The modern synthetic theory embodies a strong faith in reductionism. It advocates a smooth extrapolation across all levels and scales – from the base substitution

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Footnote 19 (continued)

make a new species except in the case of polyploidy. New species are due to gradual accumulation and integration of small genetic differences." If we now interpret "small genetic differences" as changes in single nucleic acid bases, Mayr's thinking accords well with the viewpoint espoused here. Often critical to the initiation of species are differences in Bateson's "residue" (Forsdyke 2010), which now appears to relate to the slow accumulation, *genome-wide*, of base differences that modify GC% values and hence oligonucleotide frequencies (Forsdyke 2021b). Mayr never appreciated this, nor did a member of the late population genetics wave, H. Allen Orr (academic genealogy: Filipchenko, Dobzhansky, Lewontin, Coyne, Orr). His paper (Orr 1996) continued to receive multiple citations, despite its disparagement of Bateson and a narrow focus on Dobzhansky-Muller incompatibilities (Forsdyke 2011; Nei and Nozawa 2011).

> to the origin of higher taxa. The most sophisticated of leading introductory textbooks in biology still proclaims: more extensive evolutionary change, macroevolution, [can] be explained as an outcome of these microevolutionary shifts. Did birds really arise from reptiles by an accumulation of gene substitutions of the kind illustrated by the raspberry eye-color gene? The answer is that it is entirely plausible, and no one has come up with a better explanation …. The fossil record suggests that macroevolution is indeed gradual, paced at a rate that leads to the conclusion that it is based upon hundreds or thousands of gene substitutions no different in kind from the ones examined in our case histories …. The general alternative to such reductionism is a concept of hierarchy – a world constructed not as a smooth and seamless continuum, permitting simple extrapolation from the lowest level to the highest, but as a series of ascending levels, each bound to the one below it in some ways and independent in others. Discontinuities and seams characterize the transitions; "emergent" features not implicit in the operation of processes at lower levels, may control events at higher levels.

The postulate of Gould (1980) that "the synthesis hardened throughout the late 40's and 50's" seems to have prompted a symposium on macroevolution, where he was strongly criticized (Charlesworth et al. 1982). The problem did not disappear. Gould (1995) noted that "a self-styled form of Darwinian fundamentalism, has risen to some prominence in a variety of fields, from the English biological heartland of John Maynard Smith to the uncompromising ideology (albeit in graceful prose) of his compatriot Richard Dawkins." Indeed, Gould (1995) noted that he himself had been publicly condemned by Smith in *The New York Review of Books*:

> Gould occupies a rather curious position, particularly on his side of the Atlantic. Because of the excellence of his essays, he has come to be seen by non-biologists as the preeminent evolutionary theorist. In contrast, the evolutionary biologists with whom I have discussed his work tend to see him as a man whose ideas are so confused as to be hardly worth bothering with, but as one who should not be publicly criticized because he is at least on our side against the creationists.

Whatever his opponents did, it sufficed. Gould's last major work (1400 pages) outdid even Mayr. Gould admitted error (Gould 2002, p 1002–1003). He died in the population geneticists' camp (Forsdyke 2017b), as did the unwaverable Lewontin (Newman et al. 2021).

Rate-limiting steps

The pace of scientific discovery appears to be limited by three main factors, the first two of which are positive. First, there are the conceptual leaps—new ways of thinking. With these, at the very summit, we associate such names as Newton, Darwin, and Einstein. Second, there are technical advances, such as the seventeenth century invention of the light microscope that demonstrated both the existence of microorganisms and that organisms like us are composed of cells. The third factor is competitions (that Dobzhansky saw in terms of horse races; Adams 2021a, b). Acting at various levels (ideas, resources), competitions can have positive aspects, but they can also delay—luring researchers down blind alleys (Eichmann 2008; Forsdyke 2012). While it is normal for those engaged in a line of enquiry to have different perspectives, when the research results of one group are easily communicated and/or are argued with greater skill, then that group can capture the narrative so tending to gain the interests of other scientists, popularizers of science and, more ominously, the granting agencies (Forsdyke 2022a). What could have been a natural divergence into two healthily interacting lines of enquiry, ends up with the dominance of one. Sometimes the latter's success is warranted, but sometime not, as is the case made here. Indeed, critical advances tend to follow the work of “underfunded solo investigators and small teams who disrupt science and technology by generating new directions on the basis of a deeper and wider information search” (Wu et al. 2018; Forsdyke 2022a).

The relative importance of the various factors may vary with time and place, as is well illustrated by Mendel (Forsdyke 2018). He began with technology—the counting of the distribution of certain characters among the offspring of a cross between two members of a species that differed in those characters (not as easy a task as some may think). There was then intercrossing among those offspring, with further enumerations generation after generation. Mendel's conceptual leap came when, from quantifying the ratios of certain characters, he deduced the presence within gametes of fundamental units that correlated with the ability to produce those characters. These we now know as "genes." Finally, subtle messages from his cloistered location (Olby 1966) had to compete with the revolutionary light cast by Darwin, with major support from the Darwinian "network" that included his influential "bulldog," Thomas Huxley. From the outset, Mendel knew of the work of Darwin. But Darwin knew little of Mendel. Fortunately, Romanes, and later Bateson, got Mendel's message (Forsdyke 2018).[5] There followed a century-long battle along many fronts between biometricians morphed into modern-day biometricians, and other evolutionists. The distinctions are not rigid, but biometricians tended to have strengths in mathematics and biology, while other evolutionists tended to have strengths in physics, chemistry and biology. Thus, there was a major interdisciplinary clash, with winners and losers, that may have profoundly affected the pace of research. As noted by Junker (1996):

> Systematics, for example, lost much of its previous importance during the 1950s and 1960s, mostly due to the prominent successes of molecular biology and other reductionist and experimental approaches. A major portion of the available resources – graduate students and financial support – was diverted into the new research areas. The coincidence of the Darwin centennial, the triumph of the modern synthesis, and the emergence of a controversy over the history and future of the evolutionary synthesis with the beginning of Mayr's interest in the history of biology, is not accidental.

Adams noted that, chameleon-like, post-WWII, "Soviet scientists had long since mastered … self-rebranding [i.e., not appearing to support genetics] to satisfy the government that controlled their funding," while "American scientists also found similar ways of adapting to the new honeypot" that had emerged (Adams 2021a, p. 220). The US Atomic Energy Commission with post-Hiroshima radiation concerns was funding population genetics (Adams 2021a, p. 219). Furthermore:

> I suspect, though, that in the United States (and possibly Britain), academic politics played a bigger role. So-called Big Science, which had developed earlier following the revolution in the USSR, took hold in the United States during World War II, and postwar America saw massive financial government support to science . . . especially to the right kind of science, useful science that was experimental, often conducted in laboratories, and addressed perceived immediate needs.

Conclusions

It is not hyperbolic to compare Lysenko's mid-twentieth century purging of geneticists from Soviet science with, in the West, the near century-long exclusion by modern-day biometricians of those with a deeper reductionist understanding of the science and its history. While in the Russian dictatorship *physical* exile to the gulags of many who would not conform was easily achieved, in Western democracies *academic* exile of opponents required an active and sustained control of the media by celebrity scientists and their network of associates well-placed in leading universities. However, while Lysenko's research was probably of little value and his motives questionable, the population geneticists made impressive research contributions and were well-intentioned. Nevertheless, they should have remained on tap, not on top. With their high authority acknowledged by publishers, journal editors, and officers of granting agencies, their network provided an abundance of peer-review "gate-keepers" whose narrow foci may have damaged promising careers and stifled opponents. Their hubristic contentment with the *status quo* was based on an incomplete understanding of the works of Romanes and Bateson, and of the underlying biochemical and cytological fundamentals. With their momentum unchallenged, now in the twenty-first century, with the help of philosophers (Delisle 2021), there is some concerted pushback by a small network of historians of science (Adams and Provine) and one science historian (the present author). However, in an age when "cancel culture" flourishes (Krylov et al. 2022), we cannot be hopeful concerning its success (Adams 2021a):

> I am neither a biologist nor a philosopher, but an historian. At one point, with the passage of time, I thought that by now, surely, many would have already realized the failings of the traditional view. But, alas, the “traditional” narrative still holds sway, …. I am not so foolish as to think that my 1990 paper’s publication will rectify the prevailing narrative, but I am very pleased to finally be able to make it available to interested colleagues and a broader readership.

Notwithstanding its implications for urgent sociopolitical issues such as Roe versus Wade (see Forsdyke 2022b), the recognition that macroevolution often involves a genome-specific character other than natural selection may take a while.[20]

Summary

The early biometricians, who attacked Mendelism, morphed into modern population geneticists, who accept Mendelism but maintain that natural selection suffices to explain both within-species evolution ("microevolution") and between-species evolution ("macroevolution"). Among students who

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[20] While this paper was under review there were three developments. 1. Population geneticists reported that the term “reproductive isolation” in the context of speciation was *first* employed in 1935; after discussion with the authors, the editor issued a correction (Reuter 2023). 2. Masatoshi Nei died. Having obtained results that “are complex and quite confusing,” he had sought with “a historical perspective” to “clarify the roles of mutation and natural selection in speciation” (Nei and Nozawa 2011). In an obituary, the senior author of Long et al. (2018) noted how Nei’s work had launched many careers in theoretical population genetics and that “Toward the end of his life, he pushed ideas about mutation-driven evolution, but despite my attempts to get a deeper understanding of what he was getting at, I never quite pulled this out of our conversations and was left feeling that I was missing out on something” (Lynch 2023). 3. A fuller translation of Russian works became available (see note 2).

came under their influence were two future historians—William Provine and Mark Adams—who provided supporting papers and a much-cited text *The Origins of Theoretical Population Genetics* (1971). However, opposition arose from biochemists (e.g., Woese, Pederson), chromosomal cytologists (e.g., White, King), a ciliate geneticist (Nanney), and Richard Grantham, whose bioinformatic analysis of DNA sequences led to his "genome hypothesis" in the 1980s. Drawing on both early studies (Gulick, Romanes, Bateson, Winge, Goldschmidt) and the later works of Chargaff and Sueoka, in the 1990s, Grantham's work was continued by a scientist-historian, Forsdyke, who proposed a molecular basis for the initiation of the divergence of one species into two (speciation) that did not require natural selection. Meanwhile, despite their earlier schooling, Provine and Adams had noted anomalies and began to question traditional "just-so-stories." The convergence of their views with those of Forsdyke, suggested that a "collective variation" postulated by Romanes and a mysterious "residue" postulated by Bateson, might relate to differences in short runs of DNA bases (oligonucleotides). Contrasts are here drawn between resolution of scientific conflicts in dictatorships, where specialist groups ("networks") need authoritarian approval, and in democracies, where approval involves public engagement. Whereas the downfall of Nikita Khrushchev quickly reversed Trofim Lysenko's hold on Russian genetics, in the West "public intellectuals" and their followers can slow reform.

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