The 1909 Darwin Celebration

Reexamining Evolution in the Light of Mendel, Mutation, and Meiosis

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ABSTRACT

In June 1909, scientists and dignitaries from 167 different countries gathered in Cambridge to celebrate the hundredth anniversary of Charles Darwin's birth and the fiftieth anniversary of the publication of *Origin of Species*. The event was one of the most magnificent commemorations in the annals of science. Delegates gathered within the cloisters of Cambridge University not only to honor the "hero" of evolution but also to reassess the underpinnings of Darwinism at a critical juncture. With the mechanism of natural selection increasingly under attack, evolutionary theory was in disarray. Against this backdrop, biologists weighed the impact of several new developments—the rediscovery of Mendel's laws of heredity, de Vriesian mutation theory, and the linkage of sex-cell division (recently named "meiosis") to the mechanism of heredity. The 1909 Darwin celebration thus represents a significant watershed in the history of modern biology that allows historians to assess the status of evolution prior to the advent of the chromosome theory of genetics.

LATE IN JUNE 1909, the University of Cambridge played host to 235 scientists from 167 different countries and 68 British institutions, along with other invited dignitaries, who gathered to celebrate the centenary of Charles Darwin's birth and the fiftieth anniversary of *On the Origin of Species*. The festivities of the three-day event were widely reported in newspapers around the globe, and by all accounts the Darwin celebration of 1909 was a huge success—one of the most magnificent spectacles ever recorded in the annals of science. The celebration exhibited "all the pomp and dignity of learning" of prewar Europe on a scale unsurpassed by other centennials of the time, many of which were conceived as much to promote certain political, commercial, or local interests as to

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honor a hero.[1] Indeed, the Darwin celebration was unique in a number of respects. As one contemporary noted, "Commemorative festivals, held at one or other ancient seat of learning, have been frequent in recent years; but their object has been to celebrate the foundation of some famous institution in the distant past. And there have been festivals of a different kind in honor of one or other of the great names on the roll of intellectual achievement, whose glory has been established and consecrated by the long lapse of time. But no such academic tribute has ever been paid to the memory of an individual within so short a time of his own life." Certainly this reflects Darwin's meteoric "rise to celebrity" in the half-century since the publication of his controversial theory of evolution by natural selection.[2] The event thus provides a means of exploring in depth the contemporary cultural assessment of Darwin. Yet interspersed with all the commemorative festivities honoring Darwin, both in Cambridge and abroad, were concurrent discussions about serious scientific issues that affected core tenets of the theory of evolution. In this respect, the celebration reveals as much about the current status of evolution as it does about the construction of the historical Darwin.

Darwinism in 1909 was in a state of disarray. With orthodox Darwinians pitted against their perceived challengers, the various proponents of different varieties of Darwinism attempted to use the occasion to assert the validity of their particular evolutionary perspective. Certainly, the event allowed neo-Darwinians to repeat their arguments in support of the efficacy of natural selection as the prime mechanism behind descent with modification. However, the occasion also provided a venue for others to highlight new developments in biology that they believed promised to redirect studies of evolution. Unlike the "old" evolution, which was characterized primarily by logical arguments supported by empirical evidence, the "new" evolution championed by many biologists was to be enriched by the findings of modern experimental research programs.[3] By bringing together leading representatives of the sundry sects of Darwinism, the commemoration concentrated attention on both problems and possible solutions.

As delegates gathered within the cloisters of Cambridge University in the summer of 1909, then, they sought not only to honor Darwin as a revolutionary scientist and cultural hero but also to use the occasion to examine the underpinnings of evolution theory in the wake of a series of new developments. Nine years after the rediscovery of Gregor Mendel's laws of heredity, biologists were struggling to assess the impact of Mendelism on evolution, particularly the study of the "physiology" of heredity that in 1906 William Bateson had

[1] "The Darwin Centenary: Commemorations at Cambridge: Brilliant Scenes and Remarkable Speeches," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909. See also Roland Quinault, "The Cult of the Centenary, c. 1784–1914," *Historical Research*, 1998, *71*:303–323. For the different character of the celebrations honoring James Watt and Michael Faraday see Christine MacLeod and Jennifer Tann, "From Engineer to Scientist: Re-inventing Invention in the Watt and Faraday Centenaries, 1919–1931," *British Journal for the History of Science*, 2007, forthcoming (I thank MacLeod for sending me a copy of this essay).

[2] [A. C. Seward,] "The Darwin Centenary at Cambridge," *Science*, 1909, *30*:52–53, on p. 52; *Times*, 22 June 1909, p. 9; and Janet Browne, "Presidential Address: Commemorating Darwin," *Brit. J. Hist. Sci.*, 2005, *38*:251–274, on p. 251. As Browne notes, "The moment is ripe to take up a post-postmodern position that reinvestigates the category of scientific hero and engages with Darwin's life after death—the management and use of the intellectual legacy, the commemorations, the mythologizing, the biographical traditions and wider problems of reputation in science that interweave in interesting ways with major conceptual shifts in evolutionary biology and the public status of the biological sciences through the late nineteenth and the twentieth centuries" (p. 252).

[3] David Hull, *Darwin and His Critics: The Reception of Darwin's Theory of Evolution by the Scientific Community* (Cambridge, Mass.: Harvard Univ. Press, 1974); and Ernst Mayr, *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (Cambridge, Mass.: Harvard Univ. Press, 1991).

christened "genetics." Mendelism, moreover, was intimately linked with Hugo de Vries's "mutation theory," first announced in 1901, which proposed that new species could arise suddenly through changes internal to the germplasm rather than through a gradual process based on the selection of small, favorable variations, as held by Darwin and neo-Darwinists. Both of these developments, in turn, were reinforced by recent advances in cytology concerning sex-cell division, especially Walter Sutton's and Theodor Boveri's independent suggestions in 1903 that the events of germ-cell formation (meiosis) mirrored on a cellular level what would be expected of Mendelian factors segregating in hybrid crosses.[4] Hence, the time was indeed propitious for the world's biologists to come together to reassess the impact of Mendel, mutation, and meiosis on the Darwinian theory of evolution.

Little did anyone know that an even more momentous discovery was on the horizon. Early in 1910, only months after the delegates returned home from Cambridge, Thomas Hunt Morgan discovered the "mutant" white-eyed male fruit fly that would soon completely change the face of the study of heredity. With the publication of *The Mechanism of Mendelian Heredity* in 1915, the Morgan group's proposed chromosome theory of heredity effectively united Mendelian heredity, mutation theory, and chromosome studies into the new Mendelian genetics. Although many were optimistic that it was only a matter of time before genetics would lead to a new understanding of evolution, these hopes, as we now know, were premature. It would be decades before genetics was unified with the mathematical analysis of population dynamics within the modern neo-Darwinian synthesis of evolution.[5] Nonetheless, the Darwin celebration of 1909 can be seen as heralding the beginning of a process that only later bore fruit. As such, it forms an important watershed in the history of modern biology: it represents a pivotal transition between the "old" phylogenetic and speculative evolution of the immediate post-Darwinian period and the "new" genetics-based and experimental "evolutionary biology" of the twentieth century.

The historic implications of the 1909 gathering were anticipated by some participants. As one astute observer noted: "For the future historian of science [the celebration] must for all time serve as a land-mark indicating the present stage of development of scientific doctrine in every department of human thought where science holds sway, and where the great principle of evolution has, under Darwin's influence, served as a guide in the interpretation both of organic and inorganic nature." From the vantage point of a century later, this prediction seems particularly apt.[6] The celebration indeed offers the historian a treasure

[4] Hugo De Vries, *Die Mutationstheorie: Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich*, 2 vols. (Leipzig: Veit, 1901–1903); Victor McKusick, "Walter S. Sutton and the Physical Basis of Mendelism," *Bulletin of the History of Medicine*, 1960, *34*:487–497; and Lilian Al-Chueyr Pereira Martins, "Did Sutton and Boveri Propose the So-Called Sutton-Boveri Chromosome Hypothesis?" *Genetics and Molecular Biology*, 1999, *22*:261–271.

[5] T. H. Morgan, A. H. Sturtevant, H. J. Muller, and C. B. Bridges, *The Mechanism of Mendelian Heredity* (New York: Holt, 1915). On Morgan's work see Garland E. Allen, *Thomas Hunt Morgan: The Man and His Science* (Princeton, N.J.: Princeton Univ. Press, 1978); and Robert E. Kohler, *Lords of the Fly:* Drosophila *Genetics and the Experimental Life* (Chicago: Univ. Chicago Press, 1994). On the modern synthesis see William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago History of Science and Medicine) (Chicago: Univ. Chicago Press, 1971); Vassiliki Betty Smocovitis, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology* (Princeton, N.J.: Princeton Univ. Press, 1996); and Jean Gayon, *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection* (Cambridge: Cambridge Univ. Press, 1998) (hereafter cited as **Gayon, *Darwinism's Struggle for Survival***).

[6] Raphael Meldola, "Evolution: Old and New," *Nature*, 1909, *80*:481–485, on p. 481. At least one contemporary biologist, however, suggested that the task of estimating "the influence of Darwin's theories on his time and on the future" might be "better accomplished on the 200th than on the 100th anniversary of his birth": August Weismann, "Charles Darwin," *Contemporary Review*, 1909, *96*:1–22, on p. 19. Indeed, the celebrations now being planned for the approaching Darwin bicentennial year will put this belief to the test!

trove of materials that can profitably be mined from a number of perspectives to provide a fine-grained assessment of the status of Darwinism on the eve of the new genetics.

Exploring commemorative practices in science, as a number of historians have recently shown, is a productive exercise for historians, providing an abundance of data for perceptive analysis. Such occasions reveal as much about the mentality of the participants as they do about the honoree, reflecting "the current standing of past individuals and events." The 1959 Darwin centennial celebration is a good case in point. As Vassiliki Betty Smocovitis has shown, this event was staged not just to honor Darwin but also "to serve a variety of personal, disciplinary, institutional, regional, and even national functions" and, in particular, to promote the "new synthetic science of evolutionary biology."[7] The 1909 Darwin celebration exhibited an assortment of aims as well. In both 1909 and 1959, organizers and participants alike held collective as well as individual "hidden agendas." Rather than heralding a new consilience in biology, however, the 1909 festivities promoted new ideas and approaches that all concerned hoped could begin to resolve long-disputed issues in evolution theory. In short, the event initiated a new attack on evolutionary problems.

In decoding the multiple meanings of the 1909 Darwin celebration, I have found Pnina Abir-Am's methodology of "historical ethnography" of scientific ritual particularly valuable. To deconstruct an anniversary celebration of molecular biologists, Abir-Am used "participant observation, informant debriefing, site description, and collection of artifacts in order to grasp the meaning of historical ritual in science."[8] The historian is fortunate in having rich materials available for exploring the 1909 Darwin celebration, including archival records and printed accounts of the event that provide the "site description"; "participant observation" via the many published accounts as well as unpublished correspondence; "artifacts," including various archival resources (accounts of the festivities in the popular press and university records; formal "addresses" that participants presented to the university; minutes of the Darwin Centenary Committee organizers; the letter book compiled by honorary secretary and publication committee secretary Albert Charles Seward; scrapbooks kept by the other honorary secretary, John Willis Clark, by the master of Christ's College, Arthur Everett Shipley, and by the participant George Henslow; and the catalogues of museum exhibitions)—all of which provide an entrée into the scientific as well as the cultural meanings of the occasion. While "informant debriefing" is now, of course, impossible, extant correspondence pertaining to the official commemorative volume, *Darwin and Modern Science*, provides "behind the scenes" information about the intent of and various controversies connected with the public festivities.

While ethnographic analysis offers a means by which to analyze the celebration itself, an analysis of the writings of biologists who participated in the widespread focus on Darwinism around 1909 furnishes the basis for evaluating new directions in contemporary evolutionary studies. Among historians, the most widely accepted view of the decades

[7] Pnina G. Abir-Am, "Introduction," in *Commemorative Practices in Science: Historical Perspectives on the Politics of Collective Memory*, ed. Abir-Am and Clark A. Elliott, *Osiris*, 2nd Ser., 1999, *14*:1–33; Quinault, "Cult of the Centenary" (cit. n. 1), p. 322; and Vassiliki Betty Smocovitis, "The 1959 Darwin Centennial Celebration in America," *Osiris*, 2nd Ser., 1999, *14:*274–323, on p. 278. See also the contributions to William Ashworth, Jon Agar, and Jeff Hughes, eds., *On Time: History, Science, and Commemoration*, *Brit. J. Hist. Sci.*, 2000, *33*, esp. Ludmilla Jordanova, "Presidential Address: Remembrance of Science Past" (pp. 387–406), and Patricia Fara, "Isaac Newton Lived Here: Sites of Memory and Scientific Heritage" (pp. 407–426).

[8] Pnina G. Abir-Am, "A Historical Ethnography of a Scientific Anniversary in Molecular Biology: The First Protein X-Ray Photograph (1984, 1934)," *Social Epistemology*, 1992, *7*:321–354. See also Abir-Am, "How Scientists View Their Heroes: Some Remarks on the Mechanism of Myth Construction" [essay review], *Journal of the History of Biology*, 1982, *15*:281–315.

around 1900 is of a period of controversy reflecting the "eclipse of Darwinism." First formulated by Julian Huxley, this notion has been most fully expressed by Peter Bowler, who suggests that the general dissatisfaction with the sufficiency of natural selection and the proliferation of numerous alternative evolutionary mechanisms in the last two decades of the nineteenth century indicate that Darwinian evolution was in decline. This unsettled state continued, Bowler notes, until the 1930s and 1940s, when "Darwinism eventually emerged from its eclipse once it could be shown that a more sophisticated interpretation of the new genetics would provide a firmer foundation for selection."[9] As we shall see, the various pronouncements connected with the Darwin celebrations of 1909 support the contention that evolutionary theory was in a state of crisis. However, as this essay attempts to show, the notion of a pervasive "eclipse of Darwinism" needs to be qualified. Indeed, 1909 can be seen as marking a significant turning point in evolution studies, heralding a time when the old evolution (primarily the "logical analysis" pursued by the first generation of Darwinians) gave way to the new, experimentally grounded study of evolution, the fruits of which only began to ripen two decades later.[10] Such a recognition has important historiographical implications, reinforcing our understanding of the history of evolution studies by clarifying the nature of new work carried out in the 1910s and 1920s. I argue that the significance of the 1909 Darwin celebration was threefold: it focused biologists' attention on the competing claims of different varieties of Darwinism; it highlighted new developments—Mendelism, mutation theory, and chromosomal mechanics—that offered promising analytical frameworks for approaching evolutionary problems using experimental methods; and it attracted to evolution studies a significant cohort of young biologists, whose subsequent mature work contributed to the evolutionary synthesis of the 1930s and 1940s. This essay thus seeks to analyze the 1909 Darwin celebration as a means to gauge "the collective thought" of the age about Darwin and Darwinian evolution and to highlight new directions in evolution studies in the decades immediately prior to the evolutionary synthesis.

DARWINIAN POMP AND CEREMONY

The year 1909, noted the *London Illustrated News*, was the "annus mirabilis" for centenaries of famous persons, including Charles Darwin, Alfred, Lord Tennyson, William Glad-

[9] "It was in this period, immediately prior to the war, that the legend of the death of Darwinism acquired currency. The facts of Mendelism appeared to contradict the facts of paleontology, the theories of the mutationists would not square with the Weismannian views of adaptation, the discoveries of experimental embryology seemed to contradict the classical recapitulatory theories of development. Zoologists who clung to Darwinian views were looked down on by the devotees of the newer disciplines, whether cytology or genetics, *Entwicklungsmechanik* or comparative physiology, as old-fashioned theorizers; and the theological and philosophical antipathy to Darwin's great mechanistic generalization could once more raise its head without fearing too violent a knock": Julian Huxley, *Evolution: The Modern Synthesis* (London: Allen & Unwin, 1942), pp. 24–25. Peter J. Bowler, *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades around 1900* (Baltimore/London: Johns Hopkins Univ. Press, 1983), pp. 5, 14. See also Provine, *Origins of Theoretical Population Genetics* (cit. n. 5); and Gayon, *Darwinism's Struggle for Survival*.

[10] Garland Allen has expressed a similar view of the dissatisfaction with the old evolution at the time: "There was a widespread belief that evolutionary theory, and the morphological research program associated with it, especially identified with the avid pursuit of phylogenies, was at best only guesswork. While granting that Darwin's theory was synthetic, critics claimed it was non-experimental, nontestable, and ultimately, speculative. Numerous phylogenies could all account for the same evidence, and with no way to distinguish between them, younger critics sought to move away from what they saw as the overriding concern with evolutionary and morphologically based questions." See Garland Allen, "The Reception of Mendelism in the United States, 1900–1930," *Comptes Rendu de l'Académie des Sciences*, 2000, *323*:1081–1088, on p. 1082.

stone, Abraham Lincoln, and Edgar Allan Poe. While Tennyson was a Cambridge man, it was held that the university could never have "planned a festival on this scale" in his honor; indeed, the *Times* claimed that it "was impossible to conceive a pious pilgrimage" of scientists "from all parts of the earth . . . to celebrate the birth of anyone" other than Darwin.[11]

Why did scientists and laymen the world over seek to honor the memory of a man who had been dead for scarcely twenty-five years? Judging from the voluminous writings on Darwin and Darwinism that began appearing in 1908 and continued unabated throughout 1910, it was largely in recognition of the enormous influence the theory of evolution had had on science and, through its application to sociopolitical thought, on society at large. As one commentator noted, "No realm of the intellectual world has failed to respond to the power of Darwin's method, the candor of his spirit, and the force of his clear insight and restrained judgment."[12] Commemorative events were not restricted to Britain but were held the world over. In Germany, where Darwinism held considerable cultural as well as scientific sway, virtually every major German city conducted observances in which Darwinians widely "celebrated their victory over other *Weltanschauungen*."[13] It is thus easy to view the 1909 celebrations as a form of hero-worship, honoring a man whose theory had revolutionized not only the life sciences but also the humanities and social sciences.[14]

[11] *London Illustrated News*, 30 Jan 1909, p. 160; and *Times*, 22 June 1909, p. 9. There was even a call in the United States to proclaim, jointly with England, 12 February a holiday to "celebrate together Lincoln, the embodiment of Anglo-Saxon devotion to Justice, and Darwin, the reincarnation of Anglo-Saxon devotion to Truth": William Roscoe Thayer, "The Centennial of Lincoln and Darwin," *North American Review*, 1908, *188*:21–24, on p. 24.

[12] T. C. Chamberlain, "Introduction," in American Association for the Advancement of Science, *Fifty Years of Darwinism: Modern Aspects of Evolution* (centennial addresses in honor of Charles Darwin before the American Association for the Advancement of Science, Baltimore, Friday, 1 Jan. 1909) (New York: Holt, 1909) (hereafter cited as **AAAS, *Fifty Years of Darwinism***), p. 4. The Cambridge celebration was not the only event organized in Britain to honor Darwin. In 1908 the Linnean Society marked the demicentenary of the first public announcement of natural selection by Darwin and Alfred Russel Wallace, on 1 July 1858, with a "Darwin/Wallace Celebration" attended by 350 scientific delegates from around the world. Oxford held its own commemoration of Darwin's one-hundredth birthday on 12 February 1909, with a gathering attended by over 600 guests. In Cambridge, the day was celebrated with invited guests dining in Darwin's old rooms in Christ's College. See "Darwin at Cambridge," *Times*, 12 Feb. 1909, p. 10; and "University Intelligence: Oxford: Professor Poulton on 'Darwinism,'" *ibid.*, 13 Feb. 1909, p. 8.

[13] Günter Altner, ed., *Der Darwinismus: Die Geschichte einer Theorie* (Darmstadt: Wissenschaftliche Buchgesellschaft, 1981), p. 441 (here and throughout the essay, all translations are mine unless otherwise indicated). See also Eve-Marie Engels, ed., *Die Rezeption von Evolutionstheorien im 19. Jahrhundert* (Frankfurt am Main: Suhrkamp, 1995). In the United States, the American Association for the Advancement of Science held a special session on Darwin at its January meeting, inviting E. B. Poulton, the leading "pure Darwinian," to be the keynote speaker. See AAAS, *Fifty Years of Darwinism*. In February the New York Academy of Sciences held a commemoration, followed by a nine-week course of lectures on "Charles Darwin and His Influence on Science." See "Darwin Celebrations in the United States," *Nature*, 1909, *80*:72–73; and the special section in *Popular Science Monthly*, Apr. 1909, *74*:315–415. For a recent examination of the multiplicity of meanings of Darwinism in popular culture see the essays in Ronald L. Numbers and John Stenhouse, eds., *Disseminating Darwinism: The Role of Place, Race, Religion, and Gender* (Cambridge/New York: Cambridge Univ. Press, 1999).

[14] As one anonymous author noted, the meaning of the celebration was complex: "That explanation is to be found, not alone in Darwin's personality and achievements, not alone in his positive contributions to scientific thought and knowledge, but in the vast and almost immeasurable influence of the ideas associated with his name on the mental outlook—the *Weltanschauung*, as the Germans call it—of mankind. There is no man living and thinking to-day who does not regard the universe, its structure, and its history from a standpoint altogether different from that from which the vast majority of mankind regarded it in the days that preceded the appearance of 'The Origin of Species.'" See "The Darwin Celebrations," no. 78, MS 54.2: Arthur Everett Shipley (Master of Christ's College in 1909), Scrapbook of Darwin 1909 Celebration, Christ's College, Cambridge, Old Library (hereafter cited as **Shipley Scrapbook**). Most of the newspaper and magazine clippings included in Shipley's scrapbook are not attributed; while I have been able to identify the provenance of many of the reports, several have eluded me. For a comparative analysis of the portrayals of Darwin during the 1959 celebrations see An-

They also symbolized the coming of age of biology as a discipline. Just as Darwin was inducted into the pantheon of hero-scientists, so too was biology accorded status similar to that of the physical sciences, including astronomy, physics, and chemistry.[15]

The multiple significance of the occasion was stressed at every turn in the three-day Cambridge commemoration, held from 22 to 24 June 1909. Members of the world's scientific elite gathered for the academic equivalent of a royal coronation. As one observer noted, "Probably never before has there assembled together such a large and representative gathering of the world's famous scientists, and that learning has its spectacular side could hardly have been more splendidly demonstrated." "From the moment of alighting at Cambridge Station," one reporter commented, "it was clear that something very unusual was in progress. A stir and bustle pervaded the place, which under normal conditions would have been wrapped in the pleasant drowsiness of its Long Vacation sleep. Cabs rattled endlessly through the streets, while at the station eminent delegates from all parts of the world wrestled with their luggage with an energy worthy of undergraduates in the May Week." Representatives of the British press were offered invitations, which guaranteed widespread media coverage, both at home and abroad.[16] Delegates themselves, soon after their return, provided descriptions of the grand event for their local newspapers and magazines.[17] The commemoration was possibly the most highly publicized of its kind to date in the annals of science.

The festivities opened on Tuesday night, when the chancellor, Lord Rayleigh, John William Strutt (former Cavendish Professor of experimental physics and recent recipient of the Nobel Prize for physics), welcomed 1,500 scientific delegates and invited guests to a reception held at the university's Fitzwilliam Museum. Dressed in evening attire or academic robes and orders, guests resembling royalty arrived on foot, in hansom cabs, or even by motorcar, met by uniformed policemen serving as attendants. In the entry hall,

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tonello La Vergata, "Images of Darwin: A Historiographic Overview," in *The Darwinian Heritage*, ed. David Kohn (Princeton, N.J.: Princeton Univ. Press, 1985), pp. 901–972, esp. pp. 914–916.

[15] Weismann claimed that Darwin's theory of evolution marked the beginning of biology: "But was there a biology then? Strictly speaking, there was not; there was zoology, botany, and even anthropology. Each of these sciences consisted of a very large and well-arranged mass of facts, but with no intrinsic coherence among them. This was supplied by the theory of evolution": Weismann, "Charles Darwin" (cit. n. 6), p. 20. Several speakers at the Cambridge festivities explicitly compared Darwin to Newton. The American zoologist Henry Fairfield Osborn commented that "if Newton opened up a new heaven, Darwin opened up a new earth," while Arthur James Balfour, former prime minister and leader of the opposition party, indeed ranked Darwin above Newton: "After all, the branch of research which he had initiated was surely the most difficult of all. Measuring the heavens and weighing the suns were tasks surely incomparably easy compared with the problems which affected the physiologist and morphologist in dealing with the living cell, be it or plant or animal or man." See *Times*, 24 June 1909, p. 10. Balfour may have been responding to a highly critical assessment of Darwin that ran in the *Times* in February, which argued that since Darwin did not solve problem of the origin of life, his theory was inadequate: "The Centenary of Darwin," *Times*, 12 Feb. 1909. (I thank an anonymous referee for pointing out that Darwin himself began this comparison by alluding to Newton in the final sentence of the *Origin of Species*.)

[16] *Cambridge Chronicle*, 25 June 1909; and Shipley Scrapbook, MS 54.2, p. 92. Only members of the British press were invited to attend the banquet. See Minutes of the Darwin Centenary Committee, 1907–1909, Min.VII.6, Cambridge University Archives, Manuscripts Room, Cambridge University Library (hereafter cited as **Darwin Centenary Committee Minutes**).

[17] See, e.g., E. B. Wilson, "The Darwin Centenary Celebrations at Cambridge," *Columbia University Quarterly*, 1909–1910, *12*:54–58; H. F. Osborn, "The Darwin Centenary: Address in Reply to the Reception of Delegates," *Science*, N.S., 1909, *30*:199–200; Hermann Diehls, "Die Darwinfeier in Cambridge 22–24. Juni 1909," *Internationale Wochenschrift für Wissenschaft, Kunst und Technik*, 1909, *3*:892–893, 933–938; Karl Breul, "Die Darwinfeier der Universität Cambridge," *Monatsblatt: Wissenschaftliche Wochenbeilage der Magdeburgischen Zeitung*, 1909 [offprint]; Elie Metchnikoff, "La fête au l'honneur de Darwin, Cambridge," *Revue Scientifique*, 1909, *18*:545–548; and Charles Bouglé, "Darwiniens à Cambridge," *Revue de Paris*, 1 Sept. 1909, no. 17, pp. 107–120.

they were greeted at the top of the grand double staircase by Lord Rayleigh, flanked by other dignitaries of the university. In addition to gathering in the galleries of paintings, guests mingled in the gardens of nearby Peterhouse College, specially illuminated for the occasion by thousands of tiny electrical fairy lamps, with music provided by the Cambridge battalion band and refreshments offered in specially erected tents.[18] One reporter noted that the men's costumes and the ladies' toilettes "made the museum a gathering of beauty and charm. But the suggested mental picture was still more impressive, for here were men and women, known in all lands for their scientific work. It was in a sense a presentation of the scientific world."[19]

On Wednesday morning, 23 June, throngs of people lined King's Parade to watch the brilliant spectacle as delegates and guests filed into the Senate House for the presentation of "addresses"—formal congratulatory texts presented to the university by the various learned societies and universities represented.[20] This pageant presented a "gorgeous medley of brilliant colours," emphasized by the contrasting tones and textures of the academic robes of the visiting scientific dignitaries and the scarlet and grey gowns of the doctors of Cambridge and Oxford. One French delegate overheard a guest exclaim, upon catching a glimpse of the splendid robe worn by the rector of the University of Bonn, "Oh! Oh! But he must be an emperor!"[21] (See Figures 1 and 2.)

[18] "The Darwin Celebrations," *Times*, 23 June 1909, p. 12. According to another account, "The priceless treasures of the galleries were for once forgotten, or almost forgotten, in the moving picture of life and colour that presented itself": "The Darwin Centenary: Commemorations at Cambridge: Brilliant Scenes and Remarkable Speeches," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909. "Fairy lamps," patented by Samuel Clarke of London in 1885, were originally candle-based lamps covered by a dome that was often colored. Clarke's fairy lamps became so popular that all small candle lamps, such as modern-day Christmas lights, continue to be known in Britain as "fairy lights."

[19] "Darwin Commemoration at Cambridge: Official Reception," *Daily Telegraph*, 23 June 1909, p. 13. "Women are among the invited guests, some as wives or daughters of distinguished men, others as having won laurels in the arena of academic strife": "Darwin Centenary: World's Scientists at Cambridge: Notable Assembly," *Standard*, 23 June 1909. Among the academic women present, as described in Breul, "Die Darwinfeier der Universität Cambridge" (cit. n. 17), p. 10, were "the two sisters Mrs. Lewis and Mrs. Bibson, who have been awarded honorary doctorates by several German and British universities for their outstanding scientific accomplishments in the area of theology and oriental philology."

[20] "The importance they attached to the occasion was shown by the elaborate form of the addresses. Even the least pretentious were enclosed in scroll cases of artistic pattern, but some of them, enclosed in finely mounted cases, were exceedingly handsome, and will form valuable mementoes of the occasion." See "The Darwin Centenary: Commemorations at Cambridge: Brilliant Scenes and Remarkable Speeches," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909. The 255 addresses are in the Cambridge University Archives (steel cupboard no. 6), Manuscripts Room, Cambridge University Library. Many are extraordinarily beautiful and express covert meaning through the choice of topics portrayed. The address presented by the Museum of Natural History, Paris, e.g., recognized both the centenary of Darwin's birth and the publication of Jean Baptiste Lamarck's *Philosophie zoologique* (1809)—hence suggesting the latter's priority in introducing the concept of species change. That presented by the German Botanical Society, Berlin, consists of a three-page summary of Darwin's importance for botany illustrated by hand-done paintings of plants he studied, including *Drosera*, dimorphic flowers, and climbing plants. The address presented by the University of Würzburg has beautiful calligraphy with gilt letters and hand-painted Coleoptera, a reference to Darwin's love of beetles. The address presented by the Swedish Royal Academy of Science is a watercolor of an island, showing a coral atoll in the distance, while the Natural History Museum of Vienna gave a lovely classic allegorical painting, portraying Darwin wrapped in a red robe. The Imperial University of Tokyo sent a hand-painted scroll, adorned with a landscape and enclosed in a special lacquer box, that describes (in Japanese with an English translation) Darwin's influence on Japanese science. I thank the former University Archivist, Elisabeth Leedham-Greene, for helping me locate these addresses.

[21] *Daily Mail*, 24 June 1909, p. 3; *Standard*, 23 June 1909; and Bouglé, "Darwiniens à Cambridge" (cit. n. 17). "Inside the Senate House the scene was of an unforgettable brilliancy. Rows upon rows of gorgeously garbed representatives of science from all over the world made the usually sombre hall glow with colour. Scarlet was the prevailing note, but a Portuguese delegate wore a costume of sky-blue with a curious hat resembling a tasselled lamp-shade. A German professor excited envy by his gown and cape of rich red velvet trimmed with broad ermine fur": *Daily Mail*, 23 June 1909, p. 5.

Figure 1. *"All the World Honours Darwin, Whose Centenary Was Celebrated at Cambridge University Yesterday,"* Daily Mirror, *24 June 1909. Photographs, top row, from left to right: I. P. Borodin (University of St. Petersburg); Horace Darwin; George Howard Darwin; Francis Darwin; and Friedrich Schultze (Rector, University of Bonn). Bottom row, from left to right: Oliver Lodge (Principal, Birmingham University); E. Ray Lankester (Royal Society of London) and Elie Metchnikoff (Pasteur Institute); Charles Darwin (photograph by Elliot & Fry); and Aarão de Lacerda (Polytechnic Academy, Oporto, Portugal) and Edmond Perrier (Director, Musée d'Histoire Naturelle, Paris).*

The chancellor opened the festivities with brief personal remarks, noting the great stir caused by the publication of *On the Origin of Species* fifty years earlier, which he was old enough to remember.[22] Afterward, four selected delegates representing their countries—Oscar Hertwig (Germany), Elie Metchnikoff (France and Russia), Henry Fairfield Osborn (United States), and E. Ray Lankester (Britain)—addressed the import of Darwin's theory of evolution and in so doing introduced contrasting national and scientific perspectives. Hertwig (speaking in German) extolled the great influence Darwin's view had exerted on

[22] Lord Rayleigh reminisced: "I esteem myself fortunate that a visit nearly 40 years ago, a visit which I owe to my friend, now Sir George Darwin, enables me to picture the scene. I was struck as were others with his wonderful modesty. In my propounding some difficulty in connection with colour vision, and the theory which attributes the colours of flowers to the preference of insects, I remember that he asked time for refection [*sic*] before making a reply." "Brilliant Scenes in the Senate House: Tributes by Distinguished Speakers," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909.

Figure 2. *Procession of delegates from the Senate House, led by the Chancellor, Lord Rayleigh (John William Strutt). A grandson of Lord Avebury (Sir John Lubbock) carries the train. (MS 54.2: Arthur Everett Shipley Scrapbook of the Darwin 1909 Celebration, Christ's College, Cambridge, Old Library.)*

German science and culture.[23] Metchnikoff spoke of Darwin's "great influence on medical science," particularly the study of microorganisms.[24] Osborn, recalling his heady days as

[23] See Oscar Hertwig, "Darwins Einfluß auf die deutsche Biologie," *Int. Wochenschr. Wiss. Kunst Tech.*, 31 July 1909, *3*:954–958. As Paul Weindling has noted, there was a certain irony in Hertwig's invitation to speak, since his attacks on Ernst Haeckel's theory of recapitulation marked him as "one of the leading German critics of Darwinism." See Paul Weindling, *Darwinism and Social Darwinism in Imperial Germany: The Contribution of the Cell Biologist Oscar Hertwig (1849–1922)* (Stuttgart: Fischer, 1991), p. 165. For a list of German publications arising from the "Darwin Jubilee" see Walther May, "Die Darwin-Jubiläums-Literatur 1908–1910," in *Der Darwinismus*, ed. Altner (cit. n. 13), pp. 454–471.

[24] Metchnikoff's handwritten speech (in large letters to make the English easily legible) is included in the Shipley Scrapbook. His formal speech contrasts greatly with his description of the Cambridge event for a Russian audience. The historian A. E. Gaissinovitch has described this report: "Giving an account of the speeches made at the anniversary celebrations held in Cambridge in 1909 to commemorate the fiftieth anniversary of the publication of the *Origin of Species*, Metchnikov pointed to the disagreements between the 'orthodox' Darwinists and the 'neo-Darwinists' in the treatment of this problem. Thus, he said, Ray Lankester, the venerable representative of the first, 'has quite definitely opposed the theory of sudden mutations, elaborated by de Vries, as well as the results of the investigations into heredity, conducted by Bateson and resting on Mendel's discovery, much spoken about during the last few years.' Then Metchnikov concentrated on the problem of the role of 'sudden changes' in the process of evolution. He was far from being a supporter of the 'orthodox' Darwinists in this question. He wrote: 'orthodox Darwinists have supported the thesis advanced by Darwin that species can emerge only as a result of vague individual changes as asserted by Darwin.' Then he continued: 'according to the orthodox adherents, science has not progressed at all since Darwin's works. But it is an incontrovertible fact that organisms [which are] subject to considerable variations, confirm to a considerable extent changes that occurred suddenly without intermediate stages. Neo-Darwinists resolutely insist on the thesis that it is the sudden changes which provide the greatest opportunities for natural selection and consequently that 'mutations' have greatly contributed to the origin of species. Then Metchnikov gave examples of the adaptive coloration of insects and flowers, showing that slight differences in coloration were not noticed by insect-eating birds and pollinating

a student at Cambridge and London in the late 1870s, described meeting Darwin when he visited Thomas Henry Huxley's laboratory and stressed the continued importance of his evolutionary views.[25] The arch-Darwinian Lankester emphasized this point, proclaiming that, after fifty years, the fundamental principles of Darwin's evolution theory were still valid.[26]

At the afternoon garden party at Christ's College, a group portrait was taken and guests visited Darwin's old rooms as well as the extensive exhibit of Darwiniana assembled in the Old Library. (See Figure 3 and cover illustration.) On display, in keeping with the format of similar Edwardian celebrations, were several portraits, busts, and statues of Darwin, along with some of his scientific instruments, specimens of fishes and birds collected during the *Beagle* voyage, and a series of manuscripts—including his notebooks, the journal kept during his voyage, the first draft of the *Origin of Species*, his "Autobiographical Recollections," and a collection of autograph letters, including a selection of correspondence with Alfred Russel Wallace, Charles Lyell, Joseph Dalton Hooker, T. H. Huxley, and Charles Kingsley—much of which forms the basis of the present-day collections in the Darwin Archive at Cambridge University and the museum at Down House.[27]

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insects. Metchnikov concluded: 'We can give many other examples illustrating that sudden changes have much more chance to be fixed by natural selection than vague individual changes.'" A. E. Gaissinovitch, "Problems of Variation and Heredity in Russian Biology in the Late Nineteenth Century," *J. Hist. Biol.*, 1973, *6*:97–123, esp. pp. 107–108; he is describing and quoting from I. I. Metchnikov, "Celebration in Darwin's Honor in Cambridge (1909)" [in Russian], in *Akademicheskoe sobranie sochinenii* [*Collected Works*] (Moscow: Gos. Izd. Med. Lit., 1955), Vol. 3, pp. 398–400.

[25] "Throughout the winter, Huxley was delivering his remarkable lectures, suggestive and with occasional flashes of humour, still strong and full of fire, but beginning to show the effect of years of over-work, of public service and research. About once a week he came among his students. One day an unusual stir or thrill passed along the tables as with him entered Darwin, his first and only visit to a modern biological laboratory. Darwin paused for a few moments conversation, and one received the strong impression of a ruddy face, benevolent blue eyes, very deep set beneath the massive overhanging brow—a wonderful effect of kindliness and of the far-off world survey of a great naturalist. . . . If he were living in these days of Waagen, of Weismann, of Mendel and of De Vries, he would be in the front line of inquiry, armed with inventive genius, with matchless assemblage of fact, with experiment and verification, and not least with incomparable candour and good will": "Brilliant Scenes in the Senate House: Tributes by Distinguished Speakers," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909. Osborn gave another account of this meeting in the *New York Evening Post*, 12 Feb. 1909. On behalf of the thirty-member American contingent who, along with the institutions they represented, had subscribed to raise the funds, Osborn also announced the presentation to Christ's College of a bronze replica of the bust of Darwin by the noted American sculptor William Couper (1853–1942) (the original was one of fourteen busts of scientists presented by the New York Academy of Sciences to the American Museum of Natural History). The bust is now mounted in the garden of Christ's College. See "The Darwin Centenary," *Times*, 27 May 1909, p. 5.

[26] Lankester was asked to replace Lord Avebury, John Lubbock, who was unable to attend owing to the death of his son Rolfe: Conf.I.5, Manuscripts Room, Cambridge University Library. The German delegate Walther May noted the contentious nature of Lankester's speech: "The last speaker took somewhat controversial ground, maintaining the validity of the theory of the natural selection of minute and ubiquitous variations, and stating that certain views advanced by modern naturalists had been duly considered by Darwin, and for sufficient reasons set on one side. It could not be doubted, he said, that Darwin would have been deeply interested in Mendel's results, but these, although throwing light on the mechanisms concerned in hereditary transmission, were not in any way opposed to Darwin's great theoretical structure." May, "Die Darwin-Jubiläums-Literatur 1908–1910" (cit. n. 23), p. 461. See also T. D. A. Cockerell, "The Darwin Celebration at Cambridge," *Pop. Sci. Month.*, Jan. 1910, *76*:23–31. Lankester's arguments were similar to those expressed in his presidential address to the British Association for the Advancement of Science in 1906, in reviewing "Darwinism": E. Ray Lankester, "President's Address," in *Report of the British Association for the Advancement of Science, 1906* (London: Murray, 1907), pp. 3–42, esp. pp. 27–32.

[27] See the description in the *Times*, 12 June 1909, p. 12. As Joseph Dalton Hooker told John Lubbock, "To me the most interesting thing of all is the Exhibition of Portraits, Books, Letters and Instruments, and other objects in connection with the Darwin and Wedgwood families": Horace G. Hutchinson, ed., *Life of Sir John Lubbock, Lord Avebury*, 2 vols. (London: Macmillan, 1914), Vol. 2, p. 269. The artwork on display included

Figure 3. *Group portrait of delegates to the 1909 Darwin celebration, taken at Christ's College, Cambridge. (MS 57: George Henslow's Scrapbook of the Darwin 1909 Celebration, Christ's College, Cambridge, Old Library.)*

On Wednesday night the delegates, invited guests, and members of the press gathered in the newly completed University Examination Hall for the banquet. The occasion was well captured by Leonard Huxley, T. H. Huxley's son, who noted that

> over five hundred sat down to the great banquet, a polyglot assembly keyed to the highest appreciation, where the admirable interest of Mr. Balfour's historic speech was only eclipsed by the sense of personal charm in Mr. W. E. Darwin's reminiscences of his father. Simple, direct, instinct with the same rich, unassuming humanity that they affectionately depicted, his words seemed to reveal from a still living source the very qualities of his father. "Now," one who had met Darwin whispered to his neighbour, "those who never saw him will be able to understand why Darwin was so much beloved by his friends."[28]

"W. B. Richmond's painting of Darwin in his LL.D. robe, lent by the Philosophical Society and hanging in their library; John Collier's portrait of Darwin in a long black cloak, holding his hat in his hand, lent by the Linnean Society; C. Fairfax Murray's two portraits of Mrs. Charles Darwin; and W. W. Ouless's well-known profile, a replica of which hangs in Christ's College Hall, lent by W. E. Darwin." The catalogue of the exhibit, "The Portraits, Prints, and Writings of Charles Robert Darwin," is in Cam.c.909.4, Rare Books Room, Cambridge University Library. Later in the summer, most of the materials were transferred to the British Museum of Natural History in South Kensington. As the *Times* reported, "The primary object of the exhibition is to illustrate the main arguments of 'The Origin of Species,' and much of the material which actually passed through Darwin's hands and the various species which he had in view when he wrote are for the first time, brought together for the inspection of the public": "A Darwin Exhibition," *Times*, 17 Aug. 1909, p. 9. For a detailed list of items on display at the British Museum of Natural History see *Facsimile of "Memorials of Charles Darwin": A Collection of Manuscripts, Portraits, Medals, Books, and Natural History Specimens to Commemorate the Centenary of His Birth and the Fiftieth Anniversary of the Publication of "The Origin of Species,"* with an introduction by Sydney Smith (London: British Museum [Natural History], 1988) [*Bulletin of the British Museum (Natural History)*, Historical Series, 1988, *14*(3):235–298].

[28] Leonard Huxley, ed., *The Life and Letters of Joseph Dalton Hooker*, 2 vols. (London: Murray, 1918), Vol. 2, pp. 467–468. For a delightful description of this event written by Margaret Darwin Keynes, George's daughter, who "was among the female Darwins who were admitted to the balcony of the Examination Hall to hear the speeches that evening," see Margaret Keynes, *A House by the River: Newnham Grange to Darwin College* (Cambridge: Privately printed, 1984), pp. 175–176.

With the banquet restricted to men, wives of the delegates and the scientific women of Cambridge dined separately at Newnham College, presided over by Eleanor Balfour Sidgwick, principal of Newnham and herself a noted mathematician and scientist.[29]

The brilliant scene was repeated the following day, when delegates again filed into the Senate House to witness the presentation of honorary Cambridge degrees to twenty-one scientists, selected in recognition of their noteworthy accomplishments.[30] Acknowledging the recent entry of women into academic science, the committee also extended invitations "to Ladies engaged in biological teaching" at the university, led by Edith Rebecca Saunders, director of the Balfour Biological Laboratory for Women at Cambridge and Bateson's Mendelian collaborator. According to custom, however, women were restricted to the gallery rather than seated with other delegates on the Senate floor, although a rare exception was made for eighty-four-year-old Henrietta Huxley, widow of T. H. Huxley.[31]

The three-day affair came to a close on Thursday afternoon with a garden party at Trinity College hosted by the Darwin family. (See Figures 4 and 5.) Although Leonard (1850–1943) was unable to attend, William Erasmus (1839–1914), George Howard (1845–1912), Francis (1848–1925), and Horace Darwin (1851–1928) were there, as were Henrietta Emma (Etty) Litchfield (1843–1927) and Elizabeth (Bessy) Darwin (1847–1926), along with other family members. Also on hand were old family friends, including ninety-two-year-old Joseph Dalton Hooker (1817–1911), his wife Hyacinth Symonds Hooker (1842–1921), and Henrietta Huxley (1825–1915). As one delegate noted, "Here were four sons and two daughters of Charles Darwin, seven grandchildren and one great-grand-child. The last mentioned, Ursula Darwin, aged ten months, daughter of Bernard Darwin, seemed to realize the dignity of her position."[32] (See Figure 6.) On Friday, special arrangements were

[29] Ethel Sidgwick, *Mrs. Henry Sidgwick: A Memoir by Her Niece* (London: Sidgwick & Jackson, 1938), pp. 66, 71–73; and Helen Fowler, "Eleanor Mildred Sidgwick, 1845–1936," in *Cambridge Women: Twelve Portraits*, ed. Edward Shils and Carmen Blacker (Cambridge: Cambridge Univ. Press, 1996), pp. 7–28. Sidgwick was coauthor with Lord Rayleigh (her brother-in-law) of two scientific papers on standards for electrical units. See also Donald Opitz, "Aristocrats and Professionals: Country-House Science in Late-Victorian Britain" (Ph.D. diss., Univ. Minnesota, 2004).

[30] The recipients were Edouard van Beneden, Prince Roland Bonaparte, Otto Bütschli, Robert Chodat, Francis Darwin (whose award was exceptional, since Cambridge does not customarily confer honorary degrees on its own graduates), Karl von Goebel, Ludwig von Graff, Richard Hertwig, Harald Höffding, Jacques Loeb, Edmond Perrier, Gustav Schwalbe, Hermann Graf zu Solms-Laubach, Clement Timiriazeff, Frantisek Vejdovsky, Max Verworn, Hermann Vöchting, Hugo de Vries, Charles Doolittle Walcott, Edmund Beecher Wilson, and Charles Rene Zeiller.

[31] CUR 133: Miscellaneous collection (by J. W. Clark?), Manuscripts Room, Cambridge University Library. In addition to Saunders, other members of Bateson's school of genetics who were present included Nora Darwin (Darwin's granddaughter), Florence Margaret Durham (Bateson's sister-in-law), Hilda Nanette Blanche Praeger Killby, Dorothea Charlotte Edith Marryat, Igerna Brünhild Johnson (Hilda) Sollas, and Muriel Wheldale, all of whom lectured on biology at the Balfour Biological Laboratory for Women. See "Centenary of the Birth of Charles Darwin and the Fiftieth Anniversary of the Publication of the Origin of Species: List of Delegates and other Guests invited by the University," in J. W. Clark Scrapbook, Cam.b.909.1, Rare Books Room, Cambridge University Library (hereafter cited as **Clark Scrapbook**). See also Marsha Richmond, "'A Lab of One's Own': The Balfour Biological Laboratory for Women at Cambridge University, 1884–1914," *Isis*, 1997, *88*:422–455; and Richmond, "Women in the Early History of Genetics: William Bateson and the Newnham College Mendelians, 1900–1910," *ibid.*, 2001, *92*:55–90. The Darwin Centenary Committee decided that "no tickets should be given to Ladies on either day for the floor of the Senate House": Darwin Centenary Committee Minutes, 13 Mar. 1909. T. D. A. Cockerell noted the exception: "On this occasion a venerable lady was observed occupying a chair, contrary to all custom, on the floor of the senate house. It was Mrs. Huxley; to whom else could the unique distinction have been offered?" Cockerell, "Darwin Celebration at Cambridge" (cit. n. 26), pp. 29–30.

[32] Cockerell, "Darwin Celebration at Cambridge," p. 31. Cockerell also described meeting Hooker at the Darwin exhibit at Christ's College, noting: "As we were looking at these things, Dr. Francis Darwin came in, leading an old man. My heart stood still for a moment to realize that this was Sir Joseph Hooker, the great botanist who was Darwin's friend and adviser more than fifty years ago. I had never expected to look upon his

Figure 4. *A garden party, held at Christ's College Wednesday afternoon and hosted by the Darwin family, brought the 1909 celebration to a close. Notice the presence of women, who attended many of the festivities both as invited guests and as wives of delegates. (MS 54.2: Arthur Everett Shipley Scrapbook of the Darwin 1909 Celebration, Christ's College, Cambridge, Old Library. Reproduced by kind permission of the Master and Fellows of Christ's College, Cambridge.)*

Figure 5. *The Darwin family, gathered in 1909. (Photograph from DAR 225:143, Darwin Archive, Manuscripts Room; courtesy of the Syndics of the Cambridge University Library.) Standing, left to right: Maud and George Howard Darwin, with daughters Gwendolyn and Margaret seated in front; Francis Darwin next to his daughter Frances and her fiancé Francis Cornford, with son Bernard and his wife Elinor seated in front; Henrietta (Etty) Darwin Litchfield; Ida and Horace Darwin, with daughters Ruth and Emma Nora seated in front.*

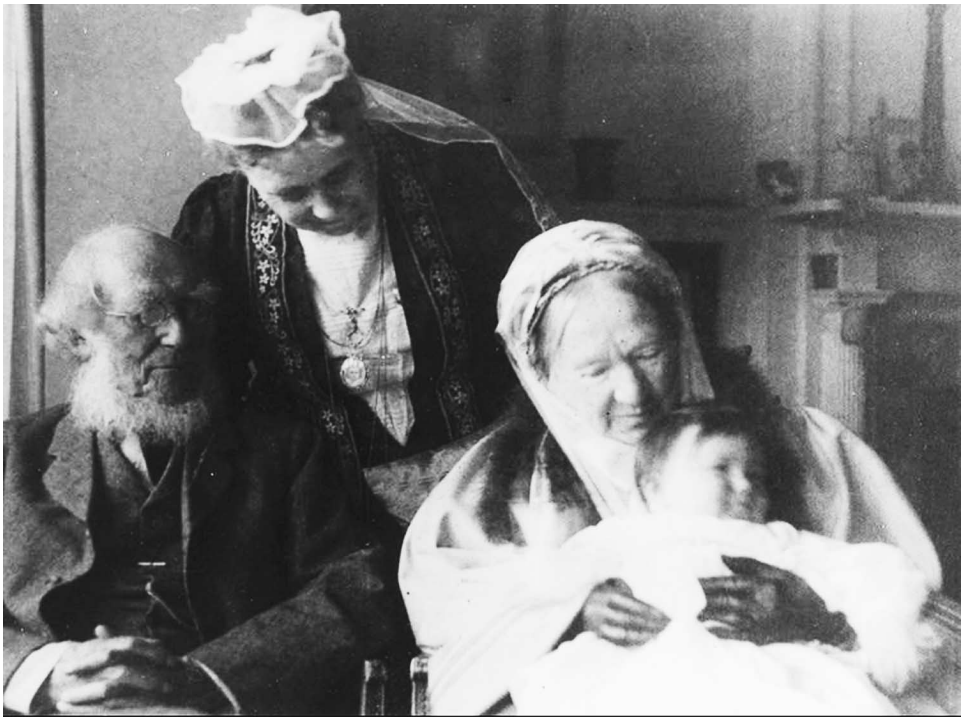

Figure 6. *Joseph Dalton Hooker, Hyacinth Hooker, and Henrietta Huxley, holding Ursula Darwin (Francis Darwin's granddaughter). (From Leonard Huxley, ed.*, Life and Letters of Sir Joseph Dalton Hooker, *2 vols. (London: Murray, 1918), Vol. 2, facing p. 468). Ursula Darwin Mommens (b. 1908) continues to be an active potter in Sussex, England. For the details behind this photograph see Margaret Keynes,* A House by the River: Newnham Grange to Darwin College (*Cambridge: Privately printed, 1984), pp. 173–174.*

made for delegates to visit Darwin's former home Down House, still owned by the family but serving as a private girls' school.

As delegates returned home to all corners of the globe, the impact of the celebration continued to resonate through the various publications prompted by the occasion. In effect, the Cambridge festivities provided texts, images, and discourse that stimulated subsequent discussions of Darwin and Darwinism. The exhibition of Darwin manuscripts and artifacts indeed became the basis for the historical record on which all future scholarship assessing the genesis of the theory of evolution would be founded. The speeches provided an outline of the significance of evolution for biology and society and delineated, at least in skeletal form, the contemporary challenges facing biologists in understanding the ultimate basis of evolutionary change. In providing this general framework, the 1909 celebration thus focused concerted attention on the central problems remaining for evolutionary biology and, in so doing, helped promote an increasing consensus about how to fit the new findings of heredity, variation, and cellular organization into evolution theory.

face, but there he was, ninety-two years old, yet quite able to enjoy the proceedings and converse with those who were presented to him. In the few words I had with him, he recalled with pleasure his botanical trip to Colorado with Asa Gray" (pp. 24–25).

DARWINISM EXTOLLED AND DARWINISM CONTESTED

The general impression left in the wake of all the pomp and ceremony, formal academic lectures, and exhibits of Darwiniana was a favorable appreciation of both Darwin and the theory of evolution. However, if we peer behind the velvety facade of the scientific spectacle we can detect significant hidden agendas, of organizers and participants alike, that complicate this overall picture. The Darwin Centenary Committee, formed in December 1907, set the tempo and mode for the commemorative events and helped shape the intellectual discourse that marked the occasion.[33] In selecting event speakers, they consciously sought to give equal time to representatives of all the major branches of "Darwinism." That is not to say, however, that certain individuals did not unduly influence particular aspects. Bateson, for example, was influential in the selection of Jacques Loeb, a leading Darwinian "heretic," as one of the two Americans to receive an honorary doctorate.[34] This choice, however, also indicates how broadly the organizers construed the boundaries of Darwinism. As many scholars have shown, this term encompassed many different meanings, both general and specific. On the one hand, "Darwinism" connotes a certain naturalistic and materialistic worldview, while on the other it signifies the common descent of organisms and change in species arising through the inheritance of variations. Even more strictly, its scientific meaning invokes the mechanism of natural selection. Yet different biologists, as is well known, held contrasting views about the role and extent of natural selection in the evolutionary process, spanning the spectrum from the ultraselectionists to neo-Lamarckians who stressed adaptation and sometimes orthogenesis and including others who advocated saltatory rather than gradual speciation.[35]

[33] The committee to consider how to celebrate the centenary was formed at the 2 Dec. 1907 meeting of the Council of the Senate. On 13 Feb. 1908 it was decided to hold a Darwin celebration, and in March the committee was augmented. It was chaired by the vice chancellor (Ernest Stewart Roberts in 1907, and later Arthur James Mason), with two honorary secretaries, the professor of botany Albert Charles Seward and John Willis Clark, university registrary and secretary of the Museums and Lecture Rooms Syndicate (which administered the life science disciplines), and included several science dons: the zoologists Arthur Shipley, William Bateson, and Adam Sedgwick; the physiologists Walter Gaskell and John Newport Langley; the professor of chemistry George Downing Living; Woodwardian professor of geology Thomas McKinney Hughes; and Rede lecturer Thomas George Bonney; along with three demonstrators: Arthur Hutchinson, mineralogy; Walter Morley Fletcher, physiology; and Reginald Crundall Punnett, animal morphology. Seward and Clark headed the eight-member Executive Committee, along with Arthur James Mason, master of Pembroke College; John Edward Marr, lecturer in geology; Shipley; Fletcher; Punnett; and a Mr. Dumford. See Darwin Centenary Committee Minutes and CUR 133, Manuscripts Room, Cambridge University Library; and Cam.b.909.1 and Cam.b.909.2, Rare Books Room, Cambridge University Library.

[34] "It was initially proposed to invite one representative, selected from the point of view of the eminence of the individual, of the United States of America, one representative of France and one of Germany to deliver a short speech in the Senate House on June 23": Darwin Centenary Committee Minutes. The foreign speakers were ostensibly chosen by Seward and Clark, in consultation with vice chancellor Arthur James Mason. Subsequently the committee decided that it was also necessary to include a British representative. On Loeb's selection see Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York/Oxford: Oxford Univ. Press, 1987), p. 115. The other American was E. B. Wilson.

[35] See esp. Michael Ruse, "Darwinism," in *Keywords in Evolutionary Biology*, ed. Evelyn Fox Keller and Elisabeth A. Lloyd (Cambridge, Mass.: Harvard Univ. Press, 1992), pp. 74–80; Jean Gayon, "What Does 'Darwinism' Mean?" *Ludus Vitalis*, 1994, *2*:105–118; and Gayon, "Neo-Darwinism," in *Concepts, Theories, and Rationality in the Biological Sciences: The Second Pittsburgh-Konstanz Colloquium in the Philosophy of Science*, ed. G. Wolters, J. G. Lennox, and P. McLaughlin (Pittsburgh, Pa.: Univ. Pittsburgh Press/Universitätsverlag Konstanz, 1994), pp. 1–25. The literature on the varieties of Darwinism is vast. Two contemporary works that identified the different schools are George John Romanes, *Darwin and after Darwin: An Exposition of the Darwinian Theory and a Discussion of Post-Darwinian Questions*, ed. C. Lloyd Morgan (Chicago: Open Court, 1892–1897), Vol. 2: *Post-Darwinian Questions: Heredity and Utility*; and Vernon L. Kellogg, *Darwinism To-Day* (New York: Holt, 1907). More recent detailed analysis was initiated by Morse Peckham, "Darwin and

Neither the organizers of nor the participants in the Cambridge celebration attempted to sweep the disagreement rife among the ranks of Darwinians under the carpet. Certainly, had they done so, the media would have called them to task. Indeed, the media accounts reveled in the controversy, repeatedly drawing the public's attention to the dissension about evolution theory prevalent among biologists. The *Times* even proclaimed, echoing recent published opinion, that "the Darwinian hypothesis is losing its hold upon men's minds."[36] The chancellor explicitly acknowledged the undercurrent of disharmony in his opening remarks at the ceremony: "I need not remind you that on many important questions raised by Darwin's labours, opinions still differ, and I imagine that he would hardly recognise as disciples some of the distinguished biologists, who meet here to do honour to his name." As one reporter noted, delegates including "the greatest Neo-Darwinian and one of the greatest Neo-Lamarckians were there; as were the most radical mechanicalist, the most advanced monist, the most ardent Mendelian, the founder of the mutations theory, one of the most influential of modern philosophers, and the four distinguished sons of the immortal master."[37] The Darwinian umbrella was wide indeed.

Reflecting the avid debate over Darwinism that had raged for many years, biologists

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Darwinisticism," *Victorian Studies*, 1959, *3*:19–40. See also Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* (Cambridge, Mass.: Harvard Univ. Press, Belknap, 1982), pp. 505–510; Thomas Junker, *Darwinismus und Botanik: Rezeption, Kritik und theoretische Alternativen im Deutschland des 19. Jahrhunderts* (Stuttgart: Deutscher Apotheker Verlag, 1989); and Bowler, *Eclipse of Darwinism* (cit. n. 9), which divides Darwinism into five analytical categories: natural selection, theistic evolution, Lamarckism, orthogenesis, and mutation theory.

[36] See the coverage of Darwin's hundredth birthday, "The Centenary of Darwin," *Times*, 12 Feb. 1909: "If Darwin's small variations are inherited they are not new, and involve no alteration in the species, since it is plain that nothing can be inherited from a parent which that parent did not possess. If they are not inherited they are acquired, though we may not be able to indicate the moment of acquirement; and in that case they are not transmissible. In the first instance, the process of mutation has never begun; in the second, it cannot go on. Modern study of variability shows that every species has a limiting curve within which considerable variation from the normal standard may occur, but that all variations, whether in the direction of excess or deficiency, revert to the average type. From this point of view, therefore, the Darwinian hypothesis is undermined. Again, De Vries and others of the later naturalists are impressed by the uselessness in the struggle for existence of the minute beginnings of a new structure, no matter how useful it might prove in its fully developed form. They therefore treat the small Darwinian variations as mere fluctuations inside the specific curve of variability, and assume that at very long intervals a species throws off a widely different form fully equipped to hold its own as a new species. As no explanation can be given of such an astonishing leap, we seem to be brought once more perilously near to the dreaded special act of creation. These recent speculations have no positive value, but they are negatively significant as showing that the Darwinian hypothesis is losing its hold upon men's minds. Like every bold generalization that arrests attention, it has done a great and useful work. It has stimulated inquiry, called forth a great amount of animated discussion, and compelled revision of many accepted and previously unquestioned opinions . . . [but] the Darwinian hypothesis remains simply an hypothesis." For an example of contemporary anti-Darwinian literature see Eberhard Dennert, *At the Deathbed of Darwinism*, trans. E. V. O'Harra and John H. Peschges (Burlington, Iowa: German Literary Board, 1904).

[37] "The Darwin Centenary: Commemorations at Cambridge: Brilliant Scenes and Remarkable Speeches," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909 (reporting Lord Rayleigh's remarks); and Vernon L. Kellogg, "Celebrating Darwin's Greatness and Darwinism's Weakness," *American Naturalist*, 1910, *44*:382–384, on p. 384. Kellogg was among the invited delegates representing the United States but apparently did not attend, since his name is not on the "Final Lists"; see Clark Scrapbook. He based this statement on publications that arose from the Darwin celebrations in New York and Cambridge. Hence, he presumed that August Weismann, "the greatest Neo-Darwinian," and Ernst Haeckel, "the most advanced monist," were present, which was not the case. He may have had Osborn in mind as being "one of the greatest Neo-Lamarckians," Jacques Loeb as "the most radical mechanicalist," Bateson as the "most ardent Mendelian," de Vries as "the founder of the mutations theory," and Harald Höffding, professor of philosophy at Copenhagen, as the influential modern philosopher. Höffding was the author of the article "The Influence of the Conception of Evolution on Modern Philosophy," in *Darwin and Modern Science: Essays in Commemoration of the Centenary of the Birth of Charles Darwin and of the Fiftieth Anniversary of the Publication of* The Origin of Species, ed. Albert Charles Seward (Cambridge: Cambridge Univ. Press, 1909) (hereafter cited as ***Darwin and Modern Science*, ed. Seward**), pp. 446–464.

took the opportunity of the Darwin celebration to discuss the status of evolution theory openly, elaborating on such issues as the extent to which natural selection shaped the course of evolution, the role of the environment in inducing hereditary changes, whether "mutations" played a significant role in species formation, the relationship of Mendel's laws and recent advances in "genetics" to evolutionary studies, and the impact of recent cytological studies of germ-cell formation for understandings of the material basis of heredity. Divisions were drawn between orthodox Darwinians, represented by Lankester and Edward Bagnall Poulton, who stressed the adaptationist elements of Darwin's theory; neo-Darwinians like Alfred Russel Wallace, who accepted the ultraselectionist and anti-Lamarckian views of August Weismann; proponents of the mutation theory of Hugo de Vries; and followers of the Mendelian program of "genetics" headed by William Bateson. While the discussions harbored undercurrents of disagreement and even discord, the public dialogue was conducted in the spirit of open intellectual debate rather than calumny. This cordial tone generally characterized the Cambridge festivities, and it carried through in most of the writings published both before and immediately following June 1909.

Different Schools of "Darwinism"

While only nominally apparent in the speeches delivered at the Cambridge celebration, the spectrum of views about the current status of evolution theory held by different biologists was certainly evident in the various publications prompted by the worldwide celebrations. As Bowler observed, "the post-Darwinian debates were not straightforward arguments about clear-cut alternatives. They ranged across a series of highly complex issues that gave the individual biologist plenty of room for maneuvering even within what was labeled as a single theory."[38] Many of the publications connected with the celebrations can be identified as falling into one camp or another, while some avoided polemics and focused instead on new data in emerging subfields of biology that ostensibly pertained to evolutionary questions.

The celebration's commemorative volume, *Darwin and Modern Science*, prepared under the auspices of the Cambridge Philosophical Society, included essays by leading biologists and scholars charged with characterizing the impact of Darwinism on science, the social sciences, religion, and philosophy—the entire spectrum encompassed by the term. This was not intended to be a hagiographic memorial volume; the committee expressly aimed for a work "in which Darwinism is examined and criticised," with the essays serving "the double purpose of illustrating the far-reaching influence of Darwin's work on the progress of knowledge and the present attitude of original investigators and thinkers towards the views embodied in Darwin's works."[39] Its American counterpart, *Fifty Years of Darwinism: Modern Aspects of Evolution*, a compilation of papers given at the memorial meeting of the American Association for the Advancement of Science in January 1909, likewise detailed new developments in evolutionary studies. While one commentator quipped that

[38] Bowler, *Eclipse of Darwinism* (cit. n. 9), p. 10. The *Reader's Guide to Periodical Literature* of 1908 and 1909 lists scores of articles on the Darwin/Wallace celebration of 1908, the U.S. celebration and the Cambridge centenary celebration of 1909, reviews of *Darwin and Modern Science*, recollections of and articles on Darwin, and assessments of the current status of evolution theory.

[39] A. C. Seward, "Preface," in *Darwin and Modern Science*, ed. Seward, pp. v–viii, on p. v. The editorial committee included members of the Cambridge Philosophical Society and the Cambridge University Press Syndicate, among them, in addition to Seward, Hugh Kerr Anderson, William Bateson, Francis Darwin, Ernest William Hobson, John Edward Marr, Adam Sedgwick, David Sharp, Arthur Everett Shipley, and William Ritchie Sorley: "Darwin Centenary Publications," *Times*, 5 June 1909, p. 6.

such works "left the definite impression on the scientific world of having celebrated Darwin's greatness and Darwinism's weakness," another found the essays in *Darwin and Modern Science* valuable, for "by bringing together the views of the different and often antagonistic writers, it enables the ordinary reader to get a clear notion of the various lines of divergence from Darwin's original position."[40] In addition to these volumes and their reviews, scores of articles were published on Darwin and evolution around this time. These rich materials provide the historian with an abundance of resources by which to assess the status of Darwinism in the "annus mirabilis" of 1909.

In his review of *Darwinism and Modern Science* and *Fifty Years of Darwinism*, the American entomologist Vernon Lyman Kellogg, author of the much-discussed recent work *Darwinism To-Day* (1907), recognized a key strategy employed by most contributors. "Each speaker," he noted, "first recognizes the lasting debt of science and of himself to the immortal master, and then gently or forcfully [*sic*] proceeds to show how the master's explanation fails to explain, and to unload and display his own precious personal baggage of 'factors'; factors of environment, of mutation, of adaptation, of determinate variation, of isolation and what not."[41] Indeed, this was the general formula: authors traced their views back to Darwin so as to establish their legitimacy, then proceeded to outline their own special interpretations and conclude that Darwin would no doubt have agreed with them had he only known of this work. Even those who had been espousing their particular points of view for decades adopted this tactic. It is thus instructive to review these arguments, both to characterize the various positions and to contrast the different views with the new perspectives that began to emerge around 1909. Because of this focus, only those authors who addressed the problems of heredity, variation, and cytology will be highlighted here. This should not obscure the fact, however, that many other scientists and scholars presented important essays on other aspects and concerns of evolution, as can readily be seen from the list of contributors to *Darwin and Modern Science*.[42]

Natural Selection

Not surprisingly, the committee made natural selection a key topic of *Darwin and Modern Science*; they wanted their volume to review Darwin's theory of natural selection and then ask, "How far sufficient and how far requiring modification?" Foremost among those who

[40] Kellogg, "Celebrating Darwin's Greatness and Darwinism's Weakness" (cit. n. 37), p. 383; and Meldola, "Evolution" (cit. n. 6), p. 484.

[41] Kellogg, "Celebrating Darwin's Greatness and Darwinism's Weakness," p. 383. On Kellogg's views of Darwinism see Mark A. Largent, "Bionomics: Vernon Lyman Kellogg and the Defense of Darwinism," *J. Hist. Biol.*, 1999, *32*:465–488.

[42] J. Arthur Thomson, "Darwin's Predecessors"; August Weismann, "The Selection Theory"; Hugo de Vries, "Variation"; William Bateson, "Heredity and Variation in Modern Lights"; Eduard Strasburger, "The Minute Structure of Cells in Relation to Heredity"; Gustav Schwalbe, "The Descent of Man"; Ernst Haeckel, "Charles Darwin as an Anthropologist"; J. G. Frazer, "Some Primitive Theories of the Origin of Man"; Adam Sedgwick, "The Influence of Darwin on the Study of Animal Embryology"; W. B. Scott, "The Palaeontological Record, I: Animals"; D. H. Scott, "The Palaeontological Record, II: Plants"; Georg Klebs, "The Influence of the Environment on the Forms of Plants"; Jacques Loeb, "Experimental Study of the Influence of Environment on Animals"; E. B. Poulton, "The Value of Colour in the Struggle for Life"; William Thiselton-Dyer, "Geographical Distribution of Plants"; Hans Gadow, "Geographical Distribution of Animals"; J. W. Judd, "Darwin and Geology"; Francis Darwin, "Darwin's Work on the Movements of Plants"; Karl Goebel, "The Biology of Flowers"; C. Lloyd Morgan, "Mental Factors in Evolution"; Hermann Höffding, "The Influence of the Conception of Evolution on Modern Philosophy"; Charles Bouglé, "Darwinism and Sociology"; P. N. Waggett, "The Influence of Darwin upon Religious Thought"; Jane Ellen Harrison, "The Influence of Darwinism on the Study of Religions"; Peter Giles, "Evolution and the Science of Language"; John Bagnell Bury, "Darwinism and History"; George Darwin, "The Genesis of Double Stars"; and William Cecil Dampier Whetham, "The Evolution of Matter."

were considered most suitable to address these questions was August Weismann, who was asked to write the lead-off scientific article, appropriately entitled "The Selection Theory," for the volume.[43] Exemplifying Kellogg's dictum, Weismann in his long piece first invoked Darwin in support of his assertion about the key role selection played in evolution.[44] Resurrecting crucial points of his famous "debate" over the inheritance of acquired characters with Herbert Spencer in the 1890s, Weismann noted that this "is the very kernel of the whole question of the reality and value of the principle of selection." He then singled out modern challenges to the supremacy of selection, explaining away the evidence cited in its support. Bateson's idea of discontinuous evolution, for example, was dismissed because the cases he cited were due (using the terminology of his germinal theory of heredity) "to an intensified germinal selection," that is, to the selection of ids containing favorable biophors. De Vries's notion of large-scale mutations, based on sporting in the evening primrose, *Oenothera lamarckiana*, was not important because the form had recently been shown to be a hybrid, not a species, and hence was at best a new variety, not a new species. Weismann also addressed what he viewed as "senseless" theoretical objections, repeated over and over again, that selection "can create nothing, it can only reject." This is certainly true, he admitted. "But in rejecting one thing it preserves another, intensifies it, combines it, and in this way *creates* what is new. *Everything* in organisms depends on adaptation."[45] To illustrate this point, Weismann described the recent study of mimicry in animals, which he believed provided some of the best evidence for selection.

Just as fitting was the choice of Ernst Haeckel, Weismann's arch critic, to present the adaptationist perspective. Haeckel began his essay, "Charles Darwin as an Anthropologist," by attacking Weismann for refusing to acknowledge the important evolutionary role played by the inheritance of acquired characteristics. Darwin, he claimed, certainly recognized this principle in his writings, as did the "great majority of speculative biologists"—including Herbert Spencer, Rudolf Virchow, Thomas Henry Huxley, Albert von Kölliker, Karl Gegenbaur, and himself. Moreover, he asserted, Weismann's theory upholding the primacy of selection was purely speculative, "a finely conceived molecular hypothesis, . . . but devoid of empirical basis." Indeed, he argued, Weismann's views should not be labeled as "Neodarwinism" or "ultradarwinism" since they did not adequately represent Darwin's theory. Haeckel claimed that Darwin's "monumental greatness" indeed rested on "the fact that not one of his many successors has succeeded in modifying his theory of descent in any essential point or in discovering an entirely new standpoint in the interpretation of the organic world."[46]

[43] Others considered included Alfred Russel Wallace, William Thiselton-Dyer, William Bateson, Hugo de Vries, and Archdale Reid: Albert Charles Seward, Copybook from *Darwin and Modern Science*, Add. 7733, Manuscripts Room, Cambridge University Library (hereafter cited as **Seward Copybook**). As Gayon noted, Weismann was known "as the founder of 'neo-Darwinism,' or, as it tended to be called at the turn of the century, 'ultra-Darwinism.'" These terms were associated "with two radical and closely linked theses: an intransigent rejection of the inheritance of acquired characters and the idea that the 'all-sufficiency of natural selection' was an explanatory principle of evolution": Gayon, *Darwinism's Struggle for Survival*, p. 148.

[44] Weismann's essay was overly long, and, owing to his poor health, E. B. Poulton agreed to shorten it for the volume. See Seward Copybook, Add. 7733; and Frederick B. Churchill and Helmut Risler, eds., *August Weismann: Selected Letters and Documents*, 2 vols. (Freiburg: Freiburg Univ. Press, 2000), Vol. 1, pp. 484, 490–495.

[45] August Weismann, "The Selection Theory," in *Darwin and Modern Science*, ed. Seward, pp. 18–65, on pp. 33, 23, 24, 61. See also Frederick B. Churchill, "The Weismann–Spencer Controversy over the Inheritance of Acquired Characters," in *Human Implications of Scientific Advance*, ed. E. G. Forbes (Edinburgh: Edinburgh Univ. Press, 1978), pp. 451–468; and Rasmus G. Winther, "August Weismann on Germ-Plasm Variation," *J. Hist. Biol.*, 2001, *34*:517–555.

[46] Ernst Haeckel, "Charles Darwin as an Anthropologist," in *Darwin and Modern Science*, ed. Seward, pp.

The diametrically opposed positions of Weismann and Haeckel regarding the mechanism of evolutionary change well illustrate a point made by another contributor, the German botanist Georg Klebs. In "The Influence of the Environment on the Forms of Plants" Klebs noted: "A glance at the controversy which is going on to-day in regard to different hypotheses shows that the same material may lead different investigators to form entirely different opinions." Indeed, one of the hallmarks of the morphologically or phylogenetically based evolution espoused by biologists of Weismann's and Haeckel's generation was its grounding in logical analysis of propositions supported by certain illustrative cases, which resulted in an impasse in unifying the divergent schools of evolutionary thought. It was precisely this stalemate that influenced Bateson and other biologists to search for a new experimental means of investigating the causes of variation and heredity.[47] The rediscovery of Mendel's laws of heredity and the rise of "Mendelism," along with the new view of mutation put forward by Hugo de Vries, led many to believe that such lines of work offered a promising approach that might help breach this philosophical and empirical deadlock. Because neo-Darwinians viewed both Bateson and de Vries as critics of the accepted tenets of Darwinian thought, these authors sought in their essays to downplay their deviance from Darwinism. While in de Vries's case this may have been sincere, in Bateson's—judging from other writings circa 1909—it was probably more a matter of expedience.

Variation and Heredity à la Mendel

In his contribution to *Darwin and Modern Science*, Bateson lavished praise on Darwin. His work, he noted, "has the property of greatness in that it may be admired from more aspects than one." Further developing an image of the "wide umbrella" of Darwinism that could shelter different views, Bateson continued: "For some the perception of the principle of Natural Selection stands out as his most wonderful achievement to which all the rest is subordinate. Others, among whom I would range myself, look up to him rather as the first who plainly distinguished, collected, and comprehensively studied that new class of evidence from which hereafter a true understanding of the process of Evolution may be developed." While he distinguished his own view about the importance of variation from Weismann's emphasis on natural selection and Haeckel's on adaptation, he stressed that he did not altogether reject a role for natural selection in evolutionary change. Although denying it the "perilous burden" that Weismann assigned it, Bateson noted that selection "permits the viable to continue and decides that the non-viable shall perish; . . . So again,

137–151, on pp. 139, 140, 141, 142. Haeckel certainly regarded natural selection as "distinctive of 'Darwinism'" (p. 137). He was originally asked to write on the "descent of man" but was requested to refocus after Gustav Schwalbe of Straßburg agreed to address this topic: Seward Copybook. An article published in an American newspaper claimed that Haeckel had been shunned by the Cambridge celebration organizing committee owing to "clerical prejudice," prompting Seward to write a letter to the editor of *Science* stating that Haeckel was originally appointed by the University of Jena as its delegate, only later to have to withdraw owing to ill health. "I need hardly add that if Professor Haeckel had not been appointed a delegate he would certainly have been invited as a private guest": A. C. Seward, "The Darwin Celebration at Cambridge," *Science*, N.S., 1909, *30*:25. On Haeckel and the inheritance of acquired characters see L. I. Blacher, *The Problem of the Inheritance of Acquired Characters: A History of* a Priori *and Empirical Methods Used to Find a Solution*, ed. and trans. Frederick B. Churchill (1971; Washington, D.C./New Delhi: Smithsonian Institution Libraries and the National Science Foundation, in association with Amerind Publishing, 1982), Ch. 5.

[47] Georg Klebs, "The Influence of the Environment on the Forms of Plants," in *Darwin and Modern Science*, ed. Seward, pp. 223–246, on pp. 240–241. See also Peter J. Bowler, "Foreword," in William Bateson, *Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species* (1894; Baltimore: Johns Hopkins Univ. Press, 1992), pp. xvii–xxvii.

as the course of descent branches in the successive generations, Selection determines along which branch Evolution shall proceed, but it does not decide what novelties that branch shall bring forth."[48] This was the "sieve" interpretation that was anathema to Weismann and other selectionists.

With regard to heredity, Bateson praised Weismann's particulate theory: "his elaborate speculations as to the genetic meaning of cytological appearances have led to a minute investigation of the visible phenomena occurring in those cell-divisions by which germ-cells arise." Yet he noted, implicitly referring to Mendelian data, that "though the particular views he advocated have very largely proved incompatible with the observed facts of heredity, yet we must acknowledge that it was chiefly through the stimulus of Weismann's ideas that those advances in cytology were made; and though the doctrine of the continuity of germ-plasm cannot be maintained in the form originally propounded, it is in the main true and illuminating." Yet, as is widely known, Bateson's acceptance of Mendelian factors did not lead him to adopt a particulate, morphological view of the material basis of heredity. Rather, he explicitly rejected identifying factors with nuclear chromosomes and expressed doubt that chromosomes "alone govern form, and are the sole agents responsible in heredity," adding, "I have never been persuaded that the rest of the cell counts for nothing." He preferred a physiological conception of Mendelian factors, noting that the "definiteness and specific order in heredity, and therefore variation," revealed by Mendelism points to "the fundamental chemical and physical nature of living things" and "the symmetry of the dividing cell" as the basis for hereditary transmission.[49]

Bateson only briefly addressed the connection between Mendelian heredity and evolution, derived from his "presence and absence" theory, which regarded variation as the product of the addition or loss of factors. According to this view, evolution resulted from the as-yet-unknown process by which different factors were removed from the germplasm through hereditary transmission, thus creating new varieties and eventually new species. "Genetic Variation is then primarily the consequence of additions to, or omissions from, the stock of elements which the species contains." For this reason, evolution was saltatory rather than a gradual process. He found this view ultimately more satisfying, concluding: "an evolution of species proceeding by definite steps is more, rather than less, easy to imagine than an evolution proceeding by the accumulation of indefinite and insensible steps."[50] Nonetheless, Bateson was not optimistic that this line of inquiry would bear fruit any time soon. He pointed to the problem of the origin of interspecific sterility as a major hurdle, alongside understanding how change in unit factors could be sufficient to result in speciation.[51] In short, Bateson distanced Mendelism from the quest to understand the basis of evolutionary change and, in effect, from later developments in Mendelian genetics.

[48] William Bateson, "Heredity and Variation in Modern Lights," in *Darwin and Modern Science*, ed. Seward, pp. 85–101, on pp. 85, 96. Bateson had long maintained this position. See Bateson, *Materials for the Study of Variation*, p. 5; and, more recently, Bateson, "President's Address, Section D.—Zoology," in *Report of the British Association for the Advancement of Science, 1904* (London: Murray, 1905), pp. 574–589, on p. 579.

[49] Bateson, "Heredity and Variation in Modern Lights," pp. 91, 97. The most complete expression of Bateson's understanding of the cytological basis of segregation is Bateson, "President's Address." The classic work on this topic remains William Coleman, "Bateson and Chromosomes: Conservative Thought in Science," *Centaurus*, 1970, *15*:228–314.

[50] Bateson, "Heredity and Variation in Modern Lights," pp. 92–93, 99. As he had noted in *Materials for the Study of Variation* (cit. n. 47), "Variation, in fact, *is* Evolution" (p. 6).

[51] Bateson built on this theme in his presidential address to the 1914 meeting of the British Association for the Advancement of Science: William Bateson, "President's Address," in *Report of the 84th Meeting of the British Association for the Advancement of Science (Australia, August 1914)* (London: Murray, 1915), pp. 3–38. See also H. Allen Orr, "Dobzhansky, Bateson, and the Genetics of Speciation," *Genetics*, 1996, *144*:1331–1335.

Mutation

To address the modern understanding of variation, the editorial committee turned to Hugo de Vries, whom the 1909 celebration organizers also selected to commend with an honorary degree.[52] In his article de Vries put forth the controversial claim that Darwin had recognized two distinct types of variation: "ordinary fluctuations which are always present, and such variations as 'happen to arise' from time to time. The latter afford the material for natural selection to act upon the broad lines of organic development, but the first do not. Fortuitous variations are the species-producing kind, which the theory requires; continuous fluctuations constitute, in this respect, a useless type."[53] Only one of the three types of "mutating variability" was the "species-producing kind," responsible for "the production of quite new characters which never existed in the ancestors. Upon this progressive mutability the main development of the animal and vegetable kingdom evidently depends." In outlining a saltationist view of evolutionary change, de Vries fell into the same camp as Bateson—likewise in his view of natural selection as the sieve that ultimately establishes the new species produced via mutation. "The origin of new species, which is in part the effect of mutability, is, however, due mainly to natural selection. Mutability provides the new characters and new elementary species. Natural selection, on the other hand, decides what is to live and what to die."[54] Hence, de Vries claimed that his mutation theory was not opposed to Darwin's views but merely provided a new understanding of the source of variation upon which natural selection could act.[55]

De Vries's identification of genetic rather than fluctuating variation as the source of evolutionary change sparked a controversy among neo-Darwinians. As Phillip Sloan has written, "Mendelism was introduced into Britain in the midst of a pre-existing debate over the role of variation in Darwinian evolution." Darwin himself contributed to this confusion, vacillating in different editions of the *Origin* between gradual and saltationist descriptions of the nature of variation.[56] By 1909, with a growing recognition that heritable variation was somehow connected with the germplasm, de Vries's interpretation gained increasing

[52] De Vries was originally considered for the articles on natural selection and the origin of species, then placed among those who were to write the three (later extended to four) essays on "Variation and Heredity." Others considered included Bateson, Francis Galton, Karl Pearson, G. U. Yule, and Wilhelm Johannsen: Seward Copybook.

[53] Hugo de Vries, "Variation," in *Darwin and Modern Science*, ed. Seward, pp. 66–84, on p. 71. Taking issue with de Vries's assertion, Seward inserted an "editorial footnote" (the only one in the volume) disputing this statement: "I think it right to point out that the interpretation of this passage from the *Origin* by Professor de Vries is not accepted as correct either by Mr Francis Darwin or by myself." See A. C. Seward to Hugo de Vries, 11 Dec. 1908, and de Vries to Seward, 19 Dec. 1908, Seward Copybook.

[54] De Vries, "Variation," pp. 75, 77. It is important to note, however, that Bateson and de Vries were estranged by 1909, with Bateson increasingly dissatisfied with de Vries's abandonment of Mendelian views. Moreover, their personal relations were also strained. While his wife and daughter stayed with the Batesons during the Darwin celebration (women were not permitted to stay in college), de Vries himself chose to stay in town, which Bateson took as a snub. See Beatrice Bateson's annotations to William Bateson's letter to C. C. Hurst, 25 June 1909, in which she stated: "Madame de Vries & daughter stayed with us, but the Professor stayed in a hotel in Cambridge and turned his back on Will at the Conversazione in the Fitzwilliam": William Bateson Correspondence, Add. MS 8634, Manuscripts Room, Cambridge University Library.

[55] As Charles Lenay notes, "For his theoretical work, De Vries claims to lean essentially on the works of Darwin," although he drew different conclusions from Darwin's data: Charles Lenay, "Hugo De Vries: From the Theory of Intracellular Pangenesis to the Rediscovery of Mendel," *Compt. Rend. Acad. Sci.*, 2000, *323*:1053–1060, on p. 1055.

[56] Phillip R. Sloan, "Mach's Phenomenalism and the British Reception of Mendelism," *Compt. Rend. Acad. Sci.*, 2000, *323*:1069–1079, on pp. 1070, 1071. For Darwin see Peter Vorzimmer, *Charles Darwin: The Years of Controversy, 1859–1882* (Philadelphia: Temple Univ. Press, 1970), p. 300.

currency among biologists.[57] Indeed, despite Bateson's perception that Mendelism was slighted during the 1909 celebration, it appears that biologists and laymen alike came away with a favorable impression of the importance of Mendel and mutation. As one reviewer noted:

> Bateson and De Vries insist that there is a definite law governing differences of any kind; that variations may arise otherwise than as the result of surroundings; and that they may persist because of something dominant and pertinacious in themselves. In other words, they believe that "natural selection" may be a necessary, but that it is not a sufficient, explanation. But they are too conscious of the difficulties of constructing any generalisation which will rest for ever absolutely true to belittle the work of one who is greater than themselves, and their essays are devoted to attempts to harmonise their results with those of the Master rather than to accentuate the differences. That spirit we commend to the more youthful writers, and we do so more urgently because it is certain that their spirited declamation will interest the general public.[58]

Moreover, in leaving open the question of the "size" of mutational change, and thereby allowing for small-scale as well as large, species-forming mutations, de Vries prepared the way for a new understanding that was critical for later developments in Mendelian genetics. The extent to which this association was occurring can be seen from the address to the British Association by Arthur E. Shipley, one of the organizers of the Darwin celebration, in August 1909:

> That mutations occur and exist is obvious to everyone, but that they are of frequent occurrence under purely natural conditions is, Sir William Thiselton-Dyer thinks, "unsupported by evidence." The delicate adjustment between an organism and its natural surroundings suggests that sudden change of a marked kind would lead to the extinction of the mutating individual. As far as I can understand the matter in dispute, Darwin and his followers held that evolution had proceeded by small steps, for which we may accept de Vries' term fluctuations; whilst the Mutationists hold that it has advanced by large ones, or mutations. But it is acknowledged that mutations are not all of the same magnitude, some, e.g., albinism; brachydactyly in man; dwarf habit or glabrousness in plants may be large; others, e.g., certain differences in shade of colour or in size, are insignificant, and indeed Punnett has suggested that under the head of fluctuating variation we are dealing with two distinct phenomena. He holds that "some of the so-called fluctuations are in reality mutations, whilst others are due to environmental influence." He thinks the evidence that these latter are transmitted is slender, and later states that "Evolution takes place through the action of selection on these mutations. Where there are no mutations there can be no evolution." The disagreement about the way in which evolution has proceeded has perhaps arisen from a misunderstanding as to the nature of the two kinds of variation described respectively as mutations and fluctuations. Mutations are variations arising in the germ-cells and due to causes of which we are wholly ignorant; fluctuations are variations arising in the body or "soma" owing to the action of external conditions. The former are undoubtedly inher-

[57] See, e.g., Bateson, "Heredity and Variation in Modern Lights" (cit. n. 48), p. 96. One reviewer of the volume echoed this view: "Some authors have tried to show that the theory of mutation is opposed to Darwin's views. But this is erroneous. On the contrary, it is in the fullest harmony with the great principle laid down by Darwin. In order to be acted upon by that great complex of environmental forces, which Darwin has called natural selection, the changes must obviously first be there." "Estimates of Darwin: Review of 'Darwin and Modern Science,'" *Standard*, 25 June 1909. See also Charles B. Davenport, "Mutation," in AAAS, *Fifty Years of Darwinism*, pp. 160–181. Davenport also suggested that the mutation theory agreed with Darwin's views.

[58] "Natural Selection Stock-Taking" [review of *Darwin and Modern Science* and *The Making of Species*, by Douglas Dewar and Frank Finn], unattributed newspaper clipping, Shipley Scrapbook. Bateson complained to Hurst that "from the Mendelian's standpoint the gathering was rather tantalising, as so many of us were assembled, but the programme gave practically no opportunity of shewing anything, or of comfortable discussion": Bateson to Hurst, 25 June 1909, William Bateson Correspondence, Add. MS 8634, Manuscripts Room, Cambridge University Library.

> ited, the latter are very probably not. But since mutations (using the word in this sense) may be small and may appear similar in character to fluctuations, it is not always possible to separate the two things by inspection alone.[59]

It is not surprising, then, to find T. H. Morgan adopting the term "mutation" to characterize the white-eyed fruit fly described in his pivotal 1910 paper. This illustrates that by 1910 a new understanding of mutation was well established, especially in the United States, where de Vries enjoyed widespread acclaim.[60]

Meiosis

The essays commemorating the Darwin celebration of 1909 not only reveal the current status of evolution theory but also indicate an important fact about contemporary biology: that specialization was making it increasingly difficult for any one scientist to comprehend, let alone synthesize, the conceptual developments in various subfields into a comprehensive view of evolutionary change. Indeed, Raphael Meldola, in his review of *Darwin and Modern Science*, pointed to Darwin's ability to synthesize data from widely divergent fields as the source of his genius. A new comprehensive overview seemed particularly urgent given the recent advances in a field that Darwin had omitted from his synthetic account of evolution, namely, cytology. Perhaps recognizing this, the organizers of the 1909 celebration had singled out Edmund Beecher Wilson to receive an honorary degree in acknowledgment of how he, "in his well-known work on 'The Cell,' enlarged on all the details of his microscopic study of karyokinesis, or the dance performed by the nuclear fragments in the process of cell-division." The editors of both *Fifty Years of Darwinism* and *Darwin and Modern Science* also clearly identified this need and, accordingly, asked Wilson and another leading figure in this field, Eduard Strasburger, to discuss the importance of recent findings in cytology for evolutionary theory for their respective volumes. Their views were clear: "any modern theory of heredity," Strasburger boldly proclaimed, "must rest on a basis of cytology and cannot be at variance with cytological facts."[61]

[59] Arthur Everett Shipley, "President's Address, Section D.—Zoology," in *Report of the British Association for the Advancement of Science, 1909* (London: Murray, 1910), pp. 484–502, esp. pp. 488–489. Shipley refers to Reginald Crundall Punnett, *Mendelism* (London: Macmillan, 1905), a revised edition of which appeared in 1907. He also illustrated his last point by referring to Wilhelm Johannsen's experiments on pure lines in beans. On de Vries's preparation for new understandings that would later become important in Mendelian genetics see Gayon, *Darwinism's Struggle for Survival*, pp. 258–259.

[60] Thomas Hunt Morgan, "Sex Limited Inheritance in *Drosophila*," *Science*, 1910, *32*:120–122, on p. 122. See also Gayon, *Darwinism's Struggle for Survival*, pp. 303–305. On de Vries's mutation theory see Garland E. Allen, "Hugo de Vries and the Reception of the 'Mutation Theory,'" *J. Hist. Biol.*, 1969, *2*:55–87. On Morgan's acceptance of the "idea of discontinuous variation as proposed by Bateson and the mutation theory proposed by de Vries" see Allen, *Thomas Hunt Morgan* (cit. n. 5), p. 110; and Allen, "Thomas Hunt Morgan and the Problem of Natural Selection," *J. Hist. Biol.*, 1968, *1*:113–139. On the general opinion of de Vries's mutation theory in the United States see Kellogg, *Darwinism To-Day* (cit. n. 35), p. 362 n 22; Provine, *Origins of Theoretical Population Genetics* (cit. n. 5), pp. 64–70; and Sharon E. Kingsland, "The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900–1912," *Isis*, 1991, *82*:479–509. For an analysis of changing views of mutation see Robert Olby, "Huxley's Place in Twentieth-Century Biology," in *Julian Huxley: Biologist and Statesman of Science*, ed. C. Kenneth Waters and Albert Van Helden (Houston: Rice Univ. Press, 1992), pp. 53–75, esp. pp. 60–64.

[61] Meldola, "Evolution" (cit. n. 6), p. 485; "Darwin Centenary: Commemorations at Cambridge: Brilliant Scenes and Remarkable Speeches," *Cambridge Chronicle and University Journal, Isle of Ely Herald, and Huntingdonshire Gazette*, 25 June 1909 (Wilson's presentation announcement); and Eduard Strasburger, "The Minute Structure of Cells in Relation to Heredity," in *Darwin and Modern Science*, ed. Seward, pp. 102–111, on p. 102. The organizers had originally wanted Theodor Boveri to write the piece. Not surprisingly, Bateson was not well pleased by Strasburger's article, calling it a "sad production" that was "so dull as to be almost unreadable, and I think very misleading. . . . I think it an article we may be heartily ashamed of, in both matter, form, and style": Bateson to Seward, 20 Oct. 1908, Seward Copybook.

The messages conveyed by Strasburger and Wilson were similar: the cell was key to understanding evolutionary change. "At least the great majority of present-day investigators in the domain of cytology," Strasburger noted, "have been led to the conclusion that the nucleus is the carrier of hereditary characters, and they also believe that hereditary characters are represented in the nucleus as distinct units." Wilson went even further and explicitly linked the cell with Mendelian heredity, emphasizing Sutton's and Boveri's recent association of chromosomal behavior with Mendelian phenomena. "Only in the chromatin-substance, again, do we see in the course of the maturation of the germ-cells a redistribution of elements that shows a parallel to the astonishing disjunction and redistribution of the factors of heredity that are displayed in the Mendelian phenomenon." This strong affirmation that the chromosomes were the material basis of heredity was significant. Only three years earlier, one biologist attending the 1906 meeting of the British Association for the Advancement of Science claimed to have witnessed a discussion of "what, if any, relation there is between heredity and chromosomes."[62] Bateson notwithstanding, by 1909 the tide among biologists was beginning to turn toward accepting the chromosomes as the material basis of heredity.

To reiterate: these topics—the connection of Mendelism, mutation, and meiosis to evolution—were not the only areas of emphasis in the essays published in the commemorative volumes. Other authors addressed topics such as Darwin's influence on embryology, paleontology, geology, botany, and psychology, as well as the geographical distribution of plants and animals, the effect of the environment on organisms, the nature of adaptation, and the role of isolation. The burning issue confronting biologists of the day, however, was the mechanism of evolution. Hence, many were particularly interested in how recent advances in understanding variation, heredity, and cellular morphology might help resolve the decades-old evolutionary debates. This concern was voiced by the author reviewing the topic of adaptation for *Fifty Years of Darwinism*. "The question of the origin of adaptive deviations," wrote Carl Eigenmann, "is the question of how and why adaptive germinal modifications arise, or how adaptive somatic modifications are transferred to the germ. . . . This is *the* question of the present generation, perhaps of the entire twentieth century."[63] The attention of biologists was thus intently focused on understanding how the new data on variation and its transmission in heredity impacted evolution theory.

CATEGORIZING THE VIEWS EXPRESSED ABOUT EVOLUTION IN 1909

What kinds of impressions would biologists who read these volumes, their reviews, and the veritable barrage of literature on Darwin and Darwinism in the years around 1909 have come away with? They were certainly offered a number of perspectives. First, the contributions of the older generation of evolutionists, represented by Weismann and Haeckel, indicated that their views had changed very little from those presented in the twenty-five years since Darwin's death. This impression was not significantly tempered, moreover, by essays written by their supporters. The selectionist and Weismannian E. B. Poulton, Oxford

[62] Strasburger, "Minute Structure of Cells in Relation to Heredity," p. 111; Edmund B. Wilson, "The Cell in Relation to Heredity and Evolution," in AAAS, *Fifty Years of Darwinism*, pp. 92–113, on p. 100; and Albert F. Blakeslee, "Twenty-five Years of Genetics (1910–1935)," *Brooklyn Botanic Garden Memoirs*, 1936, *4*:29–40, on p. 34. I have not been able to identify the session of the BAAS meeting at York at which this may have occurred.

[63] Carl H. Eigenmann, "Adaptation," in AAAS, *Fifty Years of Darwinism*, pp. 182–208, on p. 191.

professor of zoology, for example, upheld the selectionist viewpoint by focusing on animal coloration, particularly types of mimicry, and he also launched a pointed attack on the opposition. One of the few biologists to criticize Darwin, Poulton pointed to the "mistaken interpretations into which even Darwin was led by following the hypothesis of Lamarck" and drew attention to the errors of those who emphasized the inheritance of acquired characters, among them Francis Darwin.[64] Yet few were likely to have been swayed by the continuing "logical" arguments for or against different varieties of Darwinism laid out in 1909.

Second, the contributions offered by the next generation of Darwinians—the cohort represented by Bateson, de Vries, and others of their age group—attempted to bridge the perceived chasm between their own views, emerging out of recent studies of variation and Mendelian heredity, and those of the older generation and modern neo-Darwinians. They generally glossed over apparent differences, pointing out that their findings complemented Darwin's evolution theory and incorporated a role for the operation of natural selection in producing evolutionary change. In comparison with the older generation, this "middle generation" of evolutionists emphasized experimental evidence (primarily gained from breeding experiments) over evolutionary theorizing. This focus on experiment appealed to many biologists. Considering "the theoretic demand upon the selection hypothesis," the American Henry Fairfield Osborn noted that "the tendency of our time is to waive aside theoretic considerations and come down to actual observations and facts and see how far they support the Darwinian and other hypotheses, and how far they call for new hypotheses and interpretations." As Jean Gayon has noted, "For most of the pioneers of Mendelism, the new experimental science of heredity was closely associated with a new non-Darwinian and mutationist theory of evolution."[65] Thus, while many may have considered the work of Bateson and de Vries as pointing the way to a new approach to evolution, these two were themselves unable to "waive aside" their own "theoretic considerations" and lead the future campaign.

Third, readers may have noticed the glaring absence in this literature of a significant contribution from the biometricians. This was due in part to the death of W. F. R. Weldon in 1906, but it also resulted from the continued ill feelings between Karl Pearson and Bateson, who played a leading role in organizing the Cambridge events. Missing from *Darwin and Modern Science*, for example, was an essay by Pearson. This was not because the organizers failed to extend an invitation but, rather, because Pearson declined the offer, perhaps because he was asked to write on eugenics rather than on variation and heredity.[66]

[64] E. B. Poulton, "Fifty Years of Darwinism," in AAAS, *Fifty Years of Darwinism*, pp. 8–56, on p. 39. See also Poulton, "The Centenary of Darwin: Darwin and His Modern Critics," *Quarterly Review*, 1909, *211*:1–38. Poulton was referring to the views expressed by Francis Darwin in his presidential address at the 1908 Dublin meeting of the British Association for the Advancement of Science. He continued his concerted attack on Mendelians and mutationists in Poulton, *Charles Darwin and the Origin of Species: Addresses, etc., in America and England in the Year of the Two Anniversaries* (New York/London: Longmans, Green, 1909). On Poulton's adaptationist views see William C. Kimler, "Advantage, Adaptiveness, and Evolutionary Ecology," *J. Hist. Biol.*, 1986, *19*:215–233.

[65] Henry Fairfield Osborn, "Darwin and Paleontology," in AAAS, *Fifty Years of Darwinism*, pp. 209–250, on p. 217; and Gayon, *Darwinism's Struggle for Survival*, p. 289.

[66] The omission was noted by reviewers. Raphael Meldola, e.g., mentioned Pearson as one whose name "we should have liked to see on the list of contributors": Meldola, "Evolution" (cit. n. 6), p. 482. Apparently influenced by Bateson's strong antipathy toward biometricians, the committee asked Pearson to contribute to the volume not on biometrics but on eugenics—specifically, the "Future developments and influence of Darwin's teaching on human progress and social legislation." In declining, Pearson stated: "I have so recently said all I have at

This absence, however, somewhat—although not entirely—marginalized biometry from discussions in the context of the Darwin celebrations.[67]

The 1909 Darwin celebration thus served to focus the concerted attention of biologists on how recent findings in the fields of variation, heredity, and cytology impacted not just evolution *theory* but also evolution *studies*. Several of the participants, for example, offered views on how biologists could best approach "*the* question of the present generation, perhaps of the entire twentieth century." Jacques Loeb argued for a physiological approach, stating that the

> systematic physico-chemical analysis of the effect of outside forces upon the form and reactions of animals is also our only means of unravelling the mechanism of heredity beyond the scope of the Mendelian law. The manner in which a germ-cell can force upon the adult certain characters will not be understood until we succeed in varying and controlling hereditary characteristics; and this can only be accomplished on the basis of a systematic study of the effects of chemical and physical forces upon living matter.

It was clear, he asserted, that mutation and Mendelian heredity "must, for the time being, if not permanently, serve as a basis for theories of evolution," but to study the material basis of heredity, biologists needed to produce "mutations by physico-chemical means." The cytologist Wilson thought a biochemical approach was promising, stating: "It is my belief that . . . in the union of cytology and biochemistry lies our greatest hope of future advance." While not all biologists agreed, a critical consensus was forming that an experimental approach was definitely called for.[68]

These notions about how to proceed in investigating the material basis of heredity indicate the range of opinion within the biological community prior to the rise of Mendelian genetics in the 1910s. It was this confluence of new approaches that many biologists incorporated into their research agendas in the immediate post-1909 period in the hope of shedding new light on problems of evolution. Among the rising generation of biologists just beginning their scientific careers, one can indeed detect a new attitude and way of approaching the problems of evolution. The younger generation of biologists rejected the older morphological approach to evolution pursued in the immediate post-Darwinian period and adopted a concertedly experimental attack on evolutionary problems. Many took seriously as a starting point the recent findings of Mendelian heredity, mutation theory, and cytological analysis as they sought new ways to resolve long-standing evolutionary questions.

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present to say on the subject suggested, that I do not feel that I can profitably write more." See Seward to Karl Pearson, 28 Mar. 1908, and Pearson to Seward, 2 Apr. 1908, Seward Copybook. As Bateson confided to Seward on 20 Mar. 1908: "I own to a feeling of shame and mortification when I find that, after all that has happened, the opinion can seriously be expressed by leading biologists that Pearson should be asked to write on Heredity and Variation for this new volume. That he should be asked to write on Eugenics matters less. This subject, if you like, is theory, and in it one man's theory is as likely to be valuable as another's at present—and for the practical purposes which theory serves, a bad one is about as useful as a good one": Seward Copybook. Pearson does not appear to have been nominated as a delegate to the Cambridge celebration or to have attended as a guest; see "List of Delegates and other Guests Invited by the University," Clark Scrapbook.

[67] See, e.g., "Programme," p. 9, in *Order of the Proceedings at the Darwin Celebration Held at Cambridge, June 22–June 24, 1909* (Cambridge: Cambridge Univ. Press, 1909), Cam.b.909.2, Rare Books Room, Cambridge University Library. (Donated by J. W. Clark, the inside front cover reads: "This programme was in the main the work of Fra. Darwin. JWC.") For a new perspective on the beneficial aspects of the conflict between biometricians and Mendelians see Sloan, "Mach's Phenomenalism and the British Reception of Mendelism" (cit. n. 56).

[68] Jacques Loeb, "Experimental Study of the Influence of Environment on Animals," in *Darwin and Modern Science*, ed. Seward, pp. 247–270, on pp. 247, 269; and Wilson, "Cell in Relation to Heredity and Evolution" (cit. n. 62), p. 109. For the views of a detractor who disparaged the connection between Mendelism, cytology, and evolution see O. F. Cook, "Evolution, Cytology, and Mendel's Laws," *Pop. Sci. Month.*, 1903, *63*:219–228.

POST-1909 DEVELOPMENTS IN EVOLUTIONARY STUDIES

By 1909, then, changes were afoot in biology that heralded a new, experimental approach to evolutionary studies. This is particularly evident in Vernon Kellogg's *Darwinism To-Day* (1907), in which the Stanford entomologist sought to counter what he regarded as uninformed and unwarranted confusion over the problems besetting contemporary Darwinism. Kellogg was particularly troubled by the recent impression that evolution was under siege, not so much among laymen as among biologists. As a result, he emphasized in his book that the theory of descent was not in question—only the mechanism of natural selection. He also proclaimed his optimism that the new experimental spirit in biology would soon settle the long-open evolutionary questions:

> The present extraordinary activity in biology is two-phased; there is going on a most careful re-examination or scrutiny of the theories connected with organic evolution, resulting in much destructive criticism of certain long-cherished and widely held beliefs, and at the same time there are being developed and almost feverishly driven forward certain fascinating and fundamentally important new lines, employing new methods, of biological investigation. Conspicuous among these new kinds of work are the statistical or quantitative study of variations and that most alluring work variously called developmental mechanics, experimental morphology, experimental physiology of development, or, most suitably of all because most comprehensively, experimental biology. Now this combination of destructive critical activity and active constructive experimental investigation has plainly resulted, or is resulting, in the distinct weakening or modifying of certain familiar and long-entrenched theories concerning the causative factors and the mechanism of organic evolution. Most conspicuous among these theories now in the white light of scientific scrutiny are those established by Darwin, and known collectively, to biologists, as Darwinism.[69]

Kellogg noted that most of the evidence cited in support of evolution and natural selection was primarily "logical" in nature. In general, the formula ran: Given certain conditions and phenomena, then we can expect such-and-such to happen. Thus, the evidence for descent "explains all the observed facts touching the appearance in time and place on this earth of organisms and the facts of their likenesses and unlikenesses to each other, and this no other theory does." The same was true for natural selection, which also

> chiefly rests on the logical conclusion that under the observed fact of over-production, struggle is bound to occur; that under the observed fact of miscellaneous variation, those individuals most fortunate in their variations will win in the struggle; and, finally, that under the observed fact of heredity, the winners will transmit to their posterity their advantageous variations, all of which inter-acting facts and logically derived processes will be repeated over and over again, with the result of slow but constant modification of organic types, that is, formation of new species.

But arguments such as these had not to date led to closure; hence the current disarray in evolution theory. What was needed, he stressed, were new experimental approaches. The "principal desideratum in recent-day investigation of evolution," Kellogg wrote, is "the *intensive study of variability*," in terms of both statistics (via biometry) and dynamics (through experiments on embryonic development and breeding analysis). Only by studying

[69] Kellogg, *Darwinism To-Day* (cit. n. 35), pp. 1–2. Betty Smocovitis credits Kellogg with helping to introduce experimental methodology into evolution studies: Smocovitis, *Unifying Biology* (cit. n. 5), pp. 117–118, 119 n 64. For a summary of methodological objections to natural selection see Mayr, *Growth of Biological Thought* (cit. n. 35), pp. 520–522.

the "origins and causes" of variation, he claimed, could biologists circumvent the impasse created by "the present strong reaction against the selection theories."[70] Kellogg's challenge soon attracted a number of adherents.

New Experimental Approaches to Evolution circa 1909

William Provine has written that "Mendelism did not seriously affect purposive theories of evolution and did not vanquish evolutionary theories based upon the inheritance of acquired characters." While this is true, many biologists at the time were hopeful that Mendelism might offer a means to advance evolutionary studies. Provine indeed noted that Yves Delage and Marie Goldsmith's *Les théories de l'évolution* (1909; translated into English in 1913) devoted a chapter to "Mendelian inheritance and its significance for evolution."[71] When coupled with the search for mutations, Mendelism provided an impetus for a new experimental attack on problems of evolution.

The calls for a new experimental approach dovetailed with the growing realization that Mendelian research based on breeding analysis required new facilities. One of the hallmarks of post-Darwinian evolution studies was the ability to carry out its pursuit within the newly erected university biological laboratories and institutes. The research program in evolutionary morphology, for example, had been vigorously advanced in Jena under Haeckel and at the School of Morphology at Cambridge, first under the direction of Francis Maitland Balfour and later by his successor, Adam Sedgwick. However, by 1909 the recapitulationist program that attempted to trace the ancestry of and taxonomic relationships among organisms was in decline. Bateson, one of the leading critics of phylogenetic embryology, well expressed the perceived failure of this program:

> Formerly it was hoped that by the simple inspection of embryological processes the modes of heredity might be ascertained, the actual mechanism by which the offspring is formed from the body of the parent. In that endeavour a noble pile of evidence has been accumulated. All that can be made visible by existing methods has been seen, but we come little if at all nearer to the central mystery. We see nothing that we can analyse further—nothing that can be translated into terms less inscrutable than the physiological events themselves.

It was breeding experiments, he believed, that pointed the way to a new attack, and to pursue this tack biologists required facilities distinct from the university laboratory.[72]

Soon after initiating a Mendelian research program, Bateson had sought funding for a biological establishment in which to conduct an experimental study of heredity, but his application to the Carnegie Institution of Washington was rejected. Other biologists also lobbied the Carnegie Institution for facilities to be dedicated to an experimental study of evolution. Roswell Hill Johnson, for example, accompanied his proposal by stressing the need for experimentation:

[70] Kellogg, *Darwinism To-Day*, pp. 19, 377, 378–379.

[71] William B. Provine, "Progress in Evolution and Meaning in Life," in *Julian Huxley*, ed. Waters and Van Helden (cit. n. 60), pp. 165–180, on p. 176; and Yves Delage and Marie Goldsmith, *The Theories of Evolution*, trans. Andre Tridon (New York: Huebsch, 1913).

[72] Bateson, "President's Address" (1914) (cit. n. 51), p. 5. On Bateson's sense of present needs see Marsha L. Richmond, "The 'Domestication' of Heredity: The Familial Organization of Geneticists at Cambridge University, 1895–1910," *J. Hist. Biol.* (forthcoming). On the decline of the recapitulationist program see Adam Sedgwick, "The Influence of Darwin on the Study of Animal Embryology," in *Darwin and Modern Science*, ed. Seward, pp. 171–184; Georg Uschmann, *Geschichte der Zoologie und der Zoologische Anstalten in Jena 1779–1919* (Jena: Fischer, 1959); and Gerald Geison, *Michael Foster and the Cambridge School of Physiology* (Princeton, N.J.: Princeton Univ. Press, 1978).

> Our knowledge of the processes of evolution has been greatly retarded by lack of experimental investigation. Nearly all of the post-Darwinian writing has been either largely deductive or else upon the variation of individuals at a particular time and place, *i.e.*, static. Evolution, above all other things, requires dynamic studies. Much dispute centers around such observation because of various causes which may have been operative. Experiment alone admits exclusion of possible interfering elements. The various points in dispute are nearly all capable of decisive experimental testing.[73]

Johnson's proposal, however, met the same fate as Bateson's.

Charles Benedict Davenport's request to establish a Station for Experimental Evolution ultimately gained the support of the Carnegie trustees. Davenport—heavily influenced by de Vries's mutation theory, Mendelian heredity, and recent cytological advances—envisioned the proposed station as a place where "quantitatively exact experiments inbreeding through many generations can be conducted and from which material can be supplied to various specialists for cytological and biochemical investigation." Unlike Bateson's, Davenport's approach to the experimental study of evolution combined Mendelian hybridization experiments with the test for de Vriesian mutation.[74] In addition, convinced of "the importance of the chromatic material in inheritance," Davenport proposed to unite these investigations with a cytological examination of the chromosomes of the resulting hybrids. The new Station for Experimental Evolution, opened at Cold Spring Harbor on Long Island in June 1904, was the prime institutional incarnation of the new experimental ethos that had entered evolutionary studies, although the Carnegie-supported Laboratory for Plant Physiology, directed by Daniel Trembly MacDougal near Tucson, Arizona, was similarly oriented.[75] It was thus particularly appropriate that Davenport was chosen as a delegate to the 1909 Darwin celebration at Cambridge.

Bateson naturally expressed regret that no similar opportunities existed in England, "where through Darwin's genius the study of evolution first became a reality." The experimental study of evolution, he asserted, required "facilities of a special kind, such as neither technical colleges nor the laboratories of the Universities are able to supply."[76] It is therefore of some interest that one outcome of the 1909 Darwin celebration was a proposal to found a professorship of genetics at Cambridge University.

In March 1908, an announcement appeared in *Nature* stating that, as part of the Darwin celebration, there was a desire

[73] Roswell H. Johnson, "Biological Experiment Station for Studying Evolution," *Carnegie Institution of Washington Year Book*, 1902, *1*:274–279, on p. 274. On Bateson's failed application see Beatrice Bateson, ed., *William Bateson, F.R.S., Naturalist: His Essays and Addresses, Together with a Short Account of His Life* (Cambridge: Cambridge Univ. Press, 1928), p. 77. See also http://www.esp.org/foundations/genetics/classical/holdings/b/wb-02g.pdf.

[74] C. B. Davenport to the Trustees of the Carnegie Institution, 5 Mar. 1903, Davenport Papers, American Philosophical Society, Philadelphia. See also Pamela E. Mack, "The Early Years of the Cold Spring Harbor Station for Experimental Evolution" (typescript), American Philosophical Society, B: M19. Introducing de Vries at the opening of the Station for Experimental Evolution in Cold Spring Harbor, Davenport referred to his *Die Mutationstheorie* as "the most important work on evolution since Darwin's 'Origin of Species,' a work destined to be the foundation stone of the rising science of experimental evolution." See "Addresses at Opening of the Station for Experimental Evolution, June 11, 1904," *Carnegie Inst. Washington Year Book*, 1904, *3*:33–49, on p. 39.

[75] C. B. Davenport, "Station for Experimental Evolution at Cold Spring Harbor, New York," *Carnegie Inst. Washington Year Book*, 1905, *4*:87–96, on p. 94; Kingsland, "Battling Botanist" (cit. n. 60); and Garland E. Allen, "Heredity, Development, and Evolution at the Carnegie Institution of Washington," in *Centennial History of the Carnegie Institution of Washington*, Vol. 5: *The Department of Embryology*, ed. Jane Maienschein, Marie Glitz, and Allen (Cambridge: Cambridge Univ. Press, 2004), pp. 145–171.

[76] William Bateson, "The Progress of Genetic Research," in *Report of the Third International Conference 1906 on Genetics* (London: Spottiswoode, 1907), pp. 90–97, on p. 97.

> to found a chair of biology, the occupant of which shall devote himself to those subjects which were the chief concern of Darwin's life-work. It is probable that this will be accomplished, for the council of the Senate has had under consideration a generous offer of support made by a member of the University who wishes to remain anonymous. . . . It shall be the duty of the professor or professors elected during the period of five years above mentioned to teach and make researches in that branch of biology now entitled genetics (heredity and variation).[77]

The immediate result of this campaign was the establishment of a new professorship of biology at Cambridge, to which Bateson was elected in June 1908. The published text of his inaugural lecture, entitled "The Methods and Scope of Genetics" and delivered in October 1908, presented the following information:

> The object of the endowment [of the professorship of biology] was the promotion of inquiries into the physiology of Heredity and Variation, a study now spoken of as Genetics.
>
> It is now recognised that the progress of such inquiries will chiefly be accomplished by the application of experimental methods, especially those which Mendel's discovery has suggested. The purpose of this inaugural lecture is to describe the outlook over this field of research in a manner intelligible to students of other parts of knowledge.[78]

Despite the seeming triumph of gaining institutional support for genetics within the university, Bateson was disappointed by the refusal to give the title of "genetics" to this professorship. But even more disturbing was the omission of funding for the erection of facilities needed to pursue large-scale plant and animal breeding, as well as the stipulation of a fixed five-year tenure for the new position. Discussions of the proposal thus continued. In his address at the opening ceremony of the Darwin celebration in the Senate House, Lord Rayleigh mentioned the intention to create a new chair in genetics at Darwin's alma mater, news that was widely reported in the press. One account paraphrased Rayleigh's remarks as follows:

> During the last generation Cambridge, especially since the time of Michael Foster, had been active in biological work. They had the men and the ideas, but the difficulty had always been lack of funds. At the present time it was desired, among other things, to establish a Chair of Genetics, a subject associated with the name of Darwin and of his relative, Francis Galton, and of the greatest possible importance, whether it be regarded from the purely scientific or from the practical side. He would like to think that the interest aroused by this celebration would have a practical outcome in better provision for the future cultivation in Darwin's own University, and that of his sons, of the field wherein Darwin laboured. (Cheers.)[79]

Ironically enough, shortly after the close of the Darwin festivities Bateson entered into negotiations with trustees of the John Innes bequest concerning his accepting the directorship of the proposed John Innes Horticultural Institute. In October 1910 he announced that he was leaving Cambridge to take up this post. A chair of genetics was eventually established at Cambridge in November 1912, and Bateson's longtime collaborator, Reginald Crundall Punnett, was appointed to it. Hence, the Cambridge professorship in genet-

[77] "University and Educational Intelligence," *Nature*, 5 Mar. 1908, *77*:428–429. The same report was carried in the *Cambridge University Reporter*, 3 Mar. 1908, p. 632; it was reprinted in B. Bateson, ed., *William Bateson, F.R.S., Naturalist* (cit. n. 73), p. 112.

[78] William Bateson, *The Methods and Scope of Genetics* (Cambridge: Cambridge Univ. Press, 1908), p. [i].

[79] "Darwin Centenary: World-Wide Testimony," *Daily Telegraph*, 24 June 1909, p. 13. On Bateson's concerns regarding the new professorship see B. Bateson, ed., *William Bateson, F.R.S., Naturalist* (cit. n. 73), pp. 121–122.

ics, which established the university as a leading center of genetics in Great Britain for the next few decades, can be traced to the 1909 Darwin celebration.[80] Nonetheless, perhaps because both Bateson and Punnett eschewed an evolutionary focus within their Mendelian research programs, genetics at Cambridge remained disconnected from evolution until the appointment of Punnett's successor, Ronald Aylmer Fisher.[81]

In addition to fostering new experimental establishments, another notable outcome of the 1909 Darwin celebration was its role in directing the attention of young biologists to the new developments in Darwinism. Both Julian Huxley and R. A. Fisher, who later played pivotal roles in promoting the new evolutionary synthesis, acknowledged that their interest in evolution was stimulated by the 1909 festivities. In his autobiography Huxley described how his attendance at the celebration influenced his future intellectual orientation and scientific work:

> As a Huxley and a budding biologist, I was invited, and was deeply impressed by the stream of addresses stressing the importance of Darwin's many-sided work.
>
> I thought of my grandfather defending Darwin against Bishop Wilberforce, of the slow acceptance of Darwin's views in face of religious prejudice, and realized more fully than ever that Darwin's theory of evolution by natural selection had emerged as one of the great liberating concepts of science, freeing man from cramping myths and dogma, achieving for life the same sort of illuminating synthesis that Newton had provided for inanimate nature. I resolved that all my scientific studies would be undertaken in a Darwinian spirit and that my major work would be concerned with evolution, in nature and in man. This was not so much a turning point in my career as a crystallization of my ideas, a clear vision and inspiration which I can truly say remained with me all through my life.

Huxley's research interests in the years immediately after 1909 ranged widely and appear only indirectly related to evolution, yet, like so many other biologists, he always kept evolutionary implications in mind when he interpreted his work; this helps explain his dedicated focus on evolutionary studies in the 1930s.[82]

Fisher, as a first-year student at Gonville and Caius College in 1909, was among the crowd viewing the pageantry of the Darwin celebration. Like Huxley, he was inspired by

[80] B. Bateson, ed., *William Bateson, F.R.S., Naturalist*, pp. 121–122 (Bateson's move to the Innes institute); and Jenny Marie, "The Situation in Genetics, II: Dunn's 1927 European Tour," *Mendel Newsletter*, N.S., Mar. 2004, no. 13, pp. 2–8. For details on the founding of the Cambridge chair of genetics see Opitz, "Aristocrats and Professionals" (cit. n. 29).

[81] For Bateson see William Bateson, "Evolutionary Faith and Modern Doubts," *Science*, 1922, *55*:55–61. On Fisher's reform of Cambridge genetics see Joan Fisher Box, *R. A. Fisher: The Life of a Scientist* (New York: Wiley, 1978).

[82] Julian Sorrell Huxley, *Memories* (London: Allen & Unwin, 1970), p. 73; and Frederick B. Churchill, "*The Elements of Experimental Embryology*: A Synthesis for Animal Development," in *Julian Huxley*, ed. Waters and Van Helden (cit. n. 60), pp. 107–126, on pp. 112–113. Huxley's focus on evolution is evident in his review of the revised edition of T. H. Morgan, A. H. Sturtevant, H. J. Muller, and C. B. Bridges, *The Mechanism of Mendelian Heredity* (New York: Holt; London: Constable, 1923), which he concluded by stating: "Although several points still remain obscure, yet, apart from this problem of the precise method of origin of variations, the body of facts gathered in the last twenty years, concerning segregation, linkage, multiple factors, multiple allelomorphs, and modifiers, not only gives the hypothetical germ-plasm a definite body and home, but is almost precisely what was required to provide a tangible working mechanism for the bulk of Darwin's own ideas; and it is a matter of constant surprise why many who profess themselves Darwinian of the Darwinians should not only not avail themselves of the new tool, but also evince positive hostility to it. The new principles are, indeed, the only tool we at present possess which is capable of putting evolutionary theories to experimental test. Yet, with a few honourable exceptions, most taxonomists and 'evolutionists' prefer to stick to speculative methods—speculative because incapable of being tested either by experiment or by calculation—and make no attempt to use the new principles in experimental attack—or, for that matter, even in interpretation." J. S. Huxley, "Mendelism in Evolution," *Nature*, 1924, *113*:518–520, on p. 520.

the accolades showered on Darwin and the intent focus on Darwinism. As Mary Bartley has noted, he soon thereafter became a member of the new circle of "young Darwinians" in Britain:

> Fisher was swept up in the excitement surrounding this celebration and by the addresses given by famous Darwinians such as Joseph Dalton Hooker and Alfred Russel Wallace. As Fisher later wrote of Cambridge during that period: "The new school of genetics using Mendel's laws of inheritance was full of activity and confidence, and the shops were full of books good and bad from which one could see how completely many writers of this movement believed Darwin's position had been discredited." One of these books to be published just after the Darwin centenary was a collection of essays written to celebrate the scientific work of Charles Darwin; Fisher received this book, *Darwin and Modern Science*, as an academic prize at Cambridge. In this volume, both August Weismann and E. B. Poulton addressed the theory of sexual selection.[83]

Weismann's and Poulton's support for the much-maligned mechanism of natural selection attracted Fisher's interest. With his keen mathematical acumen, he turned his attention to the "statistical" approach to evolution followed by the biometricians. He was not alone. As Provine has noted, "Beginning in the late 1910s, the theoretical population geneticists Fisher, Haldane, and Wright argued that evolution in nature could be modeled quantitatively." Through his study of dominance and fitness, published in *The Genetical Theory of Natural Selection* (1930), Fisher became a leading figure in the "unification of biology" or evolutionary synthesis of the 1930s and 1940s.[84]

Other young biologists outside Britain and the United States also responded to the call for a new experimental approach to evolution. Two years after the Darwin celebration, for instance, German biologists gathered in Munich to assess evolution "in modern lights." The lead organizer of this event was Richard Hertwig, professor of zoology and director of the Munich Zoological Institute and a former student of Haeckel's, who had been honored at the Darwin celebration as the recipient of an honorary degree. Hertwig invited his assistant, Richard Goldschmidt, to be among the speakers at the 1911 conference on evolution. Having switched to work in genetics in 1909 after reading Wilhelm Johannsen's *Elemente der exakten Erblichkeitslehre*, Goldschmidt welcomed breeding analysis as a means of circumventing the limitations of morphology. In his talk, entitled "Evolution in Light of Recent Genetics," Goldschmidt cited his recent study of sex determination and the formation of geographical races in the moth *Lymantria*.[85] When compared with other writings on evolution in the previous two decades, this essay evidences an entirely new line of attack.

[83] Mary M. Bartley, "Conflicts in Human Progress: Sexual Selection and the Fisherian 'Runaway,'" *Brit. J. Hist. Sci.*, 1994, *27*:177–197, on p. 180.

[84] R. A. Fisher, "The Correlation between Relatives on the Supposition of Mendelian Inheritance," *Transactions of the Royal Society of Edinburgh*, 1918, *52*:399–433; Provine, "Progress in Evolution and Meaning in Life" (cit. n. 71), pp. 176–177; and Fisher, *The Genetical Theory of Natural Selection* (Oxford: Clarendon, 1930). On Fisher's role in the evolutionary synthesis of the 1930s and 1940s see Smocovitis, *Unifying Biology* (cit. n. 5), pp. 119–120; Provine, *Origins of Theoretical Population Genetics* (cit. n. 5); and Gayon, *Darwinism's Struggle for Survival*.

[85] Richard Goldschmidt, "Die Artbildung im Licht der neueren Erblichkeitslehre," in *Die Abstammungslehre: Zwölf gemeinverständliche Vorträge über die Deszendenztheorie im Licht der neueren Forschung*, ed. O. Abel (Jena: Fischer, 1911), pp. 22–60. On Goldschmidt see Marsha L. Richmond, "Richard Goldschmidt and Sex Determination: The Growth of German Genetics, 1900–1935" (Ph.D. diss., Indiana Univ., 1986); and Richmond, "The Making of a Heretic: Richard Goldschmidt and Physiological Genetics" (in preparation). Gayon includes Goldschmidt among "the pioneers of Mendelism," along with A. D. Darbishire, R. H. Lock, R. C. Punnett, W. Johannsen, L. Cuénot, W. Castle, and T. H. Morgan: Gayon, *Darwinism's Struggle for Survival*, p. 259.

Goldschmidt's view of how genetics could contribute to evolutionary studies provides an interesting contrast to Bateson's skepticism. As he told his audience, no problem connected with heredity—including evolution—remained untouched by Mendelism. Indeed, he believed that the laws pertaining to inheritance in hybrids, along with the phenomenon of mutation, held the key to understanding species change. Again differing with Bateson, Goldschmidt fully accepted a significant role for natural selection and looked to the chromosomes as the material basis of heredity and variation. Moreover, he drew attention to the difference between the experimentally based genetic analysis and the older phylogenetic and speculative approaches of Haeckel and Weismann, stating that while the "sobriety of current evolution studies (with their curves, numerical series, and combinations of symbols)" may not attract as great a following as did the creative fantasy involved in "reconstructing phylogenetic trees from amoebas to humans," it was through such means that an "entirely new spirit" had been introduced into evolution and the problems of variation, heredity, and speciation laid open to exact understanding.[86] He also believed that his *quantitative* view of heredity fit well with a Darwinian view of the formation of geographical races, regarded as the first step toward speciation, and better accounted for adaptation. As he noted in 1920, referring to his view of the gene as enzyme, "the quantitative condition of a factor can be an adaptive character, which places reactions important for life in the proper temporal coordination with respect to other important adaptive characters. In this way these characters are of primary significance for the process of species formation." Although Goldschmidt later rejected the role of selection in the formation of geographical races and species change—a fact noted by many historians—this was clearly not the case early in his career, when he accepted "selection in the modernized Darwinistic sense."[87]

The new experimental approach to evolutionary studies around 1909 did not, of course, result in an immediate breakthrough in resolving the points of dispute among Darwinists. As Fisher noted in recalling the 1909 celebration on the occasion of the 1959 Darwin commemorations, "It was a period of exciting new advances on the genetical front, but it is clear in retrospect that no progress had been made in understanding the bearing of the new knowledge on evolutionary theory, and that the leaders of biological thought had largely lost sight of the cogency of the principle of Natural Selection in supplying the driving force of evolutionary progress and its detailed guidance." The major hurdle that retarded progress for the next twenty years, in his view, was integrating the understanding of mutation with evolution theory, for which he laid the blame squarely on the shoulders of de Vries and Bateson:

> The early Mendelians could scarcely have misapprehended more thoroughly the bearing of Mendel's discovery, and of their own advances, on the process of evolution. They regarded

[86] Goldschmidt, "Die Artbildung im Licht der neueren Erblichkeitslehre," pp. 46, 55, 58, 60. As Olby has noted, "Johannsen challenged biometricians, Darwinians, and the followers of August Weismann with his penetrating redefinition of heredity, spiced with some scorn. The hallmark of Johannsen's contribution was the introduction of new terms with the deliberate aim of banishing what he regarded as the many erroneous associations which old terms carried. Thus the term germplasm had a Weismannian context, and that was a 'purely speculative morphological view of heredity without any suggestive value.' The whole 'transmission conception' of heredity, too, had to be discarded for he warned that no profound insight into the biological problem of heredity would be gained this way. Just as the conception of phlogiston was diametrically opposed to the chemical reality, so was the transmission conception to the biological reality." Robert C. Olby, "Mendel, Mendelism, and Genetics," *MendelWeb*, 1997, http://www.mendelweb.org/MWolby.intro.html.

[87] Richard Goldschmidt, "A Preliminary Report on Some Genetic Experiments Concerning Evolution," *Amer. Natur.*, 1918, *52*:36–40; and Goldschmidt, *Die quantitative Grundlage von Vererbung und Artbildung: Vorträge und Aufsätze über Entwicklungsmechanik der Organismen* (Berlin: Springer, 1920), pp. 102, 153.

> species as passively awaiting the next favourable mutation, instead of recognizing them as abundantly supplied with heritable variation, prepared in advance for changes in all directions and sensitively poised to respond to every kind of selective influence. They confused the discontinuity of particulate transmission with discontinuity in the evolution of new species. They thought of Mendelism as having dealt a death blow to selection theory, whereas in reality it had cleared the field of all its competitors.[88]

Indeed, it was not Mendelism but Mendelian genetics that led the way, although Ernst Mayr has argued that experimental work in genetics and cytogenetics actually hampered evolutionary studies until this complex confusion began to be untangled in the 1930s.[89] Nonetheless, the discussion about how to mesh the new findings in Mendelism, mutation studies, and the cytology of germ cells with evolutionary studies revivified the new Darwinism of the twentieth century.

CONCLUSION

The 1909 Darwin celebration in Cambridge can be seen as a watershed event in the history of early twentieth-century biology. In terms of the sheer "pomp and ceremony" of the occasion, the observance was among the most spectacular commemorative events in the annals of science. This scientific ritual was not, of course, intended solely for the consumption of biologists but was also aimed at informing the general public about Darwin and the contemporary understanding of evolutionary theory. While Darwin's public persona and celebrity status were already well constructed by the time of his death, civic interest in Darwin had been heightened by the publication of the three-volume *Life and Letters of Charles Darwin* (1887), edited by Francis Darwin, and the additional two-volume *More Letters of Charles Darwin* (1903), coedited by Francis Darwin and A. C. Seward. Coinciding with the Cambridge festivities came the publication of *The Foundations of "The Origin of Species,"* Darwin's earliest drafts (1842 and 1844) of his evolutionary views.[90] Complementing this new source of printed data about Darwin and his work was the impressive material display of Darwiniana assembled for the Cambridge festivities, later transferred to South Kensington and exhibited for over eight months at the British Museum of Natural History. The exhibit was indeed so popular that a second printing of the accompanying guide was required.[91] As such, the 1909 Darwin celebration

[88] R. A. Fisher, "Natural Selection from the Genetical Standpoint," *Australian Journal of Science*, 1959, *22*:16–17, on p. 16. As Orr notes, "a surprisingly large number of biologists held that, while Mendelism might explain the trivial and uninteresting differences seen within species, Morganist genes could never explain species differences": Orr, "Dobzhansky, Bateson, and the Genetics of Speciation" (cit. n. 51), p. 1332.

[89] Gayon, *Darwinism's Struggle for Survival*, Ch. 8; and Ernst Mayr, "Where Are We? Genetics and Twentieth Century Darwinism," in *Cold Spring Harbor Symposia on Quantitative Biology*, Vol. 24 (Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory, 1959), pp. 1–14. See also Michel Veuille, "Genetics and the Evolutionary Process," *Compt. Rend. Acad. Sci.*, 2000, *323*:1155–1165.

[90] Browne, "Presidential Address: Commemorating Darwin" (cit. n. 2); Francis Darwin, ed., *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter* (New York: Appleton, 1903); F. Darwin and A. C. Seward, eds., *More Letters of Charles Darwin: A Record of His Work in a Series of Hitherto Unpublished Letters* (New York: Appleton, 1903); and F. Darwin, ed., *The Foundations of "The Origin of Species," Two Sketches Written in 1842 and 1844* (Cambridge: Cambridge Univ. Press, 1909) (delegates were given an earlier, unpublished edition, *The Foundations of "The Origin of Species," A Sketch Written in 1842*). The 1842 manuscript was discovered in a staircase cupboard at Down House after the death of Emma Darwin in 1896: R. B. Freeman, *Charles Darwin: A Companion* (Folkestone, Kent/Hamden, Conn.: Dawson/Archon, 1978), pp. 258–259.

[91] "A Darwin Exhibition," *Times*, 17 Aug. 1909, p. 9. The exhibit opened in July 1909; a second edition of the guidebook was called for in February 1910. See Sydney F. Harmer's preface and Sydney Smith's introduction to *Facsimile of "Memorials of Charles Darwin"* (cit. n. 27).

represents one of the earliest and most extensive "public relations" projects launched by working scientists, aimed at highlighting scientific genius, the process of scientific discovery, contemporary theoretical advances, and the social impact of scientific theories for mass public consumption.[92] As one reporter noted, the Cambridge celebration "is not a matter for the learned only, but for all of us. To no other man has it been given to effect a revolution in human thought so large, so pervading, so sudden, and yet so enduring. Darwin taught mankind to see all things in a new light, not only the operations of nature, great and small, the mysteries of existence and the innumerable objects of research, but the common things of every-day life."[93] Certainly the image of Darwin as scientific and cultural hero was significantly enhanced in multiple ways by the 1909 festivities.

But the primary significance of this event was not its cultural influence but its impact on biology. In bringing together some of the world's most prominent biologists to commemorate the life and work of Charles Darwin, the event focused attention on the theoretical basis of evolution and recent developments in biology that shed new light on the nature of heredity and variation. At a time when Darwinism was being actively debated, biologists seized the opportunity to express their carefully considered views regarding the mechanism of evolutionary change, integrating recent discoveries into the "hard core" theoretical components of Darwin's conception and later neo-Darwinian assumptions. The views expressed in 1909, representing "the latest authoritative word in evolutionary matters," thus provide the historian with a valuable vantage point from which to gauge the status of Darwinism at a critical juncture, just prior to the introduction of the new Mendelian chromosome theory of heredity.[94]

Fifty years of progress in biological studies since the publication of *Origin of Species* had seen a wealth of new findings coming from embryology, systematics, cytology, and breeding studies—including Mendelian inheritance, de Vriesian mutation theory, and cytological advances that identified the chromosomes with the mechanics of meiosis. The time was indeed ripe in 1909 for biologists to take stock of the respective roles that natural selection, variation, heredity, and the environment played in effecting evolutionary change. This is not to claim, of course, that the impetus leading to an experimental study of evolution immediately bore fruit. It took many years before the early promise of Mendelism, mutation, and cytology would fully impact evolutionary theory. It is nonetheless important to acknowledge the different climate for evolutionary studies after 1909 in comparison to earlier decades. Doing so allows us to recognize definite features of a new intellectual reconstruction and realignment that privileged experimental and quantitative approaches to evolution rather than the essentially qualitative, case-study orientation of previous years. Moreover, making use of this vantage point allows us to identify the vanguard of the new movement. It was not led by the older generation of evolutionists, nor even by the contemporary critics of neo-Darwinism. Rather, the new approach was adopted by young biologists, who in their mature years would eventually assume the mantle of leaders in the new evolutionary debates of the 1930s and 1940s.

[92] Other centennial celebrations honoring British scientists and engineers after 1909 were more in the vein of "civic celebrations" than "academic scientific centenaries." See MacLeod and Tann, "From Engineer to Scientist" (cit. n. 1); and Anthony S. Travis, "Decadence, Decline, and Celebration: Raphael Meldola and the Mauve Jubilee of 1906," *History and Technology*, 2006, *22*:131–152. Cambridge was also the site for the G. G. Stokes Jubilee (1899) and the Clark Maxwell Centenary (1931). As Abir-Am noted, most recent events can be viewed as "disciplinary" commemorations: Abir-Am, "Introduction," in *Commemorative Practices in Science* (cit. n. 7), p. 27.

[93] "The Darwin Centenary at Cambridge," *Times*, 22 June 1909, p. 9.

[94] Kellogg, "Celebrating Darwin's Greatness and Darwinism's Weakness" (cit. n. 37), p. 384.

As Fisher noted in 1959, "A centenary celebration is an occasion for retrospect, yet I submit, though the view is an old-fashioned one, that the purpose of retrospect is to prepare ourselves for the future, by avoiding the unnecessary repetition of the errors of the past." In his view, the earlier celebration of 1909 had also been beneficial in directing a new generation to read Darwin's *Origin of Species*. Fisher indeed argued that the lack of direct knowledge of Darwin's own theory was one reason why "in the generation following Darwin's death his theory of Natural Selection was almost totally misunderstood by teachers and writers."[95] For the historian of biology, the open debate promoted by the 1909 Darwin commemoration, in which biologists sorted through both the pros and the cons of elements of Darwinian theory, helps to explain the relatively rapid acceptance of the "new genetics" after 1910 and the "new evolution" after 1930.[96] Hence, in focusing the attention of biologists and laymen alike on the elements of Darwin's theory of evolution, and thereby offering essential clarification of the various positions and evidence along with interpretations of how new findings fit into the whole, the 1909 Darwin celebration served a critical function. It stimulated the future development of biological science, attracting young men (and women) to a renewed study of evolution using newly available mathematical and empirical techniques. It also fostered an intellectual climate in which future developments in genetics, along with those in neighboring fields, could more easily be integrated into a new evolutionary consensus.

[95] Fisher, "Natural Selection from the Genetical Standpoint" (cit. n. 88), p. 17.

[96] As Bowler noted, "Thus it was that Darwinism eventually emerged from its eclipse once it could be shown that a more sophisticated interpretation of the new genetics would provide a firmer foundation for selection": Bowler, *Eclipse of Darwinism* (cit. n. 9), p. 14.