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Author(s): Conway Zirkle
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Gregor Mendel & His Precursors

BY CONWAY ZIRKLE *

IF Gregor Mendel's famous *Versuche über Pflanzenhybriden* had been published originally during the first or second decade of the twentieth century, it would doubtless have been considered an excellent, if somewhat routine, contribution to genetics. Most departments of botany would have judged it to be an acceptable dissertation for the doctorate in philosophy but its author, aged 43, would have seemed to be starting rather late on his scientific career. The fact that the spirit of the paper, the author's mode of reasoning and presentation of data, fit so well into our present scientific standards is of course to be expected because our present outlook in genetics is conditioned in great part by the discovery in 1900 of this very paper.

In 1865, however, the situation was very different. Mendel's ideas were definitely foreign to the dominant biological thought of the period. Of course, we have no way of knowing how many biologists read his paper when it first appeared and we have rather charitably excused our predecessors for missing its signficance by assuming that only a few of them ever saw it. True, it was published in a relatively obscure periodical but its title and place of publication were recorded in the *Royal Society Catalogue of Scientific Papers*, along with Mendel's other published works. Some biologists certainly read it. It was cited and parts of it were even quoted by Hoffman (1869). Focke (1881) mentioned Mendel fifteen times, but showed by a rather supercilious remark that he did not grasp the importance of Mendel's work. From p. 110:

"Mendel's numerous crossings gave results which were quite similar to those of Knight, but Mendel believed that he found constant number-relationships between the types of the crosses." (Quoted from Roberts, 1929.)

It is evident that Nägeli also did not grasp the import of the contribution, even with Mendel's personal assistance. This is now a matter of record, for the letters written by Mendel to Nägeli from 1866–1873 have been published. How foreign Mendel's outlook was to the biological *Zeitgeist* of the mid-nineteenth century can be emphasized by calling attention to the fact that his great contribution appeared three years *before* Darwin published his provisional hypothesis of pangenesis.

Mendel's paper is truly remarkable. We are struck at once with its notable economy of effort. There seems to have been no waste motion either in designing the experiments, in collecting the data, or in interpreting the results. Mendel chose the proper genus (Pisum) for his investigation, conducted his researches cleanly, and seemed to have known just what he should expect to discover. His work is beautifully unified and complete, more so, in fact, than that of the three biologists who discovered him, de Vries, Correns, and von Tschermak.

We can explain very easily how it happened that Mendel's work was ignored by his contemporaries. The real problem is to explain how it ever came into being. Mendel was an amateur working in a field which had been investigated extensively for over a hundred years. Previously he had not distinguished himself as a biologist. On the contrary, he had failed in his examinations when he attempted to qualify himself to teach natural science in the Znaim High School. Whatever talents he had certainly seemed to be other than scientific. He was an earnest and devout priest, a good administrator who made an excellent impression on all who knew

* University of Pennsylvania.

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him, but no one recognized him as one of the greatest of the nineteenth century investigators.

The problem before us is, did Mendel have any guide posts in making his discoveries, any hints from the existing biological literature? Or was the design of his work just a lucky shot in the dark, a clever hunch which happened to be both true and of tremendous scientific importance? Of course, nothing in pre-Mendelian genetics can detract from Mendel's own accomplishments, for it is easy to show that he saw very clearly where his predecessors did not see at all, even when they had some of the crucial data. Probably no final answer to the question can ever be given. We can place the question in its proper setting, however, and show how much of Mendelism was known before Mendel published, and we can list the earlier pertinent contributions which were probably known to him. We may even find good evidence that Mendel was familiar with the greater part of this earlier work.

In order to show the relevance of this work to Mendel's, we should break down his contributions into their basic elements or factors, for it was these factors which had been described separately by his predecessors. Until Mendel published, however, we have no evidence that they had ever come together in the mind of any one individual. If Mendel were aware of these discoveries and of their logical connections he would certainly have known what results he had a right to expect and thus he could have designed his experiments accordingly.

To begin our analysis of Mendel's observations: first, he found that if two varieties of peas which differ in regard to a single characteristic are crossed, the hybrid will resemble one parent to the exclusion of the other. The character which shows in the hybrid is *dominant*, the one which does not show is *recessive*. This is the principle of dominance. Second, Mendel observed that, when the hybrid was inbred, both dominant and recessive characters appeared in its progeny. This is the principle of segregation. Third, he observed that, when the two types reappeared they did so in numbers which bore a definite ratio to each other, approximately three dominants to one recessive. This is the famous Mendelian ratio. Fourth, when he inbred this second bybrid generation he found that the recessive bred true and produced only recessives, that one third of the dominants also bred true and produced only dominants, but that two thirds of the dominants produced both types of progeny, again in the ratio of three to one. Fifth, he found that, when the parents differed in regard to two or more factors, the same 3–1 ratio held for each factor but that each factor was transmitted independently. This is the principle of independent assortment. The corollary to all of the above discoveries is that heredity is controlled by a number of particles which are transmitted independently of each other and which can pass unaltered from one generation to the next. They can also enter into or leave various combinations without changing their nature.

It is difficult to assign credit to the first botanist who discovered dominance. It was recorded casually by a number of eighteenth century amateurs who had little conception of its significance. For example, Cotton Mather (1716) and Paul Dudley (1724) noted that yellow corn (*Zea mays*), pollinated by red, produced red grains, but in this case the matter was complicated by xenia, a factor which need not concern us here. In 1799, however, Thomas Andrew Knight recorded the fact of dominance in Mendel's own genus, *Pisum*. He fertilized white peas with the pollen of a gray seeded variety and found that the hybrid plants bore gray seeds. He even back crossed the hybrids to the recessive parent and recorded a variety of new kinds in the progeny, and he specifically stated that the white type (recessive) reappeared.

A few years later, on 20 August 1822, a paper by Alexander Seton was read to the Horticultural Society of London. Here Seton described his experiments of pollinating a green pea with the pollen from a white seeded variety. All of the peas produced were green (an instance of dominance) but, when these peas were planted,

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almost all of the pods they bore had seeds of both types (segregation in the second hybrid generation), "mixed indiscriminately and in undefined numbers; they were all completely either of one colour or the other, none of them having an intermediate tint." On 15 October of the same year, John Goss presented a paper to the same society. He described how he had crossed a blue seeded pea with pollen from a yellow-white variety. The hybrid seeds were like the male parent (dominance) but when the second hybrid generation appeared it had "produced some pods with all blue, some with all white and many with both blue and white seeds in the same pod" (Mendelian segregation). Goss carried his experiments through a third generation and reported that the blue peas (recessive) produced only blue peas but that the white peas (dominant) "yielded some pods all white, and some with both blue and white seeds intermixed." Apparently he had the two types of dominants, those that bred true and those which threw recessive segregants. These two types were described by Mendel forty three years later.

On 3 June 1823, a paper by Knight, which was in part a commentary on the work of Seton and Goss, was read to the Society. In this paper Knight described dominance in peas (gray seed coats over white) and, on back crossing the hybrid to the recessive type, he found that both dominants and recessives reappeared in the progeny, but he did not make any counts. It is important to record that these three papers, by Seton, Goss, and Knight, were all published in the same book, in volume five of the *Transactions of the Horticultural Society of London* (1824).

In 1826 Augustin Sageret published the results he obtained by hybridizing the muskmelon with the cantaloupe. He listed five contrasting characters of the two parents. The hybrid did now show a blending or intermediate form of these characters but took some from one parent, some from the other. ". . . the resemblance of the hybrid to its two ascendants consisted not in an intimate fusion of the diverse characters peculiar to each one but rather in a distribution, equal or unequal, of the same characters." Sageret thus described very clearly the independent assortment of what we now call Mendelian factors.

In 1849 appeared a book, *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* by C. F. v. Gärtner. This work is the one real connecting link between Mendel and the discoveries which have been cited. Gärtner's book contained a copious summary and discussion of the knowledge of hybridization which existed up to its date of publication. Gärtner himself had noted both the uniformity of the first hybrid generation and the extreme diversity of forms in the second and succeeding generations. He stated that both parental types and entirely new ones reappeared in these later generations and that the variability, which was so striking, was found in all of the characteristics of the progeny. A few years later Naudin (1863) contrasted the uniformity of the first hybrid generation with "the extreme medley of forms" in the second, "some approaching the specific type of the father, others that of the mother." In 1865, the year in which Mendel presented his paper, Verlot noted the fact that in a hybrid progeny certain individuals bred true but others produced numerous atavisms. (Roberts, 1929.)

The question now presents itself: how much of the work which we have described was familiar to Mendel? In attempting to answer we are faced with the basic difficulty of not being able to draw negative conclusions from negative evidence. Mendel himself described none of the earlier research and was very casual in mentioning the investigators who preceded him. He merely wrote, "To this object numerous careful observers, such as Kölreuter, Gärtner, Herbert, Lecoq, Wichura and others, have devoted a part of their lives with inexhaustible perserverance. Gärtner especially in his work *Die Bastarderzeugungen im Pflanzenreich* has recorded very valuable observations; and quite recently Wichura published the results of some profound investigations into the hybrids of the willow."

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This statement is brief but it gives us some valuable clues. Mendel's crucial citation of course is that of Gärtner, who, in addition to describing his own results, discussed the work of nearly two hundred of his predecessors. We can be certain that Mendel knew both of Gärtner's work on *Pisum* and of the many instances he recorded of a second hybrid generation showing characters which were hidden in the first. Then too, Gärtner referred to Sageret thirty times and quoted his basic discoveries, particularly (p. 282) where Sageret had stated that the individual characteristics of the parents did not blend in the hybrid but maintained their proper forms. Mendel could have read here of the independent assortment of unit characters.

Gärtner also cited the work of Knight on peas, particularly Knight's statement on the reappearance of parental characters in the second hybrid generation (pp. 54, 80). Gärtner did not list Seton and Goss in his author index but he did refer to their work (p. 85). After describing the outcome of his various pollinations on *Pisum sativum viride* he wrote, "These results agree essentially, however, with those published by Goss and Seton." Also he cited Knight's paper which was in part a commentary on Seton's and Goss' observations and which was printed in the same volume of the *Transactions of the Horticultural Society* which contained the work he was discussing.

We do not know whether Mendel, during the eight years in which he was pursuing his own researches on *Pisum*, ever consulted the original papers of Knight on the genetics of this genus, even though he must have known of their existence through the citations by Gärtner. Today, of course, an examination of the original contributions would be a routine procedure. If Mendel had consulted Knight's papers he could hardly have missed seeing the works of Seton and Goss. Knight referred to them by page number, and Seton's paper was illustrated by a large color plate showing different types of peas in a half opened pod.

We may conclude that Mendel knew of the results obtained by Knight, Sageret and Gärtner and had the work of Seton and Goss called to his attention. But even if he had read all of the original contributions he still would have found no traces of definite numerical ratios in the different types because the earlier plant hybridizers seemed to have paid no attention whatever to the relative numbers of the segregating forms.

There has been, of course, a certain amount of speculation, some of it recent, as to where Mendel got his appreciation of the importance of definite ratios as a clue to the basic mechanism of heredity. For example Woodger (1948) wrote, "Mendel can have had but scanty data to reflect upon. But his hypothesis could have been reached by reflecting upon the 50:50 sex ratio in conjunction with certain very general principles. It may be that Mendel did reach his hypothesis in some such way as this and devised his experiments as a means of testing it."

Also the sex-linked heredity of color blindness and of haemophilia was well known when Mendel wrote, but the Mendelian basis of this type of heredity is not at all obvious and it was not established until some time after Mendel's own work was rediscovered. Actually, a precise hybrid segregation ratio had been published eleven years before Mendel's paper. Its publication was extraordinarily obscure but, *mirabile dictu*, the probabilities are that Mendel knew of it. Mendel seemingly was led to it through the fact that he raised and bred honey bees. This brings us to Johann Dzierzon.

Dzierzon, like Mendel, was not appreciated by his contemporary scientists. He published copiously but the *Royal Society Catalogue of Scientific Papers* succeeded in missing all of his works. Today, however, his reputation is secure and his very original contributions are cited frequently. *Der Grosse Brockhaus* (1930) lists him as follows:

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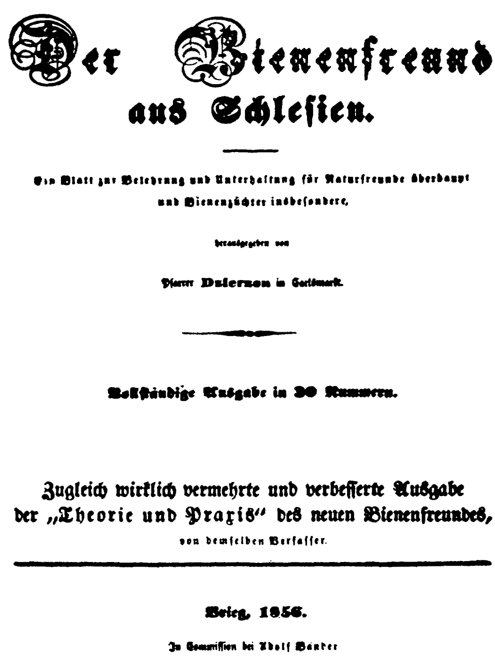
Dzierzon, Johann; theologian and bee-breeder, born in Lowkowitz, Upper-Silesia, 16 Jan. 1811; died there, 26 Oct. 1906. As a bee-breeder, he proved the worth of the hive with movable frames; he discovered further the parthenogenesis of the honey bee in which the females (queens and workers) are produced from fertilized eggs but the males (drones) develop from unfertilized virgin eggs. He wrote: 'Theorie und Praxis des neuen Bienenfreundes' (2. Aufl. 1857), 'Rationelle Bienenzucht' (2 Aufl. 1878).

Dzierzon's discovery that drones were hatched from unfertilized eggs was so novel at the time that it gave rise to a violent controversy.[1] In one of his experiments, to check his hypothesis, he crossed German with Italian bees and found that the unmated hybrid queens produced German and Italian drones in equal numbers, a definite one to one ratio. This observation is recorded in *Der Bienenfreund aus Schlesien*, a relatively rare periodical of which only three copies are noted by the *Union List of Serials* as being in the libraries[2] in the United States.

Der Bienenfreund aus Schlesien was an eight page, monthly periodical, which was issued in thirty installments between January 1854 and July 1856. The first hybrid ratio ever to be published, as far as we know, was in No. 8, *Die Drohnen*, dated August 1854. The following quotation is from pages 63–64. To the best of the writer's knowledge it has not previously been translated into English.


Der Bienenfreund aus Schlesien.

Ein Blatt zur Belehrung und Unterhaltung für Naturfreunde überhaupt und Bienenzüchter insbesondere,

herausgegeben von

Pfarrer Dzierzon in Carlsmarkt.

Vollständige Ausgabe in 30 Nummern.

Zugleich wirklich vermehrte und verbesserte Ausgabe der „Theorie und Praxis" des neuen Bienenfreundes,

von demselben Verfasser.

Brieg, 1856.

In Commission bei Adolf Bänder

Continued observations of hybrid stocks may help us ultimately to lift the veil more and more, to penetrate the darkness and, finally, to bring the mysterious truths to the light of day. If the eggs which produce drones do not need to be fertilized, Italian mothers must always produce Italian drones and German mothers German drones even when they have been impregnated by drones of the other race. The Silesian Beekeeper [Pfarrer Dzierzon] has hybrid stocks of both types and has observed them continually in so far as the limited time permitted, but he encountered new insoluble riddles. All of the Italian mothers of hybrids have fully substantiated the conjecture, and have produced the finest Italian drones, one stock perhaps even finer than the true breed, finer than the mother's stock itself. From two German mothers of hybrid stocks, the first showed likewise only the usual black drones, the second did the same except that, unexpectedly, a few scattered drones were found which glittered with gold and had even more yellow than any single one from the pure Italian stock. Of course it may be possible that, here too among the workers, one part of whom have the color of domestic bees, another part the color of the Italian, a beautiful Italian laid eggs which produced the few yellow drones. The Silesian Beekeeper, however, is not particularly inclined to explain the phenomenon in this manner, he does not wish to subject himself to the suspicion that it is his preference for his hypothesis which makes him resort to this explanation, since, in fact, the laying of eggs by worker bees is a very rare exception if a queen be present. Would it be possible that, even if the vesicle carrying the semen did not vivify the eggs which produce the drones, a certain aura [seminalis?] from it would affect their type and color? Certainly only experts can give an opinion on this matter. The living germ of the

[1] The controversy occured in spite of the fact that, over a half century earlier, the production of drones from unfertilized eggs had been discovered by François Huber and correctly described by him in his *Nouvelles observations sur les abeilles*, Genève, 1792. This book is a collection of letters, the discovery being recorded in letter number three, dated 21 Aug., 1791.

[2] These libraries are: Univ. of California, College of Agriculture, Davis, California; St John's Univ., Collegeville, Minn.; Univ. of Wisconsin, Madison, Wis.

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worker bees is awakened exclusively by the contents of the fertilization vesicle, which comes from the drone, and yet half of the bees appear exactly like the mother. But here the relationship is entirely different since the entire matter of the egg comes from the substance of the mother.

If one thinks of hybridization in accordance with Dr. Dönhoff's excellent analogy of a tissue in which, at one time the warp, at another the woof, becomes dominant, then the worker bees must in part resemble the mother and in part the drones because both male and female participated in their creation. It must be different with the drones, however, if the eggs which produce them do not need fertilization. But great precaution is necessary here to guard us from erroneous conclusions. One must be absolutely certain that the queen belongs by birth to the pure race. If she herself originates from a hybrid brood, it is impossible for her to produce pure drones, but she produces half Italian and half German drones, but strangely enough, not according to the type [not a half and half intermediate type] but according to number, as if it were difficult for nature to fuse both species into a middle race.

The genetic implication of this passage is obvious. Two types of drones being derived from unfertilized eggs means that two types of eggs were laid. If hybrid females produced two kinds of eggs in equal numbers, then the production by hybrid males of two types of sperms also in equal numbers is indicated by the internal logic of the situation. (This of course does not apply to bees for reasons which we need not mention here. A drone can produce only *one* kind of sperm.) Random fusion of such eggs and sperms could produce only a 1:2:1 ratio. In the presence of dominance, so well recorded by Knight, Sageret, Gärtner *et al.*, this would appear as a 3:1 ratio.

What evidence do we have that Dzierzon's work was known to Mendel? Dzierzon was a fellow cleric who lived in nearby Silesia. His numerous papers, although unknown to the Royal Society, were well known to practical bee breeders. We can do no better than to quote from the authoritative *Life of Mendel* by Hugo Iltis (1932). From p. 212:

Mendel's main interest in his bees, however, was not to get their honey, but to study the effects of crossing extraneous races of bees with the native ones. To each hive was attached a slate, on which was noted when the queen had been installed, out of which crossing she had sprung, when the bees had swarmed, with the dates of the nuptial flight and of the slaughter of the drones. Careful notes were also kept regarding the colours, the charactertistics of the flight, the inclination to sting, the industry of the bees, etc. It seems probable that in these experiments on bees, Mendel was guided by the hope of obtaining data which would confirm his theory of heredity. Mendel, one may presume, was acquainted with a hypothesis which at this time was being hotly debated among beekeepers, one propounded in 1854 by the Silesian parish priest Dzierzon.

Dzierzon's view that unfertilized queens, or queens whose supply of male sperm has been exhausted, continue to produce drones (these latter arising parthenogenetically out of unfertilized ova), has been fully confirmed by modern research.

Iltis next cites the post-Mendelian cytological research which confirms the parthenogenetic production of drones and then describes the genetic investigations of Newell.

Newell (1915) had gone to some pains to bring the genetics of honey bees into the Mendelian picture. He stated, among his conclusions, the following:

"Pure Italian queens mated to Carniolan drones produce only Italian drones; and Carniolan queens mated to Italian drones produce only Carniolan drones. This is strictly in accordance with the theory of Dzierzon. However, the daughters of Italian queens which have been mated to Carniolan drones produce both Italian and Carniolan drones, produce them in equal numbers and do not produce any other kind. The F_1 queens of the reciprocal cross likewise produce drones of these two kinds and in equal numbers."

The latter part of this quotation and indeed the whole paper show that Newell was unaware that his discovery of the definite ratio (1:1) in the drones produced from hybrid queens had been recorded sixty-one years earlier by Dzierzon himself. To quote from Iltis again (p. 216):

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In Mendel's days, however, these facts [the 1:1 ratio of drones from hybrid queens] were unknown, and Dzierzon's theory was still unproved. Nevertheless, in view of Mendel's peculiar faculty for analyzing such problems, it is likely enough that, setting out from Dzierzon's theory, he may have anticipated the segregation of the rudiments in the formation of the ova of the hybridized females, and consequently the origination of distinct forms of drones; and he may have undertaken his experiments upon the crossing of bees in the hope of finding a proof of the accuracy of his theory. To effect these crossings Mendel had thought out methods of his own and had had special apparatus of one kind and another made; and it has been a great loss to science that his records of his experiments have disappeared.

We can agree that the disappearance of these records is a great loss to science and that the opinion of Iltis, who has made a definitive study of Mendel, is correct in regard to Mendel's faculty of analysis. In view of the fact, however, that Dzierson's hybrid ratio preceded Mendel's, another motive for Mendel's study of the genetics of the honey bee suggests itself. If his own work had been stimulated originally by Dzierzon's, and after his great contribution to genetics had fallen with such a thud among the plant breeders, he might well have undertaken to repeat Dzierzon's hybrid experiments on bees and have tried to extend them further, hoping to find, among *Den Bienenfreunden*, more intelligent and understanding colleagues.

Modern biologists have, in general, been unaware of Dzierzon's hybrid 1:1 ratio. To the best of the writer's knowledge, the only one who has called attention to it is Professor P. W. Whiting (1935) who has cited it in two of his papers, in one of which he quoted the crucial sentence.

To conclude, we may be certain that Mendel was acquainted with the work of Knight, of Sageret and of Gärtner and probably also knew of Dzierzon's hybrid ratio. In addition he had clues which led to the work of Seton and of Goss. All of these contributions should have aided him in designing his experiments and have alerted him in what to look for. Of course his knowledge of this previous work would not detract from his own great accomplishments in the least. All of the earlier work together does not constitute Mendelism. Mendel's own experiments are so much more extensive and precise than those which went before that we are still justified in crediting him as the founder of a science.

We are also justified in emphasizing a remarkable coincidence. Before Mendel, the component parts of Mendelism had been discovered separately, some by the plant hybridizers and some by the bee breeders. Very few biologists were cognizant of the data which had been acquired in both of these fields. Mendelism was the creation of an investigator who both hybridized plants and bred bees.

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Some Letters from Charles Darwin to Jeffries Wyman

EDITED BY A. HUNTER DUPREE *

THE year 1860 was a momentous one for Charles Darwin. Following the day of publication of the *Origin of Species* [1] during the previous November, reviews, commentary, praise, and abuse cascaded upon him. The height of the printed attack came in the *Edinburgh Review* of April, 1860, written anonymously but known to everyone as the work of Richard Owen, whose high scientific reputation lent weight to his opposition.[2] At the meeting of the British Association at Oxford in June, T. H. Huxley — as Darwin's defender — clashed first with Owen and then with Bishop Samuel Wilberforce so sensationally that similes of battle and carnage seem inevitable in referring to the argument.[3] In the midst of these stirring events a small but able group of scientists who accepted Darwin's ideas, at least in part — Huxley, Sir Charles Lyell, Joseph D. Hooker, and in America Asa Gray — winnowed through the mountain of objections and exceptions looking for material which would either modify or bolster the *Origin*. But Darwin, not satisfied with passively accepting comments, sought out men who might be able and willing to give constructive criticism.

Jeffries Wyman (1814–1874), the Hersey Professor of Anatomy at Harvard University, was too reticent to enter into the grand war of ideas over natural selection, but his full and precise scientific knowledge could provide grist for Darwin's mill.[4] Member of a prominent New England medical family and trained in Paris as well as at Harvard, Wyman was one of the founders of the study of comparative anatomy, ethnology, and archaeology at Harvard, a fact somewhat obscured by the dramatic

* Texas Technological College.

[1] Charles Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (London, 1859).

[2] Leonard Huxley, *Life and Letters of Sir Joseph Dalton Hooker, O. M., G. C. S. I., Based on Materials Collected and Arranged by Lady Hooker* (London, 1918), I, 514–515.

[3] Francis Darwin, ed., *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter* (London, 1887), II, 320–323.

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