Darwin and Domestication: Studies on Inheritance

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Darwin's finches are not mentioned at all in the *Origin of Species* (1859); the ornithological star of that great book is the domesticated pigeon.

Stephen Jay Gould[1]

INTRODUCTION

On the Origin of Species begins with a chapter on domesticated plants and animals. In this chapter, Charles Darwin sets forth the central analogy of the book: just as breeders select their finest specimens to improve the stock, so natural selection favors the strongest and healthiest as parents for the next generation. Though Darwin emphasized this analogy throughout the *Origin*, he did not restrict his use of domesticates solely to explain selection; he also used these plants and animals to address the other half of his theory: the question of inheritance.

From 1855 to 1858, and continuing to a lesser degree into the 1860s, Darwin conducted breeding experiments on domesticated animals. Although domesticates, such as breeds of pigeons, cabbages, and sheep, are mentioned in Darwin's Transmutation Notebooks (1837—1839),[2] he did not begin a serious study of domestication until nearly twenty years later. Having written the notebooks and two sketches of his natural selection theory, and spent eight years on the systematics of barnacles, he turned to questions that had been plaguing him since he read his grandfather Erasmus Darwin's *Zoonomia*:[3] How are individuals and

1. Stephen Jay Gould, "Darwin at Sea — and the Virtues of Port," in *The Flamingo's Smile* (New York: Norton, 1985), pp. 347—359.

2. Paul H. Barrett, Peter J. Gautrey, Sandra Herbert, David Kohn, and Sydney Smith, eds., *Charles Darwin's Notebooks: 1836—1844* (Ithaca, N.Y.: Cornell University Press, 1987).

3. Darwin read *Zoonomia; or, The laws of organic life* (1794—96) before he

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species generated? Natural selection provided a mechanism for structural modification and eventual speciation, but it said little about the generation of individuals. Without some way to explain the inheritance of characters acted on by natural selection, his theory would be incomplete. The work on domesticates that Darwin conducted in the 1850s and 1860s was an attempt to complete the picture.

Several authors have emphasized the role that domesticated animals played in Darwin's initial formulation of the theory of natural selection,[4] but few have mentioned the influence of his experimental work with domesticates during the period when he was actively collecting information from journals, writing hundreds of letters to all parts of the world, and looking for any kind of factual support for his theory. James Secord has provided an excellent social treatment of the Victorian breeders' community in which Darwin was deeply involved; but Darwin's actual experiments are not mentioned.[5] Just prior to the publication of the *Origin*, Darwin was refining his theory; he was actively pursuing questions on the nature of variability and the mechanism of inheritance.

SOURCES

Darwin's work on domestication can be pieced together from various sources. The Transmutation Notebooks are a rich source for his early ideas on inheritance, generation, and variability, and domesticated animals are frequently mentioned. The "Sketch of 1842" and the "Essay of 1844" provide a starting point for the relationship between domestication and natural selection theory.[6] Unfortunately, *Natural Selection*, written during the period when

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began his first transmutation notebook in 1837. The B notebook begins with an extensive commentary on *Zoonomia*.

4. See L. T. Evans, "Darwin's Use of the Analogy between Artificial and Natural Selection," *J. Hist. Biol., 17* (1984), 113—140; R. M. Young, "Darwin's Metaphor: Does Nature Select?" *Monist, 55* (1971), 442—503; David Kohn, "Theories to Work by: Rejected Theories, Reproduction, and Darwin's Path to Natural Selection," in *Studies in the History of Biology*, ed. W. Coleman and C. Limoges (Baltimore: Johns Hopkins University Press, 1980), pp. 67—170; Michael Ruse, "Charles Darwin and Artificial Selection," *J. Hist. Ideas, 36* (1975), 339—350.

5. James A. Secord, "Nature's Fancy: Charles Darwin and the Breeding of Pigeons, "*Isis, 72* (1981), 163—186; idem, "Darwin and the Breeders," in *The Darwinian Heritage*, ed. D. Kohn (Princeton: Princeton University Press, 1985), pp. 519—542.

6. See Gavin de Beer, *Evolution by Natural Selection* (Cambridge: Cam-

Darwin was conducting his experiments on domesticated pigeons, does not have the chapter on domestication intact; this chapter was probably removed when Darwin wrote *The Variation of Animals and Plants under Domestication* (1868) and was subsequently destroyed.[7] The published sources, *Origin* and *Variation*, each cite experiments conducted by Darwin in the 1850s. His correspondence from 1855 to 1857 provide insights into the larger questions he was attempting to answer and gives other areas he was actively pursuing during this period. Marginal comments made in books and journals also provide clues, although it is difficult to know whether these represent fleeting thoughts or major areas of concern. Notes on his experiment on pigeon development and the results of a few of his crossing experiments exist in his embryology folder.[8] From these sources, all limited to a greater or lesser extent, I have tried to piece together Darwin's domestication work. To base my argument solely on his use of domesticates in the *Origin* would provide little more than the well-known artificial selection analogy. By looking at several sources, including the material that Darwin used in *Variation*, a more complete picture of the questions he was attempting to answer can be seen. Since Darwin did not begin to raise domesticated pigeons until 1855, the primary focus of this paper will be from 1855 to 1858, with a secondary focus on the experiments conducted for him by breeders in the 1860s.

QUESTIONS IN THE NOTEBOOKS

From 1837 to 1839 Darwin, having just returned from the *Beagle* voyage, filled several notebooks on the transmutation of species. He looked to domestic productions for information on animals and plants in nature. In these notebooks, domesticated pigeons alone are mentioned more than forty times.[9] Most of the ideas he was to develop in later works made their first appearance in the notebooks. Generation, or the manner in which organisms

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bridge University Press, 1958); the "Sketch of 1842" and "Essay of 1844" are on pp. 41—88 and 91—254, respectively.

7. See *Charles Darwin's Natural Selection: Being the Second Part of His Big Species Book Written from 1856 to 1858*, ed. R. C. Stauffer (Cambridge University Press, 1975).

8. DAR 205, Darwin Archive, Cambridge University Library.

9. Donald Weinshank, Stephan J. Ozminski, Paul Ruhlen, and Wilma M. Barrett, *A Concordance to Darwin's Notebooks 1836—1844* (Ithaca, N.Y.: Cornell University Press, 1990).

and species came into existence, was a major focus of this period. To explain generation, Darwin looked to inheritance and the subsequent evolution or unfolding of inheritance through development. While today inheritance and development are generally considered to be two distinct processes, for Darwin they were tied together in a dynamic process of change over time. Development was not strictly tied to early stages of embryonic life, but continued throughout the life of the organism. Certain characteristics appeared at the same age from generation to generation. Somehow, the entire organism was refashioned in the same manner as its parents. Darwin relied on his belief that ontogeny reveals traces of phylogeny; development of the individual carries specific information on the history of the group.[10]

Of special concern to Darwin in the Transmutation Notebooks were problems of inheritance. Did the male or female contribute more to the offspring? If the male contributed greatly, why did the offspring often have characteristics of both parents? Similarly, in a cross of two different breeds, which breed contributed more strongly? Why did some of the offspring from a cross between two different breeds resemble neither parent but instead resemble the common ancestor of both breeds? Did the male have the power to influence future matings of the female? Could she somehow be "tainted" by an initial mating? What would her offspring look like? The answers to these questions would have enormous impact on his theory: without an organized system of inheritance that remained intact generation after generation, natural selection would be unable to add up any of the small changes to produce large-scale changes in morphology. Darwin realized that inheritance was a large gap in his theory, and he began to look for "laws" that could be co-opted for his own purposes.

In several places in the notebooks, Darwin mentions "Yarrell's Law" in connection with domesticated animals. This law was named for William Yarrell, a London bookseller and author of *A History of British Birds*, who later convinced Darwin to raise pigeons.[11] This law maintains that when two different breeds are crossed, the older variety produces the greater effect on the

10. Dov Ospovat traces Darwin's views on ontogeny and phylogeny from his initial reliance on the chain-of-being interpretation to his later branching interpretation of von Baer in *The Development of Darwin's Theory: Natural History, Natural Theology, and Natural Selection, 1838–1859* (Cambridge: Cambridge University Press, 1981).

11. T. R. Forbes, "William Yarrell, British Naturalist," *Proc. Amer. Phil. Soc., 106* (1962), 505–515.

offspring. Darwin wrote in 1838: "Mr. Yarrell states that if any odd pidgeon crossed with common pidgeon, offspring must be like latter, because oldest variety."[12] This law was of great interest to Darwin, as he was trying to understand why certain breeds seemed to have a greater ability to "impress" their characteristics on the offspring. He explained the law as the result of old established varieties having had a longer and therefore a more ingrained developmental history than the newly established varieties, whose developmental history thus had much less influence on the next generation. Darwin's interest in Yarrell's law is clearly tied to his understanding of inheritance and developmental changes: since more recent changes have less impact in development, a cross of an established breed with a more recent one would naturally result in the offspring appearing like the established breed. Darwin later pursued an instance of Yarrell's Law, reversion to ancestral characteristics, in his experiments on both pigeon and fowl.

During the Notebook period, Darwin pursued the subject of breeding on his own. He wrote a 21-item questionnaire "About the Breeding of Animals" in 1839, which he sent to breeders asking them to observe patterns of inheritance in their own animals.[13] Possibly due to the length and detail of the questions, this effort brought little response from the breeders. The questionnaire shows the kinds of questions Darwin was asking before he experimented on his own; not surprisingly, many of them reflect Yarrellian ideas of inheritance. Question 4 asks: "In crossing between an old-established breed, or local variety, which from time to time immemorial has been characterized by certain peculiarities, or the animal in its aboriginal state, with some new breed, does the progeny in the first generation take more after one than the other?" Continuing to emphasize contemporary theories of inheritance, Darwin asked in number 6: "Where very different breeds of the same species are crossed, does the progeny generally take after the father or the mother?" In this question, Darwin was concerned whether certain characteristics were chiefly "male" and others "female." At the same time he wrote this questionnaire, he began his "Questions and Experiments" notebook on plants and animals.[14] Many of the questions in this

12. Barrett et al., *Charles Darwin's Notebooks* (above, n. 2), "Notebook C," p. 239.

13. Charles Darwin, *Questions about the Breeding of Animals*, ed. Gavin de Beer, (London: Society for the Bibliography of Natural History, 1968).

14. Charles Darwin, "Questions and Experiments," ed. Paul H. Barrett, in

notebook involved domesticates and were grouped into categories to be answered by certain animal and plant experts, such as Yarrell, Joseph Hooker, and Edward Blyth: "As peaches sport into Nectarines (does reverse happen?) what is effect of crossing peaches & nectarines: same question with regard to Primroses";[15] "If two half bred animals exactly alike be interbred will offspring be uniform?"[16] Darwin returned to many of these same questions in experiments he did in the 1850s.

THE "SKETCH OF 1842" AND THE "ESSAY OF 1844"

In the "Sketch" and the "Essay," domesticates are mentioned with reference to a few categories: reversion to ancestral characters, use and disuse of certain characters, the effect of the male on the reproductive system of the female, the preponderance of certain breeds over others, and the appearance of certain characters at specific times in development. In both works, Darwin clearly emphasizes inheritance and its role in his theory of natural selection. In the first chapter of the "Sketch," he discusses two main issues regarding inheritance: the possible limit to variation, and the maintenance of uniformity in a breed. Both of these processes are necessary if natural selection is to work; variations must continue to be produced, and yet the changes cannot be so great that mating is impossible. In the notebooks, Darwin emphasizes that natural selection could adapt organisms to slow change; abrupt changes produced inviable "monsters." In the "Sketch," he uses domesticates to emphasize slow change and the need to maintain uniformity: "Free crossing great agent in producing uniformity in any breed."[17] To account for the variations on which selection acts, he also relies on evidence from domesticates: "With the amount of food man can produce he may have arrived at the limit of fatness or size, or thickness of wool, but these are the most trivial points, but even in these I conclude it is impossible to say we know the limit of variation."[18] He concludes that since domesticated breeds continued to vary even under intense selection, then variations must continue to be produced.

Barrett et al., *Charles Darwin's Notebooks*, 487–516. Barrett suggests that Darwin began this notebook in mid-1839 and that entries were made in it at least until the mid-1840s and possibly later.

15. Ibid., p. 515.
16. Ibid., p. 492.
17. De Beer, *Evolution by Natural Selection* (above, n. 6), p. 42.
18. Ibid., p. 58.

CONNECTIONS TO CIRRIPEDES

Having written the notebooks, the essay, and the sketch, Darwin began what was to be an eight-year study on barnacles. Several authors have pointed out that the barnacle work was not simply a work of classification, but involved larger questions on the nature of development and its relationship to ontogenetic as well as phylogenetic change.[19] Dov Ospovat argued that Darwin emphasized an approach to development similar to that of Karl Ernst von Baer, in which the more generalized characteristics of a large group of animals will appear earlier than the more specialized characters. However, Stan Rachootin shows that Darwin's analysis of barnacle development, including the homologies of their larval and adult limbs, was primarily influenced by the work of Auguste Brullé, who suggested that the more modified a part is, the earlier it will appear in development. Further, Rachootin argues that Darwin continued his interest in Brullé when he approached the subject of pigeon embryology in the 1850s. Working with barnacles, Darwin had begun to explore questions of variability in real organisms and the manner in which these variations were expressed in development. When pressed by Hooker as to the importance of the barnacle work on larger issues, he wrote: "You ask me what effect studying species has had on my variation theories; I do not think much — I have felt some difficulties more. On the other hand I have been struck . . . with the variability of every part in some slight degree of every species. When the same organ is rigorously compared in many individuals, I always find some slight variability."[20] By the time Darwin began his next large-scale project on organisms, albeit domesticated ones, he was prepared to test questions of embryology, morphology, variation, and inheritance.

In the early 1850s, Darwin had begun to question seriously the mechanism of inheritance. Although his hypothesis of pangenesis was still more than ten years away from its published form in *Variation* (1868), many of the examples the theory attempts to explain — reversion, hybridism, prepotency and telegony — are found in his work on domesticated animals. As has been sug-

19. Michael Ghiselin, *The Triumph of the Darwinian Method* (Chicago: University of Chicago Press, 1969), pp. 103—130; Ospovat, *Development of Darwin's Theory* (above, n. 10), pp. 146—169; Stan Rachootin, "Darwin's Embryology," Ph. D. diss., Yale University, 1984.

20. Frederick Burkhardt and Sydney Smith, *The Correspondence of Charles Darwin* (Cambridge: Cambridge University Press, 1989), IV, 344.

gested by Robert Olby, and most recently by M. J. S. Hodge, Darwin's questions on sexual generation had been evident since the notebook period and had continued throughout his scientific career.[21] Hodge goes so far to suggest that "Darwin may have moved, even as early as 1841, to credit unfertilized ova with the totipotency that had always impressed him in buds and flatworm fragments."[22] Thus, I believe Darwin's work on domesticates in the 1850s was spurred on by the need to answer long-standing questions of inheritance, most of which first appear in the pages of his Transmutation Notebooks.

DARWIN AS A BREEDER

To study inheritance, Darwin used research organisms with particularly suitable characteristics. When it came to the inheritance of certain features early in development, he chose the domesticated pigeon. To study revision to ancestral characters, domesticated breeds of pigeon and chicken were useful because the common ancestor for each was agreed upon and Darwin could compare the presumed ancestor with the offspring generated to look for reversion. Domesticated birds were also useful as he looked for examples of telegony and the phenomenon of use and disuse. Certain breeds of fowl showed strange development in the frontal bones of the cranium. When he wanted to investigate variability in the size and number of vertebrae, he chose rabbits. Animals were not singled out: domesticated peas showed variability in the size and shape of the fruit; cabbages showed variations in the size and shape of the stem, but the reproductive morphology of the individual flowers remained remarkably similar. In essence, for Darwin, each domesticate was an exemplar of a particular phenomenon of interest.

Since Darwin knew very little about animal and plant breeding, he turned to horticulturalists, pigeon fanciers, farmers, and anyone who could provide him with answers to particular queries. He subscribed to several journals for the "country gentleman," such as the *Gardener's Chronicle* and the *Field*, which had articles on all aspects of animal and plant breeding. By 1855, Yarrell had "persuaded" him to take up pigeon breeding and he constructed a pigeon house in the garden at Down.[23]

21. Robert C. Olby, *Origins of Mendelism* (New York: Schocken Books, 1966), pp. 86—102; M. J. S. Hodge, "Darwin as a Lifelong Generation Theorist," in Kohn, *Darwinian Heritage* (above, n. 5), pp. 207—244.

22. Hodge, "Generation Theorist," p. 230.

23. Burkhardt and Smith, *Darwin Correspondence*, V, 294.

PIGEONS AND DEVELOPMENT

Darwin spent by far the greatest amount of time and effort studying pigeons. But surely not your run-of-the-mill park pigeon. Rather, he chose the very proper Victorian domesticated pigeon for his researches on inheritance. From 1855 to 1858, just prior to the publication of the *Origin* (1859), he bred domesticated pigeons. He also created a worldwide network of pigeon informants who were always at the ready to provide the illustrious Mr. Darwin with skins, skeletons, live material, and tidbits of information.[24] Having had little response from the breeding questionnaire in 1839, this time he targeted specific breeders to provide him with information. In 1856 he even wrote to animal collector-naturalist Alfred Russel Wallace in order to hire him to shoot pigeons and send the skins back from the Malay Archipelago.[25] Darwin joined several of London's pigeon fancying clubs and learned the ins of the "fancy" so clearly described by James Secord.[26]

Why study pigeons? Clearly part of the answer is related to Darwin's keen interest in domesticated varieties as analogues to incipient species produced in nature. In the *Origin*, and in the "big book" *Natural Selection*, he uses the domesticated pigeon as his prime analogy for changes wrought by selection. He begins both books with the analogy from artificial selection. However, the artificial selection analogy explains only part of his interests; he also used pigeons to address issues that had challenged him since the transmutation notebooks: the nature of variations, and the inheritance of those variations in ontogeny.

Darwin deemed pigeon breeds as exceptional due to several important features of their biology. First, pigeons mate for life, so matings are easily controlled. He exploited this fact when he conducted several artificial hybridization experiments. Second, pigeons were one of the few domesticated animals for which the common ancestor was generally agreed upon in Darwin's day — namely *Columba livia*, the rock dove. Indeed, he spends a major part of his pigeon discussion in *Variation* attempting to establish this as a fact beyond any reasonable doubt. Third, pigeons are born naked — thus providing Darwin with easily visible developmental characters (see Fig. 1). Evidence for the importance of this

24. See ibid., pp. 510—511, for a list of over thirty of Darwin's pigeon correspondents.

25. Burkhardt and Smith, *Darwin Correspondence*, VI, 290.

26. Secord, "Nature's Fancy" (above, n. 5).

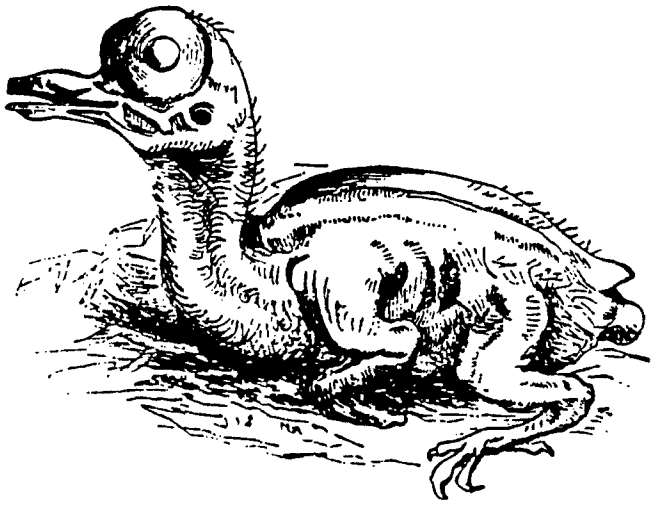

Figure 1. The picture of this squab was taken from Darwin's copy of E. S. Dixon, *The Dovecote and the Aviary* (London: John Murray, 1851), p. 58. Notice the naked, extremely immature state of the young pigeon aged one day.

feature can be seen in a fragment of a letter written to Darwin from the Reverend Edmund Saul Dixon, author of *The Dovecote and the Aviary* (1951).[27] Dixon answered a question of Darwin's on seeing "embryonic resemblances" in newly hatched fowl:

> I may now say that in new-hatched chicks it is all too late to look for the embryonic resemblances. . . . But I would undertake to decide the variety of any chick with whose breed I was well acquainted, immediately on its eclosion from the shell. Nay when an egg has been accidentally broken after a fortnight's hatching, I have been able to declare of what sort it would have been, had it survived. Many observant poultry-rearers will do the same.[28]

In several letters to his cousin William Darwin Fox written during the 1850s, Darwin asked him for young pigeons in order "to ascertain whether the *young* of our domestic breeds differ as

27. Edmund Saul Dixon, *The Dovecote and the Aviary: Being Sketches of the Natural History of Pigeons and Other Domestic Birds in a Captive State, with Hints for their Management* (London: John Murray, 1851).

28. I thank the late Sydney Smith for pointing out the Dixon letter and its significance for Darwin's work on pigeon embryology. The fragment is in DAR 205.5.

much from each other as do their parents."[29] Between 1857 and 1858 Darwin took measurements from these pickled squabs in an attempt to determine the stage at which the different races could be distinguished from each other.

Although Darwin pursued breed differentiation in the 1850s, a passage in his "Questions and Experiments" notebook (1839–1844) suggests that he was interested in this question some ten years earlier: "Is form of globule of blood in allied species similar. — if not how is it in allied varieties."[30] In 1855, he attempted to look at characters in the blood in order to study breed differentiation in pigeons. In this study, he tied together characters evident in the blood of pigeons with the phylogeny of certain breeds. His study involved the help of the anatomist George Gulliver (1804 — 1882), who studied variability in the size and shape of blood corpuscles. Measuring the diameter of blood corpuscles was all the rage in the mid-1850s, much like gel electrophoresis one hundred years later. Organisms of all sorts that showed variability in external characters were studied in this manner to look at internal variability.[31] In 1855, Darwin sent Gulliver the blood of three breeds of pigeons: the Barb, the short-faced tumbler, and the Dragon (which is much like the Carrier), and asked him to obtain the blood of a wild pigeon to use as a standard.[32] Why did he send the blood of these breeds? He had other breeds by 1855 — others such as the pouter, with its greatly enlarged crop, and the fantail, which had been selected for greater numbers of tail feathers. These breeds appear on the surface to be morphologically very distinct. Clearly, if Darwin wanted to examine diversity he would have sent the blood of some of these bizarre forms. I think he chose the birds he did in order to use the morphological character of the blood in the construction of a phylogeny.

In the nineteenth century many bird phylogenies were done using the size and shape of the beak as a diagnostic feature of the group. Darwin constructed a similar phylogeny for domesticated pigeons using beak size, but using the embryonic forms of the

29. Burkhardt and Smith, *Darwin Correspondence*, V, 337, letter to Fox of May 23, 1855. Other letters to Fox concerning this study were on March 19, 1855; July 22, 1855; and March 15, 1856.

30. Darwin, "Questions and Experiments" (above, n. 14), p. 494.

31. George Gulliver edited *General and Minute Anatomy of Man and the Mammalia* (1842) by Friedrich Gerber, in which he added a chapter on "Observations of the Blood — Corpuscles of Birds." In this chapter, Gulliver described differences between the blood of various kinds of birds, including that of the pigeon family.

32. Burkhardt and Smith, *Darwin Correspondence*, V, 528.

beaks (see Fig. 2). He wrote: "Misled by the extraordinary shortness and form of the beak, I did not at first perceive the near affinity of this race to that of the Carriers . . . , this view is supported . . . strongly by the fact that young Barbs and Dragons, within 24 hours after being hatched, resemble each other more closely than do young pigeons of other and equally distinct breeds."[33] It is interesting to note that Darwin sent Gulliver the blood of the Dragon and the Barb: these two are effectively sister taxa in group II, according to his evolutionary tree. He also sent the blood of the short-faced tumbler, which appears in group III, and he asked Gulliver to use the blood of a dove-cot pigeon as a standard, found in group IV. If he had wanted to span the spectrum of morphological diversity he could have easily sent the blood of a pouter, a carrier, and a fantail. Instead, he is particularly interested to learn about internal variability between breeds that he suspects are very closely related — such as Barbs and Carriers — and to compare these to an outgroup. By this comparison, I believe Darwin was looking for internal similarities between very closely related breeds as evidence of their recent common ancestry.

INTERNAL VERSUS EXTERNAL CHARACTERS AND PREPOTENCY

In another chapter of Darwin's work on domestication, he explored questions of heredity that he had been thinking about nearly twenty years earlier. He was specifically concerned about the proportions of the male and female contributions to the morphology of the offspring. In the summer of 1856, he wrote to his chief pigeon confidant, William B. Tegetmeier, that "Mr Orton has lately published some lectures with the old theory of externals following males and internals females."[34] This letter referred to the ancient belief (presented by Alexander Walker in his 1838 book *Intermarriage*[35] and revived by Reginald Orton, an eye surgeon and fowl breeder[36]) that the male was responsible for the external features of the offspring, and the female provided the nurturing material out of which the internal characters developed.

33. Charles Darwin, *The Variation of Animals and Plants under Domestication* (London: John Murray, 1868), I, 151–153.

34. Burkhardt and Smith, *Darwin Correspondence*, VI, 210.

35. Alexander Walker, *Intermarriage* (London, 1838).

36. D. Power, "Reginald Orton," in *The Dictionary of National Biography*, ed. Sir Leslie Stephen and Sir Sydney Lee (London: Oxford University Press, 1895), XII, 1166–67.

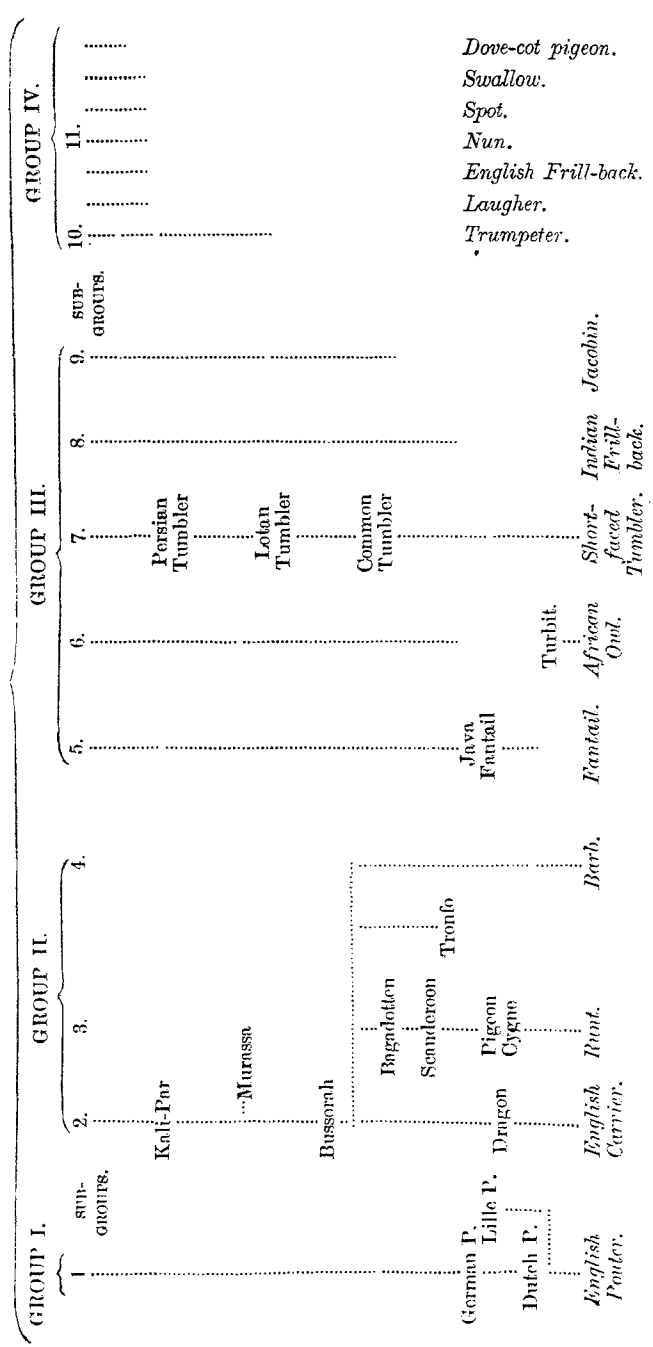

Figure 2. Darwin's pigeon phylogeny from *The Variation of Animals and Plants under Domestication* (London: John Murray, 1868), I, 136.

This belief can be found as early as Aristotle, and was discussed by Darwin's grandfather, Erasmus Darwin, in his work *Zoonomia.*

Although Orton became the catalyst for Darwin's investigation of external and internal inheritance, Darwin was reminded of this theory of inheritance just after he returned from the *Beagle* voyage. In 1837, he recorded in his C notebook the remarks of William Yarrell: "Mr. Y. is inclined to think that the male communicates the external resemblances [more] than the female."[37] Fortunately for the historian, Darwin made marginal comments in his books.[38] Some of his annotations on his copy of Orton's pamphlet suggest tests of these principles in pigeons. For instance, where Orton wrote:

> I would call your consideration to a very curious circumstance pertaining to the voice of the mule and the hinny. . . . The mule *brays* while the hinny *neighs.* The why and wherefore of this is a perfect mystery until we come to apply the knowledge afforded us by the law I have given. The male gives the locomotive organs, and the muscles are amongst these; the muscles are the organs which modulate the voice of the animal,[39]

Darwin wrote in the margin, "How will it be in Trumpeters?" In other words, if a female trumpeter pigeon were crossed with another variety of pigeon, say a turbit, would the offspring have the characteristic trumpeter voice? Or can only the male trumpeter transmit its characteristic voice in the offspring? Thus Darwin could (and probably did) conduct an experiment to test for such a method of inheritance in pigeons. In two letters to Tegetmeier written in early 1856, he asked for "a pair of Indian laughing Pigeons" and later thanked him for "authentic information with respect to the Laughing Pigeons,"[40] Darwin subsequently obtained the birds and "heard one make a very odd note, which I suppose was laughing,"[41] In his authoritative book on pigeons, Tegetmeier stated that the voice of the Laugher was "far more irregular and

37. Barrett et al., *Charles Darwin's Notebooks* (above, n. 2), "C notebook," p. 275.

38. Mario di Gregorio, *Charles Darwin's Marginalia* (New York: Harland Press, 1991).

39. Reginald Orton, *On the Physiology of Breeding: Two Lectures Delivered to the Newcastle Farmer's Club* (London: London Times Office, 1855).

40. Burkhardt and Smith, *Darwin Correspondence*, VI, 87, 110.

41. Ibid., p. 160.

varied than that of the Trumpeter."[42] Thus, with the laughing pigeons Darwin might have been looking for an even more pronounced and bizarre variation of the voice than he would have seen with trumpeters.

Another annotated passage quite clearly led to a pigeon experiment. Orton wrote:

> I caused some hens to breed with a Cochin cock . . . the half-bred (offspring) . . . were all, when hatched, like the Cochin cock, profusely feathered on the legs and feet. . . . We see here that according to the law, the male parent implanted his characteristics; but what was curious, in a few weeks in some of the half-breeds all, and in many, most of the leg feathers were shed. . . . Now why was this? The cock had implanted his external characteristics — the hen had given her vital organs. The feathers of the male were there; but the vital organs necessary to their growth were not there and consequently after a time, for want of nutriment these feathers were shed.[43]

Darwin wrote in the margin: "Hen Trumpeter & Cock Turbit — feathered." By designing an experiment with a feather-footed female and a naked-footed male, he could see if the male truly gave the external features to the offspring. The proof that he did such an experiment can be seen from a note deposited in the "Embryology" file: "Hybrid from Cock Turbit & Hen Trumpeter, the young one died about a fortnight old. — Had such feathered legs — Same female parent. Some little skin between outer toes."[44] We can see from Darwin's experiment and from his marginalia that he did not accept Orton's theory. He found feather-legged offspring as a result of the above cross, suggesting that the female, not the male, was responsible for this external feature.

Darwin's motive for crossing trumpeters and turbits was not simply to examine Orton's theory of inheritance. He was also interested in prepotency, the observation that in crosses of different races, one race would prevail in the offspring. Again, the early notebooks show that he was thinking about these same questions of inheritance many years earlier. In his "Questions and Experiments" notebook, he wrote of an experiment that might be

42. William B. Tegetmeier, *Pigeons: Their Structure, Varieties, Habits and Management* (London: Rutledge and Sons, 1868), p. 160.

43. Orton, *Physiology of Breeding*, p. 14.

44. DAR 205.7 (2): 186.

worthwhile: "To cross some artificial male with female of old breed & see result. — According to Mr. Walker the form of male ought to preponderate; according to Mr Yarrell the latter ought: either in first breed or permanently."[45] Here Darwin suggests a test to see which of these laws held true.

In *Variation*, Darwin discusses the issue of prepotency in domesticated pigeons:

> The most curious instance known to me of weak power in both sexes is in the trumpeter pigeon. This breed has been well known for at least 130 years: it breeds perfectly true, as I have been assured by those who have long kept many birds: it is characterized by a peculiar tuft of feathers over the beak, by a crest on the head, by a singular coo quite unlike that of any other breed, and by much feathered feet. I have crossed both sexes with turbits of two sub-breeds ... and reared many mongrels and recrossed them; and though the crest on the head and feathered feet were inherited (as is generally the case with most breeds), I have never seen a vestige of the tuft over the beak or heard the peculiar coo.[46]

By the time he wrote this passage, he had crossed enough trumpeters with other breeds to determine that feathered feet were almost invariably to be found in the offspring when either the male or the female parent had feathered feet. Furthermore, the feathered feet seemed to appear in all crosses of feather-footed trumpeters with other breeds. Thus, on the basis of his own experimentation, Darwin came to reject the notion of inheritance that Orton had put forth in his 1855 lecture. His experiment had also provided evidence against Yarrellian ideas of inheritance.

Variation also records Darwin's conclusion on the inheritance of internal and external features. Shortly after the paragraph quoted above, he wrote:

> I am aware that such cases as the foregoing have been ascribed by various authors, not to one species, race, or individual being prepotent over the other in impressing its character on its crossed offspring, but to such rules as that the father influences the external characters and the mother the internal or vital organs. But the great diversity of the rules given by various

45. Barrett et al., *Charles Darwin's Notebooks* (above, n. 2), "Questions and Experiments," p. 493.

46. Darwin, *Variation*, II, 66.

> authors almost proves their falseness. . . . If we confine our view to the domesticated races of a single species, or perhaps even to the species of the same genus, some such rules may hold good; for instance, it seems that in reciprocally crossing various breeds of fowls the male generally gives colour; but conspicuous exceptions have passed under my own eyes.[47]

Thus, at the end of his pigeon experimentation, Darwin circumscribed Orton's theory almost to the point of totally rejecting it. But he did not use his experiment to prove Orton or Yarrell false. Though he was very worried about false facts, he rarely dismissed any theory as completely untrue. Evidence against Yarrell did not stop him from mentioning Yarrell's Law favorably in *Variation*, or from continuing to investigate the phenomenon of prepotency throughout the 1850s and 1860s. Darwin saw greater weaknesses in Orton's theory and found him to be not very useful. Indeed, after reading about internal versus external features in Walker's 1838 book *Intermarriage*, he attached a four-page outline rejecting Walker's view.[48] That he was still attempting to study internal versus external features in the 1850s indicates that he had serious questions regarding the mechanism of inheritance and he was still willing to investigate theories that he regarded as questionable. When it came to his published conclusions in *Variation*, though, he seemed to trust the results of his own experiments enough to shy away from the older theories and to look for another explanation.

REVERSION

The subject of reversion appears early in the notebook period. Darwin was fascinated that long-lost characters sometimes appeared in the offspring; he believed that under certain circumstances, such as a change of external conditions, these characters would resurface. A more detailed mechanism for this phenomenon would be encompassed in his pangenetic view in 1868. When he looked at reversion in the 1850s, he used pigeon breeds as his experimental subjects. In crossing two different pigeon breeds, he would occasionally obtain offspring that did not resemble either parent but showed the slaty blue color or the double black wing

47. Ibid., p. 68.

48. Darwin's copy of Walker's book is in the Darwin Archive, Cambridge University Library. See di Gregorio, *Darwin's Marginalia* (above, n. 38), pp. 834—835, for a transcription of Darwin's comments on Walker's theory.

bars of the putative ancestral rock dove (see Fig. 3). Perhaps he was concerned about reversion because if it were found to be very common, the changes molded by natural selection would be continuously set back to the ancestral condition.

In 1857, Darwin actively explored reversion with the help of breeder William B. Tegetmeier. He wrote to Tegetmeier to ask his advice on reversion in fowl: "If you were to cross black Spanish with Black or Silver Polands, do you suppose ever red or other marked new colour would appear?"[49] Here Darwin was interested in the red markings of *Gallus bankiva*, the Wild Jungle Fowl from which domesticated varieties probably arose. On May 18, 1857, he referred to Tegetmeier's reply: "Thanks for the information about crossed Fowls: I am *surprised* that red does not appear in some crosses."[50] Almost certainly discontent with Tegetmeier's reply, but too busy to pursue the subject, Darwin left the question of reversion in fowl until almost a year later, when he suggested the following to Tegetmeier: "I want to try the following experiment, viz to get a cock & some Hens of several breeds, which never have red feathers in them; & then let them cross, & their mongrel children cross again & see whether red birds will not appear."[51] He specified the following birds for the cross: an old Spanish Cock [a black bird] and several white females of other breeds. He recorded the colors of the offspring the following summer on August 5:

> I have an astonishing lot of mongrels, mostly black, some white & but a very few mottled. One of the young cocks, however, has lately acquired a few reddish brown freckles; & all these mongrels seem very liable to change their plumage as they grow older. — I rather expect that the offspring of my mongrels next year will make some approach to the plumage of the Gallus bankiva.[52]

In this experiment, Darwin kept track of the sex and the moult in which red features appeared. He was not expecting any bright red offspring; the odd red feather would suffice. He gave a more complete record of his results in a September 13 letter:

> It is curious how much plumage has altered during growth with

49. Burkhardt and Smith, *Darwin Correspondence*, VI, 393.
50. Ibid., p. 397.
51. Charles Darwin to W. B. Tegetmeier, November 16, 1858, in the Library of New York Botanical Garden (hereafter, NYBG).
52. Ibid., August 5, 1859.

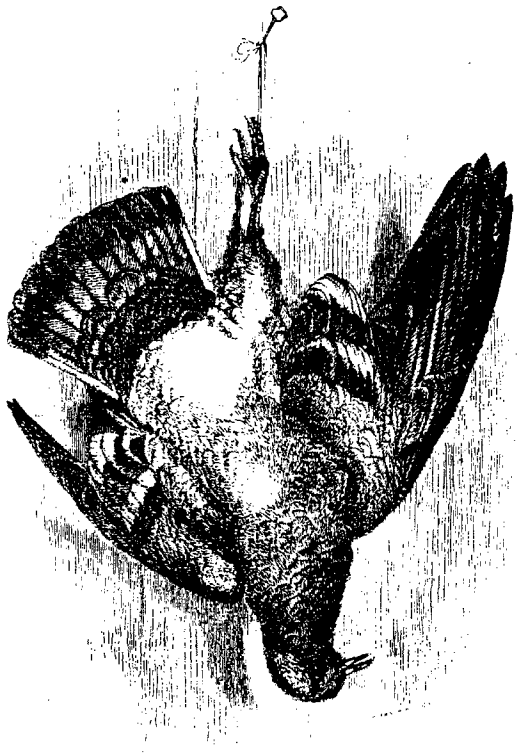

Figure 3. The rock pigeon, *Columba livia*, from *The Variation of Animals and Plants under Domestication* (London: John Murray, 1868), I, 135. Darwin seems to have had this bird drawn upside-down to emphasize the black tail bar and the double black wing bars of the ancestral condition.

> some of the Fowls. — But the most curious fact for me is that a young cock from White Game Hen which was black has lately assumed reddish neck Hackles & light yellowish red feathers on back. — Another more striking example of this fact, was given by a young cock from white Silk Hen; which was jet black in the down & in first plumage but is now getting *splendid red hackles* on neck & on back over tail; so that it will make in first generation some approach to Wild Gallus. — This is good case as I believe the Silk Breed is a very ancient & true breed in the East. — I shall be very curious to see result next year.[53]

53. Ibid., September 13, 1859.

Darwin saw reversions early in the first generation but waited until the offspring began to moult to make further observations:

> The result has now become interesting. The chickens from Spanish Cock & White Silk fowl were just black in the first plumage, but late in autumn to my astonishment red feather after red feather very strangely appeared in the *Cocks* & now one of the Cocks is nearly as splendid as the wild Gallus Bankiva. Another quite white, but now has very much red about it, i.e. the hackles red. Are not these curious facts?[54]

In his discussion of reversion in the *Origin*, Darwin considered the ability to revert an internal feature of every organism:

> When a character which has been lost in a breed, reappears after a great number of generations, the most probable hypothesis is, not that the offspring suddenly takes after the ancestor some hundred generations distant, but that in each successive generation there has been a tendency to reproduce the character in question, which at last, under unknown conditions, gains ascendancy.[55]

The "tendency to produce the character in question" later became a function of gemmular inheritance. In Darwin's pangenesis chapter in *Variation* he notes that, "the tendency to reversion is often induced by a change of conditions, and in the plainest manner by crossing," and that reversion "sometimes may be observed with advancing age even in the same individual."[56] To Darwin, a change of external conditions would somehow affect the reproductive elements. A crossing of two distinct breeds effected the same response. These external and internal challenges, apparently so different, showed by their comparable effects that they were mediated by similar processes.

Darwin's exploration of reversion indicates that he was quite willing to investigate the processes that are in direct opposition to the transmission and inheritance of new variability. Reversions to the ancestral state would necessarily interfere with the appearance of new characters. Perhaps he was concerned that this tendency to

54. Ibid., January 20, 1860.

55. Charles Darwin, *On the Origin of Species* (London: John Murray, 1859), pp. 160—161.

56. Darwin, *Variation*, II, 394—395.

revert might be more evident than anyone had imagined. From this experiment, I think that he saw that reversion did indeed occur, but generally because unusual conditions were present.

The importance of reversion appears again and again in Darwin's published works; he mentions particular crosses to study reversion in both the *Origin* and *Variation*. If long-lost characters could resurface, then perhaps form would not change over time but would be continuously reset to the ancestral condition. In the *Origin*, Darwin seemed concerned about the possibility but believed that "the struggle between natural selection on the one hand and the tendency to reversion and variability on the other hand, will in the course of time cease."[57] In *Variation*, he recounts several of his experiments on reversion (probably done in the late 1850s and early 1860s) in both pigeons and fowl. By the time he writes about reversion in *Variation*, he is convinced of the importance of this phenomenon: "Reversion in the ordinary sense of the word, comes into action so incessantly, that it evidently forms an essential part of the general law of inheritance."[58] Darwin's breeding experiments clearly led him to think more seriously about reversion, and he knew that any theory of inheritance must explain how reversions could occur.

TELEGONY

In the final episode I will present, Darwin experimented with what August Weismann later named "telegony": reproduction at a distance, or the direct effect of the male gametes on the female reproductive system. Like the other theories of inheritance mentioned earlier, Darwin's interest in telegony can be found from the notebook period through *Variation*. When he discussed telegony he often brought up the example of Lord Morton's mare: the Arabian mare "bore a hybrid to a quagga," and her subsequent offspring, after matings to horses, were supposedly tainted by the quagga.[59]

The particular case I will consider occurred in 1866, after Darwin had finished his pigeon experiments. He knew that a breeder of fowl had noticed unusual egg color when he crossed certain breeds. He turned to Tegetmeier not only for his expert

57. Darwin, *Origin*, pp. 153—154.

58. Darwin, *Variation*, II, p. 400.

59. See R. W. Burkhardt, Jr., "Closing the Door on Lord Morton's Mare: The Rise and Fall of Telegony," *Stud. Hist. Biol., 3* (1979), 1—21.

opinion, but because he wished Tegetmeier to follow up on this supposed case of telegony. The breeder, Zurhorst, had crossed a Spanish hen (Spanish fowl produce white eggs) to a Cochin cock (Cochin hens lay dark eggs); the color of the resulting eggs was dark rather than the usual creamy white. Darwin appreciated that this was an extraordinary result, and he wrote to Tegetmeier to pursue it further: "Do you think you could get Mr. Zurhorst to try his experiment again this Spring on the eggs from the Cochins crossed by Spanish & let me see the eggs?"[60] Not only did Tegetmeier talk to Zurhorst, but both of the men agreed to try the experiment again. The results were negative — that is, the eggs were white. Darwin wrote to Tegetmeier on July 9: "I am sorry but not at all surprised to hear result of your experiment with the Cochins and Spanish fowls; I think Mr. Zurhorst must have made a mistake."[61]

Darwin wanted to know if Zurhorst was right. If the white-egged hen, mated to a cock of the dark-egged breed, produced dark eggs, this would mean that the male had impressed his character on the female such that she would lay dark eggs. Even though neither Tegetmeier nor Zurhorst could repeat the results, Darwin did not give up easily. On December 4, he wondered if he should use Zurhorst's results:

> You will remember the note you sent me about Mr. Zurhorst & the eggs, & it seems so distinct that although your experiments were contradictory, I am tempted to cite the case. Pray tell me what you think. If Mr. Z. actually saw the eggs himself I would rely on him. Perhaps you will be so kind as to give me his address & I will write to ask.[62]

Tegetmeier wrote back a few days later:

> From the conversation I have had with him [Zurhorst] respecting the eggs I do not think his information is sufficiently definite to be of use. . . . It really amounts to only this, that a Spanish hen running with his Cochins had dark eggs. Whether she did so before or not he does not know. My single experiment was that in spanish hen running with Cochins, laid *perfectly white* eggs that were fertilized by the Cochin.[63]

60. NYBG, January 16, 1866.
61. Ibid., July 9, 1866.
62. Ibid., December 4, 1866.
63. Tegetmeier Correspondence, December 10, 1866, Darwin Papers, CUL.

Tegetmeier, the ultimate authority on such matters, gave his advice, and Darwin took it. The case is not cited in *Variation*.

Why would Darwin have gone to such trouble to pursue this case? Darwin's answer can be seen if we look at the case in terms of larger questions of inheritance. By showing that a male bird had the ability to alter the female to produce the abnormally colored eggs, he could then have shown that the male element fundamentally altered the female reproductive system such that she would henceforth lay abnormally colored dark eggs. In Darwin's view, the male would have been the catalyst for disruption within the female. However, he could not get Tegetmeier's assent that the dark eggs existed, and so he chose to avoid the case.

FURTHER INTEREST IN DOMESTICATES IN PUBLISHED WORKS

Although by late 1857 Darwin had to decided to give up his pigeon house and do away with his birds, his interest in domesticates continued. He pursued the phenomenon of use and disuse in domesticated ducks and rabbits by looking for differences in the weight and size of body parts between the domesticated and feral forms. Indeed, many of the examples he gives in *Variation* focus on the differences that appear between domestic and feral forms. He was extremely interested in correlation of parts, because if one structure were modified, other parts would also tend to be modified. In the *Origin*, he writes: "Breeders believe that long limbs are almost always accompanied by an elongated head. . . . Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly unconsciously modify other parts of structure, owing to the mysterious laws of the correlation of growth."[64]

Darwin studied sexual dimorphism in domesticated chickens in his work leading to the publication of *The Descent of Man* (1871). In a curious experiment that he asked Tegetmeier to perform in the 1860s, he pursued sexual selection in domesticated pigeons. Since pigeons show very little sexual dimorphism, it is not obvious that he would have turned to pigeons. He asked Tegetmeier to "dye with magenta a pigeon or two. . . . I shall be very curious to hear how an entirely crimson pigeon will be received by the others as well as his mate."[65] The *Descent of Man* recorded that

64. Darwin, *Origin*, pp. 11–12.

65. Francis Darwin and A. C. Seward, *More Letters of Charles Darwin* (New York: D. Appleton, 1903), I, 58.

the stained pigeons were "not much noticed by the others."[66] Darwin also explored what he called "analogous variation," a kind of parallel evolution in which different breeds independently show tendencies to vary in the same characteristics. He observed this phenomenon when he examined "pencilled" and "spangled" feathers in varieties of fowl, namely the Spangled and Pencilled Hamburghs. These two breeds had been independently developed at known places and times, yet they exhibited the same color pattern on their feathers. As seen in these various cases, Darwin chose particular domesticates because they provided him with useful information on subjects of intense interest; most importantly, they allowed him to address the subject of inheritance which connects all of these phenomena.

PANGENESIS

Darwin presented his "Provisional Theory of Pangenesis" near the end of *Variation*. In this chapter, he accounted for inheritance, physiology, and development by assuming the existence of submicroscopic particles that were present in every living tissue: "I assume that cells, before their conversion into completely passive or 'formed material,' throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment, multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules for the sake of distinctness may be called cell-gemmules, or . . . simply gemmules."[67] Gemmules were used to account for nearly every inheritable peculiarity known. Characters that appeared at a certain stage of development were explained as a series of particulate interactions: "the organic units, during each stage of development throw off gemmules, which, multiplying, are transmitted to the offspring. In the offspring, as soon as any particular cell or unit in the proper order of development becomes partially developed, it unites with (or, to speak metaphorically, is fertilised by) the gemmule of the next succeeding cell, and so onwards."[68] By using aggregating gemmules, Darwin could explain the formation of each structure. In this way he could explain feather-footed pigeons and fowl (feather gemmules drawn

66. Charles Darwin, *The Descent of Man, and Selection in Relation to Sex* (London: John Murray, 1871), II, 118.

67. Darwin, *Variation*, II, p. 374.

68. Ibid., p. 389.

to positions on the leg homologous to their stations on the wing), hackles on the head of the Polish Fowl (hackles are usually found on the neck of fowl), and insects with one side of their bodies like the male and the other half like that of the female (like gemmules seek out like).

Darwin used pangenesis to explain some of the more troublesome cases evident from his work on domesticates. Telegony, or the power of the male to influence future offspring of a given female, was "intelligible through the diffusion, retention, and action of the gemmules included within the spermatozoa of the previous male."[69] By giving gemmules the power to be modified throughout the life of an organism and then be transferred to the next generation, he insisted that inheritance should be looked at as a form of growth. Viewed in this light, inheritance was not a black box but simply another form of growth and change which spanned generations.

For reversion, dormant gemmules were the hypothetical cause, and Darwin's own observations on crossed pigeons the example:

> When two animals of antagonistic characters are crossed . . . dormant gemmules derived from the same part in some remote progenitor might easily gain the ascendancy, and cause the reappearance of long-lost characters. For instance, when black and white pigeons, or black and white fowls, are crossed, — colours which do not readily blend, — blue plumage in the one case, evidently derived from the rock-pigeon, and red plumage in the other case, derived from the wild jungle-cock, occasionally reappear.[70]

By using gemmules, Darwin could show a dilution effect occurring over time: eventually there will be a smaller and smaller tendency to revert, as recently developed structures are adding new gemmules to the organism. Reversion is no longer an inexplicable occurrence but is a function of the interaction between gemmules.

CONCLUSIONS

While Wallace disagreed with Darwin that domesticates provided a great deal of useful information on wild populations,[71]

69. Ibid., p. 388.

70. Ibid., p. 401.

71. See Alfred Russel Wallace, "On the Tendency of Varieties to Depart Indefinitely from the Original Type," *J. Linn. Soc., Zool., 3* (1859), 45–62.

Darwin continued to draw on his domesticated animals and plants to inform him on the workings of his theory. Unlike Wallace, his exposure to natural populations was extremely limited after his return from the *Beagle* voyage. By the 1850s, he had settled into a life at Down House and was becoming more and more withdrawn from London scientific circles. He turned to his network of informants, visits from colleagues such as Hooker and T. H. Huxley, subscriptions to various journals, and his own experimental studies at Down.

This work on domesticates was clearly related to other natural history studies conducted by Darwin and others during the same period. For example, during the 1850s when Darwin worked on domesticates, he was also engaged in questions of geographic distribution. To study the dispersal and subsequent viability of introduced seeds, he soaked various seeds in a tub filled with seawater and counted which of the seeds floated after a given period; later he planted the seeds in the yard at Down to look for potential viability. There was no attempt at controlled, replicated experiments in these studies, or in his work with domesticates, nor should there have been. To Darwin the results of one experiment represented a potential truth of nature, and he was quick to seize upon these results as supporting evidence for his theory.

I have suggested in this paper that his work on domesticates was not simply meant to provide an analogy for natural selection but rather became a research program to investigate other aspects of his natural selection theory, especially inheritance and variability; these subjects were integral parts of his theory of natural selection, but by 1859 he had not found a mechanism to account for them. The experiments brought home the difficult problems of inheritance, and Darwin specifically formulated pangenesis to account for these problems. Pangenesis was not an afterthought but an integration of several decades of thinking on inheritance. It was a unified theory to explain the complicated results he witnessed in his own experiments.

Much of the Darwin scholarship has focused on Darwin's path toward the discovery of natural selection. Natural selection *per se* was a major interest, but not the only area of interest to Darwin. Inheritance was an area of serious concern for him both before and after he had formulated natural selection. His experimentation with domesticates was an attempt to look beyond natural selection and to concentrate on the difficult subject of inheritance. He found inheritance especially troublesome, requiring a "provisional hypothesis" to account for it. To see domesticates, as they are described in the *Origin*, as merely an analogy for natural

selection, does not account for the importance Darwin placed on them. For him they were not man's monstrous productions, but worthy experimental subjects providing him with crucial information on inheritance.

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