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Citation
Sterrett, Susan G. "Darwin's Analogy Between Artificial and Natural Selection: How Does it Go?" *Studies in History and Philosophy of the Biological and Biomedical Sciences* vol. 33 no. 1 (2002): 151-168.

Darwin's analogy between artificial and natural selection: how does it go?

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Received 11 May 2001; received in revised form 30 October 2001

Abstract

The analogy Darwin drew between artificial and natural selection in *On the Origin of Species* has a detailed structure that has not been appreciated. In Darwin's analogy, the kind of artificial selection called Methodical selection is analogous to the principle of divergence in nature, and the kind of artificial selection called Unconscious selection is analogous to the principle of extinction in nature. This paper argues that it is the analogy between these two different principles familiar from his studies of artificial selection and the two different principles he claims are operative in nature that provides the main structure and force of the analogy he uses to make his case for the power of natural selection to produce new species. Darwin's statements explicitly distinguishing between these two kinds of principles at work in nature occur prominently in the text of the *Origin*. The paper also shows that a recent revisionist claim that Darwin did not appeal to the efficacy of artificial selection is mistaken.

Keywords: Darwin; Adaptation; Divergence of character; Artificial selection; Natural selection; Analogy

1. Analogous products and analogous principles

Charles Darwin chose to open his eagerly awaited *On the Origin of Species* with a chapter devoted to domesticated plants and animals, entitled 'Variation under domestication'. It is only in the fourth chapter, entitled 'Natural Selection', that Darwin presents his proposal as to how new species arise in nature. And, in that chapter, too, he begins by comparing the techniques employed by humans in breeding dom-

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esticated plants and animals, which he calls artificial selection, with the process in nature that he calls natural selection. In fact, he explicitly talks about finding principles in nature that are 'analogous' to principles of artificial selection.

But exactly how does the analogy go? The analogy drawn between what Nature has done and what humans have done is supposed to help us understand how species originated. It is based on comparing the diverse species the reader knows to exist in plants and animals in nature and the diverse varieties the reader has just been told can be produced in domesticated plants and animals. Darwin claims that there are analogues of the principles of artificial selection in nature, then shows how those principles produce diverse varieties in domesticated animals and diverse varieties and species in nature. What I will show in this paper is that it is the analogy between two different principles familiar from his studies of artificial selection and the two different principles he claims are operative in nature that provides the main structure and force of the analogy he uses to make his case for the power of natural selection to produce new species. That is, the kind of artificial selection called Methodical selection is analogous to the principle of divergence in nature, and the kind of artificial selection called Unconscious selection is analogous to the principle of extinction in nature.

One can of course construct other analogies from Darwin's text as well. There is a substantial literature on the nature and significance of the analogy between artificial and natural selection. Among those who have argued for the significance of the analogy are Michael Ruse (1971, 1973, 1975), L. T. Evans (1984), Robert Young (1985, 1993), Ken Waters (1986), Doren Recker (1987), James Lennox (1995), Ernst Mayr (1991), Daniel Dennett (1990) and S. Schweber (1977). Some of these analogies are based upon the metaphor Darwin draws between a 'being' or 'unerring power' that performs natural selection (on all the plants and animals that have ever existed) and humans performing selective breeding (on the animals and plants under their control). Thus we find in the literature discussions attributing to Darwin some basic points of analogy between nature's agency (in producing species) and man's agency (in producing varieties), and points of analogy between the processes of artificial selection and natural selection. Alternatively, some see Darwin as alluding to a generalization of the two processes, namely, 'selection'. There are in addition detractors of the analogy, dating from Darwin's day — most notably Alfred Russel Wallace (1895). I shall have more to say about a recent example that appeared in this journal (Richards, 1997) at the end of this essay.

My main concern in this essay is to show that the analogy has a structure that has not hitherto been recognized: the appeal to natural analogues of the two *different kinds* of artificial selection Darwin describes in the chapter on 'Variation under domestication'. Once this structure is seen, the analogy is seen to be crisp and far from anthropomorphic. Further, the analogy is meant not only to convince the reader of the plausibility and efficacy of natural selection, but to help explain *how* natural selection gives rise to both the adaptation and diversity of natural forms.

2. Fanciers and flock owners: their goals and skills

If a simple analogy between 'man' and Nature is sought for in the text of *On the Origin of Species*, one could be forgiven for asking just what it is to which natural selection is supposed to be analogous. For, upon close examination of the examples Darwin gives in educating the reader about the methods of artificial selection (i.e., examples wherein a human permits only certain of the individual plants and animals under his or her care to mate with certain others, and prevents others from reproducing at all) we find that some of these examples differ from others in important ways.

In some examples of artificial selection, the breeder's actions are conscious attempts to produce offspring that exaggerate or combine some characteristics of the current stock of animals. For example, the pigeon fancier's intentional breeding of new varieties of pigeons having extreme and striking characteristics is of this sort. So, too, is the intentional breeding of new varieties of sheep to produce wool with characteristics that will be more useful to people than the wool of those varieties of sheep then in existence. Such activities, Darwin is concerned to impress upon the reader, require great natural skill and years of training:

> Not one man in a thousand has accuracy of eye and judgment sufficient to become an eminent breeder. If gifted with these qualities, and he studies his subject for years, and devotes his lifetime to it with indomitable perseverance, he will succeed, and may make great improvements; if he wants any of these qualities, he will assuredly fail. Few would readily believe in the natural capacity and years of practice requisite to become even a skillful pigeon fancier. (Darwin, 1964, p. 32)

But other examples of artificial selection Darwin gives contrast sharply with this characterization, which is stated in the context of discussing how pigeon fanciers and sheep herd owners intentionally create new varieties. Creation of new varieties is not the only goal at which selective breeding may aim. For, animal breeders of an already established breed select, too: they select only (what they deem to be) the best specimens of the breed used to produce the progeny that will be the next generation of the herd or flock. Such breeders are not intending to produce new varieties and what they do, Darwin says, does not require much skill. In fact, Darwin referred to the corresponding horticulture methodology as 'artless', though, he said, the results effected over long periods of time — such as fruit trees bearing much larger, juicier fruit than their ancestors of many generations hence — were often impressive. To emphasize that very little skill is required, Darwin imagines the kind of artificial selection that would occur if humans did not even realize that characters were inherited. This is the lowest level of skill imaginable, one he is not even sure exists in humans. Yet even it can achieve much:

> If there exist savages so barbarous as never to think of the inherited character of the offspring of their domestic animals, yet any one animal particularly useful to them, for any special purpose, would be carefully preserved during famines and

> other accidents, to which savages are so liable, and such choice animals would thus generally leave more offspring than the inferior ones; so that in this case there would be a kind of unconscious selection going on. (Darwin, 1964, p. 36)

In contrast to how highly he esteems the art of the pigeon fancier and how under appreciated their skill, Darwin thinks the skill of horticulturists is generally highly overrated:

> I have seen great surprise expressed in horticultural works at the wonderful skill of gardeners, in having produced such splendid results from such poor materials; but the art, I cannot doubt, has been simple, and, as far as the final result is concerned, has been followed almost unconsciously. It has consisted in always cultivating the best known variety, sowing its seeds, and, when a slightly better variety has chanced to appear, selecting it, and so onwards. (Darwin, 1964, p. 37)

What artificial selection of either kind aims at is preserving desired characteristics of the plant or animal. Often, however, new varieties are (unintentionally) produced even when the breeder or horticulturist thinks that all he is doing is maintaining a breed standard or type. When new varieties are produced via such a process, the selection for new characters is 'unconscious', reflects the bias of that individual breeder, and, rather than resulting in a number of varieties that are strikingly different from each other, may well result in the condition wherein the breeder's whole stock, though very different from the parent stock from which it descended, is quite homogenous. The change in the breed that is effected by this process, if any, is that of one variety being replaced by another. In these cases of 'artless' breeding, unlike in the case of the pigeon fanciers who aim at creating divergent varieties, it is only when there are different breeders who do not hold a common standard of perfection that we witness diverse varieties generated from the same stock. Darwin attributes this kind of diversity to the flock owners having slightly different standards for the breed, for he implicitly indicates that when different flock owners have the *same* standard in mind, there is uniformity of character even among different flocks: 'when many men, without intending to alter the breed, have a nearly common standard of perfection, and all try to get and breed from the best animals, much improvement and modification surely but slowly follow from this unconscious process of selection' (Darwin, 1964, p. 102).

Thus these two kinds of examples of artificial selection differ. They differ in the skill they require (artless versus extremely difficult); they differ in the goal aimed at by the human employing selection (breeding the best specimens versus breeding with an eye to altering the breed to conform to an as yet unrealized standard); and they differ in the results that may be effected (replacement of one variety by another 'improved' variety versus creating diverse co-existent varieties). As the reader may realize, there is not always a clear line between the two processes; Darwin says in 'Variation under domestication' that they can only be clearly distinguished in extreme cases. Yet he mentions both, referring to them as, roughly, Unconscious and Methodical selection, respectively.

3. Selection, adaptation and divergence

Given the important qualitative differences in Darwin's examples of artificial selection, it is not surprising that some have concluded that he lacked an unambiguous notion of artificial selection. I claim, though, that if we look at the structure of the analogy Darwin drew we will see that it *requires* differentiating between these two different kinds of artificial selection. He is not ambiguous, but has clarified two extremes of artificial breeding practices. Darwin's explanation of how nature has generated the variety of species she has includes both kinds of selection working in conjunction. The kind that Darwin referred to as Unconscious selection works to preserve the character of a species; if favourable variations occur, they produce a variety that replaces the previous species with an 'improved' one. As I shall explain, this kind of selection is appealed to to explain the adaptation of a species to what Darwin called a 'place' in the polity of nature. The kind of selection Darwin called Methodical works to effect divergence of character within a species, creating exaggerated variations that become more and more distinct from one another, resulting in what become, first, distinct varieties and eventually different species. This kind of selection is appealed to to explain what Darwin called the 'principle of divergence' in Nature.

Once the differences in what Darwin called Methodical selection and Unconscious selection are recognized, one sees not confusion but a more delineated analogy. The resulting analogy between artificial and natural selection is far more structured than simply anthropomorphizing nature by drawing an analogy between a human breeder and Nature. This is in fact an analogy Darwin drew in *On the Origin of Species by Means of Natural Selection*. For there, as elsewhere, Darwin is explicit that both processes involved in artificial selection that he describes have their analogue in nature. Why have the studies of the analogy generally not distinguished between the two kinds of selection? I can only surmise that it is because Darwin's readers have been concerned to identify what it is that all the examples of artificial selection have in common. At any rate, Darwin's explicit statements that there are two different principles of artificial selection have, it seems to me, been nearly always either neglected or attributed to confusion. If we instead look at how Darwin uses them in his argument, we see that there is an analogy drawn between nature and breeders that maps these two different applications of artificial selection (roughly speaking, fanciers and flock owners) onto two different kinds of processes in nature. The structure of the analogy gains detail and the correspondence between principles of artificial and natural selection becomes direct once we see that these two processes — roughly, (i) the preservation (and possibly 'improvement') of characters achieved by the flock owner and (ii) a divergence of characters in different varieties produced by fanciers.

I do not mean to deny that there is anything to the claim that Darwin was proposing a mechanism by which species are formed, and that the examples he gives are meant to illustrate a mechanism common to all the cases of artificial selection he gives. For, of course, there *are* some things that the fancier seeking novel varieties and the flock owner seeking perfect specimens have in common. For example, both the flock owner and the fancier recognize the fact that characters are hereditary, the fact that

such modifications as occur are accomplished by small steps that accumulate over generations by influencing which individuals leave progeny, and the fact that forms are continuous. That is, although the pigeon fancier is changing features dramatically and the flock owner is not, even in the case of the fancier seizing on a novel variation (for example, a variation in the number of tail feathers) to produce a new variety (for example, the fan-tailed pigeon) by judicious selection, there is still continuity of form. The fancier effects changes slowly in the sense that small changes in the form of the individual animals bred are accumulated over many generations to result in the exaggerated features that distinguish the variety. However, the fact that sometimes the two kinds of selection are not clearly distinguished in a particular process, and that one can also make sense of these examples as illustrations of a common mechanism, does not contradict my claim. My claim is simply that Darwin draws an analogy in what he called 'one long argument' in the *Origin* that makes use of the distinction between the two kinds of artificial selection I have described.

This is the claim that the rest of my paper will endeavor to establish and explain. Although I will refer to things Darwin says in works other than the *Origin*, what he says there is sufficient to make good my claim. That is, I am not claiming that the structure of Darwin's analogy is a hidden master idea Darwin had that can only be recognized by surveying a variety of his writings, nor that the analogy needs to be uncovered by looking at writings not readily accessible to his contemporaries or not commonly read today. Once the structure of the analogy is pointed out, it can be seen plainly in the *Origin*, indeed in the most frequently anthologized excerpts. It can also be seen in other places: in particular, the main structure of the analogy, including the two clearly distinguished processes and the key examples used later to illustrate them, occur in the earliest exposition of his theory that Darwin provided to anyone: the letter to Asa Gray in which he confided his insights years before he began writing the *Origin*.

4. One complicated analogy

As I have said, Darwin begins *On the Origin of Species by Means of Natural Selection* with three chapters spent educating the reader about the facts of variation under domestication, the facts of variation under nature, and what is meant by 'the struggle for existence'. In Chapter 4 of the work, he then employs the facts he has laid down in the first three chapters to explain natural selection. Since my interest here is in analyzing the analogy Darwin uses in explaining natural selection, I shall begin by looking at how he employs the facts about artificial selection in his explanation of natural selection. He explicitly explains how analogues of principles of artificial selection are involved in the origin of species by means of natural selection in the sections just before he presents the 'Diagram of Divergent Taxa', a tree-like diagram showing how (on his account) species arise over the course of time.

Darwin motivates his account of the effects of natural selection by posing a question: 'Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature? I think we shall see that it can act most effectually'(Darwin,

1964, p. 80). He had actually mentioned the term 'natural selection' in an earlier chapter on domesticated animals. There he had remarked that when dogs were kept by humans who were not always able to provide food for them, and hence sometimes relied on the dogs to catch their own prey, the fact that the dogs had to struggle for their own food, along with the fact that 'individuals of the same species, having slightly different constitutions or structure, would often succeed better in the one country than in the other' implied that 'natural selection' could result in different 'sub-breeds' being formed in different parts of the country (Darwin, 1964, p. 38). And, in his *The Variation of Animals and Plants Under Domestication* (which was written to be part of the longer work to which the *Origin* is supposed to be a preliminary sketch), natural selection is discussed as something at work even in domesticated animals completely under the care of man — on some occasions natural selection works against, and on some occasions with, man's efforts. That is, sometimes the animals men would choose to destroy perish anyway due to natural means, even under domestication, but sometimes animals man would like to preserve are prevented from being born or thriving by natural means. A memorable example of nature working against man's efforts is that of breeding birds with such short beaks that they cannot break out of their shells, so that the fancier breeding an extremely short-faced bird needs to break the chick's shell in order for it to hatch. Thus it has been remarked that the 'best' birds, where best means meeting the fancier's taste for extremes, have died in the shell. But artificial selection does not *always* work against natural selection:

> [Professor Wyman] informs me that, being surprised at all the pigs in a part of Virginia being black, he made inquiries, and ascertained that these animals feed on the roots of the *Lachmanthes tinctoria*, which colours their bones pink, and, excepting in the case of the black varieties, causes the hoofs to fall off. Hence, as one of the squatters remarked, 'we select the black members of the litter for raising, as they alone have a good chance of living'. So that here we have artificial and natural selection working hand in hand. (Darwin, 1998, p. 212)

So Darwin mentions the notion of natural selection earlier in the *Origin* than the chapter devoted to it. What *is* new in the chapter entitled 'Natural Selection' is that the situation being considered is no longer that of animals and plants under domestication. Hence the topic is not the varieties produced by man by whatever means, but the varieties and species that occur in the wild. The struggle for existence is called upon here to explain how, in the absence of a breed standard in the mind of a human, some individuals in the wild may be considered 'favored' over others: instead of 'variations useful to man', in the wild there are 'variations useful in some way to each being in the great and complex battle of life'. Darwin is clear that what is useful is a matter not only of geographical location and climate, but that it is also — and largely — dependent upon the whole network of interdependencies between other animals and plants. He remarks that immigration or extinction of even an apparently insignificant creature or plant in what he called 'the polity of nature' in an animal's surroundings can make the difference between life or death. Here

selection arises, not from being chosen by a human for breeding and hence for producing the progeny that forms the next generation of a flock, but from the fact that in the wild 'individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind' (Darwin, 1964, pp. 80–1).

The features I have just mentioned are recognized by most commentators who lay out Darwin's explanation of the workings of nature in the wild by analogy with the actions of humans in domesticating animals and plants. Time and again Darwin compares Nature as an agent to 'Man' as an agent; for example: 'As man can produce and certainly has produced a great result by his methodical and unconscious means of selection, what may not nature effect?'(p. 83). He gives specific examples, such as: 'If it profit a plant to have its seeds more and more widely disseminated by the wind, I can see no greater difficulty in this being effected through natural selection, than in the cotton-planter increasing and improving by selection the down in the pods on his cotton-trees' (p. 86). He also thinks that, and explains why, Nature is better at it, and her productions are superior, in the sense that they are 'infinitely better adapted to the most complex conditions of life, and … bear the stamp of far higher workmanship' (p. 84). But he goes on to develop the comparison between the agency of humans and the agency of nature further. When it comes to illustrations of the action of natural selection, he is more detailed: 'I can see no more reason to doubt [that the slimmest and fleetest wolves would be preserved or selected] than that man can improve the fleetness of his greyhounds by careful and methodical selection, or by that unconscious selection which results from each man trying to keep the best dogs without any thought of modifying the breed' (p. 90). The two kinds of selection are explicitly mentioned here, and later in the chapter he explains analogues in nature of each of these kinds of artificial selection.

After a general sketch of how natural selection might work to create new species, Darwin addresses the question of how 'the lesser difference between varieties becomes augmented into the greater difference between species':

> As has always been my practice, let us seek light on this head from our domestic productions. We shall here find something analogous. A fancier is struck by a pigeon having a slightly shorter beak; another fancier is struck by a pigeon having a rather longer beak; and on the acknowledged principle that 'fanciers do not and will not admire a medium standard, but like extremes,' they both go on (as has actually occurred with tumbler pigeons) choosing and breeding from birds with longer and longer beaks, or with shorter and shorter beaks. (pp. 111–112)

He points out that in this kind of case, the breeds diverge in character 'both from each other and from their common parent' (p. 112). Now, the 'from each other' is important, as is the 'from their common parent'. Darwin had just mentioned many cases of the kind of selection, both natural and artificial, that results in 'extermination' of the breed of the stock from which the current breed was bred: 'Many curious instances [of the selection of improved forms by man] could be given showing how quickly new breeds of cattle, sheep and other animals, and varieties of

flowers, take the place of older and inferior kinds' (p. 111). Now he is discussing the 'from each other' as well as the 'from their common parent'.

Besides the case of fanciers, there are cases of horse breeders, some of whom prefer swift horses, some of whom prefer strong and bulky horses. In these cases, he says 'we see in man's productions the action of what may be called the principle of divergence, causing differences, at first barely appreciable, steadily to increase, and the breeds to diverge in character both from each other and from their common parent' (p. 112).

But if we are to regard Nature as an agent, it may seem time to drop the metaphor, for the cases Darwin is describing here are of two distinct human agents with different standards in mind. Does the analogy between the agency of humans and the agency of nature break down at this point, then? No, it doesn't — it just gets more structured. Here is what Darwin says:

> But how, it may be asked, can any analogous principle apply in nature? I believe it can and does apply most efficiently, from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers. (Darwin, 1964, p. 112)

Thus, nature does the same work that multiple human agents (for example, different fanciers, different horse breeders) do via the 'many and widely diversified places' different species can occupy 'in the polity of nature'. For it is species or varieties, and not individuals, that occupy these places. Thus, just as we need to relativize selection of the 'best' to a particular fancier or breed standard in artificial selection, so selection of 'favorable variation' in nature is relativized to a 'place' — not a geographical place, but a 'place in the polity of nature' (p. 112). A place in the polity of nature includes relations of a species to predator, prey, competitors, and mutualisms with other plants and animals. The analogy, then, between artificial selection and natural selection includes mapping the principle of divergence in artificial selection to the principle of divergence in nature. A fancier's unfulfilled desire for a certain extreme is analogous to an unoccupied place in the polity of nature. This analogy is quite direct, except for a reversal of the active and passive — i.e., the way Darwin puts it, the pigeon fancier seizes on some hitherto unexploited novelty; a species seizes on an unoccupied place in nature. The way Darwin's choice of wording would identify which is agent and which patient is really not relevant to the analogy, though: since nature's intent is not an essential part of natural selection, the intent of the fancier is only a superficial feature of *this* analogy of Darwin.

Yet in this analogy there is something in nature that provides what we might consider analogous to the motivating force of the tendency of fanciers to prefer extremes. It is hinted at by the principle that 'the greatest amount of life can be supported by great diversification of structure'. It is the force in nature that he sometimes referred to as 'wedging', wherein species are 'wedged' into unoccupied (or not fully occupied) places in the polity of nature as a consequence of the struggle

for existence. The way he puts the point in *On the Origin of Species* is that 'each species and each variety of grass is annually sowing almost countless seeds; and thus, as it may be said, is striving its utmost to increase its numbers' (pp. 113–4). How this kind of force leads to diverse species is best illustrated by his explanation of the advantage that a variety of a carnivorous species that is 'less carnivorous' might have: 'The more diversified in habits and structure the descendants of our carnivorous animals became, the more places they would be enabled to occupy'. As for animals, so for plants:

> It has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised. The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground. (p. 113)

The principle of divergence is thus a point of analogy between artificial and natural selection, and a quite direct one at that: different fanciers preferring extremes are analogous to different and diversified places in the polity of nature. As fanciers produce varieties that differ greatly from each other, nature produces varieties that eventually become different species. The analogy is so direct that Darwin sometimes refers to 'the' principle of divergence being operative in each case. But it is no flaw in an analogy if some of the correspondences are between identicals.

Under a separate heading ('Extinction'), Darwin discusses the process that is analogous to the kind of unconscious selection in which one variety replaces another: i.e., a breeder whose flock is homogenous but differs from the stock from which the individuals descended. Related examples are the English racehorse and the English pointer, which 'diverge in character from their original stocks, without either having given off any fresh branches or races' (p. 120). Rather than divergence of character, there is a sort of longitudinal progression, wherein earlier varieties are completely replaced by later ones. Darwin is absolutely explicit that there is an analogy between extinction of earlier forms in natural selection and in artificial selection; he says 'We see the same process of extermination amongst our domesticated productions, through the selection of improved forms by man' (p. 110). He cites as an especially striking case the breeding of cattle in Yorkshire, wherein long-horns replaced ancient black cattle, and then short-horns replaced long-horns. He explains the principle of extinction as a matter of extinction of intermediate forms: 'it is the most closely-allied forms, — varieties of the same species, and species of the same genus or of related genera — which, from having nearly the same structure, constitution, and habits, generally come into the severest competition with each other' (p. 111).

5. Principles in (slow motion) action

Darwin's statements explicitly distinguishing between these two kinds of principles at work in nature — i.e., divergence of character and extinction (of earlier

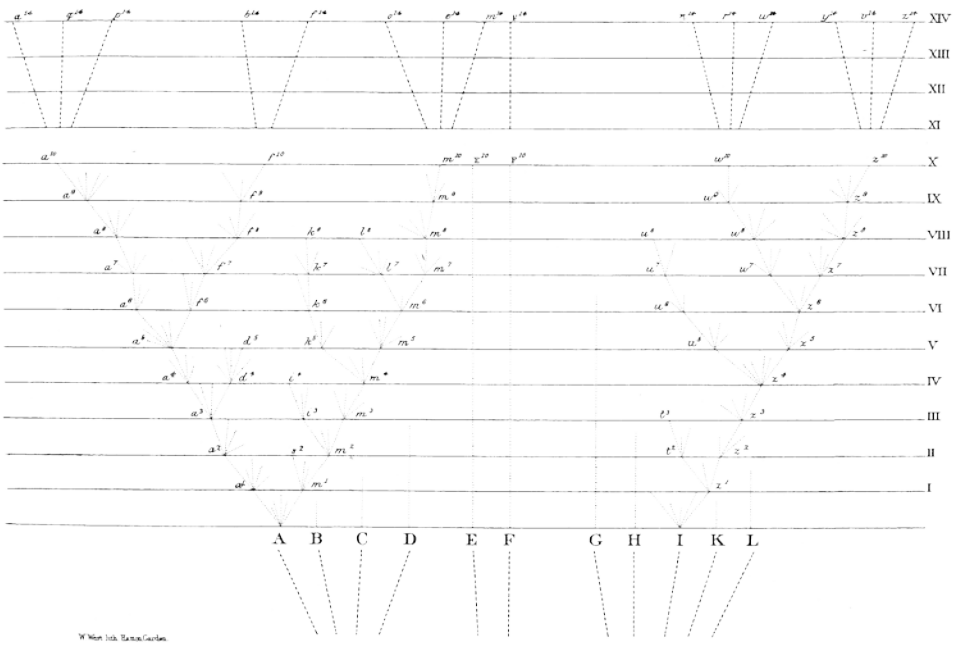

Fig. 1. Diagram of divergent taxa (From <>Darwin, 1964, ch, 4<>; courtesy of the Whipple Library, University of Cambridge).

forms) — and mapping them onto two kinds of artificial selection, are in the chapter in the *Origin* entitled ‘Natural Selection’. They are not in the least obscure or difficult passages. They occur prominently in the main part of the chapter, with headings highlighting the topics (‘Extinction’ and ‘Divergence of Character’). Directly after laying out the correspondence between each principle of artificial selection and its corresponding principle in nature, Darwin shows how they work in conjunction to produce new and diverse species over the course of many millions of generations.

The diagram represents time vertically in the sketch, the bottom of the page being the earliest point in time represented, and the top of the page being the latest point in time represented. The time scale is marked off into fourteen equal segments by fifteen horizontal lines. Darwin tells us to imagine, for the sake of discussion, that a thousand generations occur between any two of these lines, although he later remarks: ‘In the diagram, each horizontal line has hitherto been supposed to represent a thousand generations, but each may represent a million or hundred million generations’ (p. 124).

The horizontal dimension of the diagram represents, qualitatively, amount of resemblance between species. That is, there are a dozen species of one genera, named A to L, represented along the bottom of the diagram. They appear at uneven distances from one another; the distance between them corresponds to how closely they resemble each other.

Darwin asks us to suppose that species A is a 'common, widely-diffused, and varying species, belonging to a genus large in its own country'. On the diagram, Darwin depicts a fan-like array of lines originating at A; he explains: 'The little fan of diverging dotted lines of unequal lengths proceeding from (A), may represent its varying offspring'. Here is where, he says, the principle of divergence comes in. Now, recall that he has given an argument for why the principle of divergence, which occurs in artificial selection, is a principle in nature. At this point in the argument, he appeals to this as established: 'this will generally lead to the most different or divergent variations (represented by the outer dotted lines) being preserved and accumulated by natural selection' (Darwin, 1964, p. 117). Thus, after a thousand generations, there are two surviving varieties descended from (A); he calls them a1 and m1. He gives arguments for why there will be great variability in a1 and m1, which I will not go into here.

What I want to draw attention to is that there are two different kinds of principles at work, corresponding to the two kinds of artificial selection, and that one explains the occurrence of branching in the diagram, the other explains changes along a given individual branch. The principle of divergence accounts for the branching, which, as time goes on, spreads species apart from each other along the horizontal dimension. This branching is analogous to what occurs in the kind of artificial selection in which a breeder intends to alter the breed. It is effected in artificial selection by different breed standards, whether this is due to two different breeders using different standards, or by a single fancier or breeder intentionally creating a new variety by selecting according to an as yet unrealized standard (i.e., a fancier who is creating more than one variety from the same stock). It is effected in natural selection by the existence of unoccupied or less than fully occupied places in the polity of nature.

What is depicted by the existence of branching along the horizontal dimension of the graph is diversification. Variety a1 begets, after another thousand generations, variety a2. This is depicted by a dotted line that veers slightly to the left; the diagram also depicts the variety m2 veering off to the right, thus depicting not only that variety a2 differs from ancestor (A) even more than a1 did, but that it differs even more from other varieties that developed from ancestor (A), as a result of the principle of divergence being at work. The principle of divergence accounts for the fact that varieties that develop from the same parental stock diverge from each other. Similar things follow from variety m1 after a thousand generations; Darwin shows m1 begetting two varieties, m2 and s2 (the numerical suffixes here indicate location along the vertical axis, i.e., m2 and s2 are both varieties as they exist after the second segment of time — 2000 generations — on the diagram). But it is m2, rather than s2, that survives to the epoch III, and the principle of divergence accounts for this: m2 differs more from both from a2 and from ancestor (A) than m1 did. And so on, so that 'the varieties or modified descendants, proceeding from the common parent (A), will generally go on increasing in number and diverging in character … After fourteen thousand generations, six new species, marked by the letters n14 to z14, are supposed to have been produced' (p. 121). As to how these species are related to each other on the horizontal dimension of the diagram, 'Owing to the divergent

tendency of natural selection, the extreme amount of difference in character between species a14 to z14 will be much greater than that between the most different of the original eleven species'. The difference in location along the horizontal dimension corresponds to occupancy in different places in the polity of nature.

However, Darwin qualifies this sketch, granting that things are not always so straightforward as in the cases depicted on the diagram: 'I am far from thinking that the most divergent varieties will invariably prevail and multiply: a medium form may often long endure, and may or may not produce more than one modified descendant.' It is important to note, though, that he actually accounts for why such diversification is only a general rule, and why there are medium forms when they do occur: 'for natural selection will always act according to the nature of the places which are either unoccupied or not perfectly occupied by other beings; and this will depend on infinitely complex relations' (p. 119).

He also remarks that conditions may be such that there is no diversification for many thousands of generations: 'In some cases I do not doubt that the process of modification will be confined to a single line of descent, and the number of the descendants will not be increased; … This case would be represented in the diagram, if all the lines proceeding from (A) were removed, excepting that from a1 to a10.' Again, it is instructive to note Darwin's explanation of the case; it appeals to the kind of artificial selection in which there is a widely recognized breed standard of an established breed: 'In the same way, for instance, the English race-horse and English pointer have apparently both gone on slowly diverging in character from their original stocks, without either having given off any fresh branches or races'(p. 120). There is change, but not diversification.

There is another kind of case in which there is neither diversification nor change in form. Such a case is indicated on the diagram by a vertical line from a species F to F16. In artificial selection, this kind of case corresponds to keeping the same breed standard, wherein, inasmuch as there is any selection, it only effects 'improvement' of the species according to the same breed standard. In natural selection, this kind of case is adaptation to a certain place in the polity of nature. The reason this kind of change does not warrant a veering off to the left or right in Darwin's diagram is that this kind of change does not correspond to a change in place in the polity of nature.

Thus, Darwin here recognizes a difference between the kind of modifications due to diversification, and the kind that does not involve diversification. In nature the difference is this: if a species diversifies in order to occupy more or different places in the polity of nature, the change in 'place' occupied by the new variety is depicted by relative distance along the horizontal dimension between different varieties or species; whereas, if a species is modified in virtue of being more perfectly adapted to a given place in the polity of nature, there is no movement along the horizontal dimension.

This brings us to the vertical dimension of the diagram. Whether or not diversification has occurred, there may well be change along the vertical dimension. Diversification of species corresponds to diverse places in the polity of nature; but, given a certain place in the polity of nature, we can consider the modification of the variety

or species occupying it. Darwin writes: ‘during the process of modification, represented in the diagram, another of our principles, namely that of extinction, will have played an important part … there will be a constant tendency in the improved descendants of any one species to supplant and exterminate in each stage of descent their predecessors and their original parent’ (p. 121). As I have said, Darwin’s notion of extermination includes extermination by a more ‘improved’ form replacing a parent form as well as of one co-existent species beating out a closely allied (we might say ‘sibling’) species. Thus, in his discussion of the changes from each of the points along the vertical scale (I, II, III, … XIV) to another, Darwin assumes that, usually, change will have occurred. By now the reader will guess what I want to say here: change along the vertical scale is due to the principle of extinction (of earlier forms). In natural selection, this is adaptation to a particular place in the polity of nature; in artificial selection, ‘improvement’ of the breed. Thus, the analogy has the following structure:

1. As *the principle of divergence in nature* (‘the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers’(p. 112)) *effects (i.e., brings about) diversification of varieties that eventually become new species* in natural selection, so the *principle of divergence in human breeding practices* (for example, that ‘fanciers do not admire a medium standard, but like extremes’, that humans breed animals for different purposes, or that different breeders breeding from the same stock might unconsciously be biased in their conception of the breed standard) *effects diversification of varieties* that become more and more distinct from each other in artificial selection.
2. As *the principle of extinction in nature* (‘there will be a constant tendency in the improved descendants of any one species to supplant and exterminate in each stage of descent their predecessors and their original parent’ — p. 121) *results in species more perfectly adapted to their places in nature*, so the *principle of extinction in breeding practices* of human breeders (‘improved’ breeds and varieties meeting a given, well defined, already realized standard with a higher and higher degree of excellence supplant less improved ones) *results in ever more ‘perfect’ breeds*.
3. As *these two principles work in conjunction in natural selection* to effect a branching ‘Tree of Life’ structure resulting in more and better adapted species, so *these two principles work in conjunction in artificial selection* to effect more widely differing and more ‘improved’ varieties.

There is more to Darwin’s argument than this analogy. In particular, that large genera and large flocks increase the number of variations that will occur plays a part in his argument for how things unfold over generations in the ‘diagram of taxa’ presented in the *Origin*. I will not go into that here, except to remark that Darwin’s argument contains (though it involves more than) this analogy. What I have sketched out above is a very important analogy in *On the Origin of Species* that is part of

what Darwin called ‘one long argument’. It is the analogy he builds up throughout the first four chapters, resulting in his explanation of how new species can arise by means of natural selection, illustrated by the branching tree diagram (Figure 1) near the end of Chapter 4, ‘Natural Selection’.

6. A recent revisionist

In some recent articles, Richard A. Richards (1997, 1998) claims that Darwin ‘was not arguing by analogy with domestic breeding to establish the causal efficacy of selection … instead of relying on the similarities between artificial and natural selection (as would be expected in an analogical argument), Darwin’s argument relies on the differences between artificial and natural selection’ (Richards, 1998, p. 106). Richards claims: ‘When we examine the summary of that argument [for the causal efficacy of natural selection] in the chapter on natural selection of the *Origin*, we find that there is but a single reference to domestic breeding, related to the usefulness of specific variations’ (Richards, 1998, p. 108). Richards considers that this lends support to his claim that the analogy Darwin employs between domestic breeding and nature ‘is not part of his argument to establish the causal efficacy of natural selection’. However, this is hardly supportive of his claim. For, at the point in the text of the *Origin* where this summary appears, Darwin had just explained that the principles at work in ‘the complex action of natural selection, entailing extinction and divergence of character, as we have seen illustrated in the diagram’, are principles of both artificial and natural selection, and he had appealed to artificial selection to show that the principles are efficacious. Thus, it is certainly superficial to claim that Darwin does not appeal to the analogy in his argument on the basis that in the short summary in Chapter 4 he did not add something to the effect that ‘the principle of extinction is at work in artificial selection as well as in natural selection, and the principle of divergence is at work in artificial selection as well as in natural selection’.

Darwin had just laid out the correspondence, thoroughly and explicitly, in explaining his diagram. And he had remarked on the process of creation by artificial selection of new and diverse breeds (at first, sub-breeds, then distinct breeds) in the section leading up to the summary. Thus it seems clear to me that what Darwin means there is that artificial selection *is* in fact efficacious: ‘we see in man’s productions the action of what may be called the principle of divergence, causing differences, at first barely appreciable, steadily to increase, and the breeds to diverge in character both from each other and from their common parent’ (Darwin, 1964, p. 112).

Richards offers this revisionist account of Darwin’s argument in an attempt to vindicate him. It should be clear that I think that Darwin does not need any help. I think Darwin draws a fine analogy. But it may be of interest to see how Richards arrives at the conclusion that Darwin draws no analogy at all between artificial and natural selection.

In citing Darwin’s views on the relation between artificial and natural selection, Richards selects only those passages in ‘Variation under domestication’ in which

natural selection works *against* artificial selection. Then, he uses such examples to claim as a principle that 'artificial selection opposes fitness'. Richards then makes this principle the foundation of an argument for the 'inefficacy of artificial selection'. But, as Darwin himself has pointed out in the passage I have cited above about the pigs in Virginia, this is not so! What Darwin said about that example was: 'here we have artificial and natural selection working hand in hand' (p. 212). Richards argues from the mistaken claim that artificial selection always opposes fitness to the claim that artificial selection can only produce large variations, not new varieties. Then he says: 'But natural selection must not only be able to produce new species, it must be able to produce, via divergence from common ancestry, all the species that have ever existed. This means that the process in nature must be unlimited. Artificial selection, by virtue of its opposition to fitness, is a dead-end process. As processes, artificial and natural selection differ in kind' (Richards, 1997, p. 95).

Richards cites Alfred Russel Wallace as an ally in his cause. It is no secret that Wallace thought that Darwin was making a mistake in using the analogy between natural and artificial selection. However, even Wallace did not hold the extreme view that Richards does. For Wallace himself addressed the specific objection that Richards raises: the objection that natural selection requires unlimited change, whereas all that artificial selection can produce is limited change. The objection was raised during Darwin and Wallace's time, and Wallace responded to it. In an 1868 essay, 'Creation By Law', in the subsection entitled 'The Objection that there are Limits to Variation', Wallace wrote: 'But the writer [of the essay making the objection] does not perceive that this argument fails to meet the real question, which is, not whether indefinite and unlimited change in any or all directions is possible, but whether such differences as do occur in nature could have been produced by the accumulation of variations by selection.' After giving numerous examples of both domesticated and wild animals, Wallace concludes: 'The known range of variation is, therefore, more than enough for the derivation of all the forms of dogs, wolves, and foxes from a common ancestor' (Wallace, 1895, p. 160).

I hope that the part of Darwin's argument I have illuminated in this paper can add something helpful to the discussion of the relationship between natural and artificial selection. It should ward off the inclination to offer either apologia for or revisions of Darwin's analogy, for it shows that the analogy is not a gross one between artificial and natural selection. Rather, Darwin's analogy has a finer structure, which I have laid out in this paper. There is an analogy drawn between a fancier's particular intent (or unfulfilled desire for a particular extreme variation) and a particular unoccupied 'place' in the polity of nature. Once it is recognized that fitness is *relative to* a 'place' in the polity of nature, the claim that artificial selection always and necessarily opposes fitness loses its credibility and Richards's basis for his claim that the analogy between artificial and natural selection cannot support the efficacy of selection dissolves.

In Darwin's words, 'natural selection will always act according to the nature of the places which are either unoccupied or not perfectly occupied by other beings; and this will depend on infinitely complex relations' (p. 119). Isn't being a domesticated animal just one more place in the polity of nature? Darwin was well aware of

mutualisms between species. The relationship between humans and the animals they domesticate is just one such mutualism.

Acknowledgements

The main idea pursued in this paper was conceived while I was attending a very enjoyable and stimulating seminar, 'The Life and Work of Darwin', co-taught by Susan Alberts and Dan McShea at Duke University in the Fall of 2000. Thanks to the participants in that seminar for helpful comments, especially to Grant Ramsey and Tamler Sommers, and to Susan Alberts, Robert Brandon, Clark Glymour, Jim Lennox, Dan McShea and Alex Rosenberg for encouragement and suggestions. Thanks also to the audience at the Center for the Philosophy of Science at the University of Pittsburgh for many interesting comments.

In earlier versions of this paper, including the talk given at the Center for Philosophy of Science at the University of Pittsburgh, I claimed that one of these principles explains what happens along the horizontal dimension, and the other principle explains what happens along the vertical dimension of the diagram. It was Grant Ramsey, currently a doctoral student at Duke University, who showed me that this was not really correct, since unconscious selection can of its own accord cause movement along the horizontal dimension of the diagram. I am grateful to him for conversations that led me to see this was not correct and that helped me to figure out what I did want to say.

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