



Modus Darwin*

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Abstract. *Modus Darwin* is a principle of inference that licenses the conclusion that two species have a common ancestor, based on the observation that they are similar. The present paper investigates the principle's probabilistic foundations.

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Similarity, ergo common ancestry. This form of argument occurs so often in Darwin's writings that it deserves to be called *Modus Darwin*. The finches in the Galapagos Islands are similar, hence they descended from a common ancestor. Human beings and monkeys are similar, hence they descended from a common ancestor. The examples are plentiful, not just in Darwin's thought, but in evolutionary reasoning down to the present.

If two finch species have a common ancestor and human beings and monkeys have a common ancestor, do those two common ancestors themselves have a common ancestor? How far does this knitting together of species proceed? Do every two contemporaneous organisms trace back to a third organism that was their common ancestor? Modern biology tells us that there is *one* tree of life; all known species on Earth are thought to be related genealogically. In the last paragraph of the *Origin*, Darwin seems a bit more circumspect. In his famous exclamation that "there is grandeur in this view of life," he says that at the beginning, life was "breathed into a few forms or into one (Darwin 1859: p. 490)." However, only a few pages before, Darwin takes a stronger position:

... I believe that animals have descended from at most only four or five progenitors, and plants from an equal or lesser number.

Analogy would lead me one step further, namely to the belief that all animals and plants have descended from some one prototype. But analogy may be a deceitful guide. Nevertheless all living things have much in common, in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth and reproduction. We see this even in so trifling a circumstance as that the same poison often similarly affects plants and animals; or that the poison secreted by the gall-fly produces monstrous growths on the wild rose or oak-tree. Therefore I should infer from analogy that probably all organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed (Darwin 1859: p. 484).

Notice that Darwin embraces the view that there is a single phylogenetic tree on the grounds that “all living things have much in common.”¹ Perhaps if plants and animals were less similar, Darwin would have opted for the hypothesis that all animals are genealogically related and that all plants are too, but that there is no ancestor that animals and plants have in common. This points to the first question we must ask about *Modus Darwin*: How much similarity is needed for common ancestry to be a good inference?

If similarity is evidence *for* common ancestry, then difference is presumably evidence *against*. In general, if E is evidence for the hypothesis H, then not-E would be evidence against H.² Species are similar in some respects and different in others. Do the dissimilarities count against the hypothesis of common origins, and favor the hypothesis of independent origination? Since human beings have language and chimps do not, isn't this evidence against the hypothesis of common ancestry? Our second question about *Modus Darwin* is how it interprets observed dissimilarity. Do creationists use the same mode of argument as evolutionists, and merely concentrate on different data?

It now is clear that evolutionary theory has nothing against the idea that different lineages should evolve in different directions. This was already implicit in Darwin's definition of evolution as *descent with modification* and quite explicit in his principle of *divergence*. Yet, Darwin seems to have thought that he had to highlight similarity to make the case for evolution, and to relegate difference to the shadows.³ If the theory is compatible with both similarity and difference, why is it the former, but not the latter, that counts as evidence for common ancestry?

Genealogical relatedness – the tree of life hypothesis – is just one half of Darwin's theory. The other half is the claim that natural selection was an important cause of the similarities and differences one sees within and among species. The third question we need to ask about *Modus Darwin* is how these two halves of his theory are related, to each other, and to patterns of organic

diversity. Do these two parts of the theory receive separate and independent confirmation, or are they somehow linked conceptually so that evidence for or against one part tends to bear on the other?

A Bayesian decomposition

Modus Darwin is not a deductively valid form of inference. Similarity does not deductively guarantee common ancestry. Perhaps, then, we should seek to determine why similarity renders the existence of a common ancestor *probable*. Bayes' theorem describes how that posterior probability – the probability of the hypothesis of common ancestry, conditional on an observed similarity – decomposes into three other quantities.

$$(1) \quad \Pr(\text{Common Ancestor} \mid \text{Similar}) = \frac{\Pr(\text{Similar} \mid \text{Common Ancestor})\Pr(\text{Common Ancestor})}{\Pr(\text{Similar})}.$$

Similarly, if we apply Bayes' Theorem to the hypothesis of separate origination, we obtain:

$$(2) \quad \Pr(\text{No Common Ancestor} \mid \text{Similar}) = \frac{\Pr(\text{Similar} \mid \text{No Common Ancestor})\Pr(\text{No Common Ancestor})}{\Pr(\text{Similar})}.$$

Equations (1) and (2) together yield the following:

$$(3) \quad \Pr(\text{Common Ancestor} \mid \text{Similar}) > \Pr(\text{No Common Ancestor} \mid \text{Similar}) \text{ iff} \\ \Pr(\text{Similar} \mid \text{Common Ancestor})\Pr(\text{Common Ancestor}) > \\ \Pr(\text{Similar} \mid \text{No Common Ancestor})\Pr(\text{No Common Ancestor}).$$

Equation (3) tells us how to determine which hypothesis has the higher posterior probability. This depends on the prior probabilities, but also on how probable each hypothesis says the observed similarity is. Observation enters this problem by way of quantities of the form $\Pr(\text{Observations} \mid \text{Hypothesis})$. R.A. Fisher called these quantities the “likelihoods” of hypotheses; the likelihood of a hypothesis should not be confused with the hypothesis' probability.

Likelihood is a good measure of the degree to which an observation *supports* a hypothesis; if two hypotheses confer different probabilities on

an observation, then the observation *discriminates* between them. It *favours* the hypothesis that confers the higher probability. If we obtain 503 heads in 1000 tosses of a coin, this supports the hypothesis that the coin is fair better than it supports the hypothesis that the coin has a 0.9 probability of landing heads. As this example illustrates, a set of observations can favor a hypothesis even though the hypothesis says that the observations were very improbable. Similarly, a set of observations can point away from a hypothesis even though the hypothesis confers a high probability on the observations. The point of likelihood is *comparative*; the question is not whether $\text{Pr}(\text{observations} \mid \text{hypothesis})$ is low or high, but whether this quantity is lower or higher than the likelihoods of other hypotheses, relative to the same set of observations.

Equation (3) decomposes the problem into two components – prior probabilities and likelihoods. We now need to see how each of these components should be evaluated. Without considering the observed similarities and differences that characterize two species, how probable is it that they trace back to a common ancestor? Is this more probable than their having separate ancestors? We want our answer to this question to be *objective*. We are not interested in how strong someone’s prior prejudices are on the subject. However, if prior probabilities are not subjective degrees of belief, on what can they be based?

Similarly, how are we to evaluate the likelihood of the hypothesis of common ancestry and the likelihood of its negation? How probable is it that two species will be similar if they have a common ancestor, and how probable is it that they will be similar if they do not? These likelihoods also seem difficult to estimate. The hypothesis of common ancestry, and its negation, are not sufficiently *specific* for us to assign values. If a fair coin is tossed 10 times, we know how probable it is that there will be 6 heads. But the hypotheses we are considering are not like this. How, then, are we to analyze the likelihood foundations of *Modus Darwin*?

Prior probabilities

Let’s begin with the question of prior probability. How many “start-ups” and “blow-ins” have probably occurred in the history of the earth? A start-up is a process wherein living things are assembled on earth from materials that are not alive. Start-ups include the processes that biologists study under the heading of prebiotic evolution. However, if intelligent design ever created life from nonlife, then a start-up can be the work of a designer. A “blow-in” is a process that brings living materials to earth from elsewhere. The concept of a start-up and that of a blow-in both require that we use some definition of

“life.” Just to make the discussion reasonably concrete, let’s suppose that an object is alive if it can make copies of itself.

How many trees of life have existed on earth, however briefly? That is, how many start-ups and blow-ins have occurred? To answer this question, we need to think probabilistically. What we’d like to know is the *expected number* of these events. If s_i is the probability that exactly i start-ups occurred and b_j is the probability that there were exactly j blow-ins (each assumed to be genealogically unrelated to the others), then the expected value of the number of trees can be expressed as follows:

$$E(\text{number of trees}) = \sum_{i=0}^{i=\infty} i(s_i + b_i).$$

How are we to estimate the value of $E(\text{number of trees})$? Recall that this is supposed to be a *a priori* expected value. This doesn’t mean that we must base our estimates solely on knowledge that is *a priori* in the traditional philosophical sense of being knowable independent of sense experience. We are perfectly entitled to use whatever empirical knowledge we have, apart from our observations concerning the similarities and differences of living things.

There is a second question about prior probabilities that is worth considering. Suppose there were thousands of start-ups and blow-ins, but that only one of them survived for more than a few years and it is this one tree that connects all present and future species and all fossils that will ever be found. In this circumstance, all the species we will ever observe, either while they are alive or after they go extinct, will belong to a single tree. So quite apart from the expected value of the number of trees, there is the expected value of C , where C is the number of trees that connect species that now are alive or that now are fossilized.⁴ The value of $E(C)$ will depend not just on the number of start-ups and blow-ins that have occurred, but on the probabilities that various trees persist long enough to connect with present species or fossils. Let p_{ij} be the probability that exactly i trees persist in this sense, given that there were exactly j start-ups and blow-ins ($i \leq j$). Let o_j represent the probability that there were exactly j origination events (start-ups and blow-ins). Then the probabilities of the various values of C are as follows:

$$\Pr(C = 1) = o_1 p_{11} + o_2 p_{12} + \dots + o_n p_{1n}$$

$$\Pr(C = 2) = o_2 p_{22} + o_3 p_{23} + \dots + o_n p_{2n}$$

$$\Pr(C = i) = \sum_{j=i}^{j=\infty} (o_j)(p_{ij}).$$

What must these probabilities look like for $C = 1$ to be more probable than its negation? One possibility is for origination events to be so vastly improbable that there probably was just one in the whole time since the earth began. A second possibility is that start-ups and blow-ins are not terribly improbable, but that once one happened, it destroyed the conditions needed for further such events to occur. A third possibility is that several start-ups or blow-ins probably occurred, but that it was very improbable that more than one of them persisted long enough to connect with present species and presently observable fossils. This might have been because different trees competed so intensely that all but one was driven to extinction long ago.

As far as I know, biologists are now not in a position to argue that the prior probability of $C = 1$ exceeds the prior probability of its negation. Present knowledge of the conditions pertaining to prebiotic evolution makes it difficult to say very much about the values of the o_j 's and of the p_{ij} 's. The same agnosticism is appropriate with respect to the question of whether the prior probability of there being one tree exceeds the prior probability that there was more than one. However, if these prior probabilities are obscure, the same will be true of the posterior probabilities. This can be seen by inspecting proposition (3). Thus, if *Modus Darwin* licenses the conclusion that a single tree of life is more probable than its negation, it is questionable whether this form of argument really makes sense.

It does not follow, however, that scientists have no basis for evaluating claims of common ancestry, or for saying that all life is related. Rather, what we need to consider is the possibility that *Modus Darwin* is species of likelihood inference. Even if observed similarities don't render the hypothesis of common ancestry more *probable* than its negation, it remains to be seen whether these observations *strongly favor* the one hypothesis over the other.

The fact that it is hard to see how *Modus Darwin* is a species of probable inference should not send alarm bells ringing among evolutionists. It often happens in science that likelihood arguments stand on their own, even when probability arguments are not to be had. For example, relativity theory is tested against Newtonian mechanics by seeing what each predicts about observations; the theories disagree about what observations one should expect. This test procedure goes forward, even if it is entirely unclear what prior probabilities those two theories possess.⁵

Likelihood

Suppose we observe that two species X and Y have trait T. If they have a common ancestor, then Y will be identical with Y_1 or with Y_2 or ... or with Y_n in Tree 1 depicted in Figure 1. If they do not have a common ancestor,

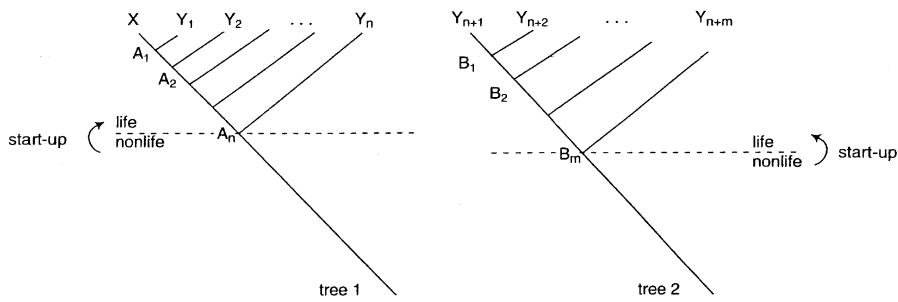


Figure 1.

then Y will be identical with Y_{n+1} or with Y_{n+2} or ... or with Y_{n+m} in Tree 2, also depicted in that figure. I have drawn these two trees to indicate that if X and Y derive from separate origination events, these events may have occurred at different times.

The hypothesis of common ancestry (CA) encompasses a variety of possibilities. X and Y might be very closely related or they may be related only more distantly. If $Y = Y_1$, then the most recent common ancestor of X and Y is A_1 ; if $Y = Y_2$, then the most recent common ancestor is A_2 ; and so on. We will say that X and Y are i -related ($1 \leq i \leq n$) when A_i is their most recent common ancestor.

What is the probability that X and Y will have trait T , if they share a common ancestor? Since the (CA) hypothesis is disjunctive, its likelihood will be a weighted summation:

$$\Pr(X \text{ and } Y \text{ have } T \mid \text{CA}) = \sum_{i=1}^{i=n} \Pr(X \text{ and } Y \text{ have } T \mid X \text{ and } Y \text{ are } i\text{-related}) \times \Pr(X \text{ and } Y \text{ are } i\text{-related} \mid \text{CA}).$$

To assign a value to the likelihood of the common ancestry hypothesis, we apparently would have to assign values to the component probabilities described. However, this isn't necessary if we wish merely to assess whether the observed similarity of X and Y favors the common ancestry hypothesis (CA) over the hypothesis of separate ancestry (SA). Comparing likelihoods requires less knowledge than estimating their values, as we now will see.

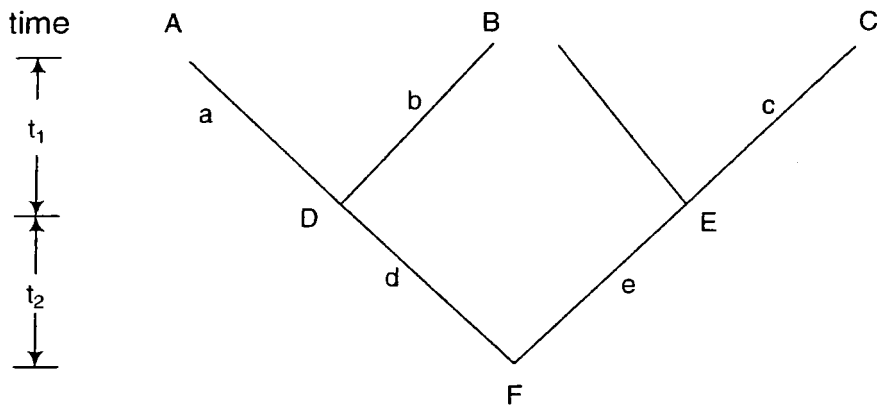


Figure 2.

Modus Darwin with uniform rates

There is an assumption that greatly simplifies the task of comparing the likelihoods of (CA) and (SA). Biologists call it the *uniform rate assumption*; it can be explained by considering Figure 2. Here we see a phylogenetic tree whose evolution from root to tips is divided into two temporal periods. t_1 and t_2 . Nodes in this tree are labeled with capital letters; these represent species. Branches are labeled with lower case letters; these represent the probabilities of various events occurring in the lineages connecting ancestors with their descendants. Suppose that the root species F has the characteristic T. We wish to describe the probability that the tip species (A, B, and C) have that trait as well. This outcome will depend on the value of $d = \Pr(D \text{ has T} \mid F \text{ has T})$ and of $e = \Pr(E \text{ has T} \mid F \text{ has T})$. It also will depend on $a = \Pr(A \text{ has T} \mid D \text{ has T})$, on $b = \Pr(B \text{ has T} \mid D \text{ has T})$, and on $c = \Pr(C \text{ has T} \mid E \text{ has T})$. The uniform rate assumption says that $a = b = c$ and that $d = e$. If two branches are contemporaneous, then any conditional probability that describes the one also describes the other. The assumption of uniform rates does not entail that rate are *constant*. Constant rates would mean that $a = d$, if t_1 and t_2 have the same durations.

If rates are uniform then X and Y have a higher probability of being similar, the more closely related they are (Sober 1988: p. 208):

$$(4) \quad \Pr(X \text{ and } Y \text{ and have T} \mid X \text{ and } Y \text{ are } i\text{-related}) > \\ \Pr(X \text{ and } Y \text{ and have T} \mid X \text{ and } Y \text{ are } j\text{-related}), \text{ if } i < j.$$

With respect to Figure 1, this means that a *lower-bound* on the likelihood of the hypothesis of common ancestry is provided by the case in which X and Y are n-related:

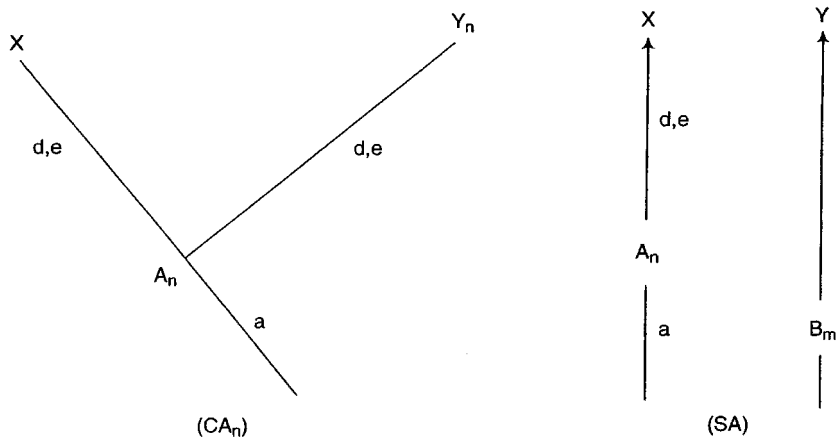


Figure 3.

$$(5) \quad \Pr(\text{X and Y have trait T} \mid \text{CA}) > \\ \Pr(\text{X and Y have trait T} \mid \text{X and Y are n-related}).$$

Thus, if we can show that

$$\Pr(\text{X and Y have T} \mid \text{X and Y are n-related}) > \\ \Pr(\text{X and Y have T} \mid \text{SA}),$$

we will have described a circumstance in which *Modus Darwin* makes sense as a mode of likelihood inference.

Our new formulation of the likelihood problem is depicted in Figure 3. On the left, we have the hypothesis that species X and Y are $n =$ related; on the right we have the hypothesis (SA) that X and Y have separate ancestors. The letters a, d, and e are probabilistic parameters, whose meaning I'll now explain. Notice that no parameters are represented in the figure for the right-hand half of (SA); I'll explain why shortly.

Although we will not discuss the probabilities of a common ancestor's existing or of separate ancestors' existing – remember that this is a likelihood argument – we will need to represent the probability that these ancestors have trait T:

$$(A) \quad \Pr(A_n \text{ has trait T} \mid \text{CA}_n) = \Pr(A_n \text{ has trait T} \mid \text{SA}) = a.$$

I call this proposition (A) because it describes the probability that an *ancestor* will have trait T.

We also need to represent the probabilities that X and Y have trait T, conditional on the possible states of their ancestors:

- (B) $\Pr(X \text{ has trait } T \mid A_n \text{ has } T \ \& \ CA) = d$
 $\Pr(X \text{ has trait } T \mid A_n \text{ does not have } T \ \& \ CA) = e$
 $\Pr(Y \text{ has trait } T \mid A_n \text{ has } T \ \& \ CA) = d$
 $\Pr(Y \text{ has trait } T \mid A_n \text{ does not have } T \ \& \ CA) = e$
 $\Pr(X \text{ has trait } T \mid A_n \text{ has } T \ \& \ SA) = d$
 $\Pr(X \text{ has trait } T \mid A_n \text{ does not have } T \ \& \ SA) = e$

I call these six propositions (B) because they describe the probabilities of various events in *branches*; they represent the probability that a branch will end in a given state, given that it begins in some state. Notice that the use of “d” in the first and third lines and of “e” in the second and fourth is a consequence of the uniform rates assumption. And the use in the fifth and sixth lines of the same parameters that were used in the first four represents the assumption that the conditional probabilities there described do not depend on whether A_n is an ancestor of both X and Y, or an ancestor only of X.

To complete the parameterization of this problem, we need to assign values to $\Pr(B_m \text{ has } T \mid SA)$, to $\Pr(Y \text{ has trait } T \mid B_m \text{ has } T \ \& \ SA)$, and to $\Pr(Y \text{ has trait } T \mid B_m \text{ does not have } T \ \& \ SA)$. The uniform rates assumption does not justify using a, d, and e for these parameters. After all, there is no reason to assume that A_n and B_m existed simultaneously. Yet, the uniform rates assumption *does* allow one to assume that

- (C) $\Pr(X \text{ has trait } T \mid SA) = \Pr(Y \text{ has trait } T \mid SA)$.

Since X and Y are simultaneously existing species, the same amount of time elapsed between, say, the coming into existence of the earth and them.

These component probabilities allow us to represent the likelihoods of the common ancestry hypothesis (CA_n) and the hypothesis of separate ancestry (SA) as follows:

$$\Pr(X \text{ has } T \text{ and } Y \text{ has } T \mid CA_n) = ad^2 + (1 - a)e^2$$

$$\Pr(X \text{ has } T \text{ and } Y \text{ has } T \mid SA) = [ad + (1 - a)e]^2$$

If we assume that $0 < a < 1$, we may derive the following result:

$$\text{If rates are uniform, then } \Pr(X \text{ and } T \text{ and } Y \text{ has } T \mid CA_n) > \Pr(X \text{ has } T \text{ and } Y \text{ has } T \mid SA) \text{ iff } (d-e)^2 > 0.$$

Combining this result with proposition (5), we obtain

- (D1) If rates are uniform and $(d-e)^2 > 0$, then $\Pr(X \text{ has } T \text{ and } Y \text{ has } T \mid CA) > \Pr(X \text{ has } T \text{ and } Y \text{ has } T \mid SA)$.

In the circumstance described, the common ancestry hypothesis is the more likely explanation of the observed similarity.

By parity of reasoning, it can be shown that a *mismatch* between species X and Y favors the hypothesis of separate ancestry over the hypothesis of common ancestry. Our first step is to place an *upper-bound* on the likelihood of the common ancestry hypothesis, relative to this observation. Given uniform rates, mismatches are more probable, the more distantly related the two species are (Sober 1988: p. 210):

$$\Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid X \text{ and } Y \text{ are } j\text{-related}) > \Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid X \text{ and } Y \text{ are } i\text{-related}), \text{ if } j > i.$$

It follows that

- (6) $\Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid CA) < \Pr(X \text{ and } Y \text{ have } T \mid X \text{ and } Y \text{ are } n\text{-related})$.

It can be shown that

$$\text{If rates are uniform, then } \Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid CA_n) < \Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid SA) \text{ iff } (d-e)^2 > 0.$$

Combining this result with proposition (6), we obtain

- (D2) If rates are uniform and $(d-e)^2 > 0$, then $\Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid CA) < \Pr(X \text{ has } T \text{ and } Y \text{ lacks } T \mid SA)$.

In the circumstance described, an observed difference between two species favors the hypothesis of separate ancestry.

The LPL principle

Darwin had no reason to think that Mendel had proposed a universal mechanism of heredity. For one thing, there is no evidence that Darwin read, or read about, Mendel's theories. And even if Darwin had read Mendel, he would not have found there an ambitious claim about the mechanism of heredity in all living things. Rather, Mendel took himself to be describing how stable hybrids are created, pea plants being his paradigm case. It was only

decades later that Mendel's ideas were transformed into *Mendelism* (Olby 1966).

Darwin didn't know about Mendelism, but he did invoke repeatedly an idea he thought was fundamental to the science of inheritance. This is the idea that "like produces like" (see, for example, Darwin 1859: p. 12). I'll call this the LPL Principle. Darwin did not insist that the LPL Principle is absolutely exceptionless; rather, he understood it as the idea that offspring tend to resemble their parents.

What does this "tendency" claim actually mean? Does it mean that if an offspring has trait T, then its parent probably had that trait as well? Or does it mean that if a parent has trait T, the its offspring will probably have that trait also? Actually, it means neither, as subsequent elaboration of the concept of heritability made clear. The claim is not that $\Pr(\text{descendant has T} \mid \text{ancestor has T}) > 0.5$, nor is it that $\Pr(\text{ancestor has T} \mid \text{descendant has T}) > 0.5$. Rather, the LPL Principle should be understood as asserting a difference in *likelihoods*. It is the claim that ancestor and descendant are *correlated*:

$$(7) \quad \Pr(\text{descendant has T} \mid \text{ancestor has T}) > \Pr(\text{descendant has T} \mid \text{ancestor lacks T}).$$

This is nothing other than the claim, in the notation introduced before, that $(d-e) > 0$. Darwin mainly thought of the LPL Principle as applying to individual organisms; however, its role in our discussion of *Modus Darwin* is to be found in its application to species.

Although the LPL Principle helps justify *Modus Darwin*, the principle is not necessary. If ancestors and descendants were *negatively* correlated and rates were uniform, *Modus Darwin* would still make sense.

Assumptions in the parameterization

Although it is easy enough to inspect (D1) and (D2) and see that two empirical assumptions are needed for these two propositions to provide a likelihood justification of *Modus Darwin*, other assumptions are there as well. These lurk a bit beneath the surface, however, since they are not expressed in (D1) and (D2), but are to be found in the parameterization of the problem provided by (A), (B), and (C).

In (A), the letter "a" is used to represent the probability than an ancestor will have trait T. By using this single letter in the two propositions in (A), we are saying that an ancestor's probability of having trait T is *independent* of whether it is an ancestor of both X and Y, or of just one of them. Similarly, notice that the letter "d" appears three times in (B); this reflects the

assumption that X's probability of having trait T, if its ancestor has trait T, is *independent* of whether X and Y have a common ancestor.

These are all empirical assumptions. Think of the case in which ancestors and descendants are individual (asexual) organisms, not species, and consider the assumption represented by the use of the letter "a." What is the probability that a parent will have a given trait? It is quite possible that parents who have just one child have one value for this probability, whereas parents who have two children have another. The "d" assumption is perhaps less questionable, though it too is empirical – a parent's probability of transmitting a trait to her offspring does not depend on whether she has one offspring or two; according to Mendelism, for example, offspring genotypes are drawn independently from the parental genotype, so what happens on one draw is not influenced by whether there are other draws.

Selection and the erasing of history

Suppose that a powerful process takes place in the lineages that connect ancestors to their descendants. Suppose that this process is so powerful that it *erases history* – a descendant's probability of having trait T is the same, regardless of what trait its ancestor possessed. Applied to the process of natural selection, the claim would be that if T is the optimal trait for a species to have, then selection will move the species to that state, regardless of where the species began ancestrally. In this case, the LPL Principle is nullified – $(d-e) = 0$. If so, the observed similarity of species X and species Y does not discriminate between the hypothesis of common ancestry and the hypothesis of separate ancestry.

We see here that the two parts of Darwin's theory bear a peculiar relation to each other. The tree of life hypothesis and the hypothesis of natural selection are logically compatible, of course. However, if natural selection is overwhelming in its power, then it will be impossible to use *Modus Darwin* to confirm the tree of life hypothesis. Natural selection can be a powerful force, as Darwin thought it was, without this problem arising. But selectionists who out-Darwin Darwin – who claim that each trait is the result of selection's rendering organisms *perfectly* adapted to their environments – in fact undermine the epistemological foundations of the hypothesis of common descent.

Natural selection is not the only process that can erase history. Any process that drives lineages to global equilibria can do this. For example, suppose evolution is controlled just by mutation. Suppose that the probability of not-T's mutating to T in a brief interval of time is u and the probability of T's mutating to not-T in that interval is v . Then, if there is a lot of time between

each ancestor and its descendants, the probability that a contemporary species will have trait T will be very close to $u/(u+v)$, regardless of what state its ancestor occupied. In this circumstance, the observation that two present day species both have trait T does not discriminate between the hypothesis of common ancestry and the hypothesis of separate origination.

Multiple traits

Propositions (D1) and (D2) describe how a single trait should be interpreted; they do not settle how *Modus Darwin* applies to data sets that involve more than one trait. We know from (D1) that each match in the data set favors the hypothesis of common ancestry and from (D2) that each mismatch favors the hypothesis of separate ancestry, but what summary judgment does the whole data set deliver about these two hypotheses?

Assumptions additional to uniform rates are needed if this question is to be answered. The uniform rates assumption, recall, describes a within-trait constraint. It says that the rules governing the evolution of trait T_1 in one branch of a tree are the same as the rules governing the evolution of T_1 in other, simultaneous branches. This says nothing as to how the rules governing the evolution of T_1 are related to the rules governing the evolution of T_2 . However, if we can assume that the traits in one's data set evolve independently of each other and have the same values for a, d, and e, then all matches are epistemologically equivalent and the same holds for all mismatches. We will term the assumption that different traits obey the same rules of evolution the assumption of *trait homogeneity*.

Even the three-part assumption of uniform rates, trait homogeneity, and trait independence does not fully answer the question of how data sets containing more than one trait should be evaluated. If species X and Y match with respect to eight traits and differ with respect to two, what summary verdict does this data set of ten traits imply? The assumptions just described do not settle how a match is related to a mismatch, so the fact that eight is greater than two is neither here nor there. At this point, we must involve ourselves in the nitty gritty of quantitative comparisons. What is the likelihood ratio of (CA) and (SA) with respect to a match, and what is the likelihood ratio of the two hypotheses with respect to a mismatch? If we know how these two ratios are related, we then can say how the entire data set should be evaluated.

What if the traits evolve independently of each other, but each has its own values for a, d, and e? It remains true that a trait on which species X and Y match favors the hypothesis of common ancestry. However, some matches strongly favor that hypothesis, while others favor the hypothesis only to a

lesser extent. Which types of matching deserve higher weight when the likelihoods of the two hypotheses are compared? The likelihood ratio of (CA) and (SA), for a given trait T on which the two species match, will be at least as large as the following:

$$\frac{\Pr(\text{X has T and Y has T} \mid \text{CA}_n)}{\Pr(\text{X has T and Y has T} \mid \text{SA})} = \frac{ad^2 + (1-a)e^2}{[ad + (1-a)e]^2}$$

If d is large and e is small, this ratio is approximately $1/a$, which is made large by making a small. This means that matchings on traits that are rarely found in ancestors, that probably won't occur in descendants if they are not found in ancestors, and which probably will occur in descendants if they are found in ancestors, deserve high weight.

So far my comments about multiple traits have been limited to the case in which traits evolve independently of each other. If traits are correlated with each other, they will not provide independent evidence that bears on the problem of discriminating between (CA) and (SA). How is one to tell whether two traits evolved independently? If both are adaptive, an engineering analysis may help. Is the sex ratio found in a species independent of the average body size? If sex ratio is an adaptive response to one factor (e.g., the degree of inbreeding), while body size is an adaptive response to another (e.g., ambient temperature), and the two factors are uncorrelated, then the traits will evolve independently if the two phenotypes are coded for by different genes. Another solution is to look at traits that are *not* adaptive. Neutral traits that are coded by different genes evolve independently – each does its own random walk. We will return to the importance of nonadaptive traits later.

Methods of phylogenetic inference

It may seem that the results reviewed so far merely recapitulate ideas that have been explored in contemporary discussions of phylogenetic inference. This is not entirely true. The methods used in phylogenetic inference *assume* that the species surveyed are genealogically related. The question is to determine which tree is best supported by the data. The issue we have addressed here is separate and conceptually prior. The question is not whether human beings are more closely related to chimps than they are to gorillas, but why we should think of these species as sharing ancestors at all.

Still, the assumptions that validate *Modus Darwin* reflect assumptions that do the same job for methods of phylogenetic inference. The LPL Principle

plays a role in both. And the idea that matches deserve more weight when they are rare reflects an asymmetry in phylogenetic inference that I termed the Smith-Quackdoodle theorem (Sober 1988). If you meet two individuals named Smith, this is *some* evidence, however slight, that they are genealogically related. The same holds for two individuals named Quackdoodle. It can be shown that the two Quackdoodle's are probably more closely related than the two Smith's. Matches that are rare deserve more weight than matches that are common.

Modus Darwin without assuming uniform rates

It is evident from (D1) and (D2) that the LPL Principle is not sufficient to justify *Modus Darwin* as a mode of likelihood inference. When rates fail to be uniform, proposition (6) can fail to be true. For example, suppose in Figure 2 that a and c are large, but b is tiny. If d and e are also large, then it will be more probable that A and C have trait T than that A and B do. With nonuniform rates, similarity can fail to reflect propinquity of descent. And even if one is prepared to accept the assumption of uniform rates, this within-trait assumption does not settle how one should analyze data sets that contain multiple traits. Assumptions concerning how different traits are related to each other also are needed.

For these reasons, it would be desirable to obtain a justification of *Modus Darwin* that does not depend on the assumption of uniform rates, nor on the assumption of trait homogeneity. Darwin would have had no problem with assuming the LPL Principle, but he was well aware that a trait that selection favors in one lineage may be disfavored in another, and that different traits can change according to different rules.

We still must deal with the problem, depicted in Figure 1, that the hypothesis of common ancestry is a disjunctive hypothesis. However, if we abandon the assumption of uniform rates, it is hard to see what general relation the likelihood of one disjunct should bear to the likelihood of another. It therefore becomes unclear how the likelihood of (CA), given an observed matching of two species, can usefully be represented. A solution to this puzzle resides in the fact that there is something that each disjunct in (CA) *deductively implies*. If ancestor and descendant are correlated on each branch in the sense of proposition (7), then each disjunct in (CA) entails that X and Y will be positively correlated; (SA), on the other hand, entails that X and Y will not be correlated, if we assume that lineages, once separated, do not causally interact with each other:

- (R) If ancestor and descendant on each branch are correlated, and if separate lineages evolve independently, then the common ancestry hypothesis entails that $\Pr(X \text{ has } T \text{ and } Y \text{ has } T) > \Pr(X \text{ has } T)\Pr(Y \text{ has } T)$ and the separate ancestry hypothesis entails that $\Pr(X \text{ has } T \text{ and } Y \text{ has } T) = \Pr(X \text{ has } T)\Pr(Y \text{ has } T)$.

This is an application of Reichenbach's (1956) *principle of the common cause* (see also Forster 1986). Whereas propositions (D1) and (D2) describe a circumstance in which the two hypotheses confer different *probabilities* on a conjunction, criterion (R) describes a wider circumstance in which the two hypotheses disagree about whether the probability of that conjunction exceeds the product of the probabilities of the conjuncts.

Let's examine in more detail the assumption, stated in (R), that separate lineages evolve independently. This means that if C is descended from B and B from A, then B "screens off" A from C, and if A is the most recent common ancestor of X and Y, then A "screens off" X from Y:

$$\begin{aligned} \Pr(C \text{ has } T \mid B \text{ has } T \text{ and } A \text{ has } T) &= \Pr(C \text{ has } T \mid B \text{ has } T) \\ \Pr(X \text{ has } T \text{ and } Y \text{ has } T \mid A \text{ has } T) &= \\ \Pr(X \text{ has } T \mid A \text{ has } T) \Pr(Y \text{ has } T \mid A \text{ has } T). \end{aligned}$$

These Markovian assumptions are not *a priori* true, but they are entirely standard in causal modeling across the sciences.

An additional part of the independence assumption is the idea that species that are not genealogically related are probabilistically independent of each other. This can fail to be true for obvious ecological reasons – for example, if one species exerts a selection pressure on the other or if both species adapt to a shared environment. However, in the absence of these ecological interactions, we expect that species that have no common ancestors will not be correlated.

Advantages of criterion (R)

Criterion (R) shows that *Modus Darwin* does not depend on the assumption of uniform rates. It also is worth noting that this criterion does not depend on the parameterization of the problem we exploited in deriving criteria (D1) and (D2); as noted earlier, that parameterization involves biological assumptions of its own. To compare the likelihoods of (CA) and (SA), it was essential to use a parameterization of the problem in which there are *shared* parameters; otherwise, the two expressions for the likelihoods would have been incommensurable. It is not necessary to do this to derive proposition (R). Nor, as we shall see, does proposition (R) depend on the assumption of trait homogeneity, whereas some sort of between-trait assumption is needed if (D1) and

(D2) are to be used to analyze the testimony of data sets that include more than one trait.

Testing for independence

How might one use proposition (R) to test whether two species have a common ancestor? One can't determine whether $\Pr(X \text{ has } T \ \& \ Y \text{ has } T) > \Pr(X \text{ has } T)\Pr(Y \text{ has } T)$ simply by considering the observation that X and Y both have trait T. That would be like trying to determine whether the results of tossing two coins are independent by observing that both landed heads on a single toss. The key is to expand our view in two directions – we need to consider more than one trait and more than two species. The first expansion is obviously mandated by (R); that proposition says that independence fails for *each* of the traits on which X and Y match, if X and Y have a common ancestor. But this, by itself, is not enough. After all, what we observe for each trait is simply whether X and Y match or fail to do so. The question is whether they match sufficiently often for us to reject the null hypothesis that says that they originated separately. However, there is no simple quantitative threshold that can be specified here. For example, even if X and Y match on 90% of the traits we consider, this is consistent with the hypothesis that they evolved independently. If each trait T_i is such that $\Pr(Y \text{ has } T_i) = 0.95$, then we'd expect them to match approximately 90% of the time if they obtained their traits independently.

By bringing in species besides X and Y, we can obtain estimates of a species' probability of exhibiting each of the traits we want to consider. Suppose we score n species for each of m dichotomous traits, as shown in the accompanying table. From these data, we can estimate, for each trait T_i , the probability (p_i) that the trait will be present in a species. The maximum likelihood estimate of p_i is the actual frequency of pluses in the relevant column.

		Traits			
		T_1	T_2	...	T_m
Species	s_1	+	–	...	+
	s_2	+	+	...	–

	s_n	–	–	...	+
Pr(s has T_i)		p_1	p_2	...	p_m

From these estimated values of p_i , we can compute the expected number of matches that two species s_i and s_j should exhibit in this data set if the species originated separately:

$$E(\text{number of traits on which } s_i \text{ and } s_j \text{ match} \mid \text{SA}) = \sum_{k=1}^{k=m} (p_k)^2 + (1 - p_k)^2.$$

Likewise the expected number of mismatches, according to the null hypothesis of separate ancestry, is

$$E(\text{number of traits on which } s_i \text{ and } s_j \text{ mismatch} \mid \text{SA}) = \sum_{k=1}^{k=m} 2(p_k)(1 - p_k).$$

We then can determine whether the number of matches in the data is sufficiently greater (or, equivalently, whether the number of mismatches is sufficiently less) than the expected value predicted by the null hypothesis of separate origination for one to reject the null hypothesis. It may turn out that the null hypothesis can be rejected for some pairs of species, but not for others; the evidence may favor the hypothesis that some pairs have common ancestors, but may point in the opposite direction for others. Notice that this test looks at *all* the data – both at matches and at mismatches. Thus construed, *Modus Darwin* abides by the principle of total evidence.

It is clear that the test procedure I have described avoids the assumption of trait homogeneity; the probability under the null hypothesis that X and Y match with respect to one trait may differ from the probability that they match with respect to another. However, it may be suggested that the test procedure assumes that all species have the same probability of exhibiting a given trait, according to the null hypothesis. I disagree. That assumption would suffice for the test to make sense, but it is not necessary. Suppose you want to estimate a coin's probability of landing heads, but it and the other coins on the table before you can be tossed only once. One option is to toss the coin of interest, note whether it lands heads or tails, and estimate its probability of landing heads as being either 1.0 or 0. A second procedure would be to toss each coin on the table and take the average. The second procedure can be better, even if you know that the coins are not precisely the same in their biases. By pooling data, one is estimating a single parameter;

by treating each coin as separate and unique unto itself, one is estimating the values of n parameters, one for each coin. Akaike's (1973) "information criterion" explains why the first procedure can be expected to yield estimates that are more accurate in predicting *new* data (Sober and Forster 1994).⁶

Relation of (CA) and (SA) to creationism

Although talk of common ancestry and separate origination naturally leads one to think of the opposition between evolution and creationism, there is an important respect in which this association is historical happenstance, not a logical consequence of the hypotheses considered. Although Darwin and contemporary evolutionary theory both assert that all present day life on Earth is genealogically related, the theory is perfectly compatible with the idea that life on Earth and life in distant galaxies (should such exist) are genealogically *unrelated*. There is no prior theoretical commitment in evolutionary theory to *all* life's being related. The theory is open to hypotheses of common ancestry and to hypotheses of separate ancestry, its being left to the data to decide which is more plausible.

Furthermore, there is nothing in our formal treatment of (CA) and (SA) that prevents one from interpreting these hypotheses as design hypotheses. Darwin saw the deep analogy between the evolution of species and the evolution of human languages. Languages are products of consciousness and are modified because language users change their states of consciousness. Languages are transmitted by learning, not by genes. However, the very same epistemological issues arise when one asks whether two languages trace back to a common ancestral language (an *ur-language*) or arose independently. As long as the relevant assumptions apply, principles (D1), (D2), and (R) can be used to test the hypotheses. What is strange about creationism is not that it advocates a hypothesis of conscious design, but that the designer it postulates is a supernatural being.

If we nonetheless seek to apply (CA) and (SA) to creationism, we must decide whether creationism is better thought of as a hypothesis of common origins or as a hypothesis of separate origination. It may seem obvious that (monotheistic) creationism advances a hypothesis of common origins; after all, it says that the diversity of the living world traces back to the mind of God. However, whether creationism should be thought of in this way depends on how the hypothesis is elaborated. If the postulated designer is said to have created each species (or each "basic kind" of organism) according to a separate and independent plan, then this form of creationism in fact asserts a hypothesis of *separate* origination. Construed in this way, creationism predicts that species should have their traits independently. This claim can

be tested by applying proposition (R). However, two complications need to be considered before this conclusion can be drawn.

The first is that creationism has traditionally assumed that some features of God's plans for different species were *nonindependent*. Why do birds have wings and bats have wings? Why do whales and sharks both have torpedo shapes? Creationists point out that different organisms sometimes live in similar environments; when this happens, God, in his benevolence, gives those organisms similar features that allow them to survive and reproduce in their environments. Creationists thereby claim to explain correlations between birds and bats, or between whales and sharks, when those correlations involve *adaptive features*. God formulated separate plans for these different species, but the plans were similar, owing to God's good will.

Creationists thereby seek to explain by the hypothesis of intelligent design what evolutionists seek to explain by the hypothesis of natural selection. However, it is not automatic that these two frameworks make the same predictions about adaptive features. The problem is for the creationist to say to whom or to what God meant to be "benevolent" – to individual organisms, to groups of conspecific organisms, to whole species, to multi-species communities, to genes, to *what*? The units of selection problem makes it clear that the interests of objects at different levels of organization can come into *conflict* (Sober and Wilson 1998). What is good for a gene may be bad for the organism in which it occurs; what is good for an organism may be bad for the group in which it lives; and so on. R. A. Fisher (1930: p. 49) observes that this point "... was unknown to the early speculations to which the perfection of adaptive contrivances naturally gave rise. For the interpretation that these were due to the particular intention of the Creator would be equally appropriate whether the profit of the individual or of the species were the objective in view. The phrases and arguments of this pre-Darwinian viewpoint have, however, long outlived the philosophy to which they belong."

In addition to the problem of specifying the level of organization towards which God's benevolent intentions were directed, the creationist also has a problem accommodating neutral and maladaptive traits. How are these to be explained by the hypothesis of an intelligent, powerful, and benevolent designer? In the following passage, Darwin makes the crucial point:

On my view of characters being of real importance for classification only in so far as they reveal descent, we can clearly understand why analogical or adaptive characters, although of the utmost importance to the welfare of the being, are almost valueless to the systematist. For animals, belonging to two most distinct lines of descent, may readily become adapted to similar conditions, and thus assume a close external resemblance; but

such resemblances will not reveal – will rather tend to conceal their blood-relationship to their proper lines of descent (Darwin 1859: p. 427).

Here Darwin is discussing the problem of inferring which genealogy is most plausible for a group of organisms, not the prior problem of saying why one should think that organisms are genealogically related. However, his point about the value of valueless traits is still fundamental. Adaptive similarities are consistent with the hypothesis of separate creation, on the assumption that the creator is benevolent. But nonadaptive similarities are another story. Surely the hypothesis of separate design offers no reason to expect a correlation among nonadaptive features.

The second complication that stands in the way of applying proposition (R) to test a creationist hypothesis of separate origination is that creationism usually assumes a deterministic framework. God's power is such that his will is done, not just with *high* probability, but with *certainty*. However, the derivation of proposition (R) depends on the assumption that probabilities are intermediate – less than 1 and greater than 0. Proposition (R) cannot be applied to test a deterministic creationist hypothesis of separate origination against the evolutionary hypothesis of a single tree of life.

We have seen that the two parts of Darwin's theory can be separated. The hypothesis that there is a single tree of life that unites all life on Earth can be tested by seeing whether the traits of different species are correlated. There is no requirement that these characteristics be the sorts of things that natural selection could be expected to have produced. As Darwin notes in the passage just quoted, it is neutral and deleterious characteristics that provide the best evidence concerning common ancestry. Similarly, even if it turns out that there is more than one tree of life – that some pairs of species do not have common ancestors – the question is still open as to whether natural selection has been an important force in shaping the characteristics of organisms. In fact, there could be *many* lines of descent (in the limit, each current species could be unrelated to all the others) and still natural selection could be the principal force causing descendants to evolve away from their ancestors.

These separate elements of Darwinian theory often get lumped together when evolutionary theory is compared with creationism. This is not surprising, given that creationists apparently have no way to test separately the two corresponding parts of their own theory. There is first the idea that different species (or "basic kinds" of organisms) were brought into being by a designer. Second, there is the idea that this designer formed a plan of a certain sort for each species or kind, which he then executed. Is the existence of a designer testable separately from the hypothesis that the designer had certain characteristics? It is not clear how the separate components of creationism can be tested independently of each other. If this is right, it is important to

see that Darwinian theory is not like this – its components can be scrutinized separately.

Concluding comments

Modus Darwin can be stated schematically – when we observe different species, we observe characteristics that we'd expect to find if they had a common ancestor, but would not expect to find if they did not. Stated in this way, *Modus Darwin* sounds like a likelihood inference. However, to check whether this is right, we had to specify what “characteristics” of species are relevant and show why the hypothesis of common ancestry (CA) and the hypothesis (SA) of separate ancestry confer different probabilities on these characteristics. The fruits of this inquiry are contained in propositions (D1) and (D2). Given the LPL Principle and the uniform rates assumption, matching traits are more probable according to (CA) than they are according to (SA). However, additional assumptions are needed if *Modus Darwin* is to permit likelihood arguments to be made about data sets that contain multiple traits. I then asked whether the uniform rates assumption and the assumption of trait homogeneity are dispensable. Proposition (R) shows that they are. Rather than talk about the probability that two species will match on a given trait, we examined the idea that the two species should be correlated. The common ancestry and the separate ancestry hypotheses have opposite implications about this, if the LPL Principle is true and if separate lineages evolve independently of each other.

The foregoing discussion may leave the impression the *Modus Darwin* rests on foundations that are a lot less transparent than the intuitiveness of the rule of inference might lead one to suspect. “There *must* be a simpler justification of *Modus Darwin*,” the reader may be inclined to say, “one that depends on less demanding assumptions or on no assumptions at all.” My reply is that I am confident that *some* substantive assumptions are needed – as in other nondeductive arguments, observations bear on hypotheses only through the mediation of auxiliary assumptions (Sober 1988). However, nothing I have said here shows that the assumptions I have described are the most austere assumptions that suffice for *Modus Darwin* to make sense. In fact, I am certain that the assumptions I have used in connection with (D1), (D2) and (R) are *not* the weakest ones possible. For example, some departure from uniform rates will still permit one to show that the common ancestry hypothesis confers a higher probability on similarity than the separate ancestry hypothesis does. And some departure from the Markov conditions can still allow one to show that (CA) and (SA) make different predictions about (degrees of) probabilistic dependence. Philosophers look for presuppositions, but the logic

of inquiry usually allows one to uncover sufficient conditions, not necessary ones. A condition that is both necessary and sufficient for *Modus Darwin* to be justified might be very complicated to formulate and difficult to interpret. Still, the possibility remains that there are weaker sufficient conditions for the correctness of *Modus Darwin* that still manage to be illuminating. The only way to see if this is true is to try to find them.

Dedication

It has sometimes been said that the debt we owe to our teachers can never be repaid. Even though I am a philosopher who delights in finding counter-examples to general principles, I feel that this little saying is true in what it says about my debt to Dick Lewontin. I spent my first sabbatical (1980–1981) in Dick’s lab at the Museum of Comparative Zoology at Harvard. I had written one or two pieces on philosophy of biology by then, but I was very much a rookie in the subject. Dick was enormously generous with his time – we talked endlessly – and I came away convinced that evolutionary biology was fertile ground for philosophical reflection. While in his lab, I worked on the units of selection problem and on the use of a parsimony criterion in phylogenetic inference. I still have not been able to stop thinking about these topics.

Dick is “natural philosopher.” I don’t mean this in the old-fashioned sense that he is a *scientist* (though of course he is that), but in the sense that he is a *natural at doing philosophy*. It was a striking experience during that year to find that Dick, a scientist, was actually interested in the philosophical questions I was thinking about and that he too found it interesting to trace out the consequences of an argument. I came to the lab with the rather “theoretical” conviction that there should be common ground between science and philosophy; the experience I had in the lab made me see that this could be true, not just in theory, but in practice.

During that year, I attended Dick’s course in biostatistics and gradually started to see how deeply the concept of probability figures in evolutionary biology. Although the present paper is not on a topic that Dick has written about, I feel that it connects with something that he cares about – the clarification of patterns of reasoning that matter in thinking about evolution. I am pleased to dedicate this paper to him.

Notes

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¹ The variorum edition of the *Origin* indicates that Darwin did not change his mind on this issue through successive editions. See Darwin (1959: p. 759).

² For example, this is true in Bayesian confirmation theory, since $\Pr(H | E) > \Pr(H)$ iff $\Pr(H | \text{not-}E) < \Pr(H)$.

³ This was especially evident in Darwin's discussion of the mental continuity between human beings and other organisms; see Sober (1998) for discussion.

⁴ Darwin recognized the difference between (T) the number of start-ups and blow-ins and (C) the number of trees that persisted long enough to connect with extant species or extant fossils. In the fifth edition of the *Origin* he adds the following remark to the passage I quoted at the beginning of the present paper: "No doubt it is possible, as Mr. G.H. Lewes has urged, that at the first commencement of life many different forms were evolved; but if so, we may conclude that only a few have left modified descendants (Darwin 1959: p. 759)."

⁵ In the case of Newtonian mechanics and relativity theory, it is doubtful that the notion of prior probability makes objective sense. This problem does not apply, however, to the case of estimating the number of phylogenetic trees, since the number of trees can be regarded as the outcome of a chance process. Here the concepts of prior probability and of prior expected value are intelligible, but their values are presently not known.

⁶ To be sure, *some* assumptions are needed for it to make sense to look at the pooled data, rather than just rely on whether the coin of interest landed heads or tails on a single toss. For example, if one were pretty sure that the other coins are very different from the target coin, this would count against consulting the pooled data. However, suppose the target coin is drawn at random from a set of coins that may differ in their biases, where the different biases form a normal distribution. In this case, attending to the pooled data makes sense.

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