

Darwin was a Teleologist*

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ABSTRACT: It is often claimed that one of Darwin's chief accomplishments was to provide biology with a non-teleological explanation of adaptation. A number of Darwin's closest associates, however, and Darwin himself, did not see it that way. In order to assess whether Darwin's version of evolutionary theory does or does not employ teleological explanation, two of his botanical studies are examined. The result of this examination is that Darwin sees selection explanations of adaptations as teleological explanations. The confusion in the nineteenth century about Darwin's attitude to teleology is argued to be a result of Darwin's teleological explanations not conforming to either of the dominant philosophical justifications of teleology at that time. Darwin's explanatory practices conform well, however, to recent defenses of the teleological character of selection explanations.

KEY WORDS: Adaptation, Darwin, final cause, natural selection, plant sexuality, teleology.

1. INTRODUCTION

In the Foreward to a recent reprint of Darwin's classic, *The Various Contrivances by Which Orchids are Fertilised by Insects*, Michael Ghiselin writes:

...a myth has grown up, partly the work of [Asa] Gray, partly the work of Darwin's son and biographer, Frances Darwin, that Darwin somehow "brought teleology back into biology." In any nontrivial sense of that word, he did the exact opposite, getting rid of teleology and replacing it with a new way of thinking about adaptation... (Darwin 1984, xiii)

This is a puzzling claim. This so-called "myth" is as much the work of Charles Darwin himself as of either individual mentioned here. In a brief appreciation of Darwin published in *Nature*, in June of 1874, Asa Gray noted "...Darwin's great service to Natural Science in bringing back to it Teleology: so that instead of Morphology versus Teleology, we shall have Morphology wedded to Teleology" (Gray 1963). Darwin quickly responded:

What you say about Teleology pleases me especially and I do not think anyone else has ever noticed the point. (F. Darwin 1887, 308)¹

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Now I suppose one can blame Francis for making this remark public, but it is hardly accurate to accuse him (or Asa Gray, or Thomas Huxley) of creating a myth – unless, of course, Darwin was being patently disingenuous. One might imagine that Darwin is again busy trying to smooth over differences in the Darwinian fold. After all, Gray was the chief exponent of rapprochement between theology and evolutionary biology. But the attempt to explain the above remark as a piece of political maneuvering on Darwin's part will not work. No doubt, Darwin and Gray mean somewhat different things when they refer to the teleology of Darwin's theory, differences which Darwin politely does not mention. But the quote from Huxley in note 1 indicates that this view of Darwin's accomplishment was shared by those who were avowed enemies of the argument from design.

The following discussion will establish the uncompromisingly teleological stance of Darwin, explain recent attempts to explain it away, and (more positively) make clear the structure of Darwinian teleological explanations.² Having done this, a good deal of the problem people have had with this aspect of Darwin's thought will find a natural explanation: His selection-based teleology simply failed to conform to any model of teleological explanation available in the 19th century. The conclusion that Darwin was not a teleologist follows inexorably from two premises: (i) The only "non-trivial" teleological explanations are those which appeal to divine design or an internal vital force; (ii) Darwinian selection explanations appeal to neither. The literature cited in note 13, below, makes it clear that the first premise is false. Selection explanations are inherently teleological, in the sense that a value consequence (Darwin most often uses the term 'advantage') of a trait explains its increase, or presence, in a population. To establish whether Darwin was a teleologist in this sense, it is requisite to take his employment of teleological explanations at face value, and examine their structure. When this is done, a robust form of teleology is revealed, one for which Darwin's contemporaries were quite unprepared, but which has been vigorously defended in recent years by biologists and philosophers of a neo-Darwinian persuasion.

2. DARWIN'S TELEOLOGY ESTABLISHED

It would be surprising if Charles Darwin did not at some point come face to face with the concept of teleology. By his own admission he admired the argument from design in Paley's work while at Cambridge, and was apparently ready to accept creation by design as the most reasonable explanation for adaptation when the *Beagle* sailed. Less than ten years later he was confident of the main outlines of a theory which explained adaptation, and the creation of new species, by references to natural causes, and was an avowed agnostic.

In his *Species Notebooks*, Darwin uses the term 'Final Cause' in a consistent way (cf. B 5, 49; C 236; D 114, 135, 167; E 48–49, 146–147; M 154; in Barrett et al. 1987, 167–455). The reference of the term seems constant. In contexts

where the central question being considered is ‘What is *S* for?’, Darwin refers to the answer to the question as stating the ‘Final Cause’ of *S*. By contrast, when he thinks it is reasonable to suppose that the fact in question is not for anything, he denies that it has a ‘Final Cause’. Perhaps the most interesting passage on Darwin’s attitude to teleology at this time is found in his notes on John Macculloch’s *Proofs and Illustrations of the Attributes of God* (Barrett et al. 1987, 631–641). Darwin is systematically testing natural selection against Macculloch’s Creator in accounting for various natural phenomena. At 58r we find the following comment on p. 234 of Macculloch’s work.

The Final Cause of innumerable eggs is explained by Malthus. – (is it anomaly in me to talk of Final Causes: consider this! –) consider these barren Virgins (Barrett et al. 1987, 637)

The fact that ‘Final Cause’ here seems to refer to the explanandum rather than the explanans might give one pause. But, though there is much that is obscure in this note, this worry, at least, can be put aside. “Explained by Malthus” surely means that the explanation of innumerable eggs is provided by Malthus.³

What is further clear is that the explanation deriving from Malthus is taken to provide an alternative to that of the natural theologian, and that raised, in Darwin’s mind, a question of the validity of his use of the term. The reference to Francis Bacon’s negative assessment of Final Causes, which Darwin may have known of through a reference in William Whewell’s contribution to the Bridgewater treatises (Whewell 1833, 355–356), indicates Darwin’s concern whether, once one gives up the designs of an intelligent, benevolent creator as the productive cause of an adaptation, one should also give up the language of Final Cause.

He apparently decided that the answer is ‘No’, for he continued using the term in the *Origin* (Darwin 1964, 216, 435, 448)⁴, and after (besides the passages discussed in detail below, see his description of Bates’ selectionist explanation of mimicry as giving its Final Cause (Barrett 1977, 2: 89). More importantly than his bare use of the term, however, are his consistent arguments that natural selection acts *for the good* of each being, and that its products *are present for* various functions, purposes and ends (Darwin 1964, 149, 152, 224, 237, 451). As John Beatty (1990, 127) and Ernst Mayr (1988, 241) point out, that was all Albert von Kölliker, a contemporary of Darwin’s and a critic of teleology, needed to be assured that Darwin was a teleologist.

This sets the context for the teleology of Darwin’s botanical works. Ghiselin has attempted to argue (though in the foreword mentioned above he admits to exaggeration), in chapter 6 of *The Triumph of the Darwinian Method*, that Darwin’s *Various Contrivances* is a “metaphysical satire”, “a deliberate, planned attack” on the natural theologians of its day (Ghiselin 1969, 135). There is no positive evidence for this hypothesis at all. But if one begins with the assumption that Darwin could not have used the term ‘Final Cause’ with a straight face, then some such hypothesis is needed to account for *Various Contrivances*; for it is, as we will see, chock full of teleological explanation.⁵

2.1. *Primulae*

Before testing Ghiselin's hypothesis about *Various Contrivances*, however, it is worth examining the teleological reasoning of the soberly titled 'On the Two Forms, or Dimorphic Condition, in the Species of *Primula*, and on Their Remarkable Sexual Relations', a paper read to the Botanical section of the Linnean Society and published in their proceedings (in Barrett 1977, 2: 45–63).⁶ Having done an elegant experimental study of homomorphic and heteromorphic fertilization in *P. vulgaris* and *veris* (Primroses and Cowslips), Darwin turns to the teleological question.

The meaning or use of the existence in *Primula* of the two forms in about equal numbers, with their pollen adapted for reciprocal union, is tolerably plain; namely, to favour the intercrossing of distinct individuals. With plants there are innumerable contrivances for this end; and no one will understand the final cause of the structure of many flowers without attending to this point. (Barrett 1977, 2: 59)

As in his pre-*Origin* usage, 'final cause' is here referentially equivalent to *the end for which* an adaptation – sexual dimorphism in this case – exists, encouraging cross-fertilization. But there is a deeper teleological puzzle in this case, since this end is in fact achieved by a variety of means. Thus why species of *Primula* adopt the particular strategy, by means of the particular structures, they do – i.e., what this particular strategy is *for* – is an open question.

There are, within the species being studied by Darwin, long- and short-styled forms of their sexual organs (see Fig. 1).

Darwin's painstaking experimental work had established that certain pollen/ova combinations were less fertile than others, though both self-fertilization and cross-fertilization were possible and mechanically facilitated by the relevant insect agents. He concludes:

We see the species of *Primula* divided into two sets or bodies, which cannot be called distinct sexes, for both are hermaphrodites; yet they are to a certain extent sexually distinct, for they require for perfect fertility reciprocal union. (Barrett 1977, 2: 57; again see Fig. 1).

An obvious question to ask, and the one that Darwin does ask, is, 'What end is served by this odd state of affairs?' But he is at a loss for a satisfactory answer.

...we know not why the species of *Primula* should have acquired this novel and curious aid for checking continued self-fertilisation through the division of the individuals into two bodies of hermaphrodites with different sexual powers, instead of by the more common method of the separation of the sexes, or by the maturity of the male and female elements at different periods, or by other such contrivances. Nor do we know why nature should thus strive after the intercrossing of distinct individuals. We do not even know the final cause of sexuality... (Barrett 1977, 2: 61)

Thus Darwin sees both a general teleological question here, the answer to which is tolerably clear, and a series of more specific questions about which he is mostly still puzzled. Nevertheless, what this passage clearly shows is that Darwin's teleological reasoning goes on within the context of evolutionary conjectures about the slow modification of forms and the slow acquisition of

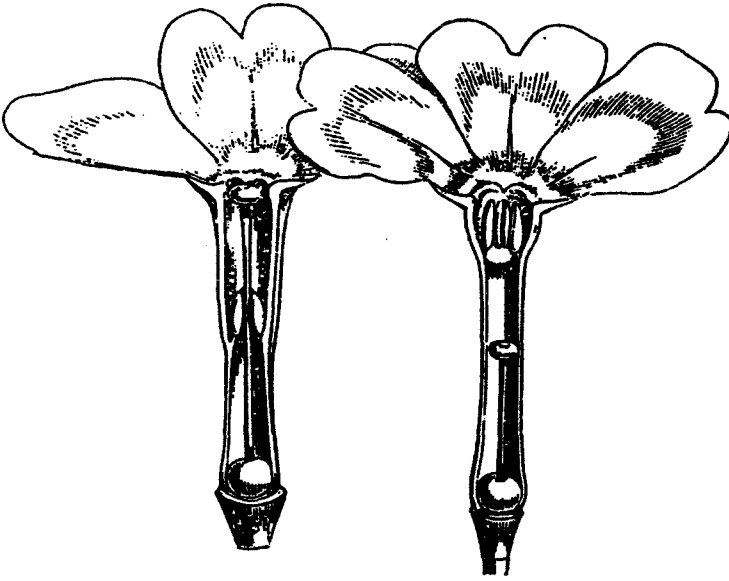


Fig. 1. Long-styled (left) and short-styled (right).

traits. Darwin's reasoning takes the following form.

1. By controlled study, the actual consequences for the species of the two hermaphroditic forms are determined. Such research aims to determine whether dimorphism prevents certain pollenizations from occurring; whether it makes certain ones more likely or more frequent and if so, which ones; whether certain pollenization events are more likely to result in fertilization than others and if so, which ones; what the consequences of dimorphism are for how the relevant insect carriers are dusted with pollen, and how this affects the process of pollenization itself; and finally, whether, as a consequence, cross-fertilization is more frequent than, less frequent than, or equal in frequency to, self-fertilization. The crucial result of his investigation, for Darwin, is to have shown,

...how potent the dimorphic condition of the pollen in *Primula* will be in favouring the intercrossing of distinct individuals. ... Whatever advantage there may be in the separation of the sexes, towards which we see so frequent a tendency throughout nature, this advantage has been so far gained that the one form is fertilised by the other, and conversely; and this is effected by the pollen of each form having less potency than that of the other on its own stigma. (Barrett 1977, 2: 59-60)

2. Having answered, as far as possible, these questions, the next step is to *identify the consequence of dimorphism which explains its presence*. The first step here is simply identifying the good served by it. Here Darwin is clear. Persistent self-fertilization decreases the fertility of a variety, while regular cross-fertilization with other varieties increases fertility and offspring vigor.

Again, both with plants and animals, there is abundant evidence, that a cross between very distinct individuals of the same species, that is between members of different strains or sub-breeds, gives vigour and fertility to the offspring (Darwin 1964, 267)

3. But Darwin is sensitive in the extreme to the possibility that the present function of a structure is not the function for which it was originally selected. Thus one needs a plausible mechanism by means of which the trait in question would have been selectively favored. Darwin clearly has such a mechanism in this case. If a species has within it slight variations in pistel and stamen lengths, and some of these variations promote, however slightly, cross-fertilization, which in turn generates a higher frequency of fertile seeds and more vigorous offspring, the bearers of these variations will be favored in the metaphorical struggle for existence. Thus such dimorphism, if it can be shown, as a consequence, to discourage self-fertilization and encourage the crossing of different forms, is clearly a candidate for a selection explanation.

To schematize the above Darwinian explanation, then (the generalized schema is in brackets):

1. Dimorphism is present in *Primula veris*. [*V* is present in *P*]
2. Dimorphism has the effect of increasing heteromorphic crosses and decreasing homomorphic fertilization. [*V* has effect *E*]
3. Heteromorphic crosses are more fertile and produce more vigorous offspring than homomorphic fertilizations. [*E* is advantageous to *P*]
4. Natural selection would thus favor increased dimorphism in *Primula veris*. [Therefore *V* in *P* would be selectively favored]
5. Dimorphism is present in *Primula veris* because it promotes intercrossing. [Therefore *E* is the cause of *V*'s presence in *P*]

Darwin, without a blink, refers to the promotion of intercrossing as the "Final Cause" of the dimorphic condition of *Primula*. Is this merely a careless mode of expression, or does the above reasoning reveal a legitimate sense in which the reproductive consequences of sexual dimorphism are the cause of its presence in *Primula*? It is unlikely that Darwin would have used such a loaded expression unreflectively; and indeed there is a clear sense in which Darwin has identified the Final Cause of the trait in question. The various environmental "checks" to population expansion, which Darwin thinks of as the principal mechanisms promoting adaptive evolutionary change, bias reproductive frequencies on the basis of whether the consequences of particular variations are advantageous or disadvantageous to their possessor's living to sexual maturity and reproducing. If a variation functions, in a particular environment, in a way that increases its relative frequency in subsequent generations, that variation is selectively favored because of that function. The (relatively) advantageous consequences of that variation are (part of) the causal basis of its presence in the population. Darwin's explanation thus displays the 'selection' teleology defended recently by a variety of biologists and philosophers of a neo-Darwinian persuasion.⁷

2.2. *Orchidaceae*

In the concluding remarks of *Various Contrivances*, Darwin shows himself particularly sensitive to the danger of inferring the past selection of a trait from its present usefulness. But he does not conclude that a change in function implies the absence of teleology.

Although an organ may not have been originally formed for some special purpose, if it now serves for this end, we are justified in saying that it is specially adapted for it. (Darwin 1984, 283)

To explain his point, he draws a most interesting and, for those who see Darwin as the vigilant enemy of teleology, troubling comparison.

On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. (Darwin 1984, 283–284)

Natural selection similarly can only work to modify existing structures as they vary slightly through time. Those structures are the products of past selection, and thus will have served various ends in the past. Darwin's chief point is relentlessly adaptationist – if the present, slightly altered structure provides an advantage, it too will be selectively favored, though the basis of that selection may be very different from the basis of its past selection. *The reference of the terms 'end' and 'purpose' throughout are to the activities performed by the part in virtue of which it has been, or is, selected.* The beneficial consequences of a variation explain why it is selectively favored.

The Orchids pose a particular problem for selection teleology which Darwin raises in these concluding pages of *Various Contrivances*.

In my examination of Orchids, hardly any fact has struck me so much as the endless diversities of structure, – the prodigality of resources, – for gaining the very same end, namely, the fertilisation of one flower by pollen from another plant. This fact is to a large extent intelligible on the principle of natural selection. (Darwin 1984, 284)

Note that the end served is the same as in *Primula*. The problem that worries Darwin is nicely illustrated by him in the following passage.

...from slow changes in the form or position of the petals, or from new sorts of insects visiting the flowers, it might be advantageous to the plant that the labellum should resume its normal position on the upper side of the flower, as is actually the case with *Malaxis paludosa*, and some species of *Catasetum*, &c. This change, it is obvious, might be simply effected by the continued selection of varieties which had their ovaria less and less twisted, but if the plant only afforded varieties with the ovarium more twisted, the same end could be attained by the selection of such variations, until the flower was turned completely round on its axis. This seems to have actually occurred with *Malaxis paludosa*, for the labellum has acquired its present upward position by the ovarium being twisted twice as much as is usual. (Darwin 1984, 284–85)

The end to be obtained is the facilitation of insect visitation (which facilitates in

turn cross-fertilization). Orchids display some rather baroque adaptations which apparently have this result. Darwin's teleological question is why there are so many strange structures with the same effect in a closely related group of plants. He indicates that the principle of natural selection can do better on this score than special creation, since, unlike an omnipotent creator, natural selection can only modify structures on the basis of variations that actually occur. Like the Rube Goldberg machine he described earlier, natural selection doesn't start from scratch – it is stuck with doing the best it can with available variations.

Nevertheless, the explanation-sketches offered here are relentlessly teleological while being relentlessly selectionist. Darwin, as both Thomas Huxley and Asa Gray claimed, saw no conflict between natural selection and teleology.

3. MISUNDERSTANDING TAKES MANY FORMS

In a recent essay, John Beatty (1990, 113–144) surveys the many reactions to Darwin's evolutionary theory with respect to its relation to teleological explanation.⁸ He neatly encapsulates his results in this two-by-two figure (Fig. 2).

	For Promoting Teleology	For Undermining Teleology
Darwin Praised	Gray	Huxley Helmholtz duBois-Reymond
Darwin Blamed	Kölliker	von Baer

Fig. 2 (after Beatty 1990).

As we have seen, Huxley's attitude is more complex than his place on this chart would suggest. While he thought Darwin's theory had dealt "the death blow" to special creation, he also insisted that "there is a wider teleology which is not touched by the doctrine of Evolution, but is actually based upon the fundamental proposition of Evolution" (in F. Darwin 1887, 316). If by "the fundamental proposition of Evolution" Huxley intended the principle of natural selection, this remark seems to describe Darwin's practice correctly. 'Natural selection' refers to a natural process which preserves traits in virtue of their advantageous

consequences. Further, the passage quoted in note 1 shows that Huxley endorsed the reconciliation of morphological and teleological approaches which Beatty argues to be Darwin's achievement.⁹

Beatty thinks this remarkable result is due to a subtle interplay between chance and utility in Darwin's theory that "lent itself to widely different interpretations"(Beatty 1990, 124). Here I would like to suggest a simpler explanation for this truly unusual reaction to Darwin. It is that Darwin essentially re-invented teleology. Encouraged by many close followers to drop the term 'natural selection', Darwin steadfastly refused. He saw, better than his followers, that it could not easily be dropped. In the context of viewing variation as the provision of a random set of alternatives, a mechanism for selecting among them is crucial. The concept of selection permits the extension of the *teleology* of domestic breeding into the natural domain, without the need of conscious design.¹⁰ As in domestic selection, the good served by a variation continues to be causally relevant to its increasing frequency, or continued presence, in a population – but the causal mechanism, and the locus of goodness, shifts.

None of the figures listed on Beatty's chart were prepared for this. Even those who were evolutionists, botanists, and partial to teleology were not. To say, for example, as Asa Gray did, that "Darwin's particular hypothesis...would leave the doctrines of Final Causes, utility, and special design, just where they were before" (Gray 1963, 119; quoted in Beatty 1990, 125) wishful thinking. In a historical context where one's teleological choices were either the goals of goal-directed vital forces or divinely designed adaptation, no one was prepared for Darwin's accomplishment: a selection-based teleology. Far from leaving the doctrine of Final Causes just where it was, Darwin had given it a fundamentally new theoretical base. Unlike Gray, Huxley seems to have, at least implicitly, understood this.

But we have now seen that Gray and Huxley in fact agreed on one important aspect of this question: Darwin had reconciled "Morphology and Teleology." Beatty, following Toby Appel's important work (1987, 207, 231–32)¹¹, points out that this was a battle, initiated by disagreements between Geoffrey St. Hiliare and George Cuvier, over whether priority should be given to explanations based on the basic anatomical plan of the class to which an organism belonged or to explanations based on the functional needs of the organism. Darwin did indeed see his theory as mediating this debate.

It is generally acknowledged that all organic beings have been formed on two great laws – Unity of Type, and the Conditions of Existence. ... On my theory, unity of type is explained by unity of descent. The expression of conditions of existence, so often insisted on by the illustrious Cuvier, is fully embraced by the principle of natural selection. (Darwin 1964, 206)

He goes on to note that his theory gives priority to conditions of existence, since the agreement in structure one sees throughout a type is due to the past adaptations of shared ancestors. In the nineteenth century, this would be understood as

taking a position on the morphology versus teleology debate, giving priority to teleology. To twentieth century readers this is not nearly so clear.

It is doubtful, however, that any of those who praised or blamed Darwin for his position on teleology ever worked very hard to see how this reconciliation actually works. Darwin speaks of the principle of natural selection “fully embracing” conditions of existence; and Huxley of a “wider teleology based on the fundamental proposition of Evolution.” Gray, on the other hand, read divine design into Darwin’s teleology in a way that disturbed Darwin deeply.¹²

Paradoxically, we are better prepared to appreciate Darwin’s accomplishment than were his contemporaries. A number of biologists and philosophers have provided accounts of the teleological explanations associated with evolution by natural selection that map onto Darwin’s teleological explanations quite well.¹³ These accounts rest, to a greater or lesser degree, on thoughtful reflection on the explanatory practices of contemporary evolutionary biology. To the extent that these practices derive from Darwin, it is perhaps not surprising that accounts of teleological explanation based on them fit Darwin’s explanatory practices so well.

4. CONCLUSION

By carefully examining Darwin’s actual use of teleological explanation, one finds an explanatory structure which is at once irreducibly teleological, and at the same time unlike any of the standard forms of teleology in the nineteenth century. Indeed it is only rather recently that there is a model of teleological explanation to which Darwin’s reasoning conforms. Moreover, though Darwin occasionally endorses his own teleology, to my knowledge he never provides a philosophical commentary on it.

This last fact is closely related to the puzzle of Darwin’s public silence on how he intends his readers to understand his use of terms such as ‘Final Cause’, ‘purpose’, ‘end for which’, ‘good for which’. After all, his letters and notebooks indicate that he thought about it a good deal. Puzzling as this is, however, it is not a *special* puzzle about his teleology. The same sources show that he thought deeply about the nature of inductive support for theories, but his published books and papers leave such issues alone. Darwin read and thought much on the philosophy of biology – he published nothing at all on the subject. There is no reason to think he would deal with the question of final causation any differently. A skilled rhetorician knows when to speak, but more importantly, when to be silent. That followers as different as T.H. Huxley and Asa Gray could both find a teleology that they could live with in Darwin’s explanatory practice indicates that, as usual, Darwin was a skilled rhetorician.

NOTES

¹ Nor were the sentiments expressed by Gray shared only by those with theological axes to grind. The passage that Ghiselin perhaps had in mind when he mentioned Francis Darwin says that “one of the greatest services rendered by my father to the study of Natural History is the revival of Teleology.” But he immediately follows this with a quote from T. H. Huxley, which reads, in part, “...the most remarkable service to the philosophy of Biology rendered by Mr. Darwin is the reconciliation of Teleology and Morphology, and the explanation of the facts of both, which his view offers.” (F. Darwin 1892/1958, 316) Notice again that it is the reconciliation of a philosophical dispute for which both Gray and Huxley praise Darwin. Ernst Mayr takes such passages as evidence of Huxley and Gray misunderstanding Darwin (Mayr 1988, 241); but Darwin’s endorsement is hard to reconcile with this viewpoint.

² The analysis, based as it is on morphological adaptations in plants, cannot be extended without argument to other sorts of traits (instincts, emotions, etc.). Nevertheless, the analysis does make it likely that any trait due solely to natural selection would be given a teleological explanation of the same sort.

³ The obscurities include what precisely Darwin means by ‘innumerable eggs’, what the referent of ‘Final Cause’ is, and whether it is Darwin’s use of Malthus’s ideas or Malthus himself that is intended. There is no help forthcoming in the immediate context of this entry.

⁴ While Mayr (1988, 240) claims the *Origin* is remarkably free of teleological language, he doesn’t mention these uses of the term ‘Final Cause’; his focus is solely on determining whether Darwin was wedded to the concept of perfect adaptation at the time he wrote the *Origin*. It is clear that Mayr is equating being a teleologist or finalist with believing either in internal vital forces or natural theology – that is, he accepts the premises mentioned at the end of my introduction, and draws the valid conclusion.

⁵ Under the subtitle ‘The Refutation of Design’, Ghiselin takes a passage of Darwin’s that is thoroughly teleological, and interprets it as an attack on the argument from design (Ghiselin 1969, 154). He closes with a quote from Darwin’s discussion of heredity in *The Variation of Animals and Plants Under Domestication* in which Darwin is criticizing Asa Gray’s claim that variations are in fact intentionally directed along beneficial lines. Presumably this is intended to show that Darwin was an enemy of teleological explanation generally (156–157). What it *does* show is (a) that Darwin does not think any aspect of the evolutionary process is divinely guided and (b) that this also applies to the origins of variations. It does *not* show Darwin to be an opponent of teleology. (I assume it is clear that these critical remarks are aimed solely at Ghiselin’s attempt to deny Darwin’s teleology. I have learned much from Ghiselin’s work on Darwin, and much about Darwin’s botanical work from the chapter currently under discussion.)

⁶ The *Primulae* fascinated Darwin for a variety of reasons. In chapter 2 of the *Origin*, for example, the two species commonly known as the cowslip and primrose were the centerpiece of Darwin’s argument that the most able botanists possessed no standardized criteria for determining whether two closely allied organisms should be ranked as varieties of a single species or distinct species (Darwin 1964, 49–50; see Beatty 1985, 271–273).

⁷ For a brief discussion and references see section 3 and note 13, below.

⁸ For further details on the various perceptions of the consequences of Darwin’s theory for teleology, see Lenoir 1982, 246–275 and Cornell 1986, 405–421. I discuss these questions briefly in Lennox 1992.

⁹ Cf. Beatty 1990, 130–31, and notes 50–53. Beatty’s conclusion that Huxley is a thoroughgoing opponent of teleology relies upon a remark in Huxley 1898, 82.

¹⁰ Though it hardly needs mentioning that Darwin freely availed himself of the network of metaphors this extension provided: “Man selects only for his own good; Nature only

for that of the being which she tends" (Darwin 1964, 83). "It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving that which is good..." (Darwin 1964, 84).

¹¹ It should be noted, however, that Appel accepts the view defended by Dov Ospovat (1981) that Darwin gave up teleology when he gave up a belief in "perfect adaptation." For example: "Darwin eventually came to reject not only teleological explanation but also perfect adaptation" (Appel 1987, 207). She claims this rejection was complete by the 1850's (231); and Darwin's claim (quoted immediately below) to be able to integrate the concept of Unity of Type with that of Conditions of Existence is referred to as "a reminder of his earlier belief in teleology" (231). Oddly, on the very next page, Appel quotes the *Origin* (1964, 435) as referring to the *purposes served* by the limbs of the progenitors of mammals.

¹² Cf. Beatty 1990, 125. These claims are often cited to show Darwin's general antipathy to teleology. What they in fact show is his antipathy to natural theology.

¹³ For example, Ayala 1970; Binswanger 1990; Brandon 1981, 1990; Williams 1966; Wimsatt 1972; Wright 1976; and for summary discussions of this work, see Lennox 1992, and Ruse 1988, chapter 5. This is not meant to imply that these analyses are identical; indeed the differences among them are in some cases very important. However they share one crucial concept that is required to make sense of Darwin's teleology, specifically the idea of traits being differentially selected due to their consequences. This 'consequence etiology' structure (to use Larry Wright's language) has recently been endorsed by Wesley Salmon 1990, 111–116.

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