Femmes finales: natural selection, physiology, and the return of the repressed

David Haig[1]

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Abstract

Nineteenth-century final causes were ‘barren virgins’, an aphorism attributed to Francis Bacon, but twentieth-century teleology was a ‘mistress’, an adage of uncertain provenance. A study of historical uses of these gendered metaphors is used to probe changing attitudes toward teleological reasoning in biology. At the beginning of the nineteenth-century, invocations of final causes were commonplace but such idioms are rarely used at its end. This change is commonly attributed to publication of the *Origin of Species* in 1859 which completed the ejection of final causes from biology. Charles Darwin, however, openly and unashamedly uses teleological reasoning and language in his botanical research. He believed he had naturalized, rather than eliminated, the concept of final cause. A more important reason for the eclipse of final causes was the shift within physiology toward the explanatory modes of the physical sciences which had long held final causes in disrepute. The rejection of final causes as explanatory principles occurred despite a persistence of teleological reasoning that was experienced as a ‘guilty secret’ likened to a mistress that a physiologist could not give up but would not acknowledge in public. Biology’s ambivalent attitude toward teleological explanations persists in the twenty-first century.

David Haig

Department of Organismic and Evolutionary Biology,
Harvard University, 26 Oxford Street,
Cambridge MA 02138.
dhaig@oeb.harvard.edu

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> *"And teleology, like a wise damsel, though temporarily ruffled, managed to gather up her skirts with dignity and make the best of it." (Thiselton-Dyer 1890)*

1. Introduction

In 1818, William Whewell wrote to John Herschel: "It is true, as Bacon says, that speculations about final causes are like vestal virgins, pretty, dedicated to Heaven, and barren: yet still it is difficult to believe that the laws which produce all this multitude of phenomena should exist if it were not that some good purpose is or may be answered by them" (in Todhunter 1876, 29). The following year, Gilbert Blane (1819, p. 69) wrote:

> *"Bacon, with that exuberance of imagination with which he was so richly gifted … says, that final causes, like the vestal virgins, are devoted to the service of the Divinity; but like them too, are unfruitful, the consideration of them not leading to scientific improvement and natural discoveries."*

Dugald Stewart (1814; p. 455) considered that the epigrammatic maxim, to which Whewell and Blane alluded, had been "oftener quoted (particularly by French writers) than any other sentence in Bacon's works."

A century and a half later—repeating a witticism of uncertain provenance—Michael Polanyi (1964, p. 66) wrote "The story goes around among biologists everywhere that teleology is a woman of easy virtue whom the biologist disowns in public but lives with in private." The two tropes have different import—Blane's 'vestal virgins' were public but sterile; Polanyi's 'woman' was private but fertile—and mark a linguistic shift from the *final causes* of early nineteenth-century natural philosophy to the *teleology* of twentieth-century biology. This paper follows this thread of gendered metaphors of final causes—of nuns, priestesses, *hetairai*, and mistresses—through the troubled but fruitful marriage of biology and final causes.

Much attention in recent philosophy of biology has been directed to the question whether developmental biology was

excluded from (or declined to join) the so-called Modern Synthesis of evolutionary biology (Laland *et al*. 2011). Much less attention has been turned to the relative absence of physiology from the Modern Synthesis, although Schiller (1959, 1968) noted the neglect of physiology by evolutionary biologists and the fact that the major physiological societies let the Darwin centenary pass unnoticed. One of the themes that emerges from my investigation is the estrangement between physiology and evolutionary biology that followed publication of the *Origin of Species*.

2. *Virgo Deo consecrata*

Francis Bacon's (1605) *Advancement of Learning* was dedicated to the new king of England. Book II opens with an address that flatters James with the fruitfulness of his marital bed compared to the barrenness of the 'virgin queen' he had succeeded:

> *"It might seem to have more convenience, though it comes often otherwise to pass (excellent king), that those which are fruitful in their generations, and have in themselves the foresight of immortality in their descendants, should likewise be more careful of the good estate of future times, unto which they know they must transmit and commend over their dearest pledges. Queen Elizabeth was a sojourner in the world in respect of her unmarried life, and was a blessing to her own times … But to your Majesty, whom God hath already blessed with so much royal issue, worthy to continue and represent you for ever, and whose useful and fruitful bed doth yet promise many the like renovations, it is proper and agreeable to be conversant not only in the transitory parts of good government, but in those acts also which are in their nature permanent and perpetual."*

Bacon returned to his contrast of sterile females and fertile males in a plea for funding experiment:

> *"Another defect I note, wherein I shall need some alchemist to help me, who call upon men to sell their books and to build furnaces, quitting and forsaking Minerva and the Muses as barren virgins, and relying upon Vulcan."*

After Bacon's fall from grace in 1621 he prepared *De Augmentis Scientiarum* (Bacon 1623) as an expanded Latin version of the *Advancement of knowledge*. In a new section on the practical doctrine of nature, Bacon compared the investigation of final causes to a barren woman: "*nam causarum finalium inquisitio sterilis est, et, tanquam virgo Deo consecrata, nihil parit*". The investigation of final causes is sterile; like a virgin consecrated to God, it gives birth to nothing.

A few fine points should be noted about what Bacon actually wrote rather than what he was subsequently said to have written. In the *Advancement of Learning*, Bacon rejects a role for final causes in physical enquiry but uses the epithet 'barren virgins' (plural) for Minerva and the Muses. In *De Augmentis Scientiarum*, he compares the investigation of final causes to a virgin consecrated to God (singular). Bacon never compares final causes to vestal virgins. The phrase *virgo Deo consecrata* was used in the Catholic church to refer to a nun, who would probably have been the principal association of the phrase for contemporary readers in the aftermath of the Reformation. By the nineteenth century, classically-trained

Britons thought little of nuns and usually associated Bacon's 'virgin consecrated to God' with the vestal virgins. In the process, the epithet 'barren virgins' had become associated with final causes rather than Minerva and the Muses.

Bacon's feminine personification of Nature and the question whether his descriptions of experimental science should be interpreted as metaphors of rape and torture have been hotly debated (Merchant 2008; Vickers 2008; Pesic 2014). This paper is not a contribution to those debates, except to note that Bacon's metaphor lacked overt elements of suppressed male desire and Bacon's own marriage was childless. Neither does this paper address Bacon's understanding of final causes. Rather it addresses how a metaphor attributed to Bacon, of final causes as barren virgins, was found useful and widely disseminated in the nineteenth century, and how a different gendered metaphor, of teleology as a hidden mistress, took its place in the twentieth century and was widely propagated despite its obscure origins.

Elizabeth's mother was beheaded so her father could marry again. She succeeded her sister who was barren in marriage and remained childless by choice to pursue other ends. Her 44-year reign was a period of relative peace and stability. The queen is dead, long live the queen!

3. Final causes in nineteenth-century British biology

My focus will be on attitudes toward final causes in nineteenth-century British biology, but I will begin by placing this in the context of developments in continental biology. One key event was the Cuvier–Geoffroy debate in Paris of 1830 (Appel 1987; Grene 2001). Untangling the issues in this debate is beyond my current purpose, except to note that it was commonly construed in Britain as a conflict between final and formal causes in morphology. On one side, Georges Cuvier argued that the arrangements of animal parts were determined by the 'conditions of existence', how they fitted the animal to its place in life. Function determined form. Cuvier equated this view with final causes. In opposition, Étienne Geoffroy St-Hilaire argued that animal forms exhibited 'unity of composition.' Different animals were related in form by structural analogies that were independent of function. Geoffroy rejected final causes.

A shift occurred in continental biology during the nineteenth century toward explanations in terms of physics and chemistry (Lenoir 1981). This shift occurred first in physiology. Emil DuBois-Reymond reported in a letter of 1842 that he and Ernst Brücke had sworn an oath that no forces other than the common physico-chemical forces were active within organisms.[1] DuBois-Reymond and Brücke, together with Hermann Helmholtz and Carl Ludwig, set out to reform German physiology on a strictly physico-chemical basis (Cranefield 1957; Lenoir 1981). They saw the organic as subject to the same fundamental laws as the inorganic. Formal and final causes were excluded in favor of efficient and material causes. In modern physiology's creation myth, the field was born in 1846 when Ludwig first used a revolving drum recorder to create a spatial record of temporal changes in an instrumented body (Borell 1987).

The attitudes toward final causes of five British thinkers will be described: William Whewell (1794–1866), a clergyman, college master, and polymath with strong links to natural theology; Richard Owen (1804–1892), a comparative anatomist who developed an idealist philosophy of archetypic forms; Thomas Henry Huxley (1825–1895), another comparative anatomist who advocated agnosticism on metaphysical questions and a positivistic philosophy of science; Charles Robert

Darwin (1809–1882), a gentleman naturalist who attempted to reconcile ‘unity of type’ and ‘conditions of existence’; and John Burdon Sanderson (1828–1905), a physician, turned physiologist, who brought the methods of modern physiology, controversially including vivisection, to Britain. The views of the younger Huxley will be considered before those of the older Darwin because, prior to 1859, Huxley had had more to say publically on final causes.

3.1. William Whewell

William Whewell’s voluminous writings often allude to barren virgins in contexts in which he defends final causes. In the third Bridgewater treatise *Astronomy and general physics considered with reference to natural theology* Whewell (1833, pp. 264–6) divorces final causes from explanation in the physical sciences:

> *“Final causes are to be excluded from physical inquiry; that is, we are not to assume that we know the objects of the Creator’s design, and put this assumed purpose in the place of a physical cause. The physical philosopher has it for his business to trace clouds to the laws of evaporation and condensation … and it is precisely because he has thus established theories independently of any assumption of an end, that the end, when after all it returns upon him and cannot be evaded, becomes an irresistible evidence of an intelligent legislator. … [Bacon] would probably have said, that to these final causes barrenness was no reproach, seeing they ought to be, not the mothers but the daughters of our natural sciences; and that they were barren, not by imperfection of their nature but in order that they might be kept pure and undefiled, and so fit ministers in the temple of God.”*

Whewell saw final causes as playing a very different role in physiology (a term which for Whewell encompassed most of biology). In his *History of the inductive sciences*, Whewell (1837, p. 389f) wrote:

> *“The assumption of hypothetical final causes in physics may have been, as Bacon asserts it to have been, prejudicial to science; but the assumption of unknown final causes in physiology, has given rise to the science. … And though it may be possible to introduce into physiology the doctrine of efficient causes, such a step can never obliterate the obligations which the science owes to the pervading conception of a purpose contained in all organization.”*

When Whewell (1837, p. 463f) came to consider the doctrines of Geoffroy and Cuvier, he emphatically sided with Cuvier against Geoffroy:

> *“The assumption of an end or purpose in the structure of organized beings, appears to be an intellectual habit which no effort can cast off. It has prevailed from the earliest to the latest ages of zoological research … and has been formally accepted by so many great anatomists, that we cannot feel any scruple in believing the rejection of it to be a superstition of a false philosophy, and a result of the exaggeration of other principles which are supposed capable of superseding its use. And the doctrine of unity of plan of all animals, and the other principles associated*

> *with this doctrine, so far as they exclude the conviction of an intelligible scheme and a discoverable end, in the organization of animals, appear to be utterly erroneous."*

Final causes were the wellspring of physiological discovery, "far from being sterile… [they] had a large share in every discovery which is included in the existing mass of real knowledge" (p. 467).

In his *Philosophy of the inductive sciences*, Whewell (1840, p. 49) opined:

> *"This Idea of a Final Cause is applicable as a fundamental and regulative idea to our speculations concerning organized creatures only. … In mere Physics, Final Causes as Bacon has observed, are not to be admitted as a principle of reasoning. But in the organical sciences, the assumption of design and purpose in every part of every whole … is the basis of sound reasoning and the source of true doctrine."*

Explanations in terms of final causes formed "no essential part" of the understanding of inorganic matter but were "fundamental and regulative" for the understanding of organized creatures. Indeed, Whewell (1840, p. 87) in one passage restricts Final Causes to the living world:

> *"The regular form of a crystal, whatever beautiful symmetry it may exhibit, whatever general laws it may exemplify, does not prove design in the same manner in which design is proved by the provisions for the preservation and growth of the seeds of plants, and of the young of animals. The law of universal gravitation, however wide and simple, does not impress us with the belief of a purpose, as does that propensity by which the two sexes of each animal are brought together."*

Why should the living world be different from the non-living world with respect to purposiveness? Surely this is a phenomenon for which one would like an explanation but I have found no place where Whewell directly addresses this question and agree with Ruse (1977) that this tension in Whewell's philosophies of physics and physiology is never satisfactorily resolved. Ruse (1977) has also helped me understand Whewell's theological tension with respect to physical laws. The necessity of physical laws leaves little room for God's creative freedom. Whewell found evidence of God's freedom in the structure of living things that showed exquisite fitness to function in details that were not determined by physical law. This is also why Whewell initially resisted the idea of Unity of Plan—as championed by Geoffroy and other morphologists—because the existence of correspondences between the skeletons of sparrows and humans that were unrelated to function suggested the existence of law-like constraints on divine design.

Richard Owen's studies on the vertebrate skeleton pushed Whewell to seek a compromise between Unity of Plan and Final Causes. In his 'Additions' to the third edition of the *History of the inductive sciences*, Whewell (1857, p. 553ff) conceded that Owen's homologies and archetypes "necessarily displace some of the old views regarding Final Causes" (559). In Whewell's revised view, "Final Causes, or Evidences of Design, appear … not merely as contrivances for evident purposes, but as modifications of a given general Plan for special given ends" (p. 560). Whewell (p. 561) reprises a

familiar theme:

> *"The reference to Final Causes is sometimes spoken of as unphilosophical, in consequence of Francis Bacon's comparison of Final Causes in Physics to Vestal Virgins devoted to God, and barren. I have repeatedly shown that, in Physiology, almost all the great discoveries which have been made, have been made by the assumption of a purpose in animal structures. … I might add that in Physiology, if they are not Mothers, they are admirable Nurses; skilful and sagacious in perceiving the signs of pregnancy, and helpful in bringing the Infant Truth into the light of day."*

With respect to Unity of Plan, he concluded:

> *"The Archetype of the Animal Structure being of the nature of an* ***Idea****, implies a mind in which this Idea existed; and that thus Homology itself points the way to the Divine Mind. But while we acknowledge the full value of this view of theological bearing of physiology, we may venture to say that it is a view quite different from that which is described by speaking of 'Final Causes,' and one much more difficult to present in a lucid manner to ordinary minds." (p. 561f)*

Whewell (1864) responded to the *Origin of Species* (Darwin 1859), in the Preface to the seventh edition of his Bridgewater Treatise, without ever naming his target. Darwin was guilty of "two enormous assumptions which deprive the reasoning of all force, and make these speculations a mere work of fancy."

> *"First, it is assumed, that the mere possibility of imagining a series of steps of transition from one condition of organs to another, is to be accepted as a reason for believing that such transition has taken place: And next, that such a possibility being thus imagined, we may assume an unlimited number of generations for the transition to take place in, and that this indefinite time may extinguish all doubt that the transitions really have taken place."*

Darwin had attempted to explain the appearance of purposiveness in the living world by the interaction of chance and necessity in a process he called natural selection that eliminated the need for intelligent design. Whewell equated Darwin's hypothesis as an explanation by blind chance.

> *"When it is asked, 'Have we any right to assume that the Creator works by intellectual powers like those of man?' we may reply, that we must assume that the powers by which the Creator works* ***are*** *intellectual; that they imply* ***intelligent*** *working; that the arrangements which we cannot describe except as* ***contrivances****, cannot be the work of blind chance."*

Finally, in the year of his death, Whewell (1866, p. 357) wrote:

> *"That in Bacon's time the reasoning from final causes had been pushed too far may easily be shown. But it is certain that, with regard to the structure of animals, the most eminent physiologists in all ages have declared that at every step they did discover evidences of design, and that by holding to that principle, they made discoveries. … Were they mistaken? Was it a false, an unreal principle that thus led them to some of the most important scientific truths which we possess? Are the vestal virgins barren by nature, or only to place their Divine authority above suspicion? They* ***have*** *had offspring; great and glorious offspring. Still, it is in the highest degree important that no one should rashly ascribe to them children. No one should claim their parentage for the children of his own brain."*

3.2. Richard Owen

Richard Owen trained with Georges Cuvier in Paris and attended parts of the Cuvier–Geoffroy debate of 1830. Owen at that time sided with Cuvier but his subsequent studies of vertebrate skeletons changed his mind. Owen (1868, §423) provides an account of his evolution from teleologist to idealist:

> *"… the question of the condition or law of special homologies pressed itself upon me, more especially in connection with the task of arranging and cataloguing the osteological part of the Hunterian Museum … they enforced a reconsideration of Cuvier's conclusions to which I had previously yielded assent. … I found that the artifice of an archetype vertebrate animal was as essential as that of the archetype plant had been to Goethe in expressing analogous ideas; and as the like reference to an 'ideal type' must be to all who undertake to make intelligible the 'unity in variety' pervading any group of organisms."*

Before his road to Damascus in the bowels of the Hunterian Museum, Owen had embraced final causes. *On the generation of marsupial animals* (Owen 1834, p. 358) is a fine example of teleological reasoning in the tradition of natural theology. A mother kangaroo needs some way to take care of her prematurely born offspring whilst caring for herself:

> *"To obviate this inconvenience a natural and portable nest is superadded to her structure, in order that she may resort, without prejudice to the young, to all the places necessary for her own safety and support; while at the same time the young one is enabled to draw an unintermitting supply of nutriment, and has also its temperature maintained by close contact with the abdominal surface of the parent, in an analogous, though more complete manner than the egg during incubation."*

The mutual adaptive adjustments of mother and joey provided "the most irrefragable evidence of creative foresight" (p. 349) but, by the time he came to write *On the nature of limbs*, Owen (1849, p. 40) had rethought the birth of the kangaroo and now had recourse to Bacon's metaphor of futile speculation:

> *"[A] final purpose is indeed readily perceived and admitted in regard to the multiplied points of ossification of the skull of the human foetus, and their relation to safe parturition. But when we find that the same ossific centres are*

> *established, and in similar order, in the skull of the embryo kangaroo, which is born when an inch in length, and in that of the callow bird that breaks the brittle egg, we feel the truth of Bacon's comparisons of 'final causes' to the Vestal Virgins, and perceive that they would be barren and unproductive of the fruits we are labouring to attain, and would yield us no clue to the comprehension of that law of conformity of which we are in quest."*

Owen (1868, p. 796) accepted the transmutation of species but rejected the Darwinian mechanism

> *"I have been led to recognise species as exemplifying the continuous operation of natural law, or secondary cause; and that, not only successively but progressively; 'from the first embodiment of the Vertebrate idea under its old Ichthyic vestment until it became arrayed in the glorious garb of the Human form.'" (quoting Owen 1849)*

He deemed "an innate tendency to deviate from parental type, operating through periods of adequate duration, to be the most probable nature, or way of operation, of the secondary law, whereby species have been derived one from the other" (p. 807). He named this the hypothesis of Derivation.

> *"According to my derivative hypothesis, a change takes place first in the structure of the animal, and this, when sufficiently advanced, may lead to modifications of habits. … A purposive route of development and change, of correlation and interdependence, manifesting intelligent Will, is as determinable in the succession of races as in the development and organisation of the individual. Generations do not vary accidentally, in any and every direction; but in preordained, definite, and correlated courses." (p. 808)*

Owen had rejected final causes as independent acts of creation that fitted each species to its conditions of existence in favor of a teleological law of derivation that led inexorably to human beings (p. 796). In an obituary of TH Huxley, Michael Foster (1896) wrote of Richard Owen "his work consisted, on the one hand, of detailed descriptions, possessing the highest merit and greatest value, of the structure of an immense number of animal forms, and, on the other hand, of generalisations and speculations of a metaphysical kind, based largely on the philosophy of Oken, and, as time has since proved, of a fruitless, barren nature."

3.3. Thomas Henry Huxley

TH Huxley is popularly portrayed as the principal public defender of Charles Darwin and scourge of Richard Owen. His strong streak of positivism is on display in his reminiscences on the reception of the *Origin of Species* (L Huxley 1900, p. 182f).

> *"I imagine that most of those of my contemporaries who thought seriously about the matter, were very much in my own state of mind … and disposed to turn aside from an interminable and apparently fruitless discussion, to labour in the fertile fields of ascertainable fact. … That which we were looking for, and could not find, was a hypothesis*

> *respecting the origin of known organic forms which assumed the operation of no causes but such as could be proved to be actually at work. … The 'Origin' provided us with the working hypothesis we sought. Moreover, it did the immense service of freeing us for ever from the dilemma—Refuse to accept the creation hypothesis, and what have you to propose that can be accepted by any cautious reasoner?"*

In his writings before the *Origin of Species*, Huxley commonly juxtaposes Physiology as the science of *function* with Ontology or Morphology as the science of *structure*. At this time, he firmly believed that function must yield explanatory primacy to structure. Thus, Huxley (1853) wrote

> *"Physiology and Ontology are two sciences which cannot be too carefully kept apart; there may be such entities as causes, powers, and forces, but they are the subjects of the latter, and not of the former science, in which their assumption has hitherto been a mere gaudy cloak for ignorance. For us, physiology is but a branch of the humble philosophy of facts … If cause, power, and force mean anything but convenient names for the mode of association of facts, physiology is powerless to reach them."*

Huxley (1856a) lumped Cuvier with Paley and natural theology:

> *"Is this utilitarian adaptation to a benevolent purpose the chief or even the leading feature of that great shadow, or, we should more rightly say, of that vast archetype of the human mind, which everywhere looms upon us through nature? The reply of natural history is clearly in the negative. She tells us that utilitarian adaptation to purpose is not the greatest principle worked out in nature, and that its value, even as an instrument of research, has been enormously overrated. … If we trace out the doctrine to its fountain head, we shall find that it was primarily put forth by Cuvier—the prince of modern naturalists. Is it to be supposed then that Cuvier did not himself understand the methods by which he arrived at his great results? that his master mind misconceived its own processes? This conclusion appears to be not a little presumptuous; but … it is correct."*

For Huxley (1856a), the study of morphology brought him closer to union with an 'infinite mind'

> *"Natural history plainly teaches us that the utilitarian principle, valuable enough in physiology, helps us no further, and is utterly insufficient as an instrument of morphological research. … it may be regarded as one of the noblest characteristics of natural history knowledge, that its highest flights point, not to a discrepancy between the infinite and the finite mind, but to a higher and closer union than can be imagined by those whose studies are confined to the physical world. For where the principle of adaptation, of mere mechanical utilitarian contrivance fails us, it is replaced by another which appeals to the æsthetic sense as much as the mere intellect."*

Huxley (1856b) reiterated his belief that Cuvier's structural practice belied his functional conclusions. Cuvier "was in error in ascribing to the laws of physiological correlation that primary importance in palæontology which he undoubtedly does

give them … palæontology, so far as it consists in the restoration of extinct forms, is entirely based upon deductions from the empirical laws of morphology; that its conclusions, so far, would be as valid if the whole science of physiology were non-extant, and if we knew nothing of final causes or adaptations to purposes." Moreover

> *"… the **physiological** laws of correlation which Cuvier laid down are not as universally and necessarily applicable as he seems to have imagined … his physiological laws of correlation are of wholly subordinate importance in palæontology, if not absolutely unimportant, the really important laws by which he worked being those morphological laws … to which he nevertheless ascribes in words, though not in practice, a subordinate place."*

Huxley was in search of transcendent principles empirically expressed in structural not functional laws.

Despite his derogation of physiology relative to morphology, Huxley was attuned to continental developments in physiology. In a paper on agamic reproduction in aphids, Huxley (1859b) excoriates Richard Owen for his invocation of a "spermatic force" and commented that the "groundwork of modern physiology is not a score of years old." A detailed study of Huxley's evolving attitudes toward physiology would be valuable, but is beyond the compass of the current work.

In a letter to Charles Lyell of June 25 1859, Huxley suggests that one species could change into another suddenly, without transitional forms, somewhat in the nature of a chemical reaction. All Huxley's studies had led him to believe in the absence of any real transitions between natural groups, great or small, but he preferred greatly the transmutation hypothesis to special creation. "I by no means believe that the transmutation hypothesis is proven, or anything like it. But I view it as a powerful instrument of research. Follow it out, and it will lead us somewhere; while the other notion is, like all the other modifications of 'final causation,' a barren virgin" (in Leonard Huxley 1900, p. 185).

Huxley's (1859a) review of the *Origin of Species* (published November 24, 1859) in *The Times* of December 26, 1859 again used Bacon's metaphor.

> *"Mr. Darwin abhors mere speculation as nature abhors a vacuum. He is as greedy of cases and precedents as any constitutional lawyer, and all the principles he lays down are capable of being brought to the test of observation and experiment. The path he bids us follow professes to be, not a mere airy track, fabricated of ideal cobwebs, but a solid and broad bridge of facts. If it be so, it will carry us safely over many a chasm in our knowledge, and lead us to a region free from the snares of those fascinating but barren Virgins, the Final Causes, against whom a high authority has so justly warned us."*

Huxley (1860) wrote a more extended review for the *Westminster Review* in which he again offered a two-fold division of biology: "That part of biological science which deals with form and structure is called Morphology—that which concerns itself with function, Physiology" (p. 543). In general, he was dismissive of the contribution of physiology to understanding the nature of species. He noted that "It is the first great law of reproduction, that the offspring tends to resemble its parent or parents, more closely than anything else" (545) but that this law was supplemented by the tendency of offspring to deviate in greater or lesser degree from their parents: "As a general rule, the extent to which an offspring differs from its

parent is slight enough; but, occasionally, the amount of difference is much more strongly marked, and then the divergent offspring receives the name of a Variety" (p. 547). Huxley describes two such marked differences that had arisen "for no assignable reason": the first a long-bodied ram with short bandy legs and the second a human child with six digits per hand and per foot (p. 547f).

> *"Two circumstances are well worthy of remark in both these cases. In each, the variety appears to have arisen in full force, and, as it were,* ***per saltum*** *… Doubtless there were determining causes for these as for all other phaenomena; but … It was no case of what is commonly called adaptation to circumstances … the variations arose spontaneously. The fruitless search after final causes leads their pursuers a long way; but even those hardy ideologists, who are ready to break through all the laws of physics in chase of their favourite will-o'-the-wisp, may be puzzled to discover what purpose could be attained by the stunted legs of Seth Wright's ram or the hexadactyle members of Gratio Kelleia."*

Huxley's (1860) review pays little attention to natural selection: the transmutation of species was the bigger question. Huxley does however reject those critics of Darwin who argued that natural selection could achieve little because nature, unlike animal or plant breeders, could not knowingly choose (p. 568):

> *"Again, it is said that there is no real analogy between the selection which takes place under domestication, by human influence, and any operation which can be effected by nature, for man interferes intelligently. … Even putting aside the question whether nature, acting as she does according to definite and invariable laws, can be rightly called an unintelligent agent, such a position as this is wholly untenable. Mix salt and sand, and it shall puzzle the wisest of men with his mere natural appliances to separate all the grains of sand from all the grains of salt; but a shower of rain will effect the same object in ten minutes. And so while man may find it tax all his intelligence to separate any variety which arises, and to breed selectively from it, the destructive agencies incessantly at work in nature, if they find one variety to be more soluble in circumstances than the other, will inevitably in the long run eliminate it."*

This passage is notable for its comparison of natural selection to a mindless*destructive* process and for the possibility it entertains of an *intelligent* nature acting by definite and invariable laws.

Huxley (1864) reviewed Albert von Kölliker's critique of the selection theory. Kölliker identified Darwin as a teleologist but Huxley wanted to nip this idea in the bud. In Huxley's view, teleology "had received its deathblow at Mr. Darwin's hands" (p. 567).

> *"If we apprehend the spirit of the 'Origin of Species' rightly, then, nothing can be more entirely and absolutely opposed to Teleology, as it is commonly understood, than the Darwinian Theory. So far from being a 'Teleologist in the fullest sense of the word,' we should deny that he is a Teleologist in the ordinary sense at all; and we should*

> *say that, apart from his merits as a naturalist, he has rendered a most remarkable service to philosophical thought by enabling the student of Nature to recognise, to their fullest extent, those adaptations to purpose which are so striking in the organic world, and which Teleology has done good service in keeping before our minds, without being false to the fundamental principles of a scientific conception of the universe. The apparently diverging teachings of the Teleologist and of the Morphologist are reconciled, by the Darwinian hypothesis." (p. 569)*

Darwin had 'reconciled' teleology and morphology by delivering a 'deathblow' to teleology.

Huxley (1869a) returned to the seductive allure of final causes in an address to the Geological Society in which he likens final causes to courtesans who lure men from gainful activity:

> *"Like most philosophers of his age, [Hutton] coquetted with those final causes which have been named barren virgins, but which might be more fitly termed the* ***hetairæ*** *of philosophy, so constantly have they led men astray."*

That same year, in a review of Haeckel's*Natural History of Creation*, Huxley (1869b) gave what may be his most extended discussion of teleology.

> *"The Teleology which supposes that the eye, such as we see it in man or one of the higher Vertebrata, was made with the precise structure which it exhibits, for the purpose of enabling the animal which possesses it to see, has undoubtedly received its death-blow. Nevertheless it is necessary to remember 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. That proposition is, that the whole world, living and not living, is the result of the mutual interaction, according to definite laws, of the forces possessed by the molecules of which the primitive nebulosity of the universe was composed. If this be true, it is no less certain that the existing world lay, potentially, in the cosmic vapour; and that a sufficient intelligence could, from a knowledge of the properties of the molecules of that vapour, have predicted, say the state of the Fauna of Britain in 1869, with as much certainty as one can say what will happen to the vapour of the breath on a cold winter's day."*

Huxley then invokes the complex mechanism of a kitchen clock:

> *"If the evolution theory is correct, the molecular structure of the cosmic gas stands in the same relation to the phenomena of the world as the structure of the clock to its phenomena."*

Two death-watch beetles live within the clock-case. The first beetle is a mechanist who "might say 'I find here nothing but matter and force and pure mechanism from beginning to end,' and he would be quite right. But if he drew the conclusion that the clock was not contrived for a purpose, he would be quite wrong." The second beetle is a teleologist who "listening to the monotonous 'tick! tick!' so exactly like his own, might arrive at the conclusion that the clock was itself a monstrous sort of death-watch, and that its final cause and purpose was to tick. How easy to point to the clear relation of the whole

mechanism to the pendulum, to the fact that the one thing the clock did always and without intermission was to tick, and that all the rest of its phenomena were intermittent and subordinate to ticking!"

Both beetles were drawn to erroneous conclusions by different philosophical presuppositions. The teleologist, in particular, had been found guilty of coleopteromorphism. Huxley continued:

> *"Substitute 'cosmic vapour' for 'clock,' and 'molecules' for 'works,' and the application of the argument is obvious. The teleological and the mechanical views of nature are not, necessarily, mutually exclusive."*

The moral was simple, we can afford to be agnostic on such barren questions: "why trouble one's self about matters which are out of reach, when the working of the mechanism itself, which is of infinite practical importance, affords scope for all our energies?" Huxley was a true heir of Francis Bacon.

Leonard Huxley (1900) paraphrased an unpublished lecture of his father from 1876,*On the Teleology and Morphology of the Hand*. His father showed

> *"… by the facts of morphology that the argument, as commonly stated, fails; that each mechanism, each animal, was not specially made to suit the particular purpose we find it serving, but was developed from a single common type. Yet in a limited and special sense he finds teleology to be not inconsistent with morphology. … To be a teleologist and yet accept evolution it is only necessary 'to suppose that the original plan was sketched out—that the purpose was foreshadowed in the molecular arrangements out of which the animals have come.'"*

Huxley's seductive sirens were metaphysical questions: the meaning or non-meaning of existence; whether the universe was directed to an end. One senses a tension in Huxley between his fascination with a cosmic teleology and his rejection of metaphysical speculation as fruitless and sterile. For the pragmatic Huxley, natural selection had rhetorical usefulness in undercutting appeals to final causes but was not useful in his empirical research. For the agnostic Huxley, the intricate contrivances of living things were explained by natural selection and therefore did not address his fundamental question whether the universe had a purpose.

3.4. Charles Robert Darwin

As an undergraduate at Cambridge, Charles Darwin admired Paley's *Natural Theology* which argued from the contrivances of nature to a divine mind with a goal. It was only in 1837, after a circumnavigation of the globe, that Darwin became a believer in the transmutation of species, and only after his reading of Malthus in September 1838 that he gained an intimation of a mechanism (Sulloway 2009). Later that year, Darwin was making notes on MacCulloch's (1837) *Proofs and illustrations of the attributes of God* (234) when he read the passage

> *"In the insect races, there is a very general case, where inconvenience or evil would have followed, as in the*

> *elephant under other circumstances, had there not been an analogous special contrivance made, to encounter a peculiar difficulty: while it is one of the examples of that continuous system of adaptation of means to ends which pervades the whole of the Creator's plans. I allude to those insects in which the mouth is a proboscis, as in the bee and the butterfly."*

Darwin jotted across the bottom of one page of his notebook and the top of the next:

> *"… says* ***inconvenience*** *would have arisen had insects not been provided. inconvenience!* ***extinction****, utter* ***extinction****! let him study Malthus & Decandoelle.— 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."*[2]

The note is enigmatic. Are the 'barren virgins' MacCulloch's arguments from design or the innumerable eggs? Whatever the interpretation, the note indicates that Darwin was thinking about final causes and knew they had been compared to sterile females. Darwin took another twenty years to publish ideas that gave a novel philosophical grounding for arguments from final causes.

On the Origin of Species (Darwin 1859) has dual epigraphs from Whewell's (1833) Bridgewater Thesis and Bacon's (1605) *Advancement of Learning*

> *"But with regard to the material world, we can at least go so far as this—we can perceive that events are brought about not by insulated interpositions of Divine power, exerted in each particular case, but by the establishment of general laws."*
>
> *"To conclude, therefore, let no man out of a weak conceit of sobriety, or an ill-applied moderation, think or maintain, that a man can search too far or be too well studied in the book of God's word, or in the book of God's works; divinity or philosophy; but rather let men endeavour an endless progress or proficience in both."*

Despite these strategic genuflections to the almighty, *On the Origin of Species* undercut natural theology by showing that organisms could become adapted to their environment without an intervening intelligence. Darwin thus answered Whewell's unasked question, why final causes should be fundamental and regulative in the living world but out of place in the non-living world. Darwin also adjudicated on the relative merits of function and structure (reversing the pro-structuralist verdicts of Huxley and Owen):

> *"It is generally acknowledged that all organic beings have been formed on two great laws—Unity of Type, and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. 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. … the law of the Conditions of Existence is the*

> *higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type."*

Darwin had "re-invented teleology" by deriving purposeful beings from the natural selection of chance variations without a directing intelligence or vital force (Lennox 1993).

Darwin's next book was *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing* (Darwin 1862a). The title is notable for its use of 'contrivance', a word strongly associated with natural theology. In offering the manuscript to John Murray, Darwin had written "Like a Bridge-water Treatise the chief object is to show the perfection of the many contrivances of orchids" and "it will perhaps serve to illustrate how natural History may be *worked* under the belief of the modification of Species" (Yam, Arditti and Cameron 2009; emphasis added).

Before the theoretical synthesis of his final chapter, Darwin painstakingly disentangles the current usefulness of intricate details of floral structure with a meticulousness that will try the patience of an uncommitted reader. He shows that current purpose need not be ancestral purpose. Final causes are *inessential*. They evolve and diversify among species.

> *"When this or that part has been spoken of as adapted for some special purpose, it must not be supposed that it was originally always formed for this sole purpose. The regular course of events seems to be that a part which originally served for one purpose becomes adapted by slow changes for widely different purposes." (p. 282)*

The final chapter eloquently expounds the creative power of natural selection:

> *"The more I study nature, the more I become impressed with ever-increasing force with the conclusion, that the contrivances and beautiful adaptations slowly acquired through each part occasionally varying in a slight degree in many ways … transcend in an incomparable degree the contrivances and adaptations which the most fertile imaginations of the most imaginative man could suggest with unlimited time at his disposal. The use of each trifling detail of structure is far from a barren search to those who believe in natural selection." (p. 352)*

His peroration concludes:

> *"Considering how precious the pollen of Orchids evidently is, and what care has been bestowed on its organisation and on the accessory parts … It is an astonishing fact that self-fertilisation should not have been an habitual occurrence. It apparently demonstrates to us that there must be something injurious in the process. Nature thus tells us in the most emphatic manner, that she abhors perpetual self-fertilisation. For may we not further infer as probable … that some unknown great good is derived from the union of individuals which have been kept distinct for many generations?"*

Asa Gray's (1862) review of the *Contrivances* was glowing

> *"We cannot close without an expression of gratitude to Mr. Darwin for having brought back teleological considerations into botany. So difficult is the study of functions in plants, so impossible often to find out the use or meaning of the various modifications of organs, and so unscientific and foolish the conjectures which are apt to be hazarded upon the subject, that Geoffroy's saying, 'science knows nothing of intention in nature' had well nigh become a conceded, even if unexpressed principle in natural history, especially in botany. Under the study of homologies—so fertile in excellent results—botany and even zoology have become almost exclusively morphological. In this fascinating book on the fertilization of Orchids, and his paper explaining the meaning of dimorphism in hermaphrodite flowers, Mr. Darwin,—who does not pretend to be a botanist—has given new eyes to botanists, and inaugurated a new era in the science."*

But Gray had not forsaken design. In a letter of February 16 1863, he confided to Alphonse de Candolle (Gray 1894, p. 498):

> *"Well, as to origin of species, you have now gone just about as far as I have, in Darwinian direction, and both of us have been led step by step by the facts and probabilities, and have not jumped at conclusions.… Under my hearty congratulations of Darwin for his striking contributions to teleology, there is a vein of petite malice, from my knowing well that he rejects the idea of design, while all the while he is bringing out the neatest illustrations of it!"*

Since its publication, the *Contrivances* has been a 'smoking gun' for those who want to conscript Darwin on the side of design or convict him of the sin of teleology, and an awkward hurdle for those who want to clear him of the charge (Hoquet 2010). Michael Ghiselin has gone so far as suggest that *Contrivances* was written as a lampoon of teleological reasoning not to be taken seriously:

> *"The book is a sort of biological* ***Candide****, which, albeit with the greatest restraint, holds up the very idea of organic design to ridicule and contempt. There are reasons to think, indeed, that it was written as a deliberate satire on the* ***Bridgewater Treatises****." (Ghiselin 1969, p. 136)*

At most, Darwin is teasingly imitative but, if so, the satire was written with affection. If the *Contrivances* had a hidden barb, the ridicule and contempt were clearly lost on Asa Gray, and why should Darwin repeat a joke that had fallen flat in his subsequent botanical work. A more convincing interpretation is that the *Contrivances* was deftly targeted to win over multiple audiences with contradictory agendas of finding design in nature and observing strict subservience to physical law (Tabb 2016). Bellon (2009, 2011) has argued that it was the doggedness of Darwin's endeavors, reported in laborious detail in the *Contrivances*, that gave moral credibility to the imaginative flights of the *Origin* and made natural selection respectable for working naturalists. Darwin had shown that his theory was useful. His experimental effort had reclaimed him the virtue of Baconian science.

The search for current utility guided Darwin's empirical research and suggested hypotheses for experiment. The exorbitant costs of cross-fertilisation demanded a compensating benefit. Nature had told him this in no uncertain terms, so he undertook experiments on self-fertilization that bore fruit in *The effects of cross and self fertilisation in the vegetable kingdom* (Darwin 1876). He was thus able to rewrite his concluding sentences for the second edition of the *Contrivances* (Darwin 1877, 239):

> *"It apparently demonstrates to us that there must be something injurious in the process,* ***of which fact I have elsewhere given direct proof****. It is hardly an exaggeration to say that Nature tells us in the most emphatic manner, that she abhors perpetual self-fertilisation." (emphasis added)*

Darwin's botanical research is a fertile garden full of ripe berries of teleological reasoning (all emphases added).

> *"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." (Darwin 1862b, p. 92)*
>
> *"The petioles which have clasped an object become much more woody, stiff, hard, and polished than those* ***which have failed in this their proper purpose.****" (Darwin 1865, p. 34)*
>
> *"The movement, excited by the absorption of such matter, though slow, suffices for its* ***final purpose****, whilst the movement excited by one of the sensitive filaments being touched is rapid, and this is indispensable* ***for the capturing*** *of insects. These two movements, excited by two such widely different means, are thus both well adapted, like all the other functions of the plant,* ***for the purposes which they subserve****." (Darwin 1875, p. 308)*
>
> *"Many flowers close at night … but we are not here concerned with their movements;* ***for although effected by the same mechanism … yet they differ essentially*** *in being excited chiefly by changes of temperature instead of light; and in being effected, as far as we can judge,* ***for a different purpose****." (Darwin 1881, p. 280)*
>
> *"There is a fourth sub-class, as far as the* ***final cause*** *of the movement is concerned; for the leaves of some plants when exposed to an intense and injurious amount of light* ***direct themselves****, by rising or sinking or twisting, so as to be less intensely illuminated." (Darwin 1881, p. 419)*

Darwin believed that natural selection had not eliminated final causes but rather explained how purposes could arise in the world without a designing intelligence. Those who recruited him as an ally against final causes were pursuing a different agenda.

Gray (1874) wrote to the journal *Nature* on Darwin's botanical research:

> *"… let us recognise 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. In many, no doubt, Evolutionary Teleology comes in such a questionable shape, as to seem shorn of all its goodness; but they will think better of it in time, when their ideas become adjusted, and they see what an impetus the new doctrines have given to investigation. They are much mistaken who suppose that Darwinism is only of speculative importance and perhaps transient interest. In its* ***working application*** *it has proved to be* ***a new power****, eminently practical and* ***fruitful****."* *(emphases added)*

Darwin responded on June 5 1874:

> *"What you say about Teleology pleases me especially, and I do not think anyone else has ever noticed the point. I have always said you were the man to hit the nail on the head." (in Francis Darwin 1898)*

Darwin's letter was published in the second volume of *The life and letters of Charles Darwin* (F. Darwin 1898). In Huxley's contribution to the first volume (Francis Darwin 1887, p. 554), Huxley quotes his own superficially similar, and earlier, statement "perhaps the most remarkable service to the *philosophy* of Biology rendered by Mr. Darwin is the reconciliation of Teleology and Morphology" (emphasis added). If Huxley felt slighted, I believe he missed the point of what had so pleased Darwin. Huxley's (1869a) brief statement on the reconciliation of morphology and teleology had appeared in an essay in which Huxley, at much greater length, dismissed the *practical* usefulness of teleology. For Gray (1874), on the other hand, Darwin's great service was the union of Teleology and Morphology in a fruitful working marriage. Darwin believed that a naturalized teleology of living things was a far from barren guide to investigation. He did not think anyone else had noted *that* point.

3.5. John Burdon Sanderson

Britain was a backwater of physiology during the middle decades of the nineteenth century because of the institutional dominance of anatomy (French 1971; Geison 1972). John Burdon Sanderson was among a group of younger British physiologists who, from the 1870s, adopted the physicalist mindset and new experimental methods of continental physiology (Richards 1986). He collaborated with Charles Darwin on the physiology of insectivorous plants. Although I had intimated that this paper would not discuss metaphors of sexual coercion, here I will make an exception. Burdon Sanderson's (1874) rhetoric in a public lecture on Venus's fly-trap is hard to interpret in any other way:

> *"The study of these external aspects leads [the true naturalist], if possessed of that curiosity which is his characteristic attribute, to study their minute structure, and this, the further he goes into it, stirs up in him the desire to penetrate further into the mysteries of their being. … But to understand nature in the sense of the naturalist we*

> *must know not only those aspects which she is willing to present to us but those she is determined to hide. For this end, when we cannot get at what we want by persuasion, we are often obliged to use compulsion. … If nature conceals the truth, we frankly deny her right to do so, and wrest it from her by force. … It is thus, and thus alone that we compel nature to tell us 'that wherein her great strength lies.'[3] … I applied the term forcible to this method because it is the plan by which, as Bacon said, we torture nature. But let us remember that this is a mere figure of speech. In disciplining nature to our ends, in forcing her to give up her secrets, we use no violence but utmost gentleness."*

Burdon Sanderson freely uses purposive language in the remainder of this public lecture but, two decades later as an elder statesman of resurgent British physiology, Burdon Sanderson (1893) brackets final causes, indeed *any* distinctively biological principle, as outside the explanatory domain of physiology:

> *"Without forgetting that every phenomenon has to be regarded with reference to its useful purpose in the organism, the aim of the physiologist is not to inquire into final causes, but to investigate processes. His question is ever How, rather than Why."*

In a eulogy on the recent death of Carl Ludwig, Burdon Sanderson (1896) divided all of biology into two branches: Physiology, the Science of Living Processes, and Ontology, the Science of Living Beings. I will quote at length a passage that deserves close reading:

> *"The Science of Physiology as we know it came into existence fifty years ago with the beginning of the active life of Ludwig, in the same sense that the other great branch of Biology, the Science of Living Beings (Ontology), as we now know it, came into existence with the appearance of the "Origin of Species". In the order of time Physiology had the advantage, for the new Physiology was accepted some ten years before the Darwinian epoch. … While Ontology regards animals and plants as individuals and in relation to other individuals, Physiology considers the processes themselves of which life is a complex. This is the most obvious distinction, but it is subordinate to the fundamental one, namely, that while Ontology has for its basis laws which are in force only in its own province, those of Evolution, Descent, and Adaptation, we Physiologists, while accepting these as true, found nothing upon them, using them only for heuristic purposes, i.e., as guides to discovery, not for the purpose of explanation. Purposive adaptation, for example, serves as a clue, by which we are constantly guided in our exploration of the tangled labyrinth of vital processes. But when it becomes our business to explain these processes—we refer them not to biological principles of any kind, but to the Universal Laws of Nature. The wonderful revolution which the appearance of the* ***Origin of Species*** *produced in the other branch of Biology promoted the progress of Physiology, by the new interest which it gave to the study, not only of structure and development, but of all vital phenomena. It did not, however, in any sensible degree affect our* ***method*** *or alter the direction in which Physiologists had been working for two decades. Its most obvious effect was to sever the two subjects from each other." (p. 1ff)*

In Burdon Sanderson's narrative, the renaissance of physiology preceded the reform of ontology. The*Origin of Species* had severed physiology from the rest of biology because physiology excluded "biological principles of any kind" from its explanations. In case he had been misunderstood, Burdon Sanderson (1896) repeated his message:

> *"The disuse of the teleological expressions which were formerly current does not imply that the indications of contrivance are less appreciated, for, on the contrary, we regard them as more characteristic of organism as it presents itself to our observation than any other of its endowments. But … we found no explanation on this or any other biological principle, but refer all the phenomena by which these manifest themselves to the simpler and more certain physical laws of the universe." (p. 5)*

3.6. Final causes in nineteenth-century British biology: an overview

> *"This return to mechanistic explanations was mainly the work of two men: the English naturalist Charles Darwin (1809–1882), who destroyed teleology, and the German physiologist and physicist Hermann von Helmholtz (1821–1894), who vanquished the vital force." (Hoffmann 2012)*

Shortly before the publication of the*Origin of Species*, the sexualization of final causes reaches an erotic climax in George Wilson's (1857, p. 349) *Chemical final causes* in which the author looks forward to an after-life of sublimated desire and eternally-deferred consummation:

> *"Final Causes are sterile, not merely like as, but for the same reason as, the Vestal Virgins were, namely, because they belong to God. These virgins, as well as others, might have become mothers; but no man dare wed them, for they were God's Brides. Neither can any man mate with Final Causes: they will bear no offspring to him. And exactly for that reason are they the most perfect of earthly witnesses to the being and perfections of God. Gentle, solemn, and beautiful, they attract men, and modestly permit them to look on their features; but awe mingles with admiration in the gazer's heart, and the ever-burning fires on the vestal-altar forbid all close or impious approach. Nevertheless, we must seek after, and love Final Causes, even with a lover's passion, although in this life they can never be ours. An irresistible impulse compels us to cling to them. It would be proof of insanity if we were only mortals … But both are the most natural and irrepressible instincts of immortals, who look forward, through God's mercy, to all eternity as their time of studentship, and to all His Infiniteness as the object of their study. For such contemplation of Final Causes will never end, any more than it will ever beget satiety."*

Wilson's devotional language was already quaint and old-fashioned in 1857 but would have been incomprehensible in a scientific context by the turn of the century.

Final cause and teleology are not univocal terms. A final cause (end) can be a thing's usefulness (utility) or the destination (goal) toward which it moved. The two are, of course, related: the use of a hammer in hitting a nail has the driven-in nail as

its goal. Another distinction is between a Platonic teleology in which final causes are the intentions of a divine mind as opposed to an Aristotelian teleology in which final causes are the usefulness of an attribute to its possessor without implications of rational intent (Lennox and Kampourakis 2013). All of these senses are muddled together in nineteenth-century arguments about the role of final causes in biology.

In assessing the positions of Whewell, Owen, Huxley and Burdon Sanderson it is useful to keep in mind a distinction between the final causes of organismic parts and the final cause of all things. The tradition of natural theology, exemplified by Whewell, argued from one to the other: *from* the usefulness of parts *to* a creative intelligence who had a goal in mind for his creation. Owen believed in a "predetermining intelligent Will" (Owen 1868, p. 789) but rejected final causes of the parts of living things, considered as separate acts of creation, in favor of a single creative act from which the living world proceeded by secondary law to a preordained end. Huxley tends to use 'teleology' when referring to cosmic purpose but 'final causes' when referring to particular things. He rejected both final causes and teleology from scientific practice but remained consistently agnostic—a term he coined—on cosmic teleology. Huxley's rejection of final causes predated the *Origin of Species*. Burdon Sanderson recognized living things as adapted but rejected final causes as explanatory. He separated questions of faith from questions of science (Ghetal Burdon Sanderson 1911, pp. 57, 159f). A belief in a mechanistic universe was not incompatible with a belief in cosmic teleology.

Darwin showed no discomfort in using teleological language to describe the behavior and structure of living things. He saw natural selection as an undirected process, without goal or intention, that gave rise to beings with purposes. His teleology was akin to Aristotle's conception of organisms containing their end within themselves (*entelecheia*) although Darwin is unlikely to have been directly influenced by Aristotle (Gotthelf 1999). Huxley, however, recruited Darwin's *Origin of Species* in his campaign for the elimination of final causes from biology. One could argue that Huxley's interpretation has prevailed over Darwin's intention.

By 1900, teleological reasoning was widely recognized as seductively barren. The general acceptance of the transmutation of species had vanquished traditional arguments for natural theology and special creation. Whewell's argument from design had lost scientific credibility and defenders of traditional theology increasingly justified their faith on other grounds. Owen's idealism and difficult personality had left him a lonely irrelevance by the time of his death while Darwin was buried in Westminster Abbey. Burdon Sanderson was Regius Professor of Medicine at Oxford. Final causes had been swept away. Darwin's brand of teleological natural history was to be a quiet backwater, an oxbow lake cut off from the mainstream of twentieth-century biology. One could argue that Huxley was not at the helm, but carried along by the flood. Nature was becoming defeminized and depersonalized. Scientific allusions to final causes as barren virgins petered out during the latter part of the nineteenth century as evidence for the demise both of arguments from design and invocations of vital forces (Lennox 1993).

Two biological revolutions occurred in the middle years of the nineteenth century. One was the physico-chemical revolution in continental physiology that occurred in the decades before 1859. Formal and final causes were rejected in favor of explanations solely by efficient and material causes. Britain was a physiological backwater during these decades. Therefore, the revolution in physiology occurred before the Darwinian revolution in continental Europe, but the relative

timing was reversed in Britain. The Darwinian revolution has been given greater prominence in the history of science than has the revolution in physiology, and this is probably appropriate if one's focus is on the public perception and reception of science. After Darwin, an appeal to the beauties of nature as a justification of faith lost credibility because he had provided a competing hypothesis. However, the physiological revolution was probably more important for the practice of twentieth-century biology and the dominant factor in the rejection of final causes in biology. It was not that adaptation by natural selection was denied by working biologists, although many did reject Darwin's mechanism, but explanations in terms of adaptive function were not considered to be scientific explanations of phenomena observable and manipulable in experimental time. Adaptive stories were decorative, like the vestal virgins, not part of 'hard' science.

4. Guilty secrets

The physico-chemical turn in physiology resulted in the peculiar situation that a science of function abjured the language of purpose. When physiologists were caught with their teleological pants down they insisted their figures of speech were not what they meant. Their thoughts were *purely* physical. Ascriptions of purpose—explanations in terms of what something is good for—became illegitimate, even shameful; a sign that the speaker had a vulgar and corrupt understanding of experimental method. Because physiologists' objects of desire were *functions* of living things, conflict occurred in their minds between permissible expression and unbidden thought. Ernst Wilhelm Brücke's most famous student, Sigmund Freud, would have diagnosed denial. Teleology had been repressed and pushed into the unspoken unconscious. Such a diagnosis could help to explain why the meme of the mistress appeared when and where it did. Teleological reasoning became a guilty secret once its open expression was no longer respectable in polite conversation.

What I will call the 'mistress meme' has no precise wording because nobody could point to a *locus classicus*. In its various forms, teleology is a lady, a woman, a maiden, or a mistress who the biologist needs but does not openly acknowledge.[4] The metaphor has different intent from Bacon's barren virgins. It implies that teleological reasoning is useful but hidden. In my attempt to uncover a source, I found the meme ascribed to many people. The two most common were Ernst Wilhelm Brücke and John Burdon Sanderson Haldane, but other ascriptions included (in no particular order) John Scott Haldane, Michael Polanyi, Peter Medawar, Walter Cannon, Hans Krebs, Frits Went, Stephen Jay Gould, and Emil DuBois-Reymond. The fact that the meme was widely disseminated despite its uncertain provenance suggests that it expressed an idea that many biologists flirted with privately but felt more comfortable expressing publicly by ascription to a respected authority.

The earliest version of the meme I have found occurs in the autobiography of Walter Cannon (1945, p. 108):

> *"My first article of belief is based on the observation, almost universally confirmed in present knowledge, that what happens in our bodies is directed toward a useful end. In finding new processes, therefore, we are justified in looking further for their utility. And in the search for utility new discoveries may result. … It may be urged that this conception is inconsistent with the idea that the province of science is strictly description. It turns away from 'how' to 'why' and thus may enter the realm of speculation. Many scientists hesitate to make that step. As the German*

> *physiologist, E. von Bruecke, remarked, 'Teleology is a lady without whom no biologist can live. Yet he is ashamed to show himself with her in public.'"*

Cannon's secondhand remark is the source of the common attribution of the aphorism to Ernst Wilhelm Brücke (1819–1892) but there is another, more plausible, candidate, his less famous grandson Ernst Theodor Brücke (1880–1941). Two other early versions help to unravel this source. First, Otto Loewi (1953) wrote

> *"I myself fully agree with an old friend of mine, the late physiologist E. von Bruecke, who once said in a lecture, 'Teleology is a lady without whom no biologist can live. Yet he is ashamed to show himself with her in public.'"*

Second, Ernst Theodor Brücke's son Franz Brücke (1961) wrote that Loewi—whom Franz Brücke had worked with in Graz—made known the saying of E. Brücke that teleology is a lady without whom no scientist can get by, but whom he does not like to be seen with in public.[5]

These sources agree that the saying originated with 'E. Brücke' whom I conclude was Ernst Theodor Brücke. First, I have found no version of the meme earlier than 1945, fifty-three years after Ernst Wilhelm Brücke's death. Second, Otto Loewi (1873–1963) knew Ernst Theodor Brücke and an 'old friend' of Loewi's is more likely to have been the grandson than the grandfather. Third, Walter Cannon (1871–1945) was instrumental in bringing both Otto Loewi and Ernst Theodor Brücke to the United States after Anschluß in Austria (Garson 2013).[6]

Otto Loewi expressed his own teleological beliefs thus:

> *"The essence of life, consisting in the tendency and potency of the organism to preserve it by all kinds of adjustments, cannot be explained by chemical or physical means. I cannot imagine that there exists any biologist nowadays, who would not approve of this statement. I am convinced that even during the epoch when the crude mechanistic concept of life predominated, most biologists must have been aware that teleology exists in living beings. How could it be otherwise? The teleological view has at all times presented the starting point in the study of chemical and physical factors involved in the single functions of the organism and in their coordination in order to relate them to their purpose. And yet almost all biologists up to this day have been reluctant to express or even touch on the teleological viewpoint." (quoted in Donnerer and Lembeck 2006, p. 109).*

Although physiologists usually ascribe the mistress meme to Ernst Wilhelm Brücke, evolutionary biologists usually ascribe it to John Burdon Sanderson Haldane. The source of this memetic lineage is a 1970 letter from Colin Pittendrigh (1918–1996) to Ernst Mayr (1904–2005), quoted in Mayr (1974):

> *"I was haunted by that famous old quip of Haldane's to the effect that 'Teleology is like a mistress to a biologist: he cannot live without her but he's unwilling to be seen with her in public'."*

Pittendrigh's 'Haldane' is not without ambiguity. John Burdon Sanderson Haldane (1892–1964) was the son of John Scott Haldane (1860–1936) and the grand-nephew of John Scott Burdon Sanderson (1828–1905). The younger Haldane is the more common ascription but, the father would be better known to an audience of physiologists, and the aphorism is sometimes attributed to him. Physiology was a family affair. The elder Haldane knew Ernst Theodor Brücke with whom he discussed the friendship of Henri Milne-Edwards, John Scott Haldane's uncle, with Ernst Wilhelm Brücke, Ernst Theodor Brücke's grandfather (see Ernst Theodor Brücke 1928, p. 81). Therefore, one or both of the Haldanes may have heard the aphorism directly from Ernst Theodor Brücke rather than indirectly via the memetic lineage originating with Walter Cannon.

John Scott Haldane applied twice for the Oxford chair in physiology vacated by his uncle after the latter's promotion to Regius chair in medicine, and was passed over both times. He then resigned his departmental position and ended his career as an unaffiliated college fellow (Sturdy 1988, 2011). He damaged his health by self-experimentation because he disliked vivisection. He rejected physico-chemical mechanisms as explanations of life, but his research on respiratory control is easy to construe as mechanistic biology. He viewed the entire universe as a single personality (Haldane 1923). He saw natural selection as part of the mechanistic view of life he despised, definitely not the source of the ubiquitous teleology he embraced in living (and non-living) things. His thought is difficult to bring into coherent focus. Let him speak for himself (Haldane 1906, p. 120):

> *"Natural selection is in itself an aimless process, incapable of bringing about organic evolution, apart from the guiding influence introduced by the fact that the nature of living organisms is to actively maintain, develop, and reproduce their specific structure and activity … The influence of natural selection, whatever it may be, is thus subordinate to the teleological factor, and even in the case of the complex activities of the nervous system the teleological conception is the only one which is ultimately capable of rendering the phenomena intelligible."*

Colin Pittendrigh (1958, p. 393), another British physiologist, coined the term *teleonomy* so that biologists could avoid using the disreputable word *teleology* for end-directed processes.

> *"[Natural selection's] overwhelming significance is that it offered, for the first time, a program for the explanation of adaptation that was entirely free of teleology and thus conformable with the dominant scientific conceptual scheme —that is physics. … It seems unfortunate that the term 'teleology' should be resurrected and, as I think, abused in this way. The biologist's long-standing confusion would be more fully removed if all end-directed systems were described by some other term."*

In his 1970 letter to Mayr (in Mayr 1974), Pittendrigh wrote:

> *"I wanted a word that would allow me (all of us biologists) to describe, stress or simply to allude to—without offense—this end-directedness of a perfectly respectable mechanistic system. Teleology would not do, carrying*

> *with it that implication that the end is causally effective in the current operation of the machine. … Haldane was, in this sense wrong (surely a rare event): we can live without teleology."*

Pittendrigh (1993, p. 20) later reminisced on the utility of his euphemism

> *"It was my intention in 1957 to help get Haldane's mistress out of the closet by describing her merits as teleonomic rather than teleological. Whether or not that did help (Monod & Davis found it useful!), the commonplace nature of programmable machines at midcentury gave teleology (as teleonomy) complete respectability in the society of biological ideas."*

Allusions to mistresses—with a nudge and a wink—now seem quaint and old-fashioned. The aphorism presumes a male researcher, a diminishing proportion of all working scientists, but the lady is not dead yet. Denis Noble (2018), onetime holder of the Burdon Sanderson Chair at Oxford, pleads for her domestic respectability:

"Biology necessarily requires the concept of function, of goals toward which a process tends to go. To slightly misquote JBS Haldane, teleology might indeed be a great mistress, but she can be an even greater openly acknowledged wife."

5. Physiology and evolutionary biology

Greek *phusis* appears in physics, physician, and physiology. English *physic* was used for a medicinal substance, a healthy practice, a remedy, the medical profession, or natural science in general. *Phusis*, *physiologia*, and their various translations, were associated from classical times with concepts of health and the *good* of the body. Because of the nature of their subjects physiologists and physicians had continued to think teleologically long after final causes had been banished from physics. When physiology turned toward strictly physical explanations in the middle years of the nineteenth century, final causes were similarly rejected. Physiology's domain had been gradually restricted from all of natural philosophy to the science of living things. Then, during the nineteenth century its domain was further restricted to the functional activities of living things as contrasted with *anatomy* concerned with their structure, and *pathology* with their malfunction.

John Burdon Sanderson's (1893, 1896) claim that the *Origin of Species* had severed physiology from evolutionary biology —with their respective questions of how? and why?—prefigured Ernst Mayr's (1961) division of biology into 'functional biology' associated with the experimental method and 'proximate causes' as answers to 'how?' and 'evolutionary biology' associated with the comparative method, historical explanations, and 'ultimate causes' as answers to 'why?' For Burdon Sanderson, the revolution in physiology preceded and was independent of the Darwinian revolution. Ernst Mayr (1982, p. 115f) concurred: "The methodology of physiology underwent drastic changes in the nineteenth century, including a much more refined application of physical methods, particularly by Helmholtz and Ludwig, and even more so, an increasing application of chemical methods. … The publication in 1859 of the *Origin of Species* caused hardly a ripple since explanation in physiology was explanation of proximate causes".

Mayr (1961) insisted that the evolutionary biologist's *why*? was the historical *how come*? rather than finalistic *what for*? He ascribed the goal-directedness of living things to their genetic program. Functional biology was concerned with how the program is decoded during the life of the organism whereas evolutionary biology was concerned with historical changes to the program and the causes of these changes. He rejected teleology and adopted Pittendrigh's term *teleonomic* to describe the apparent purposiveness of organisms. Goal-directed behaviors were the expression of the genetic program but the evolutionary process itself was not goal-directed.

Despite Mayr's intent, his distinction between proximate and ultimate causes has been widely interpreted as the distinction between mechanism and adaptive function, rather than the distinction between present causes and historical causes (Haig 2013). That is, ultimate cause has been equated with *what for*? In this interpretation, proximate causes can be considered synonymous with Aristotelian efficient causes and ultimate causes with Aristotelian final causes. This has been the distinction of greatest concern for those who wish to explain behaviors and structures in terms of what they are good for. Mayr shifted ground during his long career and sometimes equated the answer to the evolutionary biologist's *why*? with adaptive function (Mayr 1974, p. 108f).

Burdon Sanderson's (1896) stricture that physiological explanations should remain undefiled by teleology remains regulative for most twenty-first century physiologists, indeed for most biologists. Edin (2008) can serve as exemplar: a "meaningful distinction can be made between functions and mere effects in biological systems without resorting to teleological arguments" (p. 203). In his view, purposive language is convenient but not explanatory.

> *"Physiologists often use the language of information theory in describing feedback systems. Events in correcting chains are described as* ***signals****, some of which are said to* ***inform*** *the system that a disturbance has taken place, while others are said to affect the system's responses to the disturbance. Moreover, the physical parts of the system which are involved in the earliest stages of correcting chains are described as* ***sensing mechanisms*** *or* ***sensors****. It should be kept in mind, however, that these evaluative or anthropomorphic sounding terms—"set point", "disturbance", "correction", "control", "signal", etc.—are used only as convenient short form that can be dispensed with in favor of purely physical descriptions." (p. 206)*

The teleological scaffolding "can be dispensed with" once the "purely physical" cathedral has been built.

Most working biologists have been indoctrinated that they should not use teleological language, but the purposive language used by Darwin survives in the writings of adaptationists, sociobiologists, and evolutionary psychologists. These fields are often considered soft and non-rigorous because of their teleological 'just-so stories'. Gould and Lewontin's (1979) critique of the adaptationist program deplored the tendency to seek a purpose for each trifling detail of structure and proposed that structural constraints "restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution." For these critics of the Panglossian paradigm, appeals to final causes remained seductive but barren. Their championing of structure over function can be considered another salvo in the Geoffroy–Cuvier debate of 1830.

No evolutionary biologist denies some role for natural selection but there are endless debates about its importance relative to other factors as sources of order and direction in the evolutionary process. Within evolutionary biology, the word ‘adaptationist’ is usually used in a pejorative sense. In general, those who downplay the significance of natural selection consider themselves more rigorous than those who focus on understanding adaptation. Michael Lynch (2007) can serve as an exemplar. He decries the excesses of adaptive story-telling “This blind acceptance of natural selection as the only force relevant to evolution has led to a lot of sloppy thinking, and is probably the primary reason why evolution is viewed as soft science” (p. xiv). By contrast, the theory of population genetics provides “a solid foundation for the development of a mechanistic framework for understanding evolutionary processes with a level of mathematical rigor that has few rivals in the life sciences” (p. 69). Population genetics reduces problems of adaptation to a ‘selection coefficient’ that is fully general in its application because empty of specific content. Understanding adaptation is difficult and easy to get wrong. Many critics of adaptationism deride, as soft, those who attempt this hard question, while feeling superior in their own study of what is more easily quantifiable because abstracted from the complexities of real organisms in the world.

Selective change in gene frequency involves the preferential retention/rejection of alternative alleles and has two aspects, sometimes called positive and negative selection (Haig 2020, p. 272). Negative selection retains old ‘more functional’ alleles and rejects new ‘less functional’ alleles. Positive selection rejects old ‘less functional’ alleles and retains new ‘more functional’ alleles. Multiple old and new alleles may be present in a population and what is ‘more functional’ in one comparison may be ‘less functional’ in another comparison. Moreover, ‘more functional’ alleles are likely to have originated as modifications of older ‘less functional’ alleles that were once ‘more functional’ than, and modifications of, even older ‘less functional’ alleles, into the depths of evolutionary time. Both forms of selection can proceed at the same time and old alleles that are now retained by negative selection may once have been new alleles retained by positive selection in what is a continuous process of shifting functions.

Gould and Vrba (1982) drew attention to the venerable distinction between past and present utility but thoroughly confused matters by excluding selection maintaining present utility, as *exaptation*, from adaptation by natural selection which they reserved for selection for *original* utility. Darwin (1862, p. 348) recognized that any complex structure will retool and reconfigure parts that had served earlier functions for performance of new functions. If current structures are modifications of earlier structures that were modifications of earlier structures, and all past utility was once present utility, then original utility recedes into the indefinite past and all adaptations become exaptations (Haig 2020, p. 273f).

Attention to the difference between past and present utility helps make sense of debates within biology over concepts of function. Amundson and Lauder (1994) offered a causal-role (CR) concept of function as an alternative to the selected-effects (SE) concept. They explained their preference for an ahistorical and non-purposive concept: “Biologists who study the form and function of organismal design recognize that it is virtually impossible to identify the past action of selection on any particular structure retrospectively, a requirement for recognizing SE functions” (p. 443). In the SE approach, “the function of a trait can be seen as its evolutionary purpose, with purpose being imbued by selective history.” The CR approach, however, is “non-historical, and identifies the function of a trait as certain of its current causal properties. The relevant properties are seen either as those which contribute to organism’s *current needs, purposes, and goals* or those

which have evolutionary significance to the organism's *survival and reproduction*" (emphases added). Amundson and Lauder observe physicalist proprieties with their insistence that a CR function is "both non-historical and non-purposive in its applications" (p. 466, footnote) despite identifying CR functions by criteria of current utility ("current needs, purposes and goals").

The contrast between CR and SE functions reprises the contrast between ahistorical (*synchronic*) and historical (*diachronic*) explanations in linguistics. One does not have to choose between them. One can accept both, but mutual acceptance requires recognizing a role for natural selection and evolutionary history in the origin of biological mechanisms (Garson 2019).

6. Have we reached the end?

> *"It was the Darwinian theory of evolution, with its combination of chance variation and natural selection, which completed the extrusion of teleology from nature. Having become redundant even in the story of life, purpose retired wholly into subjectivity." (Jonas 1966)*

Bacon excluded final causes from the laboratory (in his day a room for the practice of alchemy). Final causes were barren because they could not be experimentally manipulated. The elimination of final causes from physics and chemistry was largely completed by the beginning of the nineteenth century but final causes were still regularly invoked in biology and medicine. Whewell expressed this dualism with his rejection of final causes as explanatory principles in physics but recognition of them as indispensable in physiology. The *avant-garde* of experimental physiology rejected this dualism in their program to unify biology with physics and chemistry in a 'physical biology'. Significantly, their rejection of final causes occurred before publication of the *Origin of Species* and strongly influenced the reception of Darwin's theory by experimental biologists.

Much of the force of the argument from adaptation to design had been the absence of a credible alternative. I contend that it was Darwin's *neutralization* of this argument by exclusion that led to the rapid acceptance of descent with modification. Natural selection provided an alternative to design. There might be other alternatives. Many biologists embraced transmutation while remaining agnostic about, or opposing, the efficacy of natural selection. Explanations in terms of divine fiat largely disappear from the biological literature in the decades after the *Origin of Species* while alternative theories of transmutation flourished. Darwin had delivered a deathblow to natural theology but had not won the field for natural selection.

Ever since Darwin, dissenters from the mechanical view of life continue to find evidence of purposiveness in nature while seeing natural selection as part of the mechanical view they wish to supplant. Thus, Weber and Varela (2002) view autopoietic systems as teleological, but dismiss natural selection as the source of this teleology:

> *"On the one hand, only by considering the embodied organism as self-producing individuality can we re-formulate*

> *a strong notion of an intrinsic teleology. On the other hand the converse is also true: in admitting biological individuality, and hence the precariousness of the living, we cannot evade the teleology that is intrinsic to life thus understood. … But this "Newton of the Grassblade" was surely not Darwin … The fuller understanding of the organism needs a different approach." (p. 120)*

On the other other hand, adaptationists see natural selection as perfectly adequate to explain the purposiveness of self-reproducing systems and would bestow Newtonian laurels on the squire of Down House (Haig 2020). Why does teleological language in biology continue to arouse passions? One explanation I have been given is that such idioms surreptitiously reintroduce supernatural agency into science, but these critics are perfectly comfortable using purposive language to describe human actions which they do not consider supernatural. I diagnose strands of Cartesian dualism and human exceptionalism: purpose and meaning are appropriate in the domain of *res cogitans* but out of place in *res extensa*. Minerva and the Muses are preceived as a nuisance and risk to themselves in the scientific laboratory.

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Footnotes

[1]"Brücke und ich, wir haben uns verschworen, die Wahrheit geltend zu machen, daß im Organismus keine anderen Kräfte wirksam sind, als die gemeinen physikalisch-chemischen" (DuBois-Reymond 1918, p. 108).

[2] This is my reading of the first writing of a passage (with subsequent amendments by Darwin removed). I acknowledge the work of Paul H. Barrett and John van Wyhe who deciphered Darwin's difficult handwriting. Images can be found at http://darwin-online.org.uk/ using search term 'barren virgins'.

[3]"Entice him, and see wherein his great strength lies" (Judges 16;5): the lords of the Philistines asking Delilah to discover the secret of Samson's strength.

[4] Francesco Vitale (2017) writes of an obsessive desire since the beginnings of modern science to clear the field of teleology and juxtaposes Bacon's 'barren virgins' with Henri Atlan's and Francois Jacob's versions of the mistress meme. We independently converged on these twin metaphors.

[5]"Er hat ja den Ausspruch E. Brückes bekanntgemacht, daß die Teleologie eine Dame sei, ohne die kein Naturwissenschafter auskomme, mit der er sich nur nicht gerne in der Öffentlichkeit zeige" (Zekert 1961).

[6] Ernst Theodor Brücke's Jewish ancestry was through his mother, Emilie Wittgenstein, an aunt of the philosopher Ludwig Wittgenstein.

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