Darwinism versus Evo–Devo: a late–nineteenth century debate

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Abstract

In his notebooks and culminating in the two volume publication on domestication of plants and animals (Darwin 1868), Charles Darwin developed a theory of inheritance, pangenesis, that fit his worldview: through a continuum of variants and intermediate forms, individuals and species graded one into another both syn– and diachronically. Pangenesis accommodated Darwin's fundamental assumptions: use–disuse, natural selection (as a factor in producing variation and then choosing from the resultant variants), and blending inheritance. He conceived of "gemmules," which were constantly thrown off from every part of an organism's body throughout its entire lifetime, as the recorders of everything that impacted an individual during its lifetime. By way of bodily "fluids," gemmules were conveyed to an individual's sex organs, to be passed on en masse *to offspring, combining upon fertilization with those contributed by the other parent. It was an ingenious idea, especially in its attempt to explain all known phenomena, including the appearance of new or different features (such as sexually dimorphic ones) later in life. Blending inheritance expanded the realm of possible variation in the next generation.*

The thrust of Darwin's theory of pangenesis was a justification of his view that the gradual nature of evolutionary change and continuous variation tied all life together in a seamless web. Ironically, the very examples Darwin enumerated for the origin of new breeds or varieties of domesticated plants and animals, and their stabilization through inbreeding and breeding with parental strains, lend themselves not to a model of gradual change and continuous variation, but to a saltationist one, in which morphological novelty emerges abruptly and yet its bearers remain capable of reproducing with the original stock.

Victorian saltationism, as articulated by St. George Mivart in (Mivart1871) in On the Genesis of Species, *envisioned alterations in development as the basis of major and instantaneous change, but it did not deal with heredity. Mivart pointed out that a major problem with Darwin's gradualism was that features critical to an organism's survival and reproductive competence would be useless unless they were functional from the beginning. In addition, as Huxley (Huxley 1860) had argued well before Mivart, natural selection played no role whatsoever in producing change. Since it was obvious that some hereditary process connected successive generations, perhaps saltationists thought it unnecessary to speculate on a mechanism of inheritance because the idea of novelty arising through alterations of developmental processes was not explained by gemmule, germ–plasm, or any other available model of inheritance. Interestingly, the contrasts between Darwin's theory of heredity and Mivart's emphasis on organismal change being due to altering developmental processes, is being replayed in the opposing views of present–day Darwinism and evo–devo.*

Introduction

A consequence of delving into the history of evolutionary thought is often seeing how a scholar, when confronted with examples of biological phenomena that could lead to diametrically opposed and contradictory models or theories, chooses one set as representing the reality of nature and regards the other as irrelevant. In such instances, the obvious question is: Why? What were the reasons behind the decision? In this regard, an interesting case is the contrast between Charles Darwin (especially his "evidence" for natural selection and gradual evolutionary change as being necessary for the origin of species and the assumptions underlying his theory of inheritance, "pangenesis") and the saltationists (especially as represented by St. George Mivart).

Darwin's bias

Although one cannot ignore *On the Origin of Species* (Darwin 1859 et seq.; herewith referred to as the *Origin*), for this discussion I shall focus on *The Variation of Animals and Plants under Domestication* (Darwin 1868; herewith referred to as *Variation*). The rationale for this emphasis is that, in *Variation*, Darwin not only argues that the character of domesticated plants and animals and the process of domestication via artificial selection make perfect analogues for the character of natural species and the process of evolution via natural selection. In this work Darwin also attempts to articulate a theory of inheritance that embraced his bias toward gradualism.

Since the basics of Darwin's assumptions as presented first in the *Origin* are well known, I shall summarize them only briefly. 1) Variation is essentially infinite and, in a perfectly preserved synchronous and diachronous world, one would be able to observe continuous variation and insensible and infinitesimal gradation between individuals, sexes, and species. 2) At any point in time, natural selection both produces and then chooses from the resultant more fit or better adapted variations. 3) The consequences of use and disuse contribute significantly to the emergence of variability. 4) Evolutionary change proceeds gradually through the accumulation of continually produced, infinitesimally small variations.

In arguing the first assumption, Darwin had to confront the discontinuities between extant species and the "gaps" in the paleontological record between extinct species as well as between extinct and extant species. This absence of evidence was explained neontologically and paleontologically by invoking the extinction or elimination of individuals that would have formed a graded series of intermediates between one species and another. The paleontological conundrum was also addressed from a taphonomic perspective: There had been intermediates, but the deposits containing them no longer existed. With the problems of discontinuity seemingly dealt with, Darwin was then free to attend to other matters, such as the origin of species:

> The differences between natural varieties are slight; whereas the differences are considerable between the species of the same genus, and great between the species of distinct genera. How do these lesser differences become augmented into the greater differences? How do varieties, or as I have called them incipient species, become converted into true and well-defined species? (*Variation*, vol. 1, p. 5)

Although he had already committed himself in the *Origin* to answering this question by invoking a gradualistic model of change, Darwin was clearly aware of examples, not only from nature, but also from plant and animal domestication, that could have led him to formulate a different model of evolutionary tempo. For example, in volume 1 of *Variation* (pp. 92–94) he commented on how the niata breed of cattle had appeared suddenly, in the course of one generation, and then described in detail how they differed from common cattle in numerous aspects of their anatomy. For example:

> In fact, on comparison with the skull of a common ox, scarcely a single bone presents the same exact shape, and the whole skull has a wonderfully different appearance. (p. 94)

Although they appeared suddenly, and their features were so different from those of common cattle, niata cattle could breed successfully with one another, as well as with common cattle. In the latter case, Darwin even discussed the specific characters that were often dominant in offspring when a niata cow was mated with a common bull, and vice versa.

Nevertheless, as profound as the differences between niata and common cattle were, and even with the former being reproductively unimpaired, Darwin rejected the case of niata cattle as being representative of how novelty might arise in the wild. His argument was that these cattle were not as adaptable as common cattle when environmental conditions occasionally and drastically changed for the worse, as in periods of drought. As such, Darwin (*Variation*, vol. 1, p. 94) concluded, "[this] shows us...how natural selection would have determined the rejection of the niata modification had it arisen in a state of nature."

But niata cattle were not the only example of the sudden appearance of marked novelty in animals or plants without loss of reproductive viability of which Darwin was aware. Indeed, it was precisely because these "monstrosities" could mate successfully with one another (as well as with "normal" individuals) that breeders could perpetuate the novelty. For instance:

> [The sprouting–broccoli] variety is a new one, and bears the same relation to common broccoli, as Brussel–sprouts do to common cabbages; it suddenly appeared in a bed of common broccoli, and was found faithfully to transmit its newly–acquired and remarkable characters (vol. 1, p. 342).

> Domestic breeds often have an abnormal or semi–monstrous character, as amongst dogs...some breeds of cattle and pigs,–several breeds of fowl,–and the chief breeds of pigeon. In such abnormal breeds, parts which differ but slightly or not at all in the allied natural species, have been greatly modified. This may be accounted for by man's often selecting, especially at first, conspicuous and semi–monstrous deviations of structure (volume 2, p. 408).

Even in terms of so–called atavistic structures, Darwin knew not only that they re–appeared suddenly, but also that they were morphologically recognizable structures. They were not mere hints of features that had been present in their bearers' ancestors. As he noted in volume 1 of *Variation*:

> Horses have often been observed, according to [the French paleontologist] M Gaudry, to possess a trapezium and a rudiment of a fifth metacarpal bone, so that "one sees appearing by

> monstrosity, in the foot of the horse, structures which normally exist in the foot of the Hipparion [an allied and extinct animal]" (p. 52; comments added).

Yet, in the face of numerous examples of the sudden appearance of novelty in domesticated plants and animals, Darwin argued that they were not reflective of what really occurs in nature:

> There is a much more important distinction between our several breeds, namely, in some having originated from a strongly-marked or semi-monstrous deviation of structure, which, however, may subsequently have been augmented by selection; whilst others have been formed in so slow and insensible a manner, that if we could see their early progenitors we should hardly be able to say when or how the breed first arose... [But] it is certain that the ancon and mauchamp breeds of sheep, and almost certain that the niata cattle, turnspit, and pug-dogs, jumper and frizzled fowls, short-faced tumbler pigeons, hook-billed ducks, &c., suddenly appeared in nearly the same state as we now see them. So it has been with many cultivated plants. The frequency of these cases is likely to lead to the false belief that natural species have often originated in the same abrupt manner. But we have no evidence of the appearance, or at least of the continued procreation, under nature, of abrupt modifications of structure; and various general reasons could be assigned against such a belief.
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> On the other hand, we have abundant evidence of the constant occurrence under nature of slight individual differences of the most diversified kinds; and we are thus led to conclude that species have generally originated by the natural selection of extremely slight differences. (vol. 2, pp. 409–410)
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> Some naturalists boldly insist that species are absolutely distinct productions, never passing by intermediate links into one another; whilst they maintain that domestic varieties can always be connected either with one another or with their parent-forms. (vol. 2, p. 409)

But does demonstrating "abundant evidence of the constant occurrence under nature of slight individual differences of the most diversified kinds" necessarily contradict inferring from observing the sudden appearance of novel features in domesticated organisms that this process also occurs in nature? Does demonstration of "abundant evidence of the constant occurrence under nature of slight individual differences of the most diversified kinds" necessarily lead only to the conclusion that "species have generally originated by the natural selection of extremely slight differences"?

The answer to both of these questions is, I believe, no. But by taking the position he did, Darwin conflated the existence of individual variation, which reflects slight degrees of difference in the expression of a particular feature or array of features, with the advent of the feature itself. And it was this unfounded conflation of two entirely different biological phenomena that informed his belief in continuous variation and continuity via an insensible gradation between species through time and at any point in time. Accordingly, and without any justification or demonstration, Darwin could then claim that "[v]ariations often pass into, and cannot be distinguished from, monstrosities; and monstrosities are of little significance for our purpose" (vol. 1, p. 322). Indeed, for the myriad examples Darwin gives in the *Origin* and in *Variation* of "monstrosities" and of slight variations of a feature or features, none supports an assumption of gradation. Darwin merely asserts that this is the case, just as, in the same quote, he can so easily declare, "monstrosities are of little significance for our purpose."

But Darwin persists in volume 2 of *Variation* in asserting the reality of insensible gradation [e.g. "...we so incessantly see in species of the same group the finest gradations between an organ in a rudimentary and perfect state, that we are led to believe that the passage must have been extremely gradual" (p. 308)]. He also attempts to explain why sudden change, at least in wild species, could not occur: "It may be doubted whether a change of structure so abrupt as the sudden loss of an organ would ever be of service to a species in a state of nature; for the conditions to which all organisms are closely adapted usually change very slowly" (p. 308).

This is an interesting approach to denying the possibility of sudden change because, here, Darwin focuses on the abrupt *loss* of structure, not, as with virtually every other example he musters in the *Origin* and *Variation* in support of gradual change, the *emergence* of structure. He then states with unfounded assurance that abrupt change not only would not benefit wild species, but also that it could not occur because organisms adapt gradually to their slowly changing surroundings. Yet Darwin knows that sudden, non–reproductively disruptive change occurs. He also knows, at least from the example of niata versus common cattle responding to drought, that the environment can change abruptly, without provoking visible organismal change at the same time. But, here and elsewhere (see quote further above) he draws a line of distinction between domesticated and wild species, and seeks to justify this distinction by asserting that no one has observed abrupt change in nature. This, of course, is an assertion without basis, because, by definition (and observation in domesticates) there is nothing to observe if change occurs suddenly. There is only the presence of something previously unknown to you whose origin would be a mystery.

Thus, while on the one hand, Darwin would like his audience to believe that, as artificial selection can gradually change the character of a domesticated species or breed, so, too, can natural selection act on wild species. On the other hand, Darwin asserts without justification that the sudden appearance (not loss) of novelty in domesticated species – that is, the emergence of "monstrosities" – has no bearing on insights into the workings of the organisms in the "wild." Still, by asking us to accept the analogy between artificial and natural selection as agents that gradually alter the character of species, and to deny any biological significance to the sudden appearance of novelty in domesticates (and thus natural species), Darwin perpetuates the misconception that individual variation in the expression of a feature is somehow relevant to the origin of the feature itself. That, by artificially shifting the bell curve of expressed variation of a feature, this serves as evidence that, under natural conditions and with enough time, a feature can be transformed into something entirely different.

Darwin's theory of pangenesis

Without doubt, the climax of Darwin's formulations in *Variation* was the model of inheritance that he called "Pangenesis." In many ways, it was quite elegant (see review in Schwartz, 1999). Through pangenesis Darwin could explain, for instance, features that appear early in development as well as those that emerge later in life (e.g. differences in secondary sexual characters). The idea was simple. All parts of an organism issue small particles, which Darwin identified as gemmules, throughout the individual's life. Consequently, the entire life history of an individual, from conception until death, is recorded in a trail of gemmules. Individually unique events, such as those that result from use or disuse, would also be recorded in the gemmules of the affected part or parts and thus affect the pool of potential variation. Traveling by way of some unspecified bodily fluid, gemmules accumulate in an individual's sex organ. Upon mating, parental gemmules blend, thereby producing additional sources of variation. Gemmules could also become latent and not expressed over a series of generations. But at some later time, they could become active again, which would account for atavisms.

Pangenesis solidified Darwin's ideas on blending inheritance (hinted at in the *Origin*, although clearly expressed in his notebooks; see Schwartz 1999) and also provided a previously unspecified mechanism for the transmission of acquired characteristics resulting from use or disuse. The theory also increased the number of ways in which individual variation could be produced. Indeed, pangenesis seemed to be able not only to account for the entirety of an organism's being, but also to provide the fodder necessary for natural selection to slowly transform one species into another.

The opposing saltationist view

Three years after the publication of Variation, St. George Mivart, one of England's leading comparative morphologists, published *On the Genesis of Species* (Mivart 1871, herewith referred to as *Genesis*). This was the saltationist's response to Darwin's notions of gradual change, the role of natural selection, the essence of variation, and the viability of pangenesis. Although in his review of the *Origin*, Huxley (Huxley 1860) was clearly strongly opposed to gradualism and a role of primacy of natural selection in producing change, Mivart makes it appear as if his fellow saltationist was not fully committed to this position:

> Professor Huxley seems now disposed to accept the, at least occasional, intervention of sudden and considerable variations. In his review of Professor Kölliker's criticisms, he himself, says, "We greatly suspect that she" (*i.e.* Nature) "does make considerable jumps in the way of variation now and then, and that these saltations give rise to some of the gaps which appear to exist in the series of known forms." (*Genesis*, pp. 103–4)

In mounting his case for saltationism, Mivart paralleled Darwin in compiling a massive array of examples from the plant and animal worlds. But instead of focusing on the minutiae of individual differences, Mivart called attention to the major ways in which species differ from one another, whether it be in the stamens and anthers of flowers, the pincers or antennae of beetles, the configuration of the vertebrate versus invertebrate eye, the presence of mammary glands in mammals, feathers in birds, and baleen in whales, or differences between organisms in their reproductive anatomies. In contrast to Darwin's rejection of sudden change solely on the basis of the argument in *Variation* on the lack of benefit of losing of an organ, Mivart emphasized the emergence of novel structure. Not, of course, that the loss of structure could not be novel – consider the reduced numbers and generations of teeth in mammals compared to reptiles, of toes in modern horses, and of limbs in snakes. But, inasmuch as Darwin himself presented examples of "gain" rather than "loss" (e.g. the vertebrate eye) in both the *Origin* and *Variation*, it was appropriate that Mivart do the same, although his interpretation of the requisites for the appearance of novelty was vastly different.

Time and time again Mivart discussed a remarkable trait and then raised the question: How could such a functionally important feature have evolved gradually, through an insensible gradation of intermediates, to its present state? How, for instance, could mammals not only have survived, but multiplied in number and become diverse, if the first mammal had merely possessed a vestige of a mammary gland, which, in turn, produced only a drop or two of milk? How could sexually reproductive organisms have persisted generation after generation if, initially, their reproductive organs were merely a hint of their necessary functional states? Turning Darwin's argument of purpose on its head, Mivart asked: How could anything but the fully formed version of a feature, particularly one that was essential for sustenance of life or procreation, be beneficial to an organism? Using flatfish (soles, flounder) as one of many examples leading to doubting Darwin's assumption, Mivart questioned the advantage of selection causing one of the fish's eyes to be dragged gradually from one side of its head, across the rough sand of the ocean floor, until it reached its present position near the eye that had been on the opposite side of the body. Clearly, on various levels, the notion of gradual change did not make biological sense.

But a saltational model for the advent of novelty – especially if functionally integral to the survival of an individual – was not only biologically sensible, it was also compatible with the pattern of life as illustrated in the fossil record.

Indeed, Mivart (pp. 129–130) quotes from Fleming Jenkin's devastating review of the *Origin* ("It is really strange that vast numbers of perfectly similar [fossil] specimens are so great; but it is also very strange that the specimens should be so exactly alike as they are, if, in fact, they came and vanished by a gradual change"), and then proceeds with his own argument: "The mass of paleontological evidence is indeed overwhelmingly against minute and gradual modification...[H]ad such a slow mode of origin, as Darwinians contend for, operated exclusively in all cases, it is absolutely incredible that birds, bats, and pterodactyles should have left the remains they have, and yet not a single relic be preserved in any one instance of any of these different forms of wing in their incipient and relatively imperfect functional condition!"

Even the bird–like fossil reptile, *Archaeopteryx*, which had been discovered in 1861, and which Darwin would use in the sixth and last edition of the *Origin* in an attempted refutation of *Genesis*, did not pose a problem for Mivart (p. 131): "But even supposing all that is asserted or inferred on this subject to be fully proved, it would not approach to a demonstration of specific origin by *minute* modification. And though it harmonizes well with 'Natural Selection,' it is equally consistent with the rapid and sudden development of new specific forms of life."

In contrast to Darwin, who invoked forces external to the organism as the primary provocateurs of change (e.g. as in gradual environmental change, or use–disuse), Mivart hypothesized the source of novelty as lying primarily internally, within the cells of the organism itself. In formulating this theory, Mivart turned to the inert inorganic world for an analogy relevant to the living one. In apparent anticipation of some of Waddington's (Waddington 1940) ideas many decades later, Mivart (*Genesis*, p. 114) suggested:

> Judging the organic world from the inorganic, we might expect, *a priori*, that each species of the former, like crystallized species, would have an approximate limit of form, and even of si-

> ze, and at the same time that the organic, like the inorganic forms, would present modifications in correspondence with surrounding conditions; but that these modifications would be, not minute and insignificant, but definite and appreciable, equivalent to the shifting of [a] spheroid on to another facet for support.

Mivart (pp. 114–115) then quotes from a Mr. Murphy ("Crystalline formation is also dependent in a very remarkable way on the medium in which it takes place...And [as] the Rev. E. Craig found that [different chemicals affected copper crystal growth]...[t]he changes take place not by the addition of new crystals, but by changing the growth of the original ones."), after which he comments: "These, however, may be said to be the same species, after all; but recent researches by Dr. H. Charlton–Bastian seem to show that modifications in the conditions may result in the evolution of forms so diverse as to constitute different organic species."

In contrast to Darwin's efforts to explain away the "gaps" in the fossil record, Mivart (p. 143) expands his model to incorporate them:

> Now all these difficulties [e.g. the absence of fossils in old strata and of intermediate forms] are avoided if we admit that new forms of animal life of all degrees of complexity appear from time to time with comparative suddenness, being evolved according to laws in part depending on surrounding conditions, in part internal–similar to the way in which crystals (and, perhaps from recent researches, the lowest forms of life) build themselves up according to the internal laws of their component substance, and in harmony and correspondence with all environing influences and conditions. [comment added]

But, what is the internal element of Mivart's saltational theory? After all, one could claim that Darwin's theory of pangenesis embodied an internal component to eventual evolutionary change. The difference between the two scholars lies in Mivart's thinking in terms of novelty emerging as a result of alterations in the regulation of an organism's development:

> Altogether, then, it appears that each organism has an innate tendency to develop in a symmetrical manner, and that this tendency is controlled and subordinated by the action of external conditions, and not that this symmetry is superinduced on *ab externo.* In fact, that each organism has its own internal and special laws of growth and development.
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> If, then, it is still necessary to conceive an internal law or "substantial form," moulding each organic being, and directing its development as a crystal is built up, only in an indefinitely more complex manner, it is congruous to imagine the existence of some internal law accounting at the same time for specific divergence as well as for specific identity.
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> A principle regulating the successive evolution of different organic forms is not one whit more mysterious than is the mysterious power by which a particle of structureless sarcode develops successively into an egg, a grub, a chrysalis, a butterfly, when all the conditions, cosmical, physical, chemical, and vital, are supplied, which are the requisite accompaniments to determine such evolution. (pp. 186–7)
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> [T]he new forms must be produced by changes taking place in organisms in, after or before their birth, either in their embryonic, or toward or in their adult, condition. (p. 233)

Reminiscent, at least in spirit, of Wright's (Wright 1932) "shifting balance theory" (represented by the topographic map of differing gene combinations) and Waddington's (Waddington 1940) "epigenetic landscape," Mivart (pp. 228–9) frames his theory of developmental reorganization in terms of a rapid transition from one stable state to another:

> The conception of such internal and latent capabilities is somewhat like that of Mr. Galton...according to which the organic world consists of entities, each of which is, as it were, a spheroid with many facets on its surface, upon one of which it reposes in stable equilibrium. When by the accumulated action of incident forces this equilibrium is disturbed, the spheroid is supposed to turn over until it settles on an adjacent facet once more in a stable equilibrium.
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> The internal tendency of an organism to certain considerable and definite changes would correspond to the facets on the surface of the spheroid.

Equally interesting is how Mivart's (*Genesis*, p. 230) language anticipates Bateson's (Bateson 1894) "undulating theory" or "theory of repeated parts":

> [A]s the atoms of a resonant body may be made to give out sound by the juxtaposition of a vibrating tuning–fork, so it is conceivable that the physiological units of a living organism may be so influenced by surrounding conditions (organic and other) that the accumulation of these conditions may upset the previous rhythm of such units, producing modifications in them–a fresh chord in the harmony of nature–a new species!

Mivart (p. 231) then asks: "Are new species now evolving, as they have been from time to time evolved? If so, in what way and by what conceivable means?" To which he responds:

> [W]e...saw that minerals become modified suddenly and considerably by the action of incident forces...
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> We have thus a certain antecedent probability that if changes are produced in specific manifestation through incident forces, these changes will be sensible and considerable, not minute and infinitesimal.
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> Consequently, it is probable that new species have appeared from time to time with comparative suddenness, and that they still continue so to arise if all the conditions necessary for specific evolution now obtain. (p. 236)
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> [A]n internal law presides over the actions of every part of every individual, and of every organism as a unit, and of the entire organic world as a whole. It is believed that this conception of an internal innate force will ever remain necessary, however much its subordinate processes and actions may become explicable.
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> That from such a force, from time to time, new species are manifested by ordinary generation just as *Pavo nigripennis* appeared suddenly, these new forms not being monstrosities but harmonious self–consistent values... (p. 239)

Countering Darwin's argument against saltation in *Variation* that only a solitary individual would be the bearer of a novelty, Mivart (p. 236) hypothesizes that "as the same causes produce the same effects, several individual parent forms must often have been similarly and simultaneously affected." As for Darwin's theory of inheritance, Mivart (p. 216) dismisses it with a quote from Delpino: "Thus, in Pangenesis, everything proceeds by force of unknown elements, and we may ask whether it is more logical to prefer a system which assumes a multitude of unknown elements to a system which assumes only a single one?"

Darwin's rebuttal

Given Mivart's rejection of virtually all of Darwin's assumptions – with the major exception of allowing that natural selection plays a role in eliminating monstrosities, rapidly eliminates antecedent species, and "favours and develops useful variations, though it is impotent to originate them or to erect the physiological barrier which seems to exist between species" (*Genesis*, p. 240) – it is not surprising that Darwin harshly criticized the former scientist the following year in the sixth (and, as it turned out, last) edition of the *Origin.*

In this edition of the *Origin*, published in 1872, the year after *Genesis*, Darwin doggedly maintained the theme of "natura non facit saltum" and devoted thirty pages specifically to Mivart's objections to his theory and his objections to Mivart's.

> Mr. Mivart believes that species change through an "internal force or tendency," about which it is not pretended that anything is known. That species have a capacity for change will be admitted by all evolutionists; but there is no need...to invoke any internal force beyond the tendency to ordinary variability, which through the aid of selection by man has given rise by graduated steps to natural races or species.
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> Mr. Mivart is further inclined to believe, and some naturalists agree with him, that new species manifest themselves "with suddenness and by modifications appearing at once." For instance, he supposes that the differences between the extinct three–toed Hipparion and the horse arose suddenly. He thinks it difficult to believe that the wing of a bird "was developed in any other way than by a comparatively sudden modification of a marked and important kind...This conclusion, which implies great breaks or discontinuity in the series, appears to me improbable in the highest degree. (*Origin*, 1872, p. 239)

Although Mivart did hypothesize an "internal force" as a generator of sudden change, his model was at least consistent with the observation of the abrupt appearance of novelty in domesticated plants and animals, the discontinuity (i.e. lack of seamless continuity) between apparent species, and the gap–riddled pattern of life history as recorded in the fossil record. In contrast, Darwin attempted to dismiss the relevance of all three of these observations, appealing, as he stated in the quote above, to a sense of probability (or, in this case, improbability). Also as seen in the quote above, Darwin pushed the envelope of credulity, not only by making it seem that the origin of new breeds of domesticated plants and animals is typically by "graduated steps," but also by adding the claim that this process has led to the emergence of new species of domesticates. In the former assertion, Darwin neglected his own recognition of the reality of niata cattle and other examples of the sudden origin of novelty, while, in the latter, he clearly entered the realm of the imaginary.

Darwin's (Darwin 1872) most relevant objection to Mivart's theory is found in his questioning the expectation that more than one individual will emerge with the same novelty. Although this suggestion is logically consistent with the argument for change via an internal force that causes developmental reorganization, Darwin (p. 240) makes light of it: "Hence in order that a new species should suddenly appear in the manner supposed by Mr. Mivart, it is almost necessary to believe, in opposition to all analogy, that several wonderfully changed individuals appeared simultaneously within the same district." Of course, "analogy" is the key word here, inasmuch as Darwin promotes the case of gradual change in domesticates through artificial selection. But, upon reflection, Darwin's counterargument merely reiterates the essence of the variation–natural selection argument that Fleming Jenkin demolished in his review of the first edition of the *Origin* (see Schwartz 1999): "This difficulty [the sudden appearance of many individuals with the same novelty]...is avoided on the theory of gradual evolution, through the preservation of a large number of individuals, which varied more or less in any favourable direction, and of the destruction of a large number which varied in an opposite direction" (Darwin 1872, p. 240; comment added). Relying on repetition rather than validation, Darwin states outright: "That many species have been evolved in an extremely gradual manner, there can hardly be a doubt" (p. 240) for "when we look to the special parts of allied species, instead of to distinct species,...numerous and wonderfully fine gradations can be traced, connecting together widely different structures" (p. 241).

Again, the question must be raised: What is the basis of these assertions? If Darwin can take issue with Mivart's hypothesis on the grounds that there is no evidence of an "internal force," are we then expected to take his word for the existence of "numerous and wonderfully fine gradations...connecting together in widely different structures"? Where is the demonstration of the reality of gemmules, of the effects of use and disuse, of blending inheritance, or of the power of natural selection to produce novel structures? Indeed, it is here we can appreciate Delpino's objection to pangenesis: Why should we invoke a multitude of unknowns when an alternative theory predicts only one mechanism?

But Darwin (Darwin 1872, p. 242) continues his attack on Mivart, concluding with an appeal to embryology:

> It is notorious that the wings of birds and bats, and the legs of horses or other quadrupeds, are undistinguishable at an early embryonic period, and that they become differentiated by insensibly fine steps. Embryological resemblances of all kinds can be accounted for...by the progenitors of our existing species having varied after early youth, and having transmitted their newly acquired characters to their offspring, at a corresponding age. The embryo is thus left almost unaffected, and serves as a record of the past condition of the species. Hence is it that existing species during the early stages of their development so often resemble ancient and extinct forms belonging to the same class. On this view of the meaning of embryological resemblances...it is incredible that an animal should have undergone...momentous and abrupt transformations; and yet should not bear even a trace in its embryonic condition of any sudden modification; every detail in its structure being developed by insensibly fine steps.

On the face of it, this passage would appear to echo von Baer's (Baer 1828) laws regarding the commonality of embryonic stages among vertebrates until the point at which each kind of animal veers off onto the ontogenetic path that will mold it into the adult of its taxon, replete with its specifically distinctive features. But it is obvious that Darwin's invocation of ontogeny is actually a foil for gradualism, using the smoothly transitional nature of organismal growth and development as supposed evidence of the gradual nature of evolutionary change. Future suggestions aside as to how novelty could become imbedded early on in ontogeny (e.g. de Beer's, 1930, theory of clandestine evolution), what is interesting about Darwin's dismissal of such a possibility and his focus on "structure being developed by insensibly fine steps" is that the only avenue he leaves open along which change can occur is by *adding* stages to the end of an individual's ontogeny. This, of course, is precisely the primary interplay between ontogeny and phylogeny that Haeckel (e.g. 1866) envisioned when he formulated the Biogenetic Law ("ontogeny recapitulates phylogeny"). Both Darwin and Haeckel envisioned links between adult individuals, with change occurring at the terminal stage of ontogeny.

Wherefore Thomas Henry Huxley?

Darwin's intensified adherence to notions of gradual transformational change from *Variation* to the last edition of the *Origin*, and his assault on Mivart in the latter work, is both interesting and curious given the reviews he received of the first edition of the *Origin*, not only from Fleming Jenkin, but also and especially from his intellectual defender, Thomas Henry Huxley. For, in his review of the *Origin*, which was published in 1860 (and reprinted thereafter, e.g. in Huxley 1876, *Lay Sermons, Addresses, and Reviews*, hereafter referred to as *Sermons*), Huxley was anything but restrained in his criticism of Darwin's rejection of rapid morphological change. For example, on p. 257 in *Sermons*, in the reprinted review of the *Origin*, Huxley writes:

> We do not speak jestingly in saying that it is Mr. Darwin's misfortune to know more about the question he has taken up than any man living.
>
> But this superabundance of matter must have been embarrassing to a writer who, for the present, can only forward an abstract of his views; and thence it arises, perhaps, that notwithstanding the clearness of the style, those who attempt fairly to digest the book find much of a sort of intellectual pemmican–a mass of facts crushed and pounded into shape, rather than held together by the ordinary medium of an obvious logical bond: due attention will, without doubt, discover this bond, but it is often hard to find.
>
> Again, from the sheer want of room, much has to be taken for granted which might readily enough be proved; and hence, while the adept, who can supply the missing links in the evidence from his own knowledge, discovers fresh proof of the singular thoroughness with which all difficulties have been considered and all unjustifiable suppositions avoided, at every reperusal of Mr. Darwin's pregnant paragraphs, the novice in biology is apt to complain of the frequency of what he fancies is gratuitous assumption.

In apparent heed of his own criticism of Darwin's unrestrained use of example, Huxley keeps his reference to individual cases to a bare minimum. Nevertheless, he does refer to one of Darwin's own citations: the abrupt appearance of a "monstrosity" that became the basis of a new breed of sheep, the Ancon or Otter sheep. He does so (p. 265) to demonstrate not only that it "appears to have arisen in full force, and...*per saltum*," but also to argue that "[i]t was no case of what is commonly called adaptation to circumstances; but, to use a conveniently erroneous phrase, that variations arose spontaneously." But, while Darwin would say that such demonstrations in domesticated animals are not applicable to wild species, Huxley takes an opposing view:

> Varieties then arise we know not why; and it is more than probable that the majority of varieties have arisen in this 'spontaneous' manner...But however they may have arisen, what especially interests us at present is, to remark that, once in existence, varieties obey the fundamental law of reproduction that like tends to produce like, and their offspring exemplify it by tending to exhibit the same deviation from the parental stock as themselves. (p. 266)

> If a variation which approaches the nature of a monstrosity can strive...to reproduce itself, it is not wonderful that less aberrant modifications should tend to be preserved even more strongly; and the history of the Ancon sheep is, in this respect, particularly instructive. (p. 267)

Anticipating Mivart's *Genesis*, Huxley used Darwin's argument for rejecting monstrosities – in this case the Ancon sheep – as a reflection of nature in the "wild" as the basis for coming to a diametrically opposed conclusion: monstrosities are biologically, and therefore evolutionarily, instructive. Further like Mivart, Huxley (e.g. see pp. 266–271) rejected natural selection as playing a role in the emergence of novel features. Unlike Mivart, however, Huxley did not speculate on how novelty is produced "spontaneously" – a fact that seems incongruous given Huxley's (Huxley 1863) emphasis only a few years later on development and the emergence of differences between taxa. Instead, Huxley took the approach of questioning on philosophical grounds the validity of Darwin's claims. For example, on pp. 294–295 of *Sermons*, he writes:

> Inductively, Mr. Darwin endeavours to prove that species arise in a given way. Deductively, he desires to show that, if they arise in that way, the facts of distribution, development, classification, &c., may be accounted for, *i.e.* may be deduced from their mode of origin, combined with admitted changes in physical geography and climate, during an indefinite period. And this explanation, or coincidence of observed with deduced facts, is, so far as it extends, a verification of the Darwinian view.

> There is no fault to be found with Mr. Darwin's method, then; but it is another question whether he has fulfilled all the conditions imposed by that method. Is it satisfactorily proved, in fact, that species may be originated by selection? that there is such a thing as natural selection? that none of the phaenomena exhibited by species are inconsistent with the origin of species in this way? If these questions can be answered in the affirmative, Mr. Darwin's view steps out of the ranks of hypotheses into those of proved theories; but, so long as the evidence at present adduced falls short of enforcing that affirmation, so long, to our minds, must the new doctrine be content to remain among the former–an extremely valuable, and in the highest degree probable, doctrine, indeed the only extant hypothesis which is worth anything in a scientific point of view; but still a hypothesis, and not yet the theory of species.

> After much consideration, and with assuredly no bias against Mr. Darwin's views, it is our clear conviction that, as the evidence stands, it is not absolutely proven that a group of animals, having all the characters exhibited by species in Nature, has ever been originated by selection, whether artificial or natural.

And on pp. 297–8,

> ...Mr. Darwin's position might, we think, have been even stronger than it is if he had not embarrassed himself with the aphorism, "*Natura non facit saltum*," which turns up so often in his pages. We believe, as we have said above, that Nature does make jumps now and then, and a recognition of the fact is of no small importance in disposing of many minor objections to the doctrine of transmutation.
>
> ...Our object has been attained if we have given an intelligible, however, brief, account of the established facts connected with species, and of the relation of the explanation of those facts offered by Mr. Darwin to the theoretical views held by his predecessors and his contemporaries, and, above all, to the requirements of scientific logic. We have ventured to point out that it does not, as yet, satisfy all those requirements; but we do not hesitate to assert that it is as superior to any preceding or contemporary hypothesis, in the extent of observational and experimental basis on which it rests, in its rigorously scientific method, and in its power of explaining biological phaenomena, as was the hypothesis of Copernicus to the speculations of Ptolemy. But the planetary orbits turned out to be not quite circular after all, and, grand as was the service Copernicus rendered to science, Kepler and Newton had to come after him. What if the orbit of Darwinism should be a little too circular? What if species should offer residual phaenomena, here and there, not explicable by natural selection?

But others did come after Darwin. Even though Darwin was a well–known naturalist prior to 1859, if we use the publication of *On The Origin of Species* as the public emergence of Darwin into the realm of evolutionary theory, we must recognize Huxley and Mivart as subsequent major critics of the credos of natural selection and gradual transformation. Curiously, though, it is Mivart who Darwin publicly attacked, and who was arguably a primary provocation for the 1872 revision of the *Origin*. Of no less import than Darwin's determined adherence to gradual transformation in this latter work was his clinging to the theory of pangenesis. Indeed, as he clearly appears to have dug in his heels on gradualism and a rejection of saltationism and the importance of "monstrosities" for understanding evolutionary change in reaction to Mivart, he seems to have done the same with regard to pangenesis and his cousin Galton's (Galton 1871) experiments that failed to support it.

By the late nineteenth century, with no less energy than Darwin brought to bear on his theories, Bateson (Bateson 1894) and de Vries (de Vries 1889) were arguing with force and conviction for the sudden origin of novelty as well as for decoupling the origin of novelty from selectionist scenarios, and relegating the role, if any, of natural selection to the survival of species. Although inspired by Darwin's theory of pangenesis, de Vries' theory of intracellular pangenesis was actually a rejection of the former notions of inheritance. And, certainly, in 1903, the capstone year of this workshop, Morgan, a trained embryologist, was as vocal as any scientist in rejecting the hyperbole and circularity of Darwinism as being of any evolutionary import.

Why, then, did the questioning of Darwinian explanations of smoothly transformational change become submerged until the recent advent of "evo–devo" thinking? Ironically, it was through the work of Morgan, who in just over a decade went from lambasting Darwinism and Mendelism in 1903 as metaphysical flights of intellectual fancy to melding the two disciplines into the population–genetics thinking that informed the evolutionary synthesis (see review in Schwartz 1999).

Conclusion

Although Darwin is often lauded for embracing embryology and development in his theory of gradual change via natural selection, his perspective was clearly at odds with Mivart's. It may be true that both scholars envisioned a source external to the individual as playing some role in the emergence of organismal change. But it is equally obvious that only at this vague level might we seek a favorable comparison between these two scientists. Otherwise, for Darwin, biologically real novelty lies only in the minutiae of individual difference, which, in turn, derives from any number of sources that, often through use or disuse, leave their marks on an individual. The notion that use–disuse can engender change by causing elements of a *postnatal* individual to become altered, and that this effect can then, via gemmules, be passed on to future generations, fits the envisioned role of natural selection: Both concepts externalize the ultimate source of organismal modification. Blending inheritance is, therefore, the only aspect of Darwin's theory of pangenesis that might conceivably be regarded as representing an internal component of an individual's biology. With the substitution of Mendelism and population genetics for blending inheritance and gemmules in early formulations of neo–Darwinism (Morgan, e.g. 1916), Darwin's theory of evolution by means of natural selection seemed to be unassailable (e.g. Simpson 1962).

Although use–disuse arguments were supposedly purged from Darwinism (by way of singling out Lamarck as the lone advocate of such lunacy; see Burkhardt 1977), it is obvious from the language of Darwinian explanation still in vogue that, in essence, they were not (e.g. see examples in Schwartz 2004, 2005). Even though Darwinism today claims a basis in genetics, the emphasis is not only on the incorrect notion of there being "genes for things" – similar to the idea that selection chooses features to serve a purpose – but also and contradictorily on the similarly biologically unreal notion that selection can direct the course of genetic change by selecting behavioral or morphological traits that anticipate their benefit to an individual. One might thus characterize present–day Darwinism as the "vacuum theory of evolution" (Schwartz 2005, in press).

In contrast, Mivart's emphasis on internal reorganization affecting an organism's development represents an entirely different biological perspective. Although hypothesizing an "external force" as the initiator of a process of change, whatever course organismal change takes is rapid and random with regard to the circumstances in which the altered organism finds itself. Most importantly, Mivart seats organismal change in the context of an internal restructuring of developmental processes. At one point in time, the developmental organization of an organism is in equilibrium, as is the spheroid lying on one of its facets. In order for change to occur, this equilibrium must be disrupted. Ultimately, the spheroid will come to rest in equilibrium on another facet; that is, developmentally, the organism will be in equilibrium in a different or novel state of organismal organization. If the resultant novelty is ill suited to its bearer's circumstance, the individual will most likely not survive. Even if one chooses to equate the "elimination" of individuals with "natural selection," this process or phenomenon is involved neither in the production of novelty, nor in the differential selection of individuals that are either more fit than others or supposedly fulfilling a particular adaptive trajectory.

With the exception of incorrectly predicting that more than one individual will emerge with the same novelty because they will respond similarly to the same provocation, Mivart's focus on development is unexpectedly compatible with the emphasis in evolutionary developmental genetic theory ("evo–devo") on novelty resulting via the differential recruitment of regulatory molecules in different signal transduction pathways (e.g. Carroll et al, 2005; Gilbert and Bolker 2001; Raff 1996; Maresca and Schwartz, n.d.; Schwartz 1999). That is, in contrast to the Darwinian population genetics model of continually changing "genes" or "genomes" underlying the emergence of minute variations of a phenotypic trait, modern cell and molecular biology have demonstrated that cell and DNA stability or homeostasis is the rule. The potential for change thus occurs when this "equilibrium" (to use Mivart's term) is disrupted and new pathways of molecular communication become available. As Gilbert and Bolker (Bolker 2001, p. 451) put it:

> Embryologists now recognize receptors and signal transducing molecules as components of the competence apparatus that enable certain cells to respond to specific inducers. These signaling pathways are the bases of embryonic induction, which is in turn the core of organogenesis. If macroevolution involves changing morphological features, then the alteration of signal transduction pathways becomes critical for any discussion of large scale evolution.

In a very basic way, then, it might not be inappropriate to delineate the beginning of a "Darwinism"–"evo–devo" debate in the late nineteenth century, between one of Victorian England's leading comparative anatomists, St. George Mivart, and Darwin himself.

Postscript

Given Darwin's seemingly career–long entrenchment in gradualism and rejection of saltationsim, it is with some surprise to read entry 130 in his Red Notebook, which according to Herbert (Herbert 1980), was written sometime during March, 1837:

> The same kind of relation that common ostrich bears to (Petisse. {lesser or Darwin's rhea} & diff kinds of Fourmillier {antbird}): extinct Guanaco {llama} to recent: in former case position, in latter time. (or changes consequent on lapse) being the relation. – As in first cases distinct species inosculate, so must we believe ancient ones: [(] not <u>gradual</u> change or degeneration, from circumstances: if one species does change into another it must be per saltum – or species may perish. = This <inosculation> representation of species important, each its own limit & represented. – Chiloe creeper {thorn–tailed Rayadito}: Furnarius {ovenbird}. <Caracara> Calandria; inosculation alone shows not gradation. {comments added}

Reading this passage and then those as well as other notebooks that followed is a frustrating experience inasmuch as there is no obvious reason for Darwin to have abandoned saltational ideas as completely as he did. Indeed, as the quotes above from *Variation* make clear, Darwin had before him the basis of a saltational theory that was even supported by evidence of heredity: not only could "monstrosities" interbreed successfully, they could also reproduce with "normal," parental–type individuals, and thereby perpetuate their novelties. Observations to the contrary, Darwin's constant assertions of a seamless web having existed among living species as well as between descendents and their extinct ancestors might betray a non–biological concern. Namely, were he to embrace saltation, the door would remain open for his religious contemporaries to invoke special creation to explain the abrupt appearance of species in the fossil record as well as the discontinuities between extant taxa. It is, therefore, perhaps a bit ironic that an intellectual enterprise – neo–Darwinism – that went and continues to go out of its way to denegrate and discredit alternative, saltation–like theories for the origin of novelty was built on such an imaginary foundation.

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