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Evolutionary provocations: Paul Sondaar, the evolution of the horse, and a new look at the origin of species

From the days of the Synthesis on, the evolution of the horse has served as one of the major examples of smoothly transitional evolution. Yet, Simpson, who promoted this scenario, had to acknowledge that this was not documented in the fossil record and, therefore, he was driven to provide an explanation of what he thought happened during the periods represented by gaps. Schindewolf, however, took the evolution of the horse and a plethora of examples from the invertebrate and vertebrate fossil records as evidence of profound organismal reorganisation associated with the origin of species. Schindewolf also backed up his ideas with developmental studies. A new theory of evolution based on regulatory genes and Mendelian inheritance demonstrates that the effects of mutation and inheritance naturally produce new species without a smoothly transitional trail of intermediates. Thus, gaps in the fossil record are real and to be expected.

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INTRODUCTION

Not quite two years ago at this writing, I was listening to Paul Sondaar as he expressed his concerns about the debates between gradualists and punctuationalists. He used the evolution of the horse as a prime example of what he thought was a unresolved conflict in a disagreement that presented itself as an either/or theoretical situation. As Paul saw it (also see Sondaar 1968), the overall picture of the evolution of the horse represented both aspects of the debate. In the enlargement and increased complexity of the teeth, there was, as Paul thought, and as Simpson (1944) and Gregory (e.g. 1951) had promoted, an apparent gradual change from *Hyracotherium* to the modern *Equus.* However, in the limbs, especially in the reduction of the digits of the feet, Paul acknowledged that there was a punctuated pattern, which was one of Schindewolf's (1950) emphases in his un-Darwinian considerations. How, Paul mused, could these seemingly contradictory evolutionary events be accommodated exclusively by one or the other model of evolutionary change?

Paul's questions came at a time when I was trying to sort out similar concerns about the relation of models of evolutionary change to both the constraints of genetic inheritance and the patterns observed in the fossil record. In part, I believe that his concerns provoked me to consider more fully the nature of the debate between gradualists and punctuationalists. Whether the conclusions I reached regarding a way in which to meld successful-

ly these two sides of the coin will stand the test of time is another matter altogether. But I can at least say that, through them, I can no longer think about evolution in the same way.

THE BACKGROUND

Although there has been an increase in the number of taxa - genera and especially species - of equoid recognized since the earlier part of this century (e.g., Carroll 1988, MacFadden 1985), the general picture of major 'evolutionary events' has remained pretty much the same. The appearance of the earliest horse, *Hyracotherium*, was characterised by a reduction in pentadactyly in which the forefoot bore four and the hindfoot three toes. The second digit of the manus [presumably the weight-bearing digit (Schindewolf 1950, Sondaar 1968)] was the thickest of the four and it was also longer than the others; the fourth digit was slightly smaller again than the first and third digits. On the hindfoot, the middle (second) digit (also probably the weight-bearing digit) was the thickest of the three and it was also somewhat longer than the first and third. In general, the cheek teeth were primitive in being low-crowned and fairly bunodont. However, the upper molars had assumed a configuration in which the buccal cusps were connected and there was also a loph that coursed distally and lingually from the internal mesiobuccal aspect of the paracone and another from that region of the metacone; in the lower molars, lophids not only circumscribed the perimeters of the trigonid and talonid, especially the latter buccally, but also connected across the tooth between protoconid and metaconid and hypoconid and entoconid.

Taxa subsequent to *Hyracotherium* were larger. Dentally, they were characterised by varying degrees of 'molarisation' of the premolars (as seen first in the middle Eocene *Orohippus*), with true lophodonty (including the development of a moderately flexed ectoloph) developed in the primitively still low-crowned molars of the Oligocene

Mesohippus. Postcranially, the fourth toe of the forefoot of *Mesohippus* was absent. Post-*Mesohippus* Eurasian and Asian equoids remained relatively primitive dentally and postcranially compared to North American taxa. In the early Miocene *Parahippus*, and especially in the slightly later *Merychippus*, the teeth were hypsodont (with cementum exposed between the vertical enamel plates), lophs were configured in much the same way as in modern horses, and the facial skeleton and mandible were also of more modern proportions and disposition (Radinsky 1984). In both fore- and hindfoot, the metapodials and three phalanges of the first and third digits were relatively much smaller overall than those of the central second digit. The late Miocene-Pliocene *Pliohippus* was larger again than *Merychippus*, with its upper teeth being more elongate mesiodistally than in the former (and thus more like the modern horse). Although greatly reduced in size, the thin metapodials and three phalanges of the first and third digits were still present, although dwarfed by the large central second digit. Absence of the phalanges of the first and third digits and severe developmental truncation of their metapodials is seen with the appearance of *Equus*.

THE INTERPRETATION

The evolution of the horse figured prominently in Simpson's (1944) discussion of models of evolutionary change. Based on the occasional occurrence of a tiny enamel spur ('crochet') on the upper molars of *Mesohippus* and *Miohippus*, its constant presence in *Parahippus*, and its significant enlargement in *Equus*, Simpson proclaimed that this supported '*the usual genetical opinion that mutations important for evolution, of whatever eventual taxonomic grade, usually arise singly and are small, measured in terms of structural change*' (Simpson 1944: 58). Simpson even calculated that, if there had been at least 15 million generations between *Hyracotherium* and *Equus* (which, of course, presumes a direct line of descent), there must

then have been 1.5 million relevant single locus mutations during that time. But while arguing that the paleontological record was in general proof enough of the gradual nature of evolutionary change, he also thought that the tempo of evolution, and especially that of the horse, could at times be quite rapid, leading to mega- or quantum evolution - but, he was quick to add, evolution is never (or hardly every) saltational.

Simpson's (1944) insistence on the improbability of saltational evolution pervades *Tempo and Mode in Evolution.* Although he acknowledged that the fossil record is plagued by gaps that prevent the observation of the smooth transitions that he insisted occurred, he sought various avenues of support to explain how they in fact were evidence of rapid but smoothly transformational evolution. The essential element in this argument was the supposition that rapid evolution would occur in small, rather than large, populations. Because of this small sample, it was to be expected that there would be only a few individuals of this 'incipient' species on their path of converting their preadaptations to useful adaptations. Thus, it was also to be expected on taphonomic grounds (and here Simpson cited the eminent taphonomist Efremov) that these rare individuals would probably not be represented in the fossil record - hence the gaps. It was only after these preadaptations became viable adaptations that the number of individuals of the new species would increase as they spread throughout their new environmental circumstances - producing a sufficiently large enough population that some individuals would be represented in the fossil record. Therefore, rather than being evidence of saltation, the gaps in the fossil record were actually proof of the sometimes rapid yet still transitional and transformational nature of smoothly evolutionary change (e.g., see Simpson 1944: 58 and 123).

Although Simpson (1944) is most frequently cited with regard to his model of quantum evolution, with rapid evolution occurring as organisms cross between different adaptive peaks [which is an idea that he actually modified from Wright's (1932 *et seq.*) concept of the shifting balance theory of adaptive peaks, for which, in a review of *Tempo and Mode*, Wright (1945) thoroughly castigated him], it is important to point out that much of his emphasis on '*continuity (with Matthew's meaning) or gradual inter - gradation*' (p. 58) derived from his attack on the developmental geneticist Richard Goldschmidt (1940) and, less caustically, his dismissal of Schindewolf's (1936) earlier work.

It is of no little significance or specific interest in the context of the focus here on the evolution of the horse that, where Simpson envisioned a smooth transition across the gaps in the fossil record, Schindewolf found evidence of non-Darwinian, saltational evolutionary change. Although Simpson reluctantly had to admit that the gaps could reflect saltational evolution [but that '*[t]here is, however, abundant and incontrovertible paleontological proof that saltation does not always occur*' (p. 58)], Schindewolf was convinced that the gaps demonstrated the lack of smoothly transitional ancestor-descendant sequences. In the absence of such transitions, there then had to be another model for evolutionary change - part of which was furnished by Goldschmidt's emphasis on major systemic mutations producing new species. It was not only from the fossil record of the horse, but also and especially from countless examples derived from both the invertebrate and vertebrate fossil records, that Schindewolf found his evidence of saltational evolution. On the grand scale of seeing (in retrospect) the emergence of the first species of a new clade, the organismal reorganisation could be profound. In the case of the horse, Schindewolf drew attention not only to the loss of digits (one in the fore- and two in the hindfoot) in *Hyracotherium*, but also to a

more profound locomotory 'reorganisation', involving many aspects of the organism, that was reflected in the feet, with the second digit becoming the major weight-bearing structure. In changes in the teeth, as well, fossil horses were exemplary of Schindewolf's concept of stepwise evolution. However, once a monophyletic group became established, Schindewolf allowed that the degrees of reorganisation (leading to a saltation) in the species within the clade might be less profound. But, great or small, these changes were still of a stepwise, rather than smoothly transitional, nature.

THE FUNDAMENTALS OF THE DISAGREEMENT

It is of historical importance to recall the events leading up to the grand evolutionary synthesis, of which Simpson, for example, was a central figure. For it was he who battled on behalf of all paleontologists for the representation of their discipline in this synthesis. He did so in the face of population geneticists, such as Wright (1945), who had no qualms about declaring publicly that the study of fossils was irrelevant to the pursuit of understanding the origin of species - a process, as popularised by Mayr (e.g. 1942), that was supposed to begin at the level of the subspecies. Although it may now seem naïve, Simpson's attempts at incorporating population genetics (as it was then understood and applied to a Darwinian model of evolution) into his paleontologically informed perspective were dictated by his having already embraced a particular model of evolutionary change, which, in turn, reinforced the way in which he viewed the fossil record, gaps and all.

Just as Mayr (1942) had done two years earlier, Simpson chose to emphasize the role of minor mutations in producing the morphological changes that would eventually accumulate to produce evolutionary change. This model had, of course, first been proposed by Thomas Hunt Morgan (e.g. 1916, 1925), who

argued that, through the vehicle of Mendelian inheritance, the accumulation of minor mutations could produce Darwinian (gradual and transitional) evolution. Although earlier in his career Morgan (1903), like virtually all of the pioneering geneticists, rejected Darwinian evolution (but unlike them, he also dismissed Mendelian inheritance), he later became the advocate of both schools of thought as a result of his experiments in fruit fly population genetics (Morgan *et al.* 1915). Whereas his fellow population geneticists had taken Mendelism as indicating that individual variations, and, therefore, species differences, were discrete and discontinuous (because the units of inheritance were themselves discrete and discontinuous entities), Morgan trivialised the significance of the effects of Mendel's units of inheritance to such a minimal order of magnitude that it was now possible to see them as conforming to Darwin's conception of continuous variation. Thus, although these units of inheritance - which were then becoming identified as genes - did behave according to Mendel's laws of segregation and independent assortment, they were responsible for such small changes in morphology that, for all intents and purposes, variation at both the genetic and morphological levels could be considered continuous. Projecting this idea over vast periods of time, one could then explain evolutionary change as the accumulation of innumerable minor genetic and, thus, morphological changes. Where Morgan 'improved' on Darwin was in the recognition of mutation, not natural selection or blending inheritance (Darwin 1859, 1868), as the source of the morphological novelties that, if selected, could serve as the basis for evolutionary change.

But while Morgan's model might account for change within a lineage, it did not - as Darwin (1859) had not been able to do either - address a process that could lead to the multiplication of species. Perhaps not unexpectedly, there was no lack of attempts at dealing with this problem. Speculations on

speciation, such as those proposed by Fisher (1930), Haldane (1932), Dobzhansky (1935, 1937), Goldschmidt (1940), and Mayr (1942), were, in one way or another, all predicated on the disruption of reproductive continuity between individuals whose ancestors had been members of the same species. Representing individuals who we might call 'gradualist Mendelians', and following in Morgan's footsteps, Fisher and Mayr, who favored the accumulation of myriad minuscule mutations, advocated the complete isolation, usually geographic, of some individuals - often a large population - from the original, parent species. Over time, genetic incompatibility would result from the accumulation of enough small mutations that populations that we could call species would be produced. Haldane, too, invoked geographic separation as the provocation of speciation. But he envisioned a small number of individuals being involved in the process and he also allowed for factors in addition to genetic ones being at the base of change, which, he argued, was often a very rapid event.

Dobzhansky proposed a number of different kinds of disruption - from geographic separation to gametic incompatibility and zygotic death - that could lead to the partitioning of one species into two. Although Dobzhansky acknowledged the potential of accumulating minor genetic differences for producing change, he also, and steadfastly, promoted the role of chromosomal rearrangements as a primary source of genetic incompatibility. Indeed, it was Dobzhansky's work on chromosomal recombination that in large part informed Goldschmidt's theory of systemic mutation. Only something that would profoundly alter the genetic constitution of an organism could, as Goldschmidt saw it, produce a new species, especially if this genetic revolution were to affect the reproductive organs of an organism. Although Goldschmidt's developmental studies on gypsy and nun moths did indeed provide evidence of profound morphological

changes, including in genital morphology, which, in turn, could logically lead to the formulation of a model of speciation based on major genetic revolutions, the problem with his theory was that it could not account for the acquisition of such alterations in more than one individual (which he also, and unfortunately, labeled as a 'hopeful monster').

Like Hugo de Vries (e.g. 1900), the Dutch plant breeder and geneticist who had proposed the Mutation Theory to explain the evolutionary role of the 'sports of nature' that arise spontaneously in the course of a single generation, Goldschmidt could not muster support for his ideas, primarily because they could not be accommodated in the prevailing views of how things were supposed to be. In de Vries' case, his Mutation Theory fell largely on deaf ears. But Goldschmidt's story was different. Almost immediately after the publication of his major opus on systemic mutation, *The Material Basis for Evolution*, Dobzhansky (1941) published a revised edition of *Genetics and the Origin of Species* in which he went out of his way to dissociate himself from Goldschmidt by ridiculing him for even thinking that chromosomal rearrangement could lead to abrupt change, and, therefore, the abrupt appearance of new species. In this second edition, Dobzhansky was even more adamant about the gradual nature of evolutionary change. The following year, Mayr's (1942) *Systematics and the Origin of Species* was published. And it, too, served as a platform for excoriating Goldschmidt. Decades later, Mayr (e.g. 1982) would promote his role in having anticipated the model of punctuated equilibria (Eldredge & Gould 1972) by advocating the idea that isolated peripheral populations would provide the vehicle for rapid allopatric speciation. But, in 1942, he favored Fisher's model of speciation, which involved the division of the parent species into large daughter populations that, over long periods of time, gradually

accumulated the minor genetic changes that would be necessary to produce new species. According to Mayr's biological species definition, individuals from different species would not be able to breed and produce fertile and viable offspring. Time and time again, Mayr emphasized the 'evidence' for gradual evolution and the 'fact' that subspecies were incipient species waiting to happen, as if that had actually been demonstrated. The process of speciation would begin, according to Mayr, when a subspecies was able to invade a vacant econiche. There was no room for Goldschmidt's ideas in Mayr's version of evolution and speciation, to which his ad hominem assaults on the former were blatant testimony.

As a paleontologist, Simpson (1944) need not have continued the diatribes against Goldschmidt. But he did so, perhaps (as might well also be ventured with regard to Dobzhansky and Mayr) because there was something threatening about the possibility that Goldschmidt might be correct. Although initially acknowledging (p. 56) '*the large mass of factual data on the problem assembled by Goldschmidt*', Simpson immediately dismissed it as being '*consistent with his [Goldschmidt's] conclusion that...differences do arise by one step.*' As Simpson chose to see it, any evidence of saltation, '*including most of the famous 'mutations' of De Vries*', were the result of chromosomal aberrations. And as aberrations, of course, they could not be regarded as viable evidence of evolutionary change. [Truly, the interpretation of an undoubted observation is in the eye of the beholder. Darwin (Barrett *et al.* 1982) rejected 'sports of nature' as sources of insight into evolutionary process. De Vries (e.g. 1900) and Bateson (e.g. 1894, 1909), however, took these natural 'oddities' as reflective of a mechanism that could affect rapid and even remarkable change. So, too, did Goldschmidt, but Simpson did not.]

Simpson's dismissals of Goldschmidt, coming as they most frequently did in the form of footnotes, reflected the position the 'fathers' of the synthesis took in defense of what they perceived as the status quo, the 'right' way to think about evolution. What is so interesting about their stance - particularly Simpson's and Mayr's - is that there was just as little (or often even no) evidence in support of their assertions as they claimed to be the case for Goldschmidt's speculations. Take, for instance, Goldschmidt's attempt to distinguish between micro- and macroevolution, which were terms he used to identify what he perceived as different processes. The former process, at which level Darwinian notions of adaptation and natural selection were relevant, he saw as applicable to the daily lives of members of a species. Macroevolution had to do with the processes involved in the formation of species and clades (which, of course, exist as a result of species diversification). Simpson's response (p. 57) was as follows: '*If one granted as a premise Goldschmidt's conviction that macroevolution, essentially one process, occurs on specific and all higher levels and microevolution, essentially a different process, on subspecific and lower levels, this admission might warrant his other generalisations. But this is not an acceptable premise. It is a hypothesis that must stand, or evidently fall, on this evidence that is so clearly opposed to it.*'

What is 'this evidence' to which Simpson alluded? As for Goldschmidt's citation of the fossil record, and of Schindewolf's work, in support of his theory of systemic mutation, Simpson (p. 58) adamantly reiterated his own claim that the evidence is actually on the side of his interpretations, which supposedly gained additional credence by their agreement with the consensus of paleontologists (a tactic also used by Mayr in his rejection of Goldschmidt, but in this case it was the majority of naturalists in whom he sought support):

'To those who have done much work on good phyletic series of fossils it will hardly seem necessary to make such an obvious statement as that good species and genera frequently arise in…[a]…gradual way, whether or not they always do; but Goldschmidt's widely publicised work denies this fact (which vitiates his basic argument) and even claims paleontological support for this denial. In spite of assertions that he has drawn facts from all fields and that paleontology will be shown to support his thesis, the section of Goldschmidt's book that purports to give a few facts from paleontology gives no facts at all and only cites one of the thousands of pertinent paleontological studies, with the statement that this 'leads to exactly the same conclusions as derived in my (Goldschmidt's) writings,' to which he refers. After having carefully read the paper cited (Schindewolf, 1936), it seems to me not only not to lead to some of the main conclusions of Goldschmidt but also to contradict them. This paper, although a theoretical work of great importance and value, is also in some respects, especially where it does approach some of Goldschmidt's conclusions, at wide variance with the consensus of paleontologists and even with some of its own author's other works.'

The fact of the matter, though, is that Schindewolf actually did enlist Goldschmidt's theory of systemic mutation in support of his saltational view of the fossil record as much as Goldschmidt found evidence of the abrupt emergence of new forms from Schindewolf's reading of the fossil record. But a point that has consistently been ignored about Schindewolf's presentation has been his use of examples from development, especially 'atavisms'. In fact, one of his major examples, which he felt also warranted illustration, was the 'reappearance' of extra toes in modern horses.

DEVELOPMENT AND REGULATORY GENETICS

Although Schindewolf was a paleontologist, and it was as a paleontologist that he was chastised by Simpson, Mayr, and others for supposedly incorrectly interpreting the fossil record as revealing the abrupt appearance of new species (and the lack of a smooth trail of intermediates leading up to the emergence of a new species), he, like Goldschmidt, tried to bring as much evidence as possible to bear on the argument. This would seem to be appropriate considering the fact that, at the time they were writing and publishing, they were going against what could already be described as received wisdom about the reality of Darwinian evolution. Indeed, by the 1940s, it was possible for someone like Simpson (1949) to feel with unqualified indignation perfectly justified in referring to anyone who did not believe in Darwinian notions of smoothly transitional evolutionary change as an anti-Darwinian. But the emergence of 'sports of nature' (which individuals with apparently atavistic features surely represent) is not by the gradual or smoothly transitional re-acquisition of a characteristic thought to have been long lost in an organism's evolutionary past. To the contrary, and this is why geneticists such as de Vries, Bateson, and even the pre-Darwinian/Mendelian Morgan were so intrigued by them, so-called atavistic characters appear suddenly - in the space of a generation - in one or more individuals.

Although de Vries based his mutation theory in large part on sports of nature (as witnessed primarily in mutant forms of the evening primrose), it was Bateson (1894) who studied developmental alterations in meristic or, as he called them, repeated parts across an array of taxa. To this end, he amassed 886 examples of plants and animals, vertebrate and invertebrate, which were characterised by having more or fewer elements in series of repeated parts. For example, he listed and illustrated flowers with extra or fewer petals, ferns with extra or fewer frond-leaf segments, starfish

with extra or fewer arms, deer with more or less arborization of antlers, humans with extra or fewer vertebrae, and chickens and horses with extra toes. In the case of horses with extra digits, Bateson, as later would be Schindewolf, was struck by the fact that when such a supernumerary is present, it may be smaller than the primary digit, but it still possesses all of the elements of a proper toe, including three phalanges, plus a keratinised hoof. Bateson likened the phenomenon of alterations in the number of repeated parts to the coming and going of the tide, which, in these cases, produced a rippling developmental effect. The greater the intensity of the developmental cascade, the greater the number of repeated parts, and vice versa. As far as he was concerned, virtually all development, and, therefore, differences between related organisms, could be accounted for by changes in the otherwise normal process of regulating development, which he referred to as homeosis. Since most if not all of the major features of an organism, whether plant or animal, can be attributed to the developmental realisation of segmentation, Bateson's idea would seem to deserve serious consideration. But since his studies of repeated parts convinced him that discontinuous rather than continuous variation characterised organisms - a position that was reinforced when he discovered Mendel's work - and, thus, that the origin of species was not a smoothly transitional process, he found himself at odds with fellow and more powerful British colleagues, such as Wheldon, who were strict Darwinians.

But the observation of a phenomenon and the explanation of the process underlying it are two entirely different propositions. Indeed, even Simpson (1944) reminded his audience of this truism in his plea for seeing the fossil record as evidence of smoothly transitional change. In this particular instance, Simpson cited the work of Henry Fairfield Osborn (e.g. 1932, 1936, 1938), who, he believed, had found paleontological evidence for the

gradual development of characters across successive populations, but who, unfortunately, had invoked both a quirky terminology and a metaphysical explanation for the underlying causes. As for Bateson, he may have suggested somewhat naïvely that the number of repeated parts resulted simply from either the lack of subdivision or the over-subdivision of elements, but his observation still holds true: differences between organisms (such as in number of pedal digits in various fossil horses) often lie in differences in degrees of segmentation or differentiation of repeated parts.

Schindewolf's interpretation of atavistic structures as providing insight into a process of abrupt evolutionary change was informed by studies in the nascent field of developmental genetics. In addition to Goldschmidt, foremost among this new breed of scientist was Grüneberg, whose experiments during the 1930s (which are summarised in his monograph of 1943) demonstrated that structures had to reach a critical developmental threshold or they would develop no further and could subsequently become resorbed. Thus, in order to be expressed, a structure must have a certain level of developmental potential. When applied to 'atavistic' structures, such as the extra digits seen in the occasional horse, it thus made sense why there would be three phalanges, replete with a keratinised hoof on the terminal phalanx: there had been sufficient developmental potential to produce a structure, albeit a structure that was perhaps reduced in size relative to the more fully expressed 'normal' state. Of course, if such developmental potential were to be lacking, so, too, would the structure.

This insight was not lost on Schindewolf, who obviously understood its implications for interpreting what he saw as the leap-frog nature of the fossil record of invertebrates and vertebrates, including the horse. The jump from *Pliohippus* to *Equus* would simply

be the reverse of the process that produces modern horses with supernumerary digits: in the origin of a new type of horse, *Equus*, cellular potential was adequate for the development of slender lateral metapodials, but not of phalanges. Thus, even the rather restricted understanding during Schindewolf's time of development was sufficient to suggest that the fossil record may not be playing tricks on paleontologists. One would expect there to be gaps between presumed ancestors and descendants because the development of structures is essentially an either/or process. This was not to deny those examples, even in the fossil record of the horse, in which the apparent evolutionary stages were not radically dissimilar, such as, in the case of the horse, enlargement and elaboration of the cheek teeth (post-*Hyracotherium* and pre-*Equus*) and the reduction in size of the lateral digits (from *Parahippus* and *Merychippus* to *Pliohippus*). But in the latter example, it was only a reduction in the size of structural elements, not in their number.

Although Eldredge & Gould (1972) did not address development when they proposed their model of punctuated equilibria - which was predicated on Eldredge's (1971) plea for seeing the fossil record as a faithful documentation of speciation resulting from allopatric speciation via peripheral isolates - they did approach the topic in their second article (Gould & Eldredge 1977). There they argued that because population genetics, upon which the model of gradual evolution was based, focused on the products of structural genes, it would be more appropriate to seek insight into mechanisms of evolutionary change by studying the regulatory genes (only then becoming known) that govern development. A change in a regulatory gene would certainly have a profound effect on its bearer and provide the 'stuff' of which new species are made. Reminiscent of Goldschmidt, Gould & Eldredge (1977) thus relegated one level of genetics, and along with it the basis for thinking that change was smoothly transitional, to

the process of microevolution, and another, which led to the formation of new species, to macroevolution. But as Goldschmidt's critics attacked him for unnecessarily, and artificially, separating a single evolutionary process into two, so, too, did population geneticists (e.g. Charlesworth *et al.* 1982) criticise Gould and Eldredge. The sentiment was simply: why invoke an unknown genetic mechanism when the one we already know is sufficient to explain all aspects of evolution?

A NEW LOOK AT EVOLUTION AND THE ORIGIN OF SPECIES

The issue at hand is actually not over separate and distinct modes of inheritance, one that is at the level of individual variation within species and the other at the level of the origin of the degree of novelty that distinguishes species. It was an unfortunate accident of history that such notables as de Vries, Bateson, and Goldschmidt were unable to articulate more fully an easily understandable and, therefore, broadly acceptable genetic model to explain the phenomena they were trying to incorporate into evolutionary theory. The same difficulty also befell Gould and Eldredge, although they were closer to the fundamental genetic levels than their predecessors had been. Perhaps, as well, the introduction of language that seemed to complicate unnecessarily the situation did not help, either. Goldschmidt's paired terms 'microevolution' and 'macroevolution' and 'micromutation' and 'macromutation', although clearly reflecting the essence of what he saw as being relevant at different levels, demand a search for two totally distinct mechanisms when, equally clearly, only one has ever convincingly been demonstrated. If we allow that the basic laws of Mendelian inheritance articulate a workable and simple mechanism of genetic transmission, then it is not a question of different modes of genetic transmission that is at issue in the debates over the origin of species. It is a matter of *what* is being transmitted and inherited. As I have discussed at length elsewhere (Schwartz 1999a, b),

although there is a tremendous difference in effect if a mutation (perhaps involving an enhancer gene) affects a homeobox (regulatory) gene instead of a structural gene, they are both genes and they are and will be transmitted in similar fashion. For example, in an experiment on mice that converted the normally dominant *Rx* homeobox gene, which is critical for proper eye and bony socket formation, to the recessive state, offspring that were homozygous for the normal allele (+/+) as well as those that were heterozygous for the normal and mutated alleles (+/-) developed eyes and bony sockets (Mathers *et al.* 1997); only homozygotes for the mutated recessive state (-/-) did not develop eyes and bony sockets. Clearly, homo- versus heterozygosity with regard to eye colour, although producing individual variation within a species, will not produce the degree of difference systematists associate with species' differences. Thus, there really is a fundamental difference between the concepts that are associated with the terms 'microevolution' and 'macroevolution'. But this difference does not result from 'micromutation' and 'macromutation' in the sense that Goldschmidt, and apparently also Gould & Eldredge (1977), meant it. The mode of inheritance and even the mechanism of mutation are not different. Only the kinds of genes - regulatory or structural - that are affected by mutation are.

It is becoming increasingly clear that most animals share many of the same homeobox genes. Differences between organisms appear to arise as a result of which genes, and where these genes, are activated. For instance (see Schwartz 1999a, b for review and references), in mobile, chordate-like tunicate larvae the *Manx* homeobox gene (which is involved in tail formation, as it is in vertebrates) is active, but in sessile tunicate larva it is not; in fish, the *Hoxd-11-13* homeobox genes are active only along the posterior side of the developing fin bud, but in tetrapods these genes are active along the posterior side as well as across the anterior face of the develop-

ing limb bud (the tetrapod *Hoxd-13* gene also has an insertion that encodes a poly-alanine stretch, which is implicated in digit number formation); the *Dlx* homeobox gene, which is necessary for tooth development, is active in vertebrates but present and inactive in tunicates; echinoderms, which begin development as bilaterally symmetrical animals, are converted into radially symmetrical organisms by the simultaneous activation in a radial pattern of three regulatory genes (*orthodenticle, engrailed*, and *distal-less*) which, in vertebrates, participate in separate and distinct aspects of structural differentiation along the body's anteroposterior axis. If a common feature of animal life is the sharing of various regulatory genes, then differences that exist between organisms that are relevant at the level of distinguishing species would be a matter of the timing of activation or deactivation of, as well as interaction between, various regulatory genes. In this context, in addition to including gene duplication or the insertion or deletion of a molecular segment, respectively, into or from a particular gene, mutation can simply be that which activates or deactivates an already-present regulatory gene (whether duplicated or otherwise altered). Since, as Bateson (1909) first realised, most nonlethal mutations arise in the recessive state, the mutation will spread 'silently' through the population by way of heterozygotes until they are sufficient in number to produce homozygotes with that mutation. The spread of the mutation would take some number of generations to reach a saturation point of heterozygotes [although the smaller the population, the faster it would spread (e.g. Haldane 1932, Wright 1932)], but the expression of the mutation would be in some number of homozygotes of the same and immediately subsequent generations, and it would be instantaneous (Schwartz 1999a, b). If the mutation happened to activate, for instance, the *Dlx* homeobox gene, then, as we know from the vertebrate fossil record, toothed organisms would appear as if out of nowhere. If it activated the *Manx* gene, then, as

we also know from the fossil record, chordates would appear as if out of nowhere. And if it activated the *Hoxd-11-13* genes across the front of the developing limb bud (and there was a spontaneous mutation that inserted a molecular segment encoding a polyalanine stretch in the *Hoxd-13* gene), then (witness *Acanthostega* and *Ichthyostega*) tetrapods would appear as if out of nowhere. At some point, the mutant recessive allele would probably be converted to the dominant state (Fisher 1930, Haldane 1932, Wright 1932). Nonetheless, however a recessive allele becomes converted to the dominant state, the basic mechanism of its spread precludes the existence of a smooth trail of intermediate forms between related taxa. If one desired, one might liken the spread of the recessive mutation to a somewhat gradual process. But because the mutation will only be expressed in homozygotes, the appearance of the morphological novelty that is associated with the mutation will be abrupt (Schwartz 1999a, b) - just as de Vries, Goldschmidt, and Schindewolf had argued was the case. Schindewolf may not have known why there had to be gaps in the fossil record, but he was convinced of the fact that gradually changing transitional forms were indeed absent from it.

Although Eldredge & Gould (1972; also Gould & Eldredge 1977) advocated rapid evolutionary change, their model of punctuated equilibria still relied on the existence of morphologically intermediate forms during the brief period of speciation. A look at Eldredge's (1971) data on lens number in trilobite species (which informed the model of punctuated equilibria) reveals, however, that, rather than there being an insensible gradation of specimens representing many possible combinations of number of lenses, there were differences over time in the relative frequencies of individuals with one or another of a very limited number of lens patterns. What seems to have happened was the increase in the number of individuals with a particular lens pattern, not a transition between interme-

diate stages from one pattern to another. This, of course, would be expected (Schwartz 1999a). For, although my model of evolutionary change allows for the emergence of more than one homozygote bearing the mutation - which was the stumbling block for de Vries, Goldschmidt, and Gould & Eldredge (1977) - if this potential species is to persist, its numbers must increase (ibid.). But one thing remains clear: the way in which the mutation will spread until its expression means there will not be gradual stages in the emergence of one species from another, and this is consistent with the existence of gaps in the fossil record. Eldredge (1971, also Eldredge & Gould 1972), was correct about the gaps in the fossil record providing clues about the origin of species. But they are not filled with fleeting glimpses of transitional forms.

A fortuitous example of my model of evolutionary change is provided by the discovery of a spontaneous mutation in a laboratory colony of mice that affected the *Hoxd-13* gene and the encoded polyalanine stretch (Johnson *et al.* 1998). The mutation arose in the recessive state and spread silently through the laboratory colony until there were enough heterozygotes for the production of a number of offspring that were homozygous for the mutation. Since the mutation caused an expansion of the polyalanine tract, affected individuals developed synpolydactyly. The researchers, of course, only discovered that this had happened upon finding a generation of offspring among which were synpolydactylous individuals. The mutation was identified with the knowledge of hindsight. Of further interest is the fact that this mutation, which affected the *Hoxd-13* gene and increased the polyalanine stretch, had previously been identified in humans with synpolydactyly (Muragaki *et al.* 1996). Thus, not only is it obvious that differences between organisms can result from differences in developmental regulation that are due to mutations producing different domains of regulatory gene activity, but, given the widespread sha-

ring of the same regulatory genes by a diversity of taxa, it is also likely that the obverse is true: similarities between organisms result from similar alterations of the same regulatory genes (Schwartz 1999a, 1999c).

The issue of determining homologous structures may still need to be sorted out in the same way it currently is: by testing alternative theories of relationship with additional data. Homoplasy can only be defined after a particular theory of relationship, and the suite of synapomorphies upon which it is based, are accepted as 'real', and other phylogenies, and the potential synapomorphies upon which they are based, are rejected as 'false'. But, in light of the fact that most organisms share many of the same regulatory genes, when potential synapomorphy becomes relegated to the ranks of homoplasy, it might still be the case that these hypothesised homoplastic morphologies are the products of the same homeobox or other regulatory genes. The difference, therefore, between homologous and homoplastic features would be due, respectively, to the inheritance from common ancestors of mutations with similar effects on the same regulatory genes versus the independent acquisition of mutations with similar effects on the same homeobox or other regulatory genes. In the realm of regulatory genes, the reason that various organisms have developed similar structures would be less a matter of them adapting to similar situations than of spontaneous (and random) mutations affecting the same set of regulatory genes - as in the case of the laboratory colony of mice that developed synpolydactyly through spontaneous mutation. Whether the bearers of such mutations would persist as viable species would, in turn, be a matter of chance (de Vries 1900; Morgan 1903; Schwartz 1999a, b, c). If I might be allowed to para-phrase de Vries: if the mutation doesn't kill you, you retain it.

CONCLUSION

Having strayed from discussion of the evolution of the horse, which, through Paul Sondaar's unplanned instigation, became the impetus for this contribution, let us return to it. It would seem to be as Schindewolf had earlier perceived: the abrupt emergence of the ancestor of the clade (*Hyracotherium*?), which was in various ways noticeably distinguished by its dental and postcranial novelties, and the subsequent diversification of species (which also appeared without smooth trails of fossil intermediates), that differed from each other in various ways. But whatever the de-grees of difference - whether in marked changes in dental morphology (such as the exposure of dentine between vertical enamel plates) or the loss of pedal digits, less profound alterations of loph patterning, or simply an increase in body size and consequent proportional changes in body parts (e.g. relatively larger second and smaller first and third digits) - they are a matter of developmental regulation, and that ultimately involves the timing and interaction of regulatory genes and the intensity of their effects (Purugannan 1998; Schwartz 1999a, b). As to what provokes the mutations that affect regulatory changes, that question is still up in the air (Schwartz 1999a, b), the recent attempt to provide an environmental model notwithstanding (cf. Rutherford & Lindquist 1998).

Clearly, as we approach the millennium mark, and this acknowledgment of Paul Sondaar's decades of influence on, and contributions to, paleontology and systematics, we are entering into a new and unexplored phase of evolutionary inquiry. To engage in it with the excitement and open-mindedness that has characterised Paul's career should be the ultimate goal.

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