

# Chapter 10

## Inertia, Trend, and Momentum Reconsidered: G. G. Simpson—An Orthogeneticist?



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*The structure of an ancestral group inevitably restricts the lines of possible evolutionary change. That simple fact greatly increases the probability that among the number of descendant lineages several or all will follow one line.*  
George Gaylord Simpson (1961)

**Abstract** George Gaylord Simpson, one of the architects of Modern Synthesis, was one of the main figures of paleontology who discredited and rejected the theory of orthogenesis in his discipline. Following the neo-Darwinian agenda, he thought that this theory had little basis to be proven. Since then, orthogenesis has been defined in textbooks as a “metaphysical,” “vitalistic,” or “theological” theory. However, in the present analysis, I demonstrate that Simpson indirectly advocated for an explanation of orthogenesis through his explanation of the concept of “parallelism.” In other words, Simpson did not end orthogenesis but rather ended up defending the phenomenon of orthogenesis through the concept of parallelism. I argue that Simpson maintained pluralistic ideas upon including constraints into his evolutionary system as a complementary factor to the argument of natural selection.

**Keywords** George Gaylord Simpson · Modern synthesis · Paleontology · Orthogenesis · Parallelism · Constraints · Macroevolution · Otto Schindewolf · William Berryman Scott · Natural selection

### 10.1 Introduction

Once upon a time, more than a hundred years ago, orthogenesis (or directed evolution) was one of the most popular and accepted theories in evolutionary biology, particularly in paleontology. But with the rise of the Modern Synthesis movement

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during the 1930s and early 1940s, geneticists and taxonomists perceived that orthogenesis was inconsistent with the assumptions of population genetics, but little could be done to disprove it. Until one day, in 1944, an American paleontologist named George Gaylord Simpson published a book whereby he reconciled population genetics with paleontological data. Following the neo-Darwinian agenda, he thought that orthogenesis had little basis to be proven. And that was how Simpson ended all theoretical consideration of orthogenesis in paleontology, and neo-Darwinians lived happily ever after.

The previous paragraph, written with a little bit of sarcasm, is a model of the type of narrative that has been used to discredit the theory of orthogenesis while highlighting the achievements of the Modern Synthesis. In any case, the narrative of the history of the Modern Synthesis, which treats this movement as a scientific revolution, has been challenged by some modern historians who attempt to reframe the history of evolutionary thought (e.g., Amundson 2005; Delisle 2009, 2011, 2017; Ochoa 2017, 2021; Stoltzfus 2017; Adams 2021; Schwartz 2021; van der Meer 2021). On that basis, this chapter aims to contribute to the historiographic development of the Modern Synthesis, but under the “no-traditional” approach. This study attempts to reconsider not only how the history of evolutionary biology has been written but also the basis on which some current evolutionary positions have developed.

In the early years of the twentieth century, anti-Darwinian theories such as saltational evolution and orthogenesis dominated in the disciplines that studied macroevolution, e.g., morphology and paleontology. In consequence, during the development of the Modern Synthesis, the first architects entered the scene slightly skeptical about supporting one of the most important assumptions of this movement, that is, that the larger-scale evolutionary phenomena (macroevolution) could be explained by observable phenomena and occurrences on a smaller evolutionary scale (microevolution). Shortly thereafter, paleontologist George Gaylord Simpson, in his book *Tempo and Mode in Evolution* (1944), stated an argument whereby paleontological data was congruent with population genetics research and, therefore, with a microevolutionary approach. When the architects took notice of this work, they were more confident in their conclusions about the premise of extrapolation. As a result, alternative theories to Darwinism were subsequently marginalized. Without a doubt, that is why we can say that Simpson’s contributions to paleontology were vital for the development of the Modern Synthesis.

Despite this narrative, we have been noticing that Simpson’s works stayed aloof from the central assumptions of Darwinism (Ochoa 2017; Popov 2018), and although he attempted to interpret the observations of paleontology with the known mechanisms of population genetics, many of his central assumptions are far from supporting a reductionist point of view. In particular, I shall demonstrate that although Simpson discredited and rejected the theory of orthogenesis in his writings, he indirectly advocated for an explanation of orthogenesis through his explanation of the concept of “parallelism” (a type of homoplasy). In other words, we shall see that Simpson did not end orthogenesis, but rather ended up defending the phenomenon of orthogenesis through the concept of parallelism. Simpson as a

character is quite complex, so we cannot say that he just reduced all paleontological observations to microevolutionary facts. Hence, this chapter endorses the idea that Simpson maintained pluralistic ideas upon including constraints into his evolutionary system as a complementary factor to the argument of natural selection.

To bring this about, I first explore in section 10.2 how the figure of Simpson was constructed in the Modern Synthesis narrative. I stress that Simpson's works stayed away from a reductionist view. In the following section 10.3, I briefly discuss the meaning of orthogenesis. Specifically, I review the ideas of two anti-Darwinian paleontologists of the early and mid-twentieth century, respectively, William Berryman Scott and Otto H. Schindewolf, who related the phenomena of orthogenesis with the modern term of "parallelism." In the last section 10.4, I analyze Simpson's ideas concerning orthogenesis, and I expose how even though he rejected the theory in his writings, I have discovered that he defended the idea of orthogenesis and even gave support and explanation for its occurrence indirectly through the term of "parallelism."

## 10.2 Creating the Hero of the Modern Synthesis

George Gaylord Simpson was a well-known American paleontologist for his role as an architect of the Modern Synthesis. Simpson began his work by studying the Mesozoic and Cenozoic mammals of North America as well as those of the Tertiary in South America. He was appointed to an Alexander Agassiz professorship at the Museum of Comparative Zoology, Harvard University. Later, he joined the University of Arizona and became professor emeritus of geosciences. Simpson inaugurated a new period in the study of vertebrate paleontology, and, along with Edward Dring Cope, Henry Fairfield Osborn, and William Berryman Scott, he figured as one of the most outstanding American paleontologists in the history of evolutionary thought. He founded the Society of Vertebrate Paleontology, belonged to distinguished scientific associations, and published many papers and books, whose subjects included paleontology and evolution (Wittington 1986).

But perhaps the most prominent influence is the publication of Simpson's book, *Tempo and Mode in Evolution* (1944), which contributed to the Modern Synthesis by making compatible the views of population genetics with paleontological data. But, why was Simpson's book so special? According to Gould (1980, pp. 157–160), firstly, *Tempo and Mode* was a unique book in the sense that it was outside from the paleontological tradition of its time. Paleontologists wrote about evolution, but most of them made fossil descriptions, or they only established their phylogeny. Few devoted considerable attention to the study of the processes and mechanisms of evolution. Secondly, the book contains graphs, frequency distributions, and representative models: "No paleontological innovation could have been more stunning than this." Simpson's book introduced the novelty of quantified information, unique in comparison with traditional paleontological works. Thirdly, and more importantly, he displayed a good argument supporting that Darwinism might be consistent

with the fossil record; therefore, no special theories of macroevolution were needed (such as saltational evolution and orthogenesis). And in the opinion of Cain (1992), *Tempo and Mode* was the bridge that linked population genetics with paleontology. This allowed greater confidence in the extrapolationist premise, that is, that microevolutionary processes could also explain the macroevolutionary realm, although the book itself gave a somewhat exclusive role to paleontology when dealing with a macroevolutionary approach.

In this regard, it is important to stress here that during the beginning of the twentieth century, most paleontologists supported ideas contrary to traditional Darwinism, for example, by considering that evolution might also occur by leaps and that variations do not occur randomly, therefore, paleontologists maintained that their discipline had autonomy in the study of macroevolution and the history of life (Bowler 1983, 2017; Gould 2002; Levit et al. 2008; Ochoa 2017). Later, the Modern Synthesis did not gain general acceptance until paleontological data were consistent with Darwinism. By regarding the meaning of the Modern Synthesis, for example, Mayr's rhetoric (1980a) tells us that these advances facilitated the removal of those "communication gaps" that did not allow understanding among paleontologists, geneticists, and naturalists. Thus, the Modern Synthesis was presented as an agreement between different research traditions, excluding anti-Darwinian theories that "had wrong ideas on the nature of inheritance and variation."

This narrative was not accidental, since, in the writings of the architects, we can observe that Simpson's work provided some confidence with respect to extrapolationist premise that macroevolution is nothing more than accumulated microevolution. This was a crucial point for the development of the Modern Synthesis.<sup>1</sup> Theodosius Dobzhansky, for example, in his monumental book *Genetics and the Origin of Species* (1937), which was published 7 years before Simpson's book, argued about the difficulties of assuming the extrapolationist premise. He stated that geneticists had been limited to studying only the phenomena of microevolution since it is not possible to experiment for millions of years; at that point, the best advice was to conceive that microevolution and macroevolution were the same but at a different timescale: "For this reason we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution, and, proceeding on this assumption, to push our investigations as far ahead as this working hypothesis will permit" (Dobzhansky 1937, p. 12). However, in a later edition of his book, Dobzhansky is more confident in his hypothesis<sup>2</sup> because he found support in the works of paleontologists and morphologists who were in favor of his research:

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<sup>1</sup>Whether microevolution is different from macroevolution has been one of the central issues in evolutionary thought; see Adams (2021) in this volume.

<sup>2</sup>However, it is important to note that Dobzhansky had doubts about the central role of natural selection in macroevolution through his life; for this discussion, see van de Meer (2021) in this volume.

All that is possible is to examine the evidence bearing on macroevolution which has been accumulated by paleontologists and morphologists, and to attempt to decide whether it agrees with the hypothesis that all evolutionary changes are compounded of microevolutionary ones. . . . The three authors [Simpson, Schmalhausen, and Rensch] find nothing in the known macroevolutionary phenomena that would require other than the known genetic principle for causal explanation. (Dobzhansky 1951, p. 17)

Likewise, Ernst Mayr, in his book *Systematics and the Origin of Species* (1942), published 2 years before Simpson's *Tempo and Mode*, is equally distrustful but at the same time enthusiastic to reach an agreement to solve the discrepancies between the disciplines that study microevolutionary principles and the disciplines that focus on a macroevolutionary approach:

Geneticists and most taxonomists have devoted most of their attention to microevolution, and the field of macroevolution was left more or less to the paleontologist and the anatomist. This has led to difficulties and misunderstandings, since paleontologists, taxonomists, and geneticists talk three different languages, and all three of them have certain mistaken ideas about the basic facts and axioms of their sister disciplines. To state that orthogenesis proves that evolution proceeds without selection would be just as erroneous as to state that orthogenetic series do not exist. (Mayr 1942, pp. 291–292)

However, in *Animal Species and Evolution* (1963), Mayr offered his vote of confidence in Simpson's works as follows: "It is not the task of this volume. . . to refute these theories [saltational evolution and orthogenesis] and to cover in detail the entire area of transpecific evolution [i.e., macroevolution]. This has been done superbly by Simpson . . . with emphasis on the paleontological evidence" (p. 586). Similarly, many years later, Mayr stressed the fact that Simpson "was one of the most important architects of the synthesis. He engineered the marriage of paleontology with genetics and more broadly with the rest of evolutionary biology" (Mayr in Mayr and Provine 1980, p. 153). Also, that "Simpson was responsible for bringing paleontology and macroevolution into the synthesis. . . He acquired this understanding by studying the genetic literature and was able, by integrating it with his fine knowledge of paleontological evidence, to arrive at an interpretation of macroevolutionary events in *Tempo and Mode of Evolution* (1944) that was fully consistent with the findings of the new genetics" (Mayr 1980a, p. 37). And finally, he states: "The gap between the findings of genetics laboratories and the findings of paleontologists seemed to be unbridgeable because of the difficulties of a genetic interpretation of macroevolution. This gap, in turn, delayed the synthesis until the division was closed by zoologists and paleontologists (Rensch and Simpson)" (Mayr 1980b, p. 134).

In short, we can ascertain that in the first writings of the founders of the Modern Synthesis, they were doubtful concerning the conclusion on macroevolution. Up until that time, disciplines such as embryology, morphology, and paleontology stayed away from the achievements accomplished by population genetics, experimental genetics, and the "new systematics." For example, the greatest adversary of the Modern Synthesis, Richard Goldschmidt, argued in *The Material Basis of Evolution* (1940) that: "The general picture of evolution resulting from such deliberations is in harmony with the facts of taxonomy, morphology, embryology,

paleontology, and the new developments of genetics. The neo-Darwinian theory of the geneticists is no longer tenable” (p. 397). But once Simpson’s *Tempo and Mode* book appeared, the architects felt more confident with respect to the extrapolationist premise. With this, I do not mean that Simpson’s work alone facilitated this endeavor, for example, surely other contributions such as those of Julian Huxley and Bernhard Rensch strengthened this point of view as well. In any case, Simpson’s writings were essential for creating this narrative of the Modern Synthesis: the microevolutionary mechanisms provided by genetics and taxonomists are congruent with what we know about paleontology and macroevolution. For example, Laporte (2000, p. 1), in his biographical work on Simpson, mentions that: “Simpson’s book applied the concepts and conclusions of the new discoveries in genetics to the large body of fossil evidence of life’s long history, and claimed that the ‘microevolution’ of the geneticist could indeed be extrapolated to explain adequately the ‘macroevolution’ of the paleontologist.”

It is interesting to note that this rhetorical assumption, characteristic and essential to the argument of the Modern Synthesis, still resonates in some recent historical works dealing with the topic of macroevolution and orthogenesis. Bowler (2017, p. 209), for example, claims that: “The work of George Gaylord Simpson would cement the palaeontologists’ rejection of the non-Darwinian stance adopted by the previous generation.” Correspondingly, Pigliucci (2017, p. 93; his italics) argues that: “It was George Gaylord Simpson’s (1944) magistral role within the Modern Synthesis to clear away any remnants of orthogenesis from paleontology . . . he convincingly argued that the sort of so-called ‘micro’-evolutionary processes accounted for by Darwinism could be extrapolated to geological timescales, thus yielding the *appearance* of macro-evolutionary changes of a qualitatively different nature. In reality, Simpson argued, the second is simply a scaled up version of the former.” Similarly, Turner (2017, p. 337) comments that: “Simpson’s *Tempo and Mode in Evolution* (1944), which is often cited as an effort to bring paleontology into the modern synthesis, represented a major theoretical turn away from earlier ideas such as orthogenesis. . . and the neo-Lamarckian theorizing about macroevolution that one finds in the work of Edward Drinker Cope.” Nevertheless, Turner wonders whether this was really the only merit that Simpson had for the Modern Synthesis: “Still one big issue that Simpson’s work had not entirely resolved was whether paleontology would have much more to contribute to neo-Darwinian evolutionary theory.”

In this regard, Sepkoski (2019) emphasizes the fact that paleontology played a very important role in the development of the Modern Synthesis, particularly due to Simpson’s influence both institutionally and theoretically. However, he argues that it seems odd to realize that many paleontologists of the 1970s and 1980s such as Stephen Jay Gould, Niles Eldredge, and Steven Stanley, among others were dissatisfied with the achievements of paleontology in the Modern Synthesis. They even argued that this discipline was relegated by the movement. For example, Gould (1980, p. 170) considered that “Simpson’s synthesis unified paleontology with evolutionary theory, but at a high price indeed— at the price of admitting that no

fundamental theory can arise from the study of major events and patterns in the history of life.”

But an important point of this discussion is that Sepkoski (2019, p. 693) noticed that *Tempo and Mode* differs considerably from the opinion of the other architects, for example, by considering the assumption that the fossil record is incomplete. On the contrary, Simpson points out that the absences in the fossil record might be real, and part of his argument in *Tempo and Modes* relies on the claim that higher taxa have evolutionary rates and modes different than those of species. One of his central contributions to this discourse is with respect to the development of the concept of “quantum evolution,”<sup>3</sup> for example. And although it is not precisely a mode that moves away from the mechanisms provided by population genetics, it is a manifesto for the no-extrapolation. However, according to Gould (2002, pp. 528–531), Simpson changes his mind regarding quantum evolution. While in *Tempo and Mode* he highlighted that quantum evolution was the most important concept of his research, in *The Major Features of Evolution* (1953) (which is considered as the second edition of *Tempo and Mode*), he doesn’t consider it as an exclusive mode, but rather as a type of phyletic evolution. This interpretation brings us to the assumption that Simpson yielded to extrapolation in later works.

In fact, Sepkoski (2019, pp. 694–695) follows Gould’s narrative, and he laments that Simpson changed his mind since the arguments in *Tempo and Mode* could be outlined as a work that would bestow theoretical autonomy to paleontology regarding evolution; and the concept of quantum evolution, specifically, was one of the most central contributions toward this endeavor. Finally, Sepkoski (2019) concluded that paleontology has played an important role in the development of the Modern Synthesis; however, this contribution was not entirely revolutionary since other perspectives came to light in subsequent years which called for a better contribution of paleontology to evolution.

In any case, I suspect that Simpson’s contribution to paleontology was eclipsed, on the one hand, by this historiographic narrative of the achievements in paleontology developed by the other architects (particularly Mayr) to corroborate the extrapolationist premise and, on the other hand, by the same paleontologists of the 1970s and 1980s who used this narrative to promote and defend their theories on macroevolution, particularly by Stephen J. Gould and Niles Eldredge during the development of punctuated equilibrium. An example of this may be seen in Gould and Eldredge’s (1977) discourse when arguing in favor of “speciation” instead of “phyletic gradualism” as the dominant mode of biological evolution: “speciation is the raw material of macroevolution, and genetic substitution within populations cannot be simply extrapolated to encompass all events in the history of life. We therefore challenged the central assumption that secured the admission of

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<sup>3</sup>To account for the origin of the species and higher taxa, Simpson argued that there were different modes of evolution. Speciation (splitting up of a population) pertains to species and subspecies. Phyletic evolution (directional shift of average characters of the entire population) was related to the genus level. Quantum evolution (a rapid change of the population from a state of instability to stability) corresponds to higher categories such as families, classes, and orders.

paleontology into the modern synthesis of evolutionary theory (Simpson 1944, 1953): change in gene frequency within populations is the building block of major evolutionary events” (p. 139).

As we can see, they quote *Tempo and Mode* and *The Major Features of Evolution* as the source of the perspective they seek to challenge. However, as we saw above, *Tempo and Mode* is beyond the reductionist approach for not simply based on the notion of “change in gene frequency within populations.” Moreover, unlike Eldredge and Gould, Simpson thought that higher taxa are real and, therefore, genuine units of evolution. Even despite what most biologists may think, he still maintained this non-reductionist point of view in *The Major Features of Evolution*:

The study of the evolution of higher categories, say for present purposes from families upward, does involve some of the most important problems of evolution. For one thing, evolution on this scale cannot be directly studied by experimental method . . . The main themes of this book relate to evolution on a broad scale, hence largely to categories above the species. The time has now come to undertake explicit consideration of what higher categories are and how they arise. (Simpson 1953, pp. 339–340)

In fact, a very different idea of Simpson as a character has also been noted by Popov (2018, p. 54), who writes far removed from historiographic orthodoxy about the subject of orthogenesis. For example, Simpson, he says, “remained aloof from his fellow ‘architects’, and seemed to enjoy his aloofness, too. ‘Orthodox’ Darwinists doubted that Simpson’s views on evolution were quite right.” Even the editors of the Russian edition of *Tempo and Mode* realized that Simpson “came to Darwinism ‘by the backdoor’ of doubts and exceptions.” Therefore: “Deviations from the traditional scheme can be easily found in his work.”

Perhaps many questions arise from all of this, like how “anti-Darwinist” could Simpson’s works end up being? If *Tempo and Mode* stays away from the assumptions of the other architects of the Modern Synthesis, why did these architects use this famous text to foster and strengthen their views? Was *Tempo and Mode* just a rhetorical means to promote the Modern Synthesis movement? And, if there was a radical change in his stance, did Simpson feel pressured by the other architects and correspondingly had to sacrifice his macroevolutionary ideas? Attempting to answer all these questions would obviously require many more historiographical studies that may exceed the objectives of this humble essay. However, I shall demonstrate that one of the most emblematic ideas of the anti-Darwinian movement and macroevolution in early-twentieth-century paleontology is present in Simpson’s works: orthogenesis. But before looking into this topic in detail, it is pertinent to know the historical context of the theory of orthogenesis, and we will see how this theory fostered the development of the modern term of “parallelism” as well.



### 10.3 On the Origin of the Term “Parallelism”: Orthogenesis and Paleontologists

One of the evolutionary controversies that have been debated is the meaning of concepts from comparative anatomy such as homology and homoplasy. Homology refers to the identity of structures in different lineages regardless of form and function, while homoplasy pertains to those similarities of form which evolved independently in two separate lineages. Regarding homoplasy, biologists recognize two kinds: parallelism and convergence. Parallelism generally refers to independent evolution in closely related groups, mainly due to internal constraints that limit and channel evolutionary change, while convergence is described as functionally similar structures which arise independently in distantly related groups but caused mainly due to the action of natural selection (Ochoa and Barahona 2014).

With this in mind, it is interesting to note that Ochoa and Barahona (2014) have found that the terms “parallelism” and “convergence” have an underlying origin in anti-Darwinian theories (see also Gould 2002, pp. 1081–1086). To clarify, in their study, they demonstrate that the term “parallelism” emerges from the theory of orthogenesis, but they also gathered that the meaning of the theory of orthogenesis is not precisely the one shown in textbooks, as we shall see hereafter.

Currently, the theory of orthogenesis has been misunderstood, and it has generally been associated with metaphysical, theological, or divine conceptions. Nevertheless, some new interpretations of orthogenesis have come to light (e.g., Grehan and Ainsworth 1985; Gould 2002; Levit and Olsson 2006; Popov 2009, 2018; De Renzi 2014; Ochoa and Barahona 2014; Ulett 2014, 2016; Ochoa 2017), and far from any progressive or teleological view, they propose that this theory had well-founded empirical and epistemological bases and whose phenomenology probably relies on developmental constraints.

In general, orthogenesis was a theory which indicated that some characters of related groups follow the same evolutionary trend and whose causes are attributed to internal factors. For example, species of different genera but belonging to the same family possess the ability to produce the same characters independently; this change, however, is not necessarily due to adaptation. Some naturalists claimed that there might be some internal factor that controlled the evolutionary pathway, e.g., genetic processes or developmental constraints, and although natural selection may also act to produce these transformations, it was limited to act with few alternatives of change (Ochoa and Barahona 2014).

Orthogenesis arose as a theory opposing Darwinism in the sense that Darwinists claimed that variation occurs spontaneously in multiple directions. On the contrary, the followers of orthogenesis argued that variations were directed and limited to a few possibilities of change, that is, that lineages were predisposed to vary toward certain directions and not others (Levit and Olsson, 2006). In any case, orthogenesis was conceptualized via three main phenomena: (1) the observation of the independent origin of characters in closely related groups; (2) the observation of characters that evolve beyond the permitted functional limits, meaning without any selective

control due to environmental pressures; and (3) the observation that there are constraints that restrict a wide range of morphological possibilities (Kellogg 1907; Ochoa and Barahona 2014; Ochoa 2017). So, having made this clear, let us take a closer look at how orthogenesis is related to the concept of “parallelism” by William Berryman Scott and Otto Schindewolf, two of the most influential paleontologists involved in evolutionary debates in the early and mid-twentieth century, respectively.

### 10.3.1 *Scott’s Parallelism*

William Berryman Scott was one of the most distinguished paleontologists of American paleontology in the late nineteenth and early twentieth centuries. He began his career along with the paleontologist Henry Fairfield Osborn<sup>4</sup> who knew him since their youth. Scott worked all his academic life in Princeton, where he initially worked as a professor in geology and paleontology, but later held the chair of the Department of Geology until his retirement. In Princeton, he founded a paleontological school turning the university into one of the largest research and teaching centers of vertebrate paleontology in North America. For a long time, Scott played an important role in the national and international affairs of the scientific community in the area of paleontology and evolution, and like Osborn, he received several awards and belonged to different scientific associations (Simpson 1948). One important aspect of Scott’s contributions is that he coined the terms “parallelism” and “convergence” in their modern sense; however, these terms were initially proposed under anti-Darwinian theories, as Ochoa and Barahona (2014) have pointed out. For example, convergence, or independent acquisition of similar characters in distant lineages, was explained by the theory of inheritance of acquired characters also known as Neo-Lamarckism, while parallelism, or independent acquisition of similar characters in closely related lineages, was explained by the phenomenon of orthogenesis. But for the moment, we shall devote more attention to this last term.

In a paper, Scott argues in favor of orthogenesis as a process that dominates the evolutionary trends of ancient mammalian lineages: “So far as the series of fossil mammals which we have been considering are concerned, the developmental history appears to be very direct, and subject to comparatively little fluctuation, advancing steadily in a definite direction, though with slight deviations” (Scott 1891, pp. 370–371). According to Scott, this constant march of change can be observed in horse evolution, for example, where premolars acquired the shape of molars one by one in the entire group. Additionally, their faces and limbs elongated, their digits

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<sup>4</sup>Osborn was a champion of the orthogenesis theory as well. He integrated natural selection as one of the several causes which explains evolutionary trends. For more information, see in this volume Ceccarelli 2021.

reduced slowly (except the middle digit which became bigger and more pronounced), and the overall stature increased. Likewise, the different genera such as *Palaeosyops*, *Diplacodon*, and *Titanotherium* from the Bridger, Uinta, and White River formations, respectively, display repeated characters that originated independently in each of their respective formations.

Scott comments that these similarities are observed in the *Oreodon* from the White River and in *Eporeodon* from John Day, and although these cases could be explained as multiple origins of the genus, some species of an ancient genus could have acquired similar characters simultaneously. From this evidence, we might conclude that “In many genera the cycle of variation appears to be a singularly small one” or that “the limited plasticity of the mammals, except along certain definite lines, is very marked” (Scott 1891, p. 371). That is, the production of variation is highly constrained by the structure of the lineage, and, therefore, the possible descending lineages would have few alternatives for change.

According to Scott, these constraints have severe consequences for lineages, since by having limited variation, if a sudden change of environment occurs, then inevitably some groups might be in danger of extinction because their bodies would not be “sufficiently plastic to adapt themselves readily to new conditions” (Scott 1891, p. 371). Scott states that if we consider the channeled change of their parts, this does not mean that the directions must be completely constant perpetually. On the contrary, these trajectories could be steady for a certain period, and later they might change course toward a completely different direction. For example, regarding the evolution of the Pecora, the hornless groups from the lower Miocene, such as *Amphitragulus*, *Paleomeryx*, etc., display a continuous increase in the size of the upper canines which are still conserved in hornless deer-like *Moschus*, *Hydropotes*, etc., whereas in typical cervids and bovids, the antlers and horns developed gradually, while the upper canines gradually decreased until they became rudiments or even disappear.

These facts allow us to postulate that change in evolutionary direction is steady and that the transformation path can change slightly; although once the trend is directed, the probability of taking a different trajectory is minimal. Of course, what drives this evolutionary trend are the constraints that are provided by the internal structure of the lineage. This is something very similar to what might be called today “developmental constraints”<sup>5</sup>: “just as the power of regeneration of lost parts diminishes as we ascend in the scale of animal life, so plasticity of organization and capacity for differentiation of structure in widely different directions diminishes also” (Scott 1891, p. 372).

However, Scott thought that variation was so constrained that the body only permits change toward a few alternative paths (or even only one). If the lineage does not have to change, the structure will remain in morphological stability, meaning that although many groups have displayed great variability across time, these alterations might be minimal; in consequence, the lineages will maintain their fundamental

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<sup>5</sup>Or we should use the term “developmental bias” to be more precise.

structures for a long time.<sup>6</sup> As we can see, this phenomenon seems to be a hard version of orthogenesis. But here the meaning of orthogenesis has to do with the constraints generated by the structure itself. Scott argues that the options for change are so narrow that there is only one avenue to go forward. In his sense, the evolutionary march advances in one direction, and that is why change is uniform.

For Scott, this constrained mechanism does not necessarily work alone, since the march of change toward specific adaptations might also be controlled by an auxiliary mechanism, natural selection: “It may, perhaps, be the outcome of future investigations, that while variations are generally due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies operating long in a uniform way, and the results controlled by natural selection” (Scott 1891, p. 388). That is to say, since Scott’s orthogenesis describes the reduction alternatives for change and although those changes proceed by themselves in a single evolutionary pathway, natural selection acts here as auxiliary mechanism pushing evolution in a single direction.

From these assumptions arises the concept of parallelism; since the evolution of characters in mammalian lineages is constrained to a few evolutionary pathways, more closely related lineages would tend to produce the same characters more frequently: “the various species of the ancestral genus may acquire the new character independently of each other (parallelism)” (Scott 1891, p. 362). Later, in another paper, he defined this concept more clearly: “By parallelism is meant the independent acquisition of similar structure in forms which are themselves nearly related . . . and thus in one or more respects come to be more nearly alike than were their ancestors” (Scott 1896, p. 185).

Another important point is that in these writings, Scott also coins the term convergence, but he separates parallelism from convergence by the mechanisms which act upon them, making it possible to distinguish them theoretically: parallelism is explained by structural constraints, as we saw above, while convergence is explained by inheritance of acquired characters. However, in terms of independent evolution, Scott stated that parallelism must be more common than convergence: “even though the resemblances have been independently acquired, because parallelism is a more frequently observed phenomenon than convergence,” and given that structural constraints induce themselves to follow channeled pathways during evolutionary change, “the more nearly related any two organisms are, the more likely are they to undergo similar modifications” (Scott 1896, p. 186). In short, the relationship of ancestry, or the shared structure among related individuals, constrains the possibilities of change, restricting the form to a few avenues whose variations are unique to each group (more closely related lineages will more likely produce similar characters in each of their descendants).

In conclusion, Scott coined the term “parallelism” based on the theory of orthogenesis. For this paleontologist, orthogenesis describes the constant evolutionary trends which occur in the evolution of closely related lineages. Therefore,

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<sup>6</sup>This phenomenon is now recognized as stasis (see Gould and Eldredge 1977).

orthogenesis could be explained by either structural constraints or by natural selection as an auxiliary mechanism acting upon a few pathways of change. With this in mind, it is important to note that Scott's orthogenesis has no mention of anything about "metaphysical" or "divine" processes. On the contrary, his orthogenesis is based on detailed observations of the fossil record which displays the evolutionary trend. We also do not find any "theological" conception in his view, since the trends are due to the structural constraints and not due to metaphysical internal programming that drives lineages toward a specific point. Likewise, these constraints might be aided by natural selection that would act by pushing the trend.

### 10.3.2 *Schindewolf's Parallelism*

Otto Heinrich Schindewolf was a German paleontologist of the mid-twentieth century, famous for his work on fossil ammonites, but, above all, he stands out for having challenged the orthodoxy of the Modern Synthesis during his time. He worked at the University of Tübingen, serving as director from 1956 to 1957. In general, Schindewolf was one of the most important and influential paleontologists of German paleontology during the period after the Second World War and beyond. One of his most notable achievements was the publication of the book *Grundfragen der Paläontologie* [*Basic Questions in Paleontology*] in 1950, which became a classic in German paleontology literature for two decades. In fact, this book and his ideas had remained hidden from American literature until an English translation appeared in 1993 (Reif 1993).

First of all, it is pertinent to comment that Schindewolf was always intrigued by the phenomenon of independent evolution. However, like many paleontologists of the time, he thought orthogenesis accounted for part of these phenomena and particularly associated this theory to the concept of parallelism. For example, Schindewolf defines parallelism in the following way: "The unfolding of the individual stocks does not take place in a single lineage but rather in a varying number of parallel lineages at the same time" (Schindewolf 1993, p. 274). Yet, to recognize this kind of independent evolution, it was necessary to observe that the lineages "differ from one another in certain characters, which are indicators of their [evolutionary] independence, but agree in other ... those that demonstrate their relatedness" (Schindewolf 1993, p. 274).

In any case, "parallel lineages exhibit similar remodeling even though they are related only at their roots and, moreover, evolve independently" (Schindewolf 1993, p. 274). As for the above definition, we can note that parallelism is explained as a phenomenon of internal channeling in lineages, a process which inevitably leads structures toward the same evolutionary conclusions, that is, orthogenesis and parallelism are governed by the same causes: "Other informative glimpses into the nature and causes of orthogenesis are provided by parallel evolution ... , an extremely common, probably even universal phenomenon of the typostatic phase of evolution" (Schindewolf 1993, p. 274). Furthermore, this channeling depends on

the common ancestry and, thus, upon a degree of ancestry: “the common ancestor must have transmitted a specific factor” whereby lineages “evolved along a directed, undeviating course” (Schindewolf 1993, p. 275).

Some examples of the parallelism shown by Schindewolf (1993, pp. 274–275) are the following: With respect to the evolution of different ammonite lineages, we can perceive that although they all stem from the same common ancestor, they independently acquire the same characters such as septa, siphon, sutures, etc. For example, in the genus *Clymenia*, there was an evolutionary trend to go from a round shell to a triangular shell. According to Schindewolf, this occurred in three different lineages that evolved independently and in parallel from the same common ancestor. The palaeodictyopterans (ancestors of all flying insects), on the other hand, display ancient characters, for example, all four wings are identical and cannot be flexed. During the Carboniferous, this group gave rise to the protoblattoids, whose wings can be folded back horizontally over the abdomen. During the course of evolution, the delicate forewings became gradually chitinous and rigid, until elytra were formed. Subsequently, the forewings took on the function of protecting the more delicate hind wings and the abdomen. Now, during the Permian, five or six lineages (e.g., beetles, cockroaches, etc.) arose from protoblattoids; it is interesting to note however that all of them underwent independent evolution shifting from forewings to elytra. Therefore, this character “was acquired independently as the result of similar latent evolutionary potential.”

In fish, changes in the caudal fin, the scales, and the skull evolved independently from a common ancestor. For example, the different groups of actinopterygians (a subclass of bony fishes) show a similar evolutionary trend: going from a heterocercal caudal fin to homocercal one; from rhomboidal ganoid scales to thin, round cycloid or ctenoid scales; trends in the shape of the cranium and the modification of the endocranium; increased ossification of the vertebral column; reduction of the clavicles; etc. In Schindewolf’s words: “these groups [Chondrostei, Holostei, and Teleostei] are polyphyletic, which means that they consist of a cluster of separate, independent lineages, which [. . .] developed [their structures] in parallel in the same direction and reached and passed through the various evolutionary stages more or less at the same time” (Schindewolf 1993, p. 275).

With these and other examples, Schindewolf postulated that parallelism, being a phenomenon of constraint which limits variation and drives lineages inside the same channeled evolutionary pathway, is a universal phenomenon and applies to all levels of taxonomic categories; that is, the structure constrains the evolutionary course at different levels steering the closely related lineages toward different modes of structural conclusion:

As our examples show, parallelism in evolution expresses itself in quite different categories and orders of magnitude. It is found in lineages within genera and families as well as in categories of higher taxonomic and evolutionary rank, where the phenomena are the same as in the smallest unit, the species. And in species, too, there is parallel evolution in numerous separate reproductive lines, as we see in individual clans, races, and subspecies. (Schindewolf 1993, p. 276)

But how can we explain this phenomenon of parallelism or orthogenesis? One type of explanation refers to structural constraints; these are due to the fact that the structure of the ancestor restricts and drives the subsequent modifications of the descendant group in question: “the set of rudiments in the first representatives of each lineage largely determines later evolution.” Therefore, every time an organ is modified, the alternatives for change become more and more reduced, so that the structure in itself would be the constraint of phenotypic possibilities: “that subsequent differentiations steps entail a progressive narrowing of evolutionary creative potential” (Schindewolf 1993, p. 273; his italics).

Part of this explanation lies in the constraints produced by a developmental system, something not very different from what we know today as developmental constraints considering that, for Schindewolf, any phenotypic flexibility exists only in the early stages of ontogeny. Once this period has passed, there is a defined and constrained avenue toward a specific point. This brings us to the conception that the individual constrains himself, meaning that the body does not easily allow possibilities for change. Therefore, in the development of a specific organ, once the change begins (although it can happen in different proportions), the evolutionary trajectories are constrained bit by bit until the potential of change is reduced: “In this manner, the compulsory course of events leading to the final stages of one ontogeny is transmitted through evolution to the following one, which then carries it further” (Schindewolf 1993, p. 273; his italics). Based on this, Schindewolf claims that, although there should be variations without any favored direction, variations with directed trajectories would have greater opportunities to be retained, at least those large-scale variations originated during the early stages of ontogeny.

Moreover, Schindewolf argues that such parallel evolution also occurs because closely related lineages have related genes and a potential to develop similar mutations; this points out that the channeling of the structure is ruled by these common genes: “We may assume, then, *that the orientation and parallelism of individual lineages is essentially guided by a common genetic base, which reacts the same way in each line*” (Schindewolf 1993, p. 276; his italics). Or differently stated, “[the] internal reasons for parallelism . . . *reside in the matching genotypes linking the lineages in question, which allow only a limited number of possible directions*” (Schindewolf 1993, p. 278; his italics).

Now, Schindewolf points out that parallel evolution is by no means guided by external factors (i.e., natural selection). He lists three main arguments to rule out this possibility:

1. *Independent evolution has occurred in different places and environments:* “The transformation of individual lineages has taken place many times under extremely different environmental conditions in widely disparate areas, and despite this, the result has been parallelism.”
2. *These similar changes have happened at different times and geological periods:* “the points at which transformation takes place in the individual parallel lineages are by no means always simultaneous, which means that the same external influences cannot be inferred. To take an example from the amphibians. . . the

phyllospondyls attain as early as the Permian the evolutionary stage of skull transformation that does not appear in the labyrinthodonts until Triassic.”

3. *Independent evolution of similar characters is always associated with closely related groups*, since non-related lineages that undergo the same environmental conditions do not develop the same structural shape in a similar way: “it is always only a certain cluster of closely related lineages that brings forth these parallel transformations, whereas other series of forms existing at the same time, which are subject to the same external influences, behave in a completely different way and show a different evolution of characters.”

Taking into account these three arguments, Schindewolf concludes that: “the critical, deciding factors are always internal and depend on the potential for evolutionary creativity of the organism itself” (Schindewolf 1993, p. 277).

With this, I do not want to portray that Schindewolf did not take into consideration the mechanism of natural selection. The issue here is that he believed that this mechanism did not play a relevant role in the evolution of higher taxa, but rather its role was microevolutionary. Natural selection would work by introducing the final and adaptive variations of already established types: “selection concerns and affects only the most superficial layer of characters” (Schindewolf 1993, p. 341; his italics).

So, by regarding Schindewolf’s ideas, we can conclude that his concept of parallelism was strongly linked to the theoretical conception of orthogenesis which entails directional changes in defined avenues. It is important to emphasize that Schindewolf’s orthogenesis resides neither in mysticisms nor purposes provided by a divine guiding force; rather, it is a phenomenon that lies on ontogenetic and genetic processes that constrain evolution to a few alternatives, without assigning these directional changes to external factors.

## 10.4 Simpson and Orthogenesis

Of course, no paleontologists of the time could let the phenomenon of orthogenesis slide, and Simpson dealt with the topic in detail. But it is important to note that Simpson, as one of the main figures of paleontology, apparently attempted to reject the theory of orthogenesis in his writings. According to Delisle (2009), he denied orthogenetic approach in three basic points: (1) empirically, because orthogenetic trends do not preside in all cases in the evolutionary history of lineages; (2) methodologically, since there must be no other kinds of mechanisms than those seen in genetic research; and (3) epistemologically, given that he rejected a domain of physicalism and determinism in the biological realm. However, we shall see that he indirectly advocated for an explanation of orthogenesis through his explanation of the term “parallelism,” since as we have seen above, the phenomenon of parallelism was a description of the phenomenon of orthogenesis.

The history of Simpson’s opinion on orthogenesis begins in *Tempo and Mode*. In chapter 5, titled “Inertia, Trend, and Momentum,” he states that orthogenesis is a



phenomenon by which lineages evolve continuously in a certain direction, even though it might result in extinction. Then, he lists a series of theories which attempt to explain this principle, among which are (1) direct interaction of organism and environment (the inheritance of acquired characters); (2) the effect of natural selection on the survival and distribution of spontaneous mutations (orthoselection); and (3) the occurrence of definite modifications of direction without reference to the environment (orthogenesis *per se*). On the latter, he discusses that there has been an extremely wide range of theories which are contrary to the others, but they have in common only the idea of either inherent trend or metaphysical conception which describes that evolution goes forward in a straight line:

Most theories of this school, however, involve an element of predestination, of a goal, a perfecting principle, whether as a vitalistic urge, or a metaphysical necessity, or a frankly theological explanation of evolution according to which it is under divine or otherwise spiritual guidance. (Simpson 1944, p. 152)

Later, he quotes some followers of this view as Henry Fairfield Osborn, Louis Vialleton, Teilhard de Chardin, and Robert Broom in spite of the fact that not all of them maintained this metaphysical or vitalistic notion.<sup>7</sup> Whatever the means which accounts for orthogenesis, we can see that he recognized it as a fact; in other words, Simpson admitted orthogenesis in a descriptive sense without a clear explanation. He mentions: “There is no possible doubt but that some degree of rectilinearity is common in evolution. It can seldom or never be maintained that the evolution . . . is exactly rectilinear or literally undeviating, but the best part of the paleontological record is made up of lines that evolve approximately in one direction over long periods of time” (Simpson 1944, p. 152). He also points out that a “tendency for phyla to continue to evolve in much the same direction for considerable periods of time, rectilinear evolution or orthogenesis in a purely descriptive sense, is a common evolutionary phenomenon” (Simpson 1944, p. 177).

With this, Simpson was not at odds with orthogenetic trends in its descriptive sense, but he was careful by interpreting all evolutionary tendencies in this way (Delisle 2009). For Simpson, orthogenesis could be understood as the evolutionary mode of “phyletic evolution,” that is, in large populations with moderate (horotelic) rates presented at lower levels within the evolutionary constancy of the adaptive zone. This, of course, shows that orthogenesis was not exclusive for all evolutionary levels, but only for levels that displayed continuous evolution in a period of environmental stability:

The probability that a tendency toward rectilinearity is not characteristic of evolution as a whole, but only of certain levels of change under certain common but far from universal conditions, is in itself a potent argument against the third school of orthogenesis, that

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<sup>7</sup>For instance, the orthogenesis theories of Osborn and Vialleton are far from being metaphysical or vitalistic. Simpson only recognized this fact in Osborn’s theory. On the other hand, Teilhard de Chardin developed a thought which had nothing to do with orthogenesis, while Robert Broom openly recognized a divine plan.

involving an inherently directional process or a metaphysical perfecting principle. (Simpson 1944, p. 153)

What mechanism could account for orthogenesis? It has been highlighted that Simpson precluded those theoretical proposals which possess deterministic or vitalistic notions because they lacked real mechanisms; as a consequence, he focused on neo-Darwinian agencies which he thought were more adequate than the others from the current science point of view (Delisle 2009). And Simpson attempted to associate those mechanisms to the paleontological data as far as possible. But how far could Simpson go with the genetics of the neo-Darwinian account?

According to Simpson, there are at least two genetic factors that might explain this phenomenon: first, that inheritance is primarily conservative: “In groups that do show rectilinearity . . . every animal is nearly like its parents in thousands of characters and may differ significantly only in a few characters.” Second, those mutations are not so random: “It is not only improbable but also inconceivable that mutations in every imaginable direction occur with equal frequency” (Simpson 1944, p. 154).

Given these considerations, it is easy to realize that Simpson admits there are certain structural and genetic constraints when analyzing the evolutionary trends of lineages:

The conservative factor of heredity greatly limits the possible avenues of evolution for any given type of organism. If an animal is like its ancestors in all but a few respects, the differences must necessarily exist in connection and in harmony with the more extensive, more complex inherited elements of structure. (Simpson 1944, p. 154)

On this, it should be noted that, in 1944, Simpson’s description of orthogenesis was very similar to Schindewolf and Scott’s explanation of orthogenesis and parallelism (see Table 10.1). Still, for Simpson, the conservation of inheritance and the limits in the trajectory of variation given by the genotype were not the only factors that provided constraint; he also considered natural selection as a mechanism that limited the change which hinges essentially on a constant environment:

The fact that species are not constructed *de novo*, but on the basis of genotypes already existing strongly limits the possible avenues of change, and the possibilities are still further limited by natural selection, the restricting influence of which is obvious and is admitted by all theorists to some extent. Most often it would happen that no sort of available modification would be definitely advantageous and next most frequently that only one would be of selective value. In this situation a character would usually tend not to change or to change only in one direction. (Simpson 1944, p. 154)

So, which of both forces, environment versus internal control, would be the predominant in constraining evolutionary change toward a definite trend? Simpson proposes that mutations, even though restricted, are still random; any advance would surely be a non-adaptive trend, and if the trajectory was frequent in a single direction, these would probably provide a degenerative and non-progressive development. Therefore, natural selection would have the final decision on any evolutionary advance, and orthogenesis might be explained rather as a kind of orthoselection (an expression coined by Ludwig Plate):

**Table 10.1** Comparison between explanations of orthogenesis and parallelism: Simpson’s orthogenesis (1944), Simpson’s parallelism (1945, 1961), Schindewolf’s orthogenesis (1950), and Scott’s orthogenesis (1891). Explanation 1 is based on structural or developmental constraints. Explanation 2 is based on genetic constraints. Explanation 3 is based on natural selection as an auxiliary mechanism. Note the great similarity between the explanations

	Explanation 1 Based on structural or developmental constraints	Explanation 2 Based on genetic constraints	Explanation 3 Based on natural selection as an auxiliary mechanism
Simpson’s orthogenesis (1944)	The conservative factor of heredity limits the possible avenues of evolutionary change	Mutations do not occur in every direction with equal frequency	Natural selection limits and steers the changes in one direction
Simpson’s parallelism (1945)	Descendant lineages evolve in the same way because they inherited genetic factors which control development	Homologous genes tend to mutate in the same way	Natural selection acts upon homologous characters exposed to the same environment
Simpson’s parallelism (1961)	The structure of an ancestral group inevitably limits the lines of possible evolutionary change	Homologous mutations and relative mutation rates produce change in the same direction	The probability that descendant lineage follows one line will be further reinforced by natural selection
Schindewolf’s orthogenesis (1950)	The structure of the ancestor (its developmental system) limits and drives the subsequent modifications of the descendant group	Common genetic base reacts in the same way and limits the number of possible directions	
Scott’s orthogenesis (1891)	The internal structure of the ancestral lineage constrains the possible avenues of evolutionary change		Natural selection acts on a few options and then pushes change in a single direction

Theories of orthogenesis, strictly speaking, by direct environmental action are consistent with many of the same observational data as theories of orthoselection. If it is true, as it seems to be, that rectilinearity is most common at certain levels of evolution and in certain types of populations, orthoselection offers an acceptable explanation for this limitation, and orthogenesis due to direct influence of the environment does not. (Simpson 1944, p. 157)

Simpson’s next strategy was to refute paleontological evidence that evolution was advancing on a strictly steady course. It has been pointed out that Simpson attempted to demonstrate that not all trends followed a narrow path; rather some divergence is perceived in some cases (Delisle 2009). He even asked if those tendencies were not more than a product of the paleontologists’ imagination. In any case, Simpson interpreted some orthogenetic examples by means of their adaptive account. The first case Simpson described was the evolution of the horse because, in his opinion, it had been a recurring example to account for orthogenesis. According to him, some of the horse’s traits that have been described as progressive during their evolution

such as the proportion of the body, skull, the brain, the limbs, the reduction of the foot, and the dental cusps evolved by some selective value. For example, intelligence was related to brain size, efficiency and speed in locomotion is linked to the evolution of limbs, and the ability to chew is associated with the modification of the molar cusps.

In his book *The Meaning of Evolution* (1949, pp. 131–159), Simpson analyzed the most cited cases of orthogenesis related with non-adaptive trends, among which were the tooth growth increase in saber-toothed tigers, the development of horns in Irish elk, the coiled shell of *Gryphaea*, and the horn of the titanotheres. With regard to saber-toothed tigers, he said that the size of the canines was very variable in different groups, and the size of the sabertooth has a strictly adaptive purpose for each of the species; then, it should not be interpreted simply as growth increase without adaptive value due to internal factors. Besides, the development of the sabertooth doesn't display any evolutionary trend by itself; rather, this argument had spread as a myth of paleontology based on a misinterpretation of the data. The same is true in the case of Irish elk since the growth increase of their horns should not be interpreted as said by the popular orthogenesis myths, that is, as disproportionate development which inevitably led them to extinction; rather the horn size was proportionate to their body, and they surely had an adaptive value as well, for instance, they used them for battle or defense.

Regarding the coiled shell of *Gryphaea*, other orthogenesis myths stated that this lineage went extinct because the exaggerated coiled shell hindered the ability to open their shells. Simpson explained that this peculiarity rather was an advantage so these oysters could settle in the soft mud of the seafloor: "There is really no good reason to believe that the change was carried to an inadapative degree by the trend" (Simpson 1949, p. 154). Furthermore, about the horn of the titanotheres, he wondered whether its incipient stage had an adaptive value. In *Tempo and Mode*, Simpson admitted that the evolution of the horns was the only evidence in favor of orthogenesis, but later he mentioned that slight variations could have driven their development along with natural selection. He emphasized this view in his books.<sup>8</sup>

Finally, it is important to point out that Simpson changed his mind significantly concerning orthogenesis. In the beginning, he admitted orthogenesis was a description of evolutionary trends and proposed constraints as a possible mechanism. However, later, he suggested that the cause of these trends would have to do with adaptation. For example, he wrote:

Thus the whole trend is adaptive from beginning to end [...]. Adaptation has a known mechanism: natural selection acting on the genetics of populations [...] In seeking the orienting factor in evolution we have seen that in some cases this must, by all reasonable inferences, be adaptation and in all, even the most doubtful, it could be adaptation. (Simpson 1949, pp. 158–159)

But what happened with those internal factors of non-random mutations and conservation of inheritance? In *The Major Features of Evolution*, we see that

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<sup>8</sup>See Simpson (1949, p. 155, 1953, pp. 270–271).

Simpson (1953, p. 272) still argues that natural selection is limited; however, now, these constraints are interpreted as the ability to produce mutations randomly and not necessarily by structural constraints as he said previously. In any case, the argument remains strictly adaptationist. Indeed, he used the phenomenon of convergence to support this fact and mentions examples of how natural selection can produce structures independent of common ancestry (see below). Therefore, Simpson is convinced that “the direction of evolution is largely determined by adaptively oriented selection acting on adaptively unoriented materials [mutations] that limit possible avenues of change” (Simpson 1953, p. 273).

Likewise, constraints also are understood as the absence of some characters, for example, many rhinos which do not have horns could have had a selective advantage by having horns, but the mutation [genetic change] that gives rise to horns never appeared. Here, the mutation is a constraint, just because without it, the rhinos would not have had horns. Subsequently, we see that he resorts to Fisher’s argument<sup>9</sup> to reject orthogenesis because he claims that the mutations alone cannot channel change toward any particular direction:

Within the firm framework of modern population genetics, it seems that mutation pressure, alone, could not orient evolution unless mutations were strongly directional and occurred with such high frequencies as to overcome omnipresent selection [. . .] The possibility is by no means excluded that in some instances and phases of evolution a predominant direction of mutation might have been an effective factor. It does, however, seem warranted to conclude from evidence already available that this is not the usual or even a common way in which orientation occurs. If direction of mutation and of selection did somehow and sometimes happen to coincide, this would unquestionably accelerate change. If very high mutation against selection occurred, this would probably be inadaptive and presumably might cause extinction. There seems to be no convincing evidence that it has ever done so, in fact. (Simpson 1953, pp. 273–274)

Interestingly, today we can write this chapter in the history of evolutionary thought under the title “that was how Simpson ended all theoretical consideration of orthogenesis in paleontology,” given that no genetic factor could account for these evolutionary trends, except for natural selection working upon randomly occurring mutations. However, we should not forget that Simpson lost the thread of the real meaning of orthogenesis. He refuted orthogenesis by solely considering that the direction is not guided by mutations alone and not that the steering would have been constrained by the internal structure of the ancestral lineage. These evolutionary trends, for Simpson, are due to natural selection acting upon mutations. In any case, where he didn’t lose the thread was in his defense by the term “parallelism,” which is precisely where his belief in orthogenesis dwells, as we will see below.

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<sup>9</sup>Ronal Aylmer Fisher, well-known for founding the population genetics, in his famous book *The Genetical Theory of Natural Selection*, argued that orthogenesis was false because experimental experience does not support the assumption that the mutations can be directed toward certain points. Most mutations, according to him, occur randomly and without any adaptive value. However, if the mutations had a steady direction, he reasons, they would have to possess a constancy of rate greater than the required selection to fix the new mutation into the population (see Ochoa 2017).

### 10.4.1 Simpson's Parallelism

In *Principles of Animal Taxonomy* (1961), Simpson defined the term parallelism as follows: "Parallelism is the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry" (Simpson 1961, p. 78; his italics). Meaning that although the characters are "absent in the common ancestry, they may arise in some or all descendant taxa as *parallel* developments channeled by characteristics, genetical or other, of the ancestry" (Simpson 1961, pp. 77–78; his italics). Later he highlights that: "parallelism is the independent occurrence of similar changes in groups from a common ancestry and *because* they had a common ancestry" (Simpson 1961, p. 103). Interestingly, this definition perfectly describes the phenomenon of orthogenesis, as we saw with Scott and Schindewolf. Remember, Simpson never denied orthogenesis in its descriptive sense (see above). Therefore, I dare say that he recognized orthogenesis as a phenomenon through the concept of "parallelism." This fact can help us to find the true beliefs of our hero.

As we saw, Scott and Schindewolf proposed explanations of orthogenesis through constraints (see Table 10.1). Yet, Gould (2002 p. 1086) mentions that in the early years of the Modern Synthesis, Darwinians paid little attention to constraints because they felt it was a process contrary to natural selection and not part of the evolutionary process. So, when Simpson recognized and advocated the concept of parallelism, he found himself to be in a theoretical dead end, because if natural selection is the mechanism that steers evolutionary trend, and if convergence is due to natural selection,<sup>10</sup> then why should we assume that parallelism is different from convergence?

In his 1945 monograph on the classification of mammals, Simpson had his first conflict with the concept of parallelism; therein he recognized that this term might be explained in the same way as convergence. This fact creates difficulties when one attempts to differentiate parallelism from convergence, and even from homology. If homology represents common ancestry, while convergence is the similarity by non-common ancestry, then parallelism looks like an additional term that contains some amount of homology and some amount of convergence (see Gould 2002, pp. 1088–1089). In any case, parallelism would be based on a phenomenon that has to do more with common ancestry:

It is a complication that a third sort of process also produces similarities: parallelism. The term is descriptive rather than explanatory and refers to the fact that distinct groups of

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<sup>10</sup>In *Principles of Animal Taxonomy* (1961), Simpson defines the term of convergence as follows: *Convergence is the development of similar characters separately in two or more lineages without a common ancestry pertinent to the similarity but involving adaptation to similar ecological status* (Simpson 1961, pp. 78–79; his italics). That is, the characters "may and frequently do also arise as independent *convergent* adaptations to similar ways of life in taxa of quite different ancestries" (Simpson 1961, p. 78; his italics). For Simpson, and unlike the case of parallelism, similarities instigated under convergence is the product of the action of natural selection on organisms living in similar environments.

common origin frequently evolve in much the same direction after the discontinuity between them has arisen, so that at a later stage the phyla may have characters in common that were not visible in the common ancestry but that tend, nevertheless, to be more or less in proportion to the nearness of that ancestry. This proportional tendency distinguishes parallelism from convergence, but the distinction is far from absolute. The two phenomena intergrade continuously and are often indistinguishable in practice. (Simpson 1945, p. 9)

Later, Simpson attempted to explain parallelism under three different situations:

1. *Homologous genes tend to mutate in the same way.* Once the two lineages split from their common ancestor, they end up with homologous genes which produce the same mutations: “such groups may and, in all probability, frequently do develop the same characters, not typical of their ancestry or directly inherited but nevertheless due to inheritance: the inheritance of genes prone to mutate in the same way” (Simpson 1945, p. 9).
2. *Proportions and some other characters are commonly the result of relative growth rates that are genetically controlled.* Once the two lineages split from their common ancestor, they tend to evolve in the same way, for example, toward a large size, because they inherited genetic factors which determinate that growth: “they may develop characters of proportion that are the same in both and that are quite different from those of the common ancestry but that were, nevertheless, inherited from that ancestry” (Simpson 1945, p. 10).
3. *Groups of common origin inherit many homologous characters, and they frequently also retain or develop similar habits and environmental preferences.* Lineages that share a common ancestor will have similar structures that will be exposed to the same environmental situations; therefore, evolution will probably take the same pathway: “Then convergence that is strictly such and not attributable to an ancestral genetic factor is likely to occur in them, and if it does, it acts in the same direction as the conservative element of homology” (Simpson 1945, p. 10).

In this light, we see that Simpson’s explanation for orthogenesis provided in 1944 is not much different from these explanations on parallelism we have just seen. They are even alike Schindewolf’s explanation for orthogenesis (see Table 10.1). Simpson had fought up until then to maintain the term parallelism, which phenomenologically can be perceived in the fossil record by paleontologists, regardless of the theory used to explain it. However, things were not working out as he had hoped.

In 1946, Otto Haas and Simpson wrote one of the best historiographical works on the concepts of comparative anatomy. In their conclusions, they defined homoplasy as “similarities between organisms or their parts, organs or structures, due not to common ancestry but to independent acquisition of the similar characters” (Haas and Simpson 1946, p. 344). In this definition, they include convergence and parallelism as special cases within homoplasy by which the increase or decrease in similarity may be assessed during evolution.

It is interesting to note that Haas and Simpson discussed plenty to validate Scott’s parallelism since they were aware that their description was based on “such vague or metaphysical ideas” as phylogenetic “predetermination” or “latent” characters. They

emphasized the importance of the geometric sense of parallelism, believing that it was the most appropriate sense for phylogenetic descriptions. Interestingly, Simpson's disagreement with the conclusions of parallelism is reflected in this paper. In fact, he supported maintaining Scott's original meaning: "one of us (Simpson 1945, pp. 9–10) has emphasized that there are at least two known genetic processes that would lead to these results without recourse to such vague or metaphysical ideas as phylogenetic 'predetermination' or 'latent' characters. . . Thus there is a real validity in the idea of parallelism in the sense of Scott and of those who have followed his definition, although the basis for this validity has usually been obscured" (Haas and Simpson 1946, p. 336). According to Haas and Simpson, there is great difficulty in accepting these phenomena because Scott did not have a knowledge of genetics which would have helped him to recognize that convergence and parallelism are the same processes. They stressed:

The intended distinction would have been validated if it had earlier been expressed in genetic terms. Redefined in such terms, parallelism would be similarity in structure due to a common genetic basis (and so far resembling homology) but not reaching morphological expression until after the separation of the two or more lines involved (and in this differing from homology). This seems really to be the concept toward which earlier students were progressing, gropingly in the absence of clearer genetic knowledge, from two different directions: when they spoke of parallelism in the sense of Scott as similarity arising in nearly related lines (i.e., with a considerable common genetic basis), and when they spoke of latent or potential homology and the like (i.e., of a common genetic basis for characters not morphologically evident until a later stage in phylogeny). (Haas and Simpson 1946, pp. 336–337)

Therefore, the phenomenon could be recognized as a special case of homoplasy (independent similarity) that reached a certain level of homology due to close ancestral relationships. Still, the question rests on whether it was appropriate to maintain the word "parallelism" for the description of this phenomenon:

It is possible to gather together broadly diverse expressions and ideas of the past and to relate them to a definite and modern restatement of a phylogenetic principle. It remains, however, to decide whether to define or redefine parallelism as the term applicable to this principle. On historical grounds this would be justified and perhaps preferable [keep the word parallelism] because this genetic definition is closer to the usage of Scott and of most later authors than is the strictly geometric definition. (Haas and Simpson 1946, p. 337)

Yet, the main issue had been deciding whether this type of parallelism was not a kind of convergence acting on different degrees with respect to common ancestry. Hence, the authors faced one of the greatest responsibilities for the future consequences of the term "parallelism": whether to opt for a term that entailed structural constraint, which relied on a few theoretical resources to be properly explained by genetics (i.e., parallelism still had only the descriptive sense without any adequate explanation by means of hereditary factors) or to opt for the geometric sense that could be more useful for a description of the phylogeny. Despite all endeavors, they ended up choosing the geometric sense of parallelism:

Nevertheless, we have decided against such a proposal (very reluctantly, as concerns one of us [Simpson]) because of the inappropriateness of the term [parallelism]. Parallelism does



have a vernacular, or at least a non-phylogenetic sense, which is applicable to the phenomenon in question only in a descriptive way, whereas the essence of genetic definition would be to supply a theory or opinion as to the cause underlying the descriptive situation. This genetic principle is not the only one that can produce a sequence descriptively parallel. Moreover, the result of this genetic factor is not necessarily parallelism in a descriptive sense. It can, indeed, be convergence in this sense although convergence has almost always been considered as essentially distinct from parallelism. One of the reasons for this view, and probably the decisive one, has been that convergence may be found between groups far distant from each other in the zoological system. (Haas and Simpson 1946, p. 337)

So, given that the original term for parallelism could not be adequately defined because there was no genetic theory that properly accounted for this phenomenon, Haas and Simpson opted to include parallelism within a general phenomenon called homoplasy. This had to be so until the boundaries between convergence and parallelism were well-defined: “However, it seems advisable to retain the last term [homoplasy] as the more comprehensive one all the same, all the more so since the boundaries between parallelism and convergence are quite indefinite and it is frequently difficult to decide which of these special terms applies” (Haas and Simpson 1946, p. 325).

Interestingly, despite these conclusions, Simpson still maintained confidence in the term parallelism as distinguishable from convergence in *Principles of Animal Taxonomy* (1961). He was not satisfied with the decision of the abovementioned paper: “Some students (for example, Haas in Haas and Simpson 1946) have preferred a more purely descriptive definition, especially by the geometrical model of parallel lines, symbolizing two lineages both changing but not becoming significantly either more or less similar” (Simpson 1961, p. 103). Simpson then mentions that parallelism has been considered useful by many taxonomists when bearing in mind common ancestry. In other words, parallelism must have something special: “The distinction of parallelism from convergence is vital” (Simpson 1961, p. 106).

Given Simpson’s continued defense in favor of the term parallelism (as a term that arose from an anti-Darwinian theory with an emphasis on constraints and channelization of change), some fundamental questions inevitably come about: Did Simpson advocate for the theory of orthogenesis through the concept of parallelism? If this is so, did he propose a mechanism based on structural constraints that supported it? Any answer to these questions could be controversial. However, from my point of view, he could have postulated an explanation for orthogenesis that linked structural constraints with the action of natural selection (just as Scott did) as well as genetic constraints as reinforcement (as Schindewolf also did at the time) (see Table 10.1):

Parallelism has several theoretical bases that help one to understand and also to recognize it. *The structure of an ancestral group inevitably restricts the lines of possible evolutionary change. That simple fact greatly increases the probability that among the number of descendant lineages several or all will follow one line.* That probability will be further reinforced by natural selection in a geographically expanding and actively speciating group if the ecologies of diverse lineages remain similar in respect to the adaptations involved in the parallelism. The degree of dependence on similar ecology resembles that of convergence, but the retention of homologous characters from the relatively near common ancestry usually

distinguishes parallelism. The parallel lineages (unlike those only convergent) furthermore start out with closely similar coadapted genetic systems, and similar changes are more likely to keep the system adequately coadapted. Tendency toward genetic parallelism is also strongly reinforced by recurrent “homologues” mutations and similar relative mutation rates. (Simpson 1961, p. 106; my italics)

To summarize, we can highlight some interesting statements about this topic. In his well-knowing book *Tempo and Mode*, Simpson recognized the phenomenon of orthogenesis, even though he discredits the theories that supported it by saying that they were based on theological, metaphysical, and vitalistic conceptions. Of course, Simpson does not agree that orthogenesis occurs without adaptation; nonetheless, he provides some explanations such as structural constraints and the mutations that do not occur in all directions (see Table 10.1). In later publications, Simpson proposed that all evolutionary trends were adaptive, and he rejected orthogenesis because mutations rates in a single direction were simply not possible, so the only guide of those evolutionary trends was natural selection. However, when he faced the issue of why parallelism should be different from convergence, he ended up defending the concept of parallelism and finally argued for structural and genetic constraints as its possible causes. So, if parallelism was the description of orthogenesis in anti-Darwinian terms, and if orthogenesis was originally based on arguments of structural constraints, I dare say that Simpson did not end orthogenesis, but rather ended up defending the phenomenon. In other words, Simpson was an orthogeneticist.

## 10.5 Conclusion: Orthogenesis Arises from Ashes Like a Phoenix

Without a doubt, Simpson’s role in paleontology and his views on macroevolution were vital for the construction of the Modern Synthesis. But the traditional narrative tells us that Simpson ended macroevolutionary anti-Darwinian theories such as saltational evolution and orthogenesis—theories that were defended by most paleontologists during the first third of the twentieth century—given that paleontological data was congruent with population genetics and microevolution after all. This narrative may have been established by the other architects who used Simpson’s portrait of macroevolution to favor their microevolutionary perspectives. In consequence, Simpson’s works only served to support the premise that macroevolutionary phenomena could be explained through the sum of microevolutionary processes. The paleontologists of the 1970s and 1980s inherited this narrative and took it as a paradigm that had to be challenged, that is, paleontology should have a greater contribution other than only corroborate the extrapolationist premise. They probably also benefited from this narrative to promote and defend their macroevolutionary theories (e.g., punctuated equilibrium).

Still, when we read Simpson’s works, we find something very different from what the traditional narrative tells us. As I have pointed out throughout this work, while Simpson is guilty of discrediting the theory of orthogenesis in paleontology, he

defends the theory indirectly through the concept of parallelism. In fact, like anti-Darwinian paleontologists, such as Scott and Schindewolf, Simpson attempted to explain orthogenesis through structural and genetic constraints (see Table 10.1). This corroborates the fact that Simpson maintained pluralistic ideas by including constraints into his evolutionary system as a complementary factor to the argument of natural selection.

If this is so, I think that Simpson's contribution to paleontology and evolution has not been appreciated correctly because of the traditional narrative. Simpson also blamed himself, during the establishment of the Modern Synthesis, since he showed that his ideas were congruent with the ideas of the other architects. Perhaps this was due to the social pressure generated by the same Modern Synthesis movement that had the desire to achieve the unification of biological science by the agreement between the different disciplines (see Smocovitis 1996). Also, as said by Delisle (2011, p. 57): "For several of its architects, the evolutionary synthesis became a theoretical trap: forced to explain all sorts of evolutionary phenomena within a narrow theoretical corpus, these scholars had to recognize, usually only implicitly, that a number of such phenomena could not properly be explained by this corpus."

On the other hand, the fact that Simpson had ideas contrary to the central assumptions of the Modern Synthesis not only rests on a reinterpretation of history but also on some current theoretical proposals about evolution (e.g., Extended Synthesis). Because if the Modern Synthesis is incongruent with macroevolution (see Adams 2021 in this volume), and if this Modern Synthesis, theoretically challenged, builds a theoretical framework that serves as a basis for any current theory of evolution, those theories that are cemented under the Modern Synthesis must, therefore, be likewise fragile and incoherent (see also Esposito 2021 in this volume). And as Delisle (2011, p. 58) claims: "current calls for an expanded and extended Darwinism need to avoid erecting a straw man when considering its history." But not everything is lost; recently, there is a theoretical proposal developed under a pluralistic approach to evolution (see Diogo 2017).

Finally, this chapter also attempts to do historical justice to all those assumptions stated under the name of "orthogenesis," considering that it has been demonstrated by this and other works that orthogenesis was not a "metaphysical," "vitalistic," or "theological" theory with "progressive" connotations (Grehan and Ainsworth 1985; Gould 2002; Levit and Olsson 2006; Popov 2009, 2018; De Renzi 2014; Ochoa and Barahona 2014; Ulett 2014, 2016; Ochoa 2017; Ceccarelli 2021). Rather, it was a theory that describes the evolutionary trends that exist in the evolution of lineages which today we recognize phenomenologically under the term of "parallelism" (Wake et al. 2011; Ochoa and Rasskin-Gutman 2015; Monnet et al. 2015), and whose causes are probably due to the developmental bias (Arthur 2004; Jablonski 2020; Moczek 2020), sometimes along with a little help from natural selection.

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