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# Ratite Phylogeny and Distribution with Comments on Evolutionary Processes

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## Abstract:

The objective of this study is to show that two alternative mechanisms of evolution, orthogenesis or genetic drift, offer a better explanation for: 1) the ubiquitous nature of character contradictions in phylogenies; 2) may resolve the non-congruence of phylogenies with a taxon's geographic distribution; 3) reconcile the conflicting ages of clade origins using molecular clock data and first appearance in the fossil record; and 4) the explosions of diversity which occur after major extinction events and during the Cambrian. Ratites which have a southern hemisphere distribution are used to illustrate these points. Natural selection does not appear to offer satisfactory explanations for these four areas of interest.

Keywords: Evolution, Natural selection, Orthogenesis, Genetic drift, Character conflicts, Geographic distribution, Homeostasis.

## Introduction

This paper presents orthogenesis and genetic drift as two alternatives to natural selection to explain character conflicts in phylogenies, extinction, periods of explosions of diversity, and distribution.

Existing literature on ratites is used to show that these problems can be satisfactorily explained by either of these two alternatives to natural selection when acting under genetic homeostasis. If we accept here as a premise that natural selection can operate on genetic change only after it is expressed in a phenotype, then it appears that it is deficient as an explanation for these problems. The purpose here is to show how deductions from this premise lead to anomalies which are not predicted by natural selection, but which are reconciled by using either orthogenesis or genetic drift as mechanisms for evolutionary change. Orthogenesis will be covered first and can be defined here as an internally driven genetic mechanism within taxa to evolve on a specific trajectory. Natural selection is proposed to be only a minor component to species change which has no effect on a taxon's trajectory of change. No mechanism is known to date which would support orthogenesis as the overriding cause of evolution, but the assumption of such a mechanism may explain a number of quandaries of evolution mentioned above.

The best definition that can be given now is a quote from "Evolution on rails: mechanisms and levels of orthogenesis" (Levit & Olsson, 2006). Their paper opens, "in the broadest sense orthogenesis is...the idea that biological evolution is governed by an intrinsic directionality. However, the very concept of orthogenesis...appeared in opposition to Darwinian selectionism, which is based on the idea that variation is very extensive or even unlimited. The champions of orthogenesis, asserted that variation is limited, and that living organisms are predisposed to vary in certain directions, and also, that this bias determines major transitions in evolution." Any more specific definition would be uncalled for given the lack of a known supporting mechanism within the genome. More recent workers in genetic variation have determined that variation can be biased (Monroe, et.al., 2022; Svensson, E. and Berger, D., 2019), but these studies have not discovered any tendency for a genome to mutate in a particular direction. The general definition above will suffice as a starting postulate which may explain patterns of diversity, distribution, extinction, and character distribution within taxonomic groups in different ways than natural selection.

The second part of the discussion will cover genetic drift as a solution to these same issues. Genetic drift, as used here, is defined succinctly by Kimura (1991) as a neutral theory of evolution, "...The great majority of evolutionary mutant substitutions at the molecular level are caused by random fixation, through sampling drift, of selectively neutral mutants under continued mutation pressure..." Unlike orthogenesis, no unknown mechanism need be invoked to explain changes in a genome, and this mechanism answers many of the same issues addressed by orthogenesis.

One way to begin a discussion of problems in evolution at a systematics level is to acknowledge one of its most glaring problems, the ubiquitous nature of character conflicts within groups. To date the phylogenetic analysis of any group of organisms which does not show a conflicting distribution of derived characters is rare indeed. The following discussion uses the ratites as one example of a taxonomic group which typifies these conflicts. Four possible mechanisms for conflicting character states are similar selection pressures, horizontal gene transfer (HGT) and related processes such as ancient introgression, genetic drift, and orthogenesis. Natural selection has been invoked as a cause of these conflicts, but HGT has been invoked with increasing frequency as well (Sackton & Clark, 2019). However, the question remains how large a role it can play, if any, beyond a species/sub-species level. Can they account for convergence of complex structures at a generic, family or higher level? Van Etten and Battacharya (2020) show that HGT occurs at may taxonomically levels in eukaryotes and can be responsible for evolutionary innovations. However, HGT is usually at a metabolic level, and not responsible for changes in gross morphology/body structures. If such structures were maintained on parallel or convergent paths by gene transfer, they would have to be continuous and complex in nature with the same suite of genetic material being transferred to different lineages. This would be a tall order for such an agent of convergence above a population or species level. More likely the limits of this agency could be likened to the metaphor of an ocean liner pulling away from its pier with family and friends throwing bouquets to their departing loved ones. At a very short distance the flowers and streamers would fall short, and the crowd on the pier would soon recede to just memories. Any convergence at a higher taxonomic level would then rest on a different cause. This would be true especially with the ratites which are scattered across the southern continents.

Orthogenesis and genetic drift are invoked as alternate explanations for these conflicts as opposed to similar selection pressures yielding convergent derived characters. There have been many workers who have tackled the phylogeny and geographic distribution of the ratite birds. All of these workers have had to employ multiple parallel development of similar derived characters in order to explain the many conflicts in their phylogenies. Some of these workers such as Cracraft (1970) near the beginning of applying phylogenetic systematics (cladistics) to a taxonomic group, and later on, Scherz (2013) tried to unravel the relationships among ratite members, but could not generate a phylogeny without character conflicts.

## Discussion

The discussion that follows attempts to resolve these conflicts which leads to deductions concerning genetic clocks, biogeography, and explosions of diversity after extinction events. Many workers (van Tuinen, et al. 1998; Scherz 2013; Hadrath & Baker 2001) derived multiple possible phylogenies of ratites and tinamous with the relationships varying based on the character set used for each. The one point of agreement common to most is the emu being the sister group to the cassowary. Besides this conclusion most studies diverge as to generic interrelationships. None of these phylogenies resolve character conflicts such as the independent acquisition or multiple losses of flight, loss of the preen gland, loss of down feathers, and the development of a cursorial body plan within the group (Scherz 2013; Harchman, et al. 2008; Maderspracher 2017), and this failure holds for both morphological and genetic characters. Furthermore, one would presume the group, being flightless would show a distribution among Gondwana continental fragments that mirrored the sequence of phylogenetic splitting. Here again, this is not the case with scenarios requiring ratites dispersing as volant taxa to different Gondwana fragments followed by independent and multiple instances of flight loss (Maderspracher 2017).

The phylogeny of the ratites when overlain on their distrubution requires one or more incidents of dispersal by island hopping, land bridges, rafting, or flight. The latter possibility corresponds with the conclusion of many authors that current flightless ratites evolved from volant ancestors which would make dispersal events more credible (Scherz 2013; Harshman et al. 2008; Yonezawa et al. 2017). Molecular evidence leads to the conclusion that tinamous lie within the ratites which yields either of two necessary results: flight was lost at least twice in ratites, or tinamous regained flight from a flightless ancestor.

There are three solutions to the contradictory character distributions, and they require parallel development of a derived character in non-sister groups. The most common explanation for this convergence is that similar selection pressures caused similar adaptive changes in the taxa in question. Similar selection pressures can be invoked to explain the ratites' development of a cursorial lifestyle, similar large body plan (kiwi excepted), and flight loss. However, the ratites occur and could very well have evolved in very dissimilar environments from open plains to closed canopy tropical jungles. A second explanation might be that the characters are not strictly homologous at one level of analysis, but might be homologous at a more general level.

First, orthogenesis will be discussed as an explanation for parallel development of derived characters and a number of deductions which follow from it. If a derived character occurs in two taxa which are not sister groups an alternate explanation could be their nearest common ancestor evolved a tendency to develop the character with selection pressures being incidental and which would have no effect on character development. Other descendent taxa which still show the primitive state have not activated this tendency and the primitive state persists. In other words, the derived state exists at a genomic level (either as a point single gene source or multiple gene level, or at an epigenetic network level in which a network of controller genes has put the taxon on a channelized pathway to a derived state) but does not occur yet in all descendent taxa.

This leaves traditional Henigian systematists in a difficult situation—if all descendent taxa don't typically exhibit a derived character state, then the distribution of shared derived characters in a taxon will not, in many if not most cases, yield a reliable, testable phylogeny. This leaves the systematist in the position of applying Occam's Razor to an unreliable set of characters in which the least number of character conflicts is assumed to be the best outcome for any hypothesized set of relationships. The corollary is that a phylogeny with more character conflicts (with characters currently used) cannot be rejected (falsified) using this principle of parsimony. Likewise, for a systematist using Bayesian inference, the model and the prior and post probabilities would lead to faulty trees due to misidentified homoplasy. The important point here is that character conflicts will come from any of the systematic methodologies currently in use, i.e. cladistics based on Hennig's parsimony criteria or Bayesian inference. The critical point is that these conflicts are irreconcilable regardless of the phylogenetic model used. At some level within a genome reliable character must exist to test competing phylogenies. After all, evolution can be defined as descent with modification, and that modification must be evident at some level. Unfortunately, if orthogenesis as defined here is the main cause of evolution, then the characters which would be reliable indicators of phylogeny have not yet been identified.

Taking orthogenesis as an operating assumption and as the driving force of evolutionary change leads to a number of deductions and the possible resolution of problems in evolution and geographic distribution. These deductions are different than one would expect in a system governed by natural selection. In order for natural selection to have an effect on any organism, a character has to be expressed beforehand. As a result, the genetic and phenotypic expression must progress hand-in-hand. In other words, genetic change and phenotypic expression are concurrent in a natural selection framework (the exception would be neutral genes which could change constantly, but have no effect on the phenotype). If a phenotype remains constant through time then selection has no way to affect change. Therefore, phenotypic change would necessarily occur at the same pace as the rate of genetic change. Explosions of diversity as seen soon after mass extinction events or during the Cambrian would not be possible since the rate at which diversity increases would be tethered to the rate of genetic change.

In an orthogenetic model, phenotypic expression can be delayed while genetic change continues apace which leads to the following deductions:

1) The disagreement between first appearance in the fossil record and the time of first appearance inferred by genetic clock studies may be due to the delay of phenotypic expression of defining characters of the group. If phenotypic characters are not apparent at the origin of a monophyletic group, then the taxon's minimum time of origin cannot be properly determined. The time of first appearance both in the fossil

record and inferred by genetic clocks could be much later than the taxon's actual origin. It is irrelevant how clocks are adjusted by different calibration techniques; significant disparity remains (Cunningham, et.al., 2016; Blair and Hedges, 2005). Under natural selection, first appearance should coincide with actual time of origin with the only lag time between the two due to the incompleteness of the fossil record. Under natural selection, in order for selection to take place, a taxon must express a character which means it is discoverable and identifiable by a collector. Orthogenesis coupled with homeostasis would shield a taxon which has become genetically distinct, but its phenotype would still lie in its ancestral state. Natural selection could not operate this way. If a taxon exhibited persistent homeostasis, then genetic changes would be neutral because they would not be expressed in a phenotype. Such genetic changes would be shielded from selection, and adaptive changes would not be possible.

2) A corollary to the delay of first appearance is the lack of fossil ratites in Gondwana sediments that predate the breakup of the super continent (Yonezawa et al. 2017). This would require dispersal of ratites over much of their current distribution in rare "sweepstakes" type events. In a selection model definable ratite fossils should appear in these sediments if they were passively dispersed by plate tectonics. Many authors (van Tuinen et al. 1998; Yonezawa et al. 2017; Cracraft 2001) have argued for the first occurrence of ratites to be in the Cretaceous. In a selection model, definable characters of a group should be evident at the group's origin. If so, then the first occurrence and time of origin should be fairly close. Since it's not, the fallback argument must be preservation or collection bias. With an orthogenetic model the first appearance should be delayed from the group's actual time of origin.
3) An effect of delayed appearance in the fossil record could be the "explosions" of diversity such as occurred in the Cambrian and after subsequent mass extinction events of later periods. If phenotypic characters are suppressed due to controller genes or gene networks being rendered inactive, and this suppression remains for a long enough time, then antecedents to the living taxa (in this case, ratites) would not be recognizable as members of the group. Genetic change would be progressing with very little phenotypic change until niches become vacated due to extinction. Once suppressor genes or gene networks are deactivated the phenotypic changes in a taxon should appear to be quite rapid; hence the explosions seen in the fossil record. It is important to note that under orthogenesis as described here, such explosions would be apparent only. The rapid rise in diversity and disparity would be an artifact of constant genetic change being masked. Blair and Hedges (2005) show that crown groups may have appeared in the late Precambrian and the Cambrian explosion therefore was not as rapid as it appears.
4) If the geographic distribution of a monophyletic group, such as the ratites (assuming they are monophyletic) does not match the order in which their ancestral geographic range has fragmented, there are two possible solutions. First, the phyletic splitting of the group could have predated the continental breakup of the southern land masses. This would lead to a non-congruence of their phylogenetic relationships and the order in which the southern continents fragmented. This

> alternative would be vigorously contested by most students of the group since it would require an origin and splitting of the group much earlier than is indicated by genetic clock studies and the fossil record. The second alternative would be that the chosen characters, both morphological and genetic, are unreliable in constructing a phylogeny. If a monophyletic taxon originates by virtue of a part of its genome acquiring a tendency to evolve a set of derived characters, but these characters are not immediately expressed, and these same characters appear in descendent taxa at different times, then a study of these characters once expressed can't be used to identify sister group relationships.

The main weakness of this model is the lack of a known genetic mechanism to explain orthogenetic/channelized change. Of the two necessary mechanisms invoked by this paper, suppressor genes have clear evidence in the appearance of atavistic traits. Some of these may be explained by neotony, but many others appear which show the underlying coding or inactive gene network for such structures still lies somewhere in the genome. However, since atavisms occur, the genome must possess redundancy, i.e. a new structure is encoded while the original structure's code or network still exists but becomes inactive. This might indicate a way for a taxon to develop mutations but have them suppressed so the obverse can occur; a new structure is encoded but remains latent while the taxon still exhibits the primitive condition. Also, if two versions of a genetic character are encoded, then this might partly explain the "junk DNA" in a genome. Gene regulatory networks (GRN's) offer a method of genetic homeostasis which would mask changes in a genome. How much and how long this masking can persist until a new attractor state is breached is unknown. This form of suppression/homeostasis would offer a mechanism for continuous genetic change without change in phenotype. Both orthogenesis and selection models would show different results for taxa attempting to radiate into already occupied niches. Selection would lead to expression of genetic change followed by either extinction of a taxon trying to invade an occupied niche, or the genetic change would be eliminated through selection. The taxon would be forced into stasis within their already occupied niche. In the latter case, no evolutionary momentum would be built up that would appear as an explosion of disparity once the invaded niche became vacant. For an orthogenetic model any phenotypic change of an invading taxon would be suppressed, but genetic change would continue unabated. If the phenotypic expression of these genetic changes occurs before the new niche became vacant, extinction could result. If genetic expression occurs after a niche is vacated, then taxonomic change and diversity could occur at a rapid pace. Distribution patterns such as those of the ratites may not be discordant with the breakup of Gondwana. Ratites may have evolved in place and remained fully volant both before and after Gondwana fragmented. Or, alternatively, if dispersal did occur rafting would have been unnecessary. If the characters being used to construct phylogenies are unreliable then the ratites may have evolved in place. This conclusion means that currently used phenotypic and molecular characters are unreliable in applying Occam's Razor to test character distributions. If suppressor and controller genes determine the fate of taxa, then the molecular characters that would be judged reliable in constructing phylogenies would lie elsewhere within the genome. A corroboration of this idea would be that current phylogenies based on nuclear DNA often don't agree with those based on mitochondrial DNA (Scherz 2013). If they don't agree then one or the other set of DNA characters is giving a false signal. In other words, phylogenies based on nuclear DNA may be flawed because the wrong portion of the genome is being sampled. Finally, is there anything that can be said about a genetic mechanism for orthogenesis? Now there seems to be no direct evidence available. However, GRN's may point the way to an explanation. If gene networks are responsible for the preservation of structures which are suppressed (Yildirim and Huang, 2018), perhaps other types of networks may be responsible for setting a taxon on more or less fixed pathway by channelizing genetic mutations in a specific direction. If a mechanism for channelizing mutations is found, then the genome could be likened to a "read-only" semiconductor chip. It cannot be perturbed by normal environmental pressures such as selection. A selection model of evolution could be likened to a programmable chip in which the chip is adaptable to environmental pressures, i.e. selection could be the causative factor in genomic change.

The third evolutionary mechanism which could explain the points mentioned above is genetic drift. One of its major advantages over orthogenesis is that it requires no as yet undiscovered genetic channeling mechanism in order to operate. Also, as Kimura (1991) states that a neutral theory of evolution caused by random fixation is directly measurable and testable. Orthogenesis, by contrast, is not measurable nor quantitative, but is supported by its explanatory value alone. The deductions which follow from orthogenesis will be compared to what might be expected from a genetic drift mechanism.

1) Genetic drift would, like orthogenesis, lead to a discrepancy between a taxon's first appearance in the fossil record and the time of origin indicated by genetic clock studies. If homeostasis shields genetic changes, then a discrepancy between these times is a necessary result. The important point here is that genetic drift would be continuous and cloaked by homeostasis whereas selection would be thwarted if it lacks any phenotypic variability to act on.
2) The lack of fossil ratites in sediments that predate the breakup of Gondwanaland would not be surprising if the group's genetic fingerprint were masked by homeostasis, and the phenotype was constrained to the point that early ratites could not be identified as such. Blair and Hedges (2005) show that the early evolution of crown group phyla may appear in the fossil record up to 100 MY before the onset of the Cambrian. However, these fossils cannot be definitively assigned to crown groups because of the lack of unambiguous derived characters. This could be an early example of a group being masked by homeostasis until they radiated after the late Precambrian cryogenic event.
3) Genetic drift will allow a taxon's genome to change over time whether or not a trait is phenotypically expressed as with orthogenesis. If homeostasis shields these changes over enough time, then explosions of diversity would be identifiable once homeostasis is relaxed. Again, Blair and Hedges (2005) offers a good example of this. The important point is that the explosion is apparent only, and the crown group representatives were probably present well before the onset of the Cambrian, and the diversity was only recognized later.
4) Non-congruence of a taxon's phylogeny and the order of geographic fragmentation could be expected with drift coupled with homeostasis. If the genetic changes were masked by homeostasis for a long enough time, then the phylogenetic splitting could have occurred before continental breakup. In the case of ratites, the phylogenetic splitting

could be due to an older geographic fragmentation than the breakup of the southern super continent.

One advantage drift has versus orthogenesis is that it would lead to "bushiness" in patterns of phylogenies. Because drift is a random process, channelized phylogenies would not be expected, and a taxon's descendant members could evolve in a multitude of directions. Gould (1989) was one worker who showed that the fossil record is replete with examples of bushiness although he did not attribute this to drift. However, bushiness of phylogenetic branching is certainly consistent with drift which could be a possible mechanism.

One major disadvantage of drift compared with orthogenesis is that it would predict an occasional reversion of a derived taxon back to an ancestral state. Bushiness should occur in all descendent taxa, some of which should radiate back to an ancestral-like state. This does not appear to happen. Such a condition, if it were to occur would produce a taxon with atavistic like characters in conjunction with a highly derived trait characteristic of a more derived ancestor.

## Conclusions

In this discussion orthogenesis and genetic drift coupled with homeostasis are invoked as possible solutions to the ubiquitous character contradictions in phylogenies. By doing so, not only have these contradictions been looked at as a normal consequence of these processes, but a number of deductions from them help explain ratite distribution, apparent rapid evolution in the fossil record and increase in diversity after extinction events, and an explanation for the strong discordance between the imputed time of origin of taxa and their first appearance in the fossil record.

The ideas presented here with respect to orthogenesis stand or fall on finding a genetic mechanism. If such a mechanism is verified, it would call into question the use of Occam's Razor and Bayesian inference in conjunction with currently used characters as a tool to test competing phylogenies of any taxonomic group. Finally, if genetic change is channelized independent of environmental influences, or if genetic drift is shown to be a predominant evolutionary force, natural selection would be called into question as an overriding agent in evolution.

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