

1 **The ‘Holy Grail’ in Phylogenetic Reconstruction: *Seeing the Forest for the Trees?***

2

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**12 Abstract**

13           Systematic/macroevolutionary biology has dedicated much of the past 50 years of its  
14 energy and resources in an effort to resolve definitively the one true ‘tree of life’ and to explain  
15 materially its cause. But, no matter the quantity/quality of data, experimentation, and analysis,  
16 the effort is hampered by persistent and ever-accumulating contradictory observations. This may  
17 be an indication that the source of the problem lies in the observer rather than the observed.  
18 Observations do not conflict with themselves; they conflict with theoretical expectations. Thus,  
19 systematic and evolutionary biology requires epistemological overhaul. Rather than continued  
20 misaligning of evidence with theory, theory must be realigned with the evidence. Evidence  
21 suggests that the Darwinian reductionist perspective is the epistemological driver of considerable  
22 conflict/contradiction in systematic/evolutionary research, and that robust non-Darwinian  
23 theories not only better reconcile observations, but also provide a superior investigative  
24 perspective.

25 **Key Words:** phylogenetics, phylogenetic comparative analysis, data conflict, Darwinism,  
26 evolutionary idiosyncraticity

27

**28 Background: conflict in phylogenetic evolutionary analysis**

29           Olmstead and Medoya (2019) remarked on phylogenetic evidence from whole genome  
30 sequencing, which they characterized as the ‘holy grail’ of molecular phylogenetics. They  
31 commiserated over persisting evidential conflict in phylogenetic reconstruction, which they  
32 noted is “as old as phylogenetic systematics.” In fact, the specter of conflict is *much* older than  
33 that. Aristotle’s *Scala Natural* highlighted ambivalent resolution of the natural relationships of  
34 flying organisms. This theory is not founded in ‘descent with modification,’ but rather

35 teleological organism-driven orthogenetic development of more perfect ‘higher’ forms. Among  
36 notable 18<sup>th</sup>–19<sup>th</sup> century systematists that addressed evidential conflict were several  
37 Creationists. These pre-phylogenetics debates hinted that character distribution mosaicism is  
38 intrinsic to biodiversity, independent of how it is parsed, and that parsing it one way or another  
39 per se does not eliminate or explain it.

40         Yet, for the past century, evolutionary systematists have probed ever deeper into  
41 organisms, expecting to find a magic bullet that retraces phylogeny perfectly. In this trajectory,  
42 the ‘holy grail’ has *not* been per se the genome, but a fully resolved and well-corroborated ‘tree  
43 of life’ (e.g., Soltis and Soltis, 2018) and its causal explanation. The earlier 20<sup>th</sup> century heralded  
44 the first subcellular bandwagons, especially cytotaxonomy. The 1960s–1970s added  
45 chemotaxonomy, ultrastructure, and protein electrophoresis; the 1980s, desktop phylogenetic  
46 computation and, concomitantly, diverse (and themselves conflicting) epistemological models  
47 and methodologies. Like greasy rags, these successive approaches, separately and together, often  
48 blurred more than they clarified the picture.

49         Then appeared DNA sequence data, which were heralded as the ultimate arbiter in  
50 systematics. Rather abruptly, the PCR-to-PAUP paradigm practically purged the entire  
51 discipline. Molecular systematics laboratories became warships. ‘More data! More sampling!  
52 More megahertz! More memory! More MCMCs! And damn the taxonomy, *barcode* those  
53 species!’ For a while, it *seemed* that this ‘shock and awe’ attack was on course to annihilate the  
54 last resistance to cladistic conquest. But the tide seemed to turn. Sometimes adding more data  
55 reduced resolution. Bombarding one unresolved node sometimes yielded, like Medusa, several in  
56 its place.

57         As Olmstead and Medoya (2019) noted, whole genome sequencing represents

58 reductionism’s last stand. Genome-scale sequencing is yielding novel information on  
 59 macroevolution, but not as much cladistic resolution as expected. But should it? Should 500,000  
 60 base pairs of arbitrarily isolated DNA sequence resolve clades better than 5000 base pairs  
 61 *preselected* for their theoretical/empirical high-quality resolvability? As Olmstead and Medoya  
 62 (2019) also noted, explanations for this flood of new conflict appeal by default to mechanically  
 63 plausible but not always demonstrable hybridization and lineage-sorting. Thus, phylogenomics  
 64 has us retreating from explanation back towards to speculation. Moreover, hybridization and  
 65 lineage sorting hardly are earth-shaking discoveries. That was the battlefield 50 years ago. And  
 66 what about transposons?

67

#### 68 **Darwinian ‘tree-thinking’ as an epistemological cause of data conflict**

69 HersHKovitz (2018a, b, 2019) addressed the question of phylogenetic data conflict, but  
 70 approached it differently. This work concluded that the source of evidential conflict in  
 71 evolutionary biology is not per se in the evidence, but in its epistemological interpretation. An  
 72 inadequate epistemology, in turn, engenders an *expectation* of observations whose *exceptions* are  
 73 described ad hoc as ‘data conflict.’ But phenomena ideally cannot generate observations in  
 74 conflict with themselves. Recall that good explanations make better predictions than poor ones.  
 75 If, as in the case of phylogenomics, a two-order of magnitude increase in observations does not  
 76 increase or even *decreases* predictability, maybe it is time to trade up to a better crystal ball.

77 HersHKovitz (2018b, 2019) inferred the cause of conflict in contemporary phylogenetics  
 78 and tree-based evolutionary analysis generally: biological reductionism, in particular *neo-*  
 79 *Darwinian* reductionism. Prevalent macroevolutionary theory and methods trace their origin to  
 80 the neo-Darwinian Modern Synthesis. This, in turn, emerged in the form of the statistical

81 population genetic incarnation of Darwin's (1859) reductionist theory of evolution by means of  
 82 Natural Selection (NS), restated succinctly as 'survival of the fittest' (Darwin, 1868).

83         The relation of NS to phylogenetic conflict is that the theory was supposed to explain  
 84 diversification not *within populations*, but *among taxa*. Although NS is conceived as initiating in  
 85 populations, validation of Darwin's theory requires its consummation with *phyletic* divergence.  
 86 Although overlooked/ignored by 20<sup>th</sup> century Aristotelian 'evolutionary' systematists, Darwin  
 87 conceived that taxa and their traits evolve integrally/synchronously and diversify  
 88 *cladogenetically*. He diagrammed macroevolution as a tree (but see Podani, 2019), or cladogram.  
 89 This diagram idealized anagenesis unidimensionally (lines) and diversification events  
 90 nondimensionally (bifurcation points). Terminal taxa, whether species or 'genera' (Podani,  
 91 2019), also were idealized nondimensionally. It is critical to appreciate that this clado-anagenetic  
 92 model is essential to NS theory. It does not explain merely anagenesis, but also the historical  
 93 consequence of species differentiation via NS. Other evolutionary mechanisms would yield other  
 94 phylogenetic patterns.

95         During the Modern Synthesis' first decades, the systematics discipline retained an  
 96 Aristotelian mindset, in which both taxa and diversification were conceived and diagrammed  
 97 multidimensionally. Indeed, texts and diagrams in 'evolutionary' taxonomy literature implied  
 98 diversification histories/mechanisms incompatible with cladistics. Armen Takhtajan, in  
 99 particular, in his 1959–2009 texts, emphasized that angiosperm families possess mixtures of  
 100 characters that he regarded as *intrinsically* primitive or specialized. He described this as  
 101 'heterobathmy.' Takhtajan vehemently rejected cladistic theory, so he did not parse conflicting  
 102 characters as parallelisms or reversals. Rather, his phylogenetic narrative resolves as a network,  
 103 such that a heterobathmic family evolved from/alongside an *assortment* of not otherwise most

104 closely related ‘primitive’ and ‘specialized’ families that collectively possessed the various  
105 individual characteristics. Thus, the heterobathmic family derived its traits effectively  
106 polyphyletically. [But see Rieppel (2016) for a discussion of Hennig’s cladistic interpretation of  
107 Takhtajan’s ‘heterobathmy.’]

108         Meanwhile, evolutionary population genetics placeheld for the neo-Darwinian  
109 macroevolutionary paradigm, pending the eventual conceptualization and development of  
110 cladistic and later tree-based macroevolutionary theory/methods. Tree-building, or, more  
111 accurately, ‘tree-thinking’ (e.g., Baum and Smith, 2012) is what consummated (and evidently  
112 consumed) the Modern Synthesis. By the time molecular systematics came along, conflicting  
113 cladistic data was well known and much debated.

114         Molecular data conflict ought to have been anticipated on the basis of transmission and  
115 molecular genetic evidence, as well as theoretical phylogenetics. Possibly molecular systematists  
116 proactively avoided it. In contrast to molecular phylogenetic data, phenotypic data were  
117 informative biologically whether or not they resolved phylogeny. But few systematists (e.g.,  
118 Herskovitz and Zimmer, 1996) concerned themselves with comparative *biology* of DNA loci. In  
119 systematics, a DNA sequence alignment was not more or less than a sterile phylogenetic data  
120 matrix. The overriding concern was whether the sequences resolved phylogeny and thus merited  
121 publication and thus advanced an academic career. Quite likely, filtering out of poorly resolvable  
122 data (and researchers who obtained them) itself enhanced the perceived reliability of molecular  
123 data in phylogenetics. The early emphasis on single, hence non-conflicting, loci tipped the  
124 balance further. But with increased locus and taxon sampling, data conflict became the rule  
125 rather than the exception. Still, there evidently persisted a superstitious belief that whole genome  
126 sequences would thresh out these conflicts.

127           A funny thing happened on the way to the genome. For example, and hardly an  
128 exception, a phylogenomic analysis among Portulacineae (especially cacti; Wang et al., 2018:  
129 *Fig. 2*) revealed that numerous statistically maximally-supported nodes in the taxon tree were  
130 supported evidentially by a *minority* of harvested loci, the majority at least weakly discordant.  
131 Another analysis, coincidentally involving cacti (Copetti et al., 2019: *Fig. 2B*), superimposed  
132 over a presumed taxon tree a diffuse cloud of gene trees and their divergence time estimates.  
133 This revealed that a large proportion of alleles had not co-diverged with speciation, but merely  
134 had assorted among lineages since the origin of the family. Other alleles manifested horizontal  
135 transfer. These results, along with phylogenomic ‘splits’ networks of *Claytonia* spp. (Stoughton  
136 et al., 2017: *Fig. 1B*), suggest that the phylogenetic ‘holy grail’ might be, after all, more like  
137 Bessey’s Cactus than a cladogram. Is it possible that the rudder of tree-thinking had rusted and  
138 steered neo-Darwinian reductionism adrift?

139

#### 140   **Resolving data conflict epistemologically rather than empirically**

141           Herskovitz (2018a, b, 2019) attempted to formulate an evolutionary synthesis of  
142 Montiaceae around data, not dogma. This synthesis aspired to span all divergence levels between  
143 outgroup and individual, and all phenomenological dimensions, ecological, morphological, and  
144 molecular. The effort was a mental exercise, focusing on conflicts and contradictions, and  
145 seeking to explain the collectively unexplained data. Nominally conflicting data were  
146 revisualized in the light of alternative theories.

147           What emerged, and not at all expectedly, was a consilient non-Darwinian evolutionary  
148 synthesis. Yet, none of the theoretical components are per se novel. All have been corroborated  
149 in scientific disciplines marginal to if not remote from ‘mainstream’ reductionist systematic and

150 evolutionary biology. These include complexity theory, systems biology, neurobiology,  
 151 cybernetics, as well as related areas of biological philosophy. In these disciplines, Darwinian  
 152 reductionist theory – and its applications – are considered obsolete, if not utterly false. The  
 153 theoretical sources and arguments are documented in HersHKovitz (2018a, b; 2019; see also  
 154 Kritz, 2017). For brevity, only a few critical references are cited here. It should be recalled, also,  
 155 that Popper (1976 [2002]) characterized Darwinism as “invaluable,” nonetheless as not a theory,  
 156 but a “metaphysical research program.” Effectively, he criticized evolutionary research that did  
 157 not test Darwinian theory per se, but merely sought Darwinian explanations under the  
 158 assumption that the theory was true and leaving unexplained or disregarding, or in any case, not  
 159 proactively seeking nonconforming observations.

160       Towards the objective of reducing perceived data discordance in phylogenetics and tree-  
 161 based evolutionary analysis, first and foremost is the understanding that living organisms are, by  
 162 definition, *autopoietic*, i.e., self-organizing/maintaining/determining/regenerating (Varela et al.,  
 163 1974; Maturana, 1999). From this principle alone, one can deduce that, in evolution, organisms  
 164 are the *drivers* and not, as NS dogmatists maintain, the *driven* (e.g., Nürk et al., 2019). Does  
 165 autopoiesis falsify NS? As a matter of fact, it does. NS does not occur, not even sometimes, not  
 166 ever (Maturana and Mpodozis, 2000). All ‘proofs’ of NS are statistical epiphenomena.

167       As corroboration, HersHKovitz (2018b, 2019) cited a recent description of NS (Pigliucci,  
 168 2010) that, remarkably, is patently *non-Darwinian*. In fact, it is a description of Natural Drift  
 169 (Maturana and Mpodozis, 2000)! More bizarre, Pigliucci (2010) penned this non-Darwinian NS  
 170 definition in a *defense* of NS against its non-Darwinian critics. No student of  
 171 systematic/evolutionary biology should overlook this watershed paradigmatic development. In  
 172 fact, autopoiesis *alone* invalidates pretty much all of a century of NS-based adaptationist



173 evolutionary ecological and phylogenetic comparative research. Autopoiesis better explains  
174 myriad conflicts in the data and interpretation.

175         But, wait, there's more.

176         As noted, phylogenetic character patterns are in 'conflict' only to the degree that they are  
177 not *predicted* by the underlying epistemological model and optimization criterion. But the self-  
178 determining quality of autopoietons (organisms) has the logical consequence that their enactivity  
179 (ontogenetic/evolutionary trajectory; Varela et al., 1992) is not (statistically or otherwise)  
180 predictable. This proves to be a quality of formal mathematical chaotic functions – determinate,  
181 yet, if the function and initial conditions are not known, unrecoverable and unpredictable  
182 (Boeing, 2016). This suggests that organismal evolution is to at least a degree a substantially  
183 chaos-like rather than strictly a stochastic process.

184         Indeed, all biological replicative functions from the level of DNA to species manifest  
185 chaotic function qualities. The neo-Darwinian reductionist paradigm idealizes replicative events  
186 as regularly occurring, and replicative mutations as having *ideally* equivalent magnitude and  
187 effect. The paradigm is well aware that the ideal is not the real, whether in the case of genes or  
188 species (e.g., punctuated equilibria). But the lesson is not appreciated, and reductionist  
189 idealizations themselves seem to persist in analytical methods, e.g., Brownian motion  
190 evolutionary null models. Equally importantly, this irregularity of timing and magnitude of  
191 change characterizes replicative events at *all* organizational levels. A further characteristic is  
192 that, with the trivial and transitory exception of DNA bases and amino acids, replicative events  
193 do not merely oscillate within fixed state spaces, as constrained in reductionist methods.  
194 Historically, they have expanded and transformed state space. These are characteristics of  
195 chaotic functions.

196           In the meantime, reductionist tree-based evolutionary analyses use contemporary  
197 empirical data to reconstruct probabilistically the ancestral conditions and the evolutionary  
198 dynamics. Based on this model, the evolutionary history is then the one that, effectively,  
199 conflicts least with the empirical data. To the degree that the true evolutionary dynamic is indeed  
200 stochastic and correctly modeled, analysis of more data (e.g., whole genome sequences) is  
201 expected to converge on the true history. But, to the degree that evolution is at least partially  
202 chaos-like, increasing data should reduce concordance, and conflict-minimization is bound to  
203 converge on error. To paraphrase an aphorism from chaos theory (Boeing, 2016), the exact  
204 ancestral conditions predict the exact evolutionary history, but the approximate ancestral  
205 conditions do not predict the approximate evolutionary history.

206           In addition to autopoiesis and chaos theory, an important aggravating source of perceived  
207 conflict can be understood in terms of hierarchy theory (Salthe and Matsuno, 1995). ‘Conflict’  
208 generally refers to discordance of trees estimated from different but presumably co-evolving  
209 characters, be they infragenic, intergenic, different morphological traits, or molecules versus  
210 morphology. Mechanisms that cause such discordance are well known. This sort of nominal  
211 conflict was embodied in the old aphorism ‘gene trees are not species trees’ (e.g., Doyle, 1992).  
212 In truth, the persistent perception of such discordance as ‘conflict’ owes to overzealous  
213 Darwinian tree-thinking. Discordance between histories at different hierarchical levels is not per  
214 se conflict.

215           To appreciate the preceding, it must be understood that all thermodynamic systems,  
216 including autopoietons, are organized hierarchically. A given hierarchical organizational level  
217 functions within its lower bound (its requisite starting conditions) and its upper bound (its  
218 tolerance range). For example, an engine piston will not work without air, fuel, and ignition. But

219 even with these, it will fail under conditions that compromise its functional integrity, e.g., any  
 220 sort of cylinder imperfection.

221         Biological organisms can be organized hierarchically in multiple levels, e.g.,  
 222 chromosomes, organelles, cells, meristems, organs, and, at the supraorganismic level, microbial  
 223 metagenomes, sexual demes, and symbionts, among others. But given that reductionist biologists  
 224 mostly are unfamiliar with autopoiesis, probably it is not either appreciated that *each* biological  
 225 level of organization *also* manifests autopoietic character. This should not be surprising, since  
 226 some levels themselves derive from once free-living autopoietons (organisms, remember?).  
 227 Retained autopoietic quality permits considerable evolutionary independence at different levels,  
 228 as long as adequate starting /operating conditions are maintained at lower/upper bounds,  
 229 respectively. The consequence is that evolution at different organizational levels is not *predicted*  
 230 to be lockstep. Their different histories might be described as incongruencies, not conflicts.

231         Thus, the meaning of the aphorism ‘gene trees are not species trees’ must be clarified. It  
 232 does not refer to a conflict inferred from discordance among different gene trees and/or  
 233 morphology. It refers to the ontological distinction between genes and species, such that gene  
 234 trees *cannot be* species trees, even when gene trees and species trees are *fully* congruent.  
 235 Axiomatically, the ‘true’ species (or taxon) tree is *not* a consensus of a plurality of concordant  
 236 gene trees, as misconceived explicitly in many molecular phylogenetic and, more so,  
 237 phylogenomic analyses. This should be clear from hybrid species formation. From the  
 238 perspective of the species level, the genes having different histories are not ‘discordant’ or  
 239 ‘conflicting.’ They are integral to the species. The species would be *different* ontologically (and  
 240 functionally, if viable at all) if the so-maligned ‘foreign’ loci were rounded up and deported. Put  
 241 another way, *all* incident loci pertain to the ‘true’ species tree.

242

243 **Epistemological solutions to phylogenetic data conflict: PEI and Wave Model**

244 Not expectedly initially, the three theoretical phenomena discussed here, autopoiesis,  
 245 chaos, and hierarchicity, threaded into a single consilient evolutionary dynamic, which I  
 246 described as the **Principle of Evolutionary Idiosyncraticity (PEI)**; HersHKovitz, 2018b, 2019).  
 247 Not merely an aesthetic term, ‘evolutionary idiosyncraticity’ was described formally as an  
 248 evolutionary product of simultaneous chaotic (determinate/unpredictable) and stochastic  
 249 (indeterminate, statistically predictable) processes. It can be summarized as **EI =**  
 250  $f(\text{chaos})f(\text{stochasticity})$ . The determinate character is inherent in autopoiesis. The stochastic  
 251 factor is a sum of the dynamics occurring at organizational levels hierarchically adjacent to a  
 252 self-organizing process. I merely conjecture that the net evolutionary effects at hierarchically  
 253 adjacent levels are stochastic. More precisely, PEI tentatively *defers* to these *adjacent*  
 254 hierarchical levels the very stochasticity that the NS paradigm presumes to encompass the *entire*  
 255 evolutionary process. Clearly the autopoieton itself does not behave stochastically, and this is the  
 256 fundamental error of the NS paradigm.

257 As a demonstration of the preceding, replication presumably is affected by incident  
 258 nucleoside concentrations, etc., at the lower bound (starting conditions), and cell environmental  
 259 parameters (tolerances) at the upper bound. The response to these conditions is not fixed, nor  
 260 stochastic, but dynamic (cf. Kritz, 2017). It varies at least somewhat unpredictably depending  
 261 upon the enaction of base incorporation into the elongating DNA molecule. This enactivity itself  
 262 modifies both the base availability pool and the functionality and thermodynamic tolerances of  
 263 the molecule. I use this example, because it demonstrates that base substitution during evolution  
 264 is not a stationary process, as neo-Darwinian reductionist molecular phylogenetic analyses

265 idealize (Hershkovitz, 2018a). This nonstationarity itself contributes significantly to unexpected  
 266 observations ('conflict'). However, this nonstationarity characterizes evolution of biological  
 267 systems at *all* hierarchical levels, yielding EI.

268         Also not initially appreciated, PEI proved to be consilient with a previously and  
 269 independently developed (and as-yet unpublished) model of species called the '**Wave Model**'  
 270 (summarized in Hershkovitz, 2019). The Wave Model is not a species concept, but an attempt to  
 271 describe and explain how entities perceived and named taxonomically as species (more  
 272 heuristically as 'specioids;' Hershkovitz, 2019) form and degenerate in the *perceptual*  
 273 dimension. Species ontology must be resolved in the perceptual dimension, because they have no  
 274 established ontology in any material dimension. Yet all phylogenetic and tree-based  
 275 macroevolutionary analyses use species as operational taxonomic units. These necessarily are  
 276 perceived and not materially real units. The Wave Model attempts to model what it is about  
 277 relations among individuals that cause them to be perceived as species by any material criterion.

278         The Wave Model compared the perception of species to the perception of water waves.  
 279 The relations 'individual/species' and 'water/wave' have several ontological and ontogenetic  
 280 similarities. Water waves, as it turns out, can be described as fractals, which are chaotic  
 281 functions. They also possess rudiments of autopoietic activity. This should not be surprising,  
 282 since life itself evolved in an aqueous environment likely facilitated by wave action. Perhaps not  
 283 coincidentally, organisms *remain* composed mainly of water. In any case, the characteristics of the  
 284 Wave Model suggest that it is a lemma of PEI.

285         The Wave Model demonstrates that it is the reductionist idealization of species as  
 286 discrete entities that has yielded the plethora of 30-some species concepts, none of which 'work.'  
 287 The taxonomic 'goodness' of species seems to be analogous to the perceived discreteness of

288 waves. And, similar to water molecules in waves, individuals perceived as conspecific need not  
289 share the same historical trajectory. (This is unless shared history is obligated by the species  
290 concept itself, as in cladistic species concepts, which are untenable.) Finally, HersHKovitz (2019)  
291 discussed evidence that corroborates the prediction that, just as not all water can be classified  
292 into waves, not all individuals can be classified into species. These conclusions are significant,  
293 because reductionist ecological and evolutionary analyses treat species as effectively  
294 independent and identically distributed entities (HersHKovitz, 2019).

295         PEI addresses another dimension of phylogenetic conflict not discussed by Olmstead and  
296 Medoya (2019). This conflict burdens reductionist tree-based macroevolutionary analysis, also  
297 known as ‘phylogenetic comparative analysis.’ In this realm, exemplified by Nürk et al. (2019),  
298 some ‘A’ is explained in terms of its phylogenetic correlation with some ‘B,’ where ‘A’ and ‘B’  
299 might be variously a phenotypic or ecological trait or simply a difference in the number of extant  
300 descendent taxa. Here, phylogeny actually *matters*, viz., as the scaffolding for hypothesis-testing.  
301 Otherwise, phylogeny per se is innocuous. Yes, phylogenies provide an objective basis for  
302 taxonomy. But towards the objective of marketing phylogenetics in the modern reductionist  
303 institution, its utility in taxonomy is not a great selling point.

304         Tree-based macroevolutionary analysis generates multiple layers of conflict/uncertainty.  
305 One form is inherited from the imported phylogenetic tree, as estimation procedures and  
306 statistical tests are sensitive to both tree topology and branch lengths and their certainties.  
307 Another arises, as in phylogenetic reconstruction itself, methodologically. All other things being  
308 equal, different data/methods disagree whether or not ‘B’ explains ‘A.’ This generates conflicts  
309 essentially identical to those in taxonomic phylogenetic reconstruction, because they trace to  
310 conflicting reconstructions of the evolution of ‘A’ and ‘B.’

311 As an aside, in the neo-Darwinian reductionist framework, a peculiar relationship exists  
312 between phylogenetic reconstruction data and phylogenetic comparative data. Phylogenetic  
313 analysis optimizes by minimizing character conflict, and this, in turn, minimizes homoplasy.  
314 Strength of correlations in phylogenetic comparative analysis, in contrast, *increases* with  
315 homoplasy of analyzed traits. This, in turn, maximizes the number of times those traits can *co-*  
316 *evolve* independently. Thus, evolution seems to stymie its own analysis. Minimal character  
317 conflict maximizes phylogenetic resolution, but constrains statistical tree-based evolutionary  
318 analysis. Maximal character conflict maximally potentiates statistical tree-based evolutionary  
319 analysis at the expense of phylogenetic certainty. It is as though, reminiscent of the Uncertainty  
320 Principle in physics, evolutionary history cannot be simultaneously precisely ‘known’ and  
321 ‘understood.’

322 From a theoretical standpoint, however, the most serious conflicts emergent in tree-based  
323 macroevolutionary analysis are the exceptions to inferred phylogenetic correlations between ‘A’  
324 and ‘B.’ This is analogous to conflict in the inferred phylogenetic relationship among taxa.  
325 Likewise, this conflict persists even in the case where all data/methods infer the same  
326 phylogenetic correlation, just as different data/methods may agree in ambiguity of support for  
327 particular phylogenetic relations.

328 Scrutiny of tree-based macroevolutionary analyses reveals that study organisms and traits  
329 commonly are cherry-picked for a priori high correlative potential, and the data then are  
330 ‘massaged’ to maximize it (Herskovitz, 2018b). Yet, invariably, taxa within the study group  
331 (and more outside of it) either behave contrary to the expectation or manifest ‘A’ *or* ‘B’ but not  
332 both. It is as though the taxa, not having studied Darwin, evolved *wrong*. In some cases, I have  
333 found independent analyses that conclude that the same ‘A’ evolved in response to some ‘C,’

334 with no mention of ‘B’ at all (Herskovitz, 2019).

335           These exceptions are what demonstrate that ‘A’ and ‘B’ are neither necessary, nor  
 336 sufficient, to ‘drive’ evolution in a predictable way (Herskovitz, 2018b, 2019). To appreciate  
 337 this, phylogenetic comparative analysis is no different from any other statistical application.  
 338 Effectively, it reduces evolution to coin-flipping, where the coins are taxa. At least in Modern  
 339 Synthesis population genetics, empirically observed ‘fitness’ is supposed to discriminate the fate  
 340 of individuals in trait classes. But, in tree-based macroevolutionary analysis, what is the  
 341 differential fate of taxa that buck the inferred evolutionary correlation? Are they less fit? The  
 342 organisms themselves seem to go on living and reproducing just fine. Herskovitz (2018b)  
 343 suggested that, but for twists of fate, induced correlations might have been nullified or even  
 344 reversed.

345           But the fatal flaw of the tree-based macroevolutionary paradigm is epistemological, not  
 346 methodological. It is consequent to the Darwinian idealization of organisms as passive actors,  
 347 evolution’s flipped coins. This ignores or effectively or explicitly denies the autopoietic property  
 348 of life. And, not coincidentally, the flaw is consequent to the Darwinian idealization of  
 349 phylogeny as bifurcating lines (a tree) and diversification events and species as ‘points.’  
 350 Barcodes, anyone? As suggested by Herskovitz (2018b), these erroneous Darwinian  
 351 idealizations underwrite the reductionist tree-based macroevolutionary paradigm. They justify, in  
 352 fact *obligate*, the successive and recursive statistical reduction of phylogenetic and taxonomic  
 353 complexity. This, in turn, partitions observations into those that concord with the presumed  
 354 phylogeny or evolutionary process and those that do not. And *this* is the source of the ‘conflict’  
 355 over which Olmstead and Medoya (2019) agonized. Evolution did not create it. Darwin did.

356           As Olmstead and Medoya (2019) noted, conflicting data typically are explained by



357 appealing to one or a few simultaneous evolutionary processes bound to generate different data  
358 patterns. But there seems to be projected a sense that one process is ‘good’ and the other ‘evil,’  
359 i.e., the one that is generating the conflict. There never is projected a sense that the mythical  
360 Darwinian clado-anagenetic process might be the culprit. And there is not at all a projected sense  
361 that a *singular* process might be generating *all* the data. In theory, evolution of incongruent data  
362 should subside only when phylogenesis and evolution *stop*, so that diversification no longer  
363 creates the specter of, e.g., hybridization or lineage sorting. *Ginkgo biloba* comes to mind.  
364 Paradoxically, this obviates phylogenetic and tree-based macroevolutionary analysis.

365         Despite appearances, this commentary in no way disparages one of history’s most  
366 perceptive and rational naturalists and, by the way, also a *taxonomist*. Darwin’s contribution was  
367 singular towards bringing then ‘Natural Theology’ belatedly into the Age of Enlightenment. But,  
368 while rational in its evident appeal to Newton’s notions of motions, Darwin’s evolutionary  
369 theory overshot the mark. Indeed, environmental forces influence the course of evolution, but  
370 they are not behind the wheel. Post-Newtonian metamorphoses of mathematics, physics, and  
371 astronomy do not diminish Newton, and neither should new evolutionary theory diminish  
372 Darwin.

373         Unfortunately, mainstream tree-based macroevolutionary theory does not seem to be  
374 advancing beyond Newtonian mechanics. Nürk et al.’s (2019) new ‘Evolutionary Arena’ (EA)  
375 platform, for (and not to single out this) example, provides not a new way of thinking about  
376 evolution, but a new way of thinking the old way. If anything, EA seems to be retrogressive, apt  
377 to overshoot Newton’s orbit on a collision course with astrology. In particular, based on  
378 discussion in Herskovitz (2018b, 2019), it seems inevitable that conclusions will vary wildly  
379 depending upon, e.g., which few among infinite ‘arena’ parameters are analyzed, which is used

380 among several artificially linearized phylogenies, which is used among various age estimate  
381 extremes, how among different ways phenotypic, genotypic, and environmental variables are  
382 described/measured, and which ‘method’ is applied. And this will be true even in the case that  
383 evolution is strictly stochastic. Between this and ignoring autopoiesis and chaos and hierarchy  
384 theory, in terms of predictive power, EA might just as well incorporate the celestial charts on the  
385 day the taxa were ‘born.’

386         PEI provides an alternative framework for conceptualizing and analyzing evolution.  
387 Under PEI, the notion of conflict can be replaced with the notion of complexity. In particular, the  
388 ‘true’ phylogeny of an equivocally resolved node such as that highlighted by Olmstead and  
389 Mendoya (2019) is *not* one or another of its linearized resolutions, but the composite of all such  
390 resolutions, or its complexity. However, under PEI, macroevolutionary analysis needs to take a  
391 different trajectory altogether. Arguments that the evolution of some ‘B’ explains the evolution  
392 of some ‘A’ are specious postdictions.

393         PEI might be criticized for its current lack of an analytical heuristic. This criticism is  
394 spurious. It took more than a century for evolutionary biology to develop the heuristics for  
395 analyzing Darwinian macroevolution, viz., phylogenetics, molecular genetics/genomics, and the  
396 phylogenetic comparative method. And 160 years on, the best heuristics remain, at best, dicey.  
397 For example, towards the objective of conflict resolution, modern phylogenetic and tree-based  
398 macroevolutionary heuristics emphasize Bayesian methods. It should be emphasized that the  
399 procedures do not *alter* discordant empirical data patterns. They provide algorithms that  
400 simultaneously iteratively optimize and weight the optimization, such that conflicting data  
401 effectively are sublimed. A critique is beyond the scope of the present commentary (see  
402 HersHKovitz, 2018a, 2019), except to say that the methods demonstrably are less reliable than a

403 Boeing 737 MAX.

404           Herskovitz (2018b) tendered suggestions for rudimentary development of EI analytical  
405 heuristics. These involved nonlinear mathematics, evaluation of performance of linear methods  
406 in reconstruction of idiosyncratic (chao-stochastic) phylogenetic functions (i.e., fractals), and  
407 epistemological hypothesis manipulation. For example, the NS paradigm considers random  
408 evolution as the null hypothesis ( $H_0$ ). But, epistemologically, NS appears to be  $H_0$ , because it is  
409 the expectation, i.e., the default explanation for departures from randomness (cf. Popper, 1976  
410 [2002]). Under EI, evolution has a determinate trajectory that might resemble NS. Because truly  
411 random evolution is *unexpected*, it is not  $H_0$ , but  $H_1$ , equivalent to NS. Additional study by  
412 qualified theoretical/philosophical biologists should help advance an EI heuristic. However,  
413 Darwinian reductionists should not expect that these heuristics will be designed to resolve linear  
414 cladograms or test Darwinian evolutionary hypotheses, because these models are unrealistic.

415           In the meantime, what is to be believed about the ‘tree of life?’ Is it wrong? Yes and no.  
416 As Podani (2019) emphasized, its idealization as a tree is overly simplistic, even if it has treelike  
417 Gestalt. Nodes such as that discussed by Olmstead and Medoya (2019) are wrong not in the  
418 sense that they are resolved incorrectly, but in the sense that they *cannot* be so resolved. No  
419 bifurcate resolution accurately describes the phylogenetic relations of those taxa. But what about  
420 apparently well-resolved nodes in the ‘tree of life?’ While still overly simplistic, in many cases,  
421 these can be accepted tentatively as historically informative *if* they are consilient. Consilience  
422 means that the same nodes emerge from analysis of different data from different organizational  
423 levels and using epistemologically distinct approaches (e.g., maximum likelihood and maximum  
424 parsimony) across broad parameter ranges. These nodes thusly, in Popper’s sense, best survive  
425 refutation.

426           Unfortunately, the tree-based reductionist macroevolutionary paradigm does not fare so  
427 well, and it is not clear whether it can be salvaged. Mainly this owes to its Newtonian  
428 interpretation of organisms. But even ignoring this, there are many other reasons, one of which is  
429 its dependence on reductionist and inherently inaccurate phylogenetic trees. And even ignoring  
430 this, existing analyses are wanting for both resistance to refutation (e.g., taxa bucking  
431 correlations and independent analyses yielding conflicting conclusions) and technical  
432 competency of analyzed data. HersHKovitz (2018a, 2019) highlighted examples involving  
433 Portulacineae, but these are typical of the paradigm more broadly (e.g., Wenzel and Carpenter,  
434 1994; Franz and Engle, 2010). Even if evolution were purely stochastic and linear, vices and  
435 artifices of existing macroevolutionary analyses likely would invalidate the conclusions of most  
436 published studies. Moreover, not even the data from such studies can be rescued, because, per  
437 the reductionist assumptions, they emphasize biologically meaningless phenotypic ‘means’ of  
438 species, and often equally meaningless means of environmental variables, such as macroclimatic  
439 mean annual temperature and precipitation. There also is a tendency to reduce parameter states  
440 arbitrarily and biologically unrealistically for statistical expedience. Such reductions might be  
441 justifiable in the case of nucleotide bases and amino acids, but they are not in the case of  
442 complex phenotypes.

443

444   **Conclusion: *Time to bail on Darwin?***

445           Returning to Olmstead and Medora’s (2019) lamentation on the persistence of  
446 phylogenetic conflict into the age of phylogenomics, the main counterpoint offered here is that  
447 ‘conflict’ in phylogenetic reconstruction *and* tree-based evolutionary analysis is not in the data,  
448 but in the epistemology. Given what we know about organisms, we should not expect all data to

449 support a single linear and bifurcating cladogram, or, in many cases, even a single best-resolved  
 450 one. Moreover, even a single best-resolved tree is not the ‘true’ one. Thus, what is perceived as  
 451 conflict is merely a consequence of overzealous tree-thinking. Characters conflict because we  
 452 *think* they do. This is Darwin’s legacy. And it is part and parcel of his widely accepted rational  
 453 Newtonian explanation of the Grand Design of life, viz., natural selection.

454         PEI emerges as a consilient evolutionary model that demonstrates that the error of tree-  
 455 thinking is precisely its simplistic, reductionist, and linearized cladistic idealization of  
 456 evolutionary history and its nondimensional idealization of cladogenesis and species. In fact,  
 457 *both* are asymptotically complex and maximally dimensional. This is precisely the ‘what’ of  
 458 biological evolution, the reason why we study it in the first place, and even the reason why *we*  
 459 *are here* to study it in the first place.

460         PEI does not conflict with ‘descent with modification,’ but it recognizes that organisms  
 461 are autopoietic, that their self-determinacy renders their evolution not utterly stochastic and at  
 462 least partially chaotic, and that their hierarchical organization permits decoupling of the  
 463 evolutionary history of organismal traits. With PEI, we can appreciate that characters conflict on  
 464 linearized trees because *they damn well can*. These properties that yield EI also likely canalize  
 465 the generation of ‘statistically significant’ phylogenetic patterns. But, like fractals, the patterns  
 466 have no *proximal* cause, i.e., there is no NS.

467         Theoretical advances in biological epistemology may present a dilemma for  
 468 systematic/macroevolutionary biologists. These advances suggest that the Darwinian model of  
 469 evolution is false, or at the very least, far too simplistic to serve the discipline usefully. But all  
 470 current heuristic methodology assumes Darwinian evolution. Should the mainstream empirical  
 471 systematics/macroevolutionary discipline bail on Darwin and be left you-know-where without a

472 paddle? Or should the band continue to play on a sinking ship and publish results and  
473 conclusions predicted to be invalid/erroneous? If, like NS, we establish that there is no Santa  
474 Claus, should we continue to explain how he delivers toys to a billion children across the globe  
475 in just one evening?

476 As Olmstead and Medoya (2019), among others, make clear, already it is clear that  
477 Darwinian phylogenetic conceptualization is obsolete. At the very least, contemporary  
478 systematic and macroevolutionary biology would do well to reconsider its obsession with tree-  
479 thinking and resolving definitively a bifurcate ‘tree of life.’ Evolution, like a forest, evidently is  
480 more than the sum of its trees.

481

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