1   **Perspectives from Montiaceae (Portulacineae) Evolution. I. Phylogeny and Phylogeography**

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7   **ABSTRACT**

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9   Montiaceae comprise a clade of at least 270 species plus about 20 accepted subspecific taxa,

10   primarily of western America and Australia. The present paper is the first of a two-part work that

11   seeks to evaluate evolutionary theory via metadata analysis of Montiaceae. In particular, it uses

12   metadata analysis to evaluate the theory in theory-laden methods that have been applied in

13   evolutionary analyses of Montiaceae. This part focuses on phylogeny and phylogeography. The

14   second part focuses on phenotypic and ecological diversification. An emergent theme in this paper is

15   the degree to which historical idiosyncrasy during Montiaceae evolution misleads quantitative

16   methods of evolutionary reconstruction and phylogeographic interpretation. This suggests that

17   idiosyncraticity itself is a fundamental property of evolution. The second part of this work elaborates

18   this notion as the Principle of Evolutionary Idiosyncraticity. The present part describes

19   idiosyncraticity in molecular phylogenetic and phylogeographic data and uses this notion to refine

20   ideas on Montiaceae evolution. Phylogenetic metadata conflicts and conflicting phylogeographic

21   interpretations are discussed. I conclude that, owing to PEI, quantitative methods of evolutionary

22   analysis cannot be globally accurate, though they are useful heuristically. In contrast, classical

23   narrative analysis is robust in the face of PEI.

24   **KEY WORDS:** Montiaceae, phylogeny, phylogeography, long-distance dispersal, idiosyncrasy,

25   Principal of Evolutionary Idiosyncraticity.

26

27   **BACKGROUND**

28

29   Montiaceae (Portulacineae) comprise a clade of ca. 270 largely herbaceous (rarely suffruticose or

30   pachycaul) species and ca. 20 additional subspecific taxa distributed mainly in western America, with

31   additional endemism in eastern North America, Siberia, Australia, New Zealand, and the Kerguelen

32   Islands. A current taxonomy of the family, applied in this work, is elaborated in [1]. Over the past three

33   decades, Montiaceae have been subjected to several evolutionary analyses. These analyses provide the

1   metadata in the present synthesis of "whole taxon" evolution. This text is the first of a two-part work that

2   critically reviews of aspects of evolutionary theory and analysis as viewed from the perspective of

3   metadata analyses of Montiaceae. This part focuses on phylogeny and historical biogeography. The

4   second part [2] focuses on the relation between phenotypic, genomic, and ecological evolution.

5   A recurring theme in this work is the extent to which conventional epistemological approaches to

6   Montiaceae evolutionary analyses have failed to predict empirically observed exceptions to their explicit

7   or implicit evolutionary rules. The epistemological approaches have optimized evolution according to one

8   or another monotonic function or criterion, either a likelihood function of a presumed evolutionary model

9   or a parsimony criterion. In individual studies, observations not conforming to the assumptions of the

10   model or criterion appear as data "idiosyncrasies." In evolutionary analytical practice, these

11   idiosyncrasies tend to be variously overlooked, observed but disregarded, or explained *ad hoc*. But what

12   is impressive is that idiosyncratic data behavior seems to emerge in all evolutionary analyses. This

13   suggests the possibility that idiosyncrasy itself is a pattern in evolution, and this is the thesis defended

14   here.

15   The present work and [2] are entitled "Perspectives *from*…" rather than "Perspectives *on*…" for a

16   reason. Indeed, they provide perspectives "on," but the effort is motivated more by what metadata

17   analysis of Montiaceae indicates about the evolutionary process in general. Rather than impose theoretical

18   and methodological dogma on the data, I attempt to let the data explain themselves. The main reason for

19   idiosyncratic data behavior (aside from data error) owes not per se to model or criterion imprecision or

20   misspecification, but to the idiosyncraticity of evolution itself. The second part of this work [2] describes

21   this as the Principle of Evolutionary Idiosyncraticity (PEI), and argues that PEI applies not only to data

22   that do not conform to the presumed optimization model or criterion, but to those that do, as well. The

23   latter simply are equivalent to localized "replicate" data that happen to predominate in many data sets,

24   sometimes because of subliminal bias to select such data sets for analysis. These create the (pseudo-

25   )patterns that seem to implicate commonality of process (e.g., cladogenesis). Presumed commonality of

26   process, in turn, forms the basis of evolutionary analytical models or criteria. The model or criterion then

27   straightjackets evolutionary analysis and interpretation, i.e., what seems to have happened most of the

28   time should happen all of the time. The second part of this work [2] explains PEI in terms of chaos theory,

29   stochasticity, and non-Darwinian evolutionary theory. And it demonstrates that PEI manifests in other

30   evolutionary analyses, as well, including *in vivo* evolutionary experiments.

31   This part begins with an evaluation of phylogenetic analyses of Montiaceae. Here first emerges

32   the dilemma consequent to application of linear models to analyze idiosyncratic processes. Conventional

33   methods of phylogenetic analysis presume a linear process and, accordingly, intrinsically impose this

34   order on data analyzed and occlude evidence for evolutionary idiosyncraticity. The present biogeographic

1   analysis of Montiaceae then emphasizes the idiosyncratic origin of biogeographic "pseudopattern."

2   Superficially, Montiaceae distributions appear to conform with an origin prior to the Pangaean or

3   Gondwanan breakup. But phylogenetic dating estimates indicate that transcontinental disjunctions reflect

4   numerous more recent long distance dispersal (LDD) events. The significance of these results in the

5   context of phylogeographic theory is elaborated.

6

7   **PERSPECTIVES FROM CURRENT EVIDENCE FOR MONTIACEAE PHYLOGENY**

8

9   This discussion does not cover each resolved and unresolved node of Montiaceae phylogeny. It

10 emphasizes aspects of the phylogeny that reemerge in subsequent discussion of phenotypic, genotypic,

11 and phylogeographic evolution. But I also discuss here aspects of phylogeny per se as they manifest

12 idiosyncrasy in phylogeny and evolution of the gene sequences used to reconstruct it. For example, a re-

13 emerging pattern in Montiaceae molecular phylogeny is clusters of shorter branches separated by fewer

14 longer ones. The significance of this pattern will be discussed in terms of assumptions of phylogenetic

15 reconstructive methods and implications for interpretation of genotypic and phenotypic evolution. I also

16 highlight idiosyncratic taxon origins, i.e., the significance of the origin of taxa whose phenotypes depart

17 markedly from those of their broader clade. The significance of apparent conflicts among genomic data

18 sets also is discussed.

19

20   **Montiaceae circumscription, sister-group, and backbone phylogeny**

21

22   Cladistic morphological analyses of Carolin [3, 4] and Hershkovitz [5, 6] radically modified

23 classical taxonomy of Portulacaceae [7, 8]. Especially Hershkovitz [6] emphasized evidence for a clade

24 comprising the taxa diversified mainly in far-western America and Australia ("western American

25 Portulacaceae"). Molecular phylogenetic analyses [9, 10] confirmed the major conclusions of the

26 morphological analyses and identified a clade comprising western American Portulacaceae plus the genus

27 *Phemeranthus*. The latter conventionally had been classified in the genus *Talinum*. Applequist et al. [11]

28 and Wagstaff & Hennion [12] later demonstrated that Hectorelleae are nested in this clade. Nyffeler &

29 Eggli [13] later classified this clade as Montiaceae. This classification is currently broadly accepted [14].

30 The present work and [2] follow taxonomy slightly modified from [1]. Full authored names of subgeneric

31 taxa are provided at the end of this text.

32   Analyses based on multiple markers [15-18] strongly support a sister relation between

33 Montiaceae and a clade comprising all other taxa of Portulacineae. The latter clade comprises seven

1   families, three of which, like Montiaceae, are segregates of classical Portulacaceae [14]. Portulacineae is

2   sister to the current circumscription of Molluginaceae [15-18].

3   Preliminary DNA analyses of Montiaceae [9, 10, 19] revealed high divergence among generic-

4   level clades but low divergence within several of them. Interspecific divergence/resolution was minimal

5   within subclades *Cistanthe*, *Calyptridium*, *Calandrinia*, and *Montiopsis*. Similar minimal

6   resolution/divergence was reported for a large *Phemeranthus* subclade [20]. At the other extreme, few-

7   locus divergence/resolution is greatest among *Montia* and many annual *Claytonia* species [21]. This result

8   seemed peculiar, given that Montieae are the most recently diverged clade of Montiaceae. However, there

9   is little divergence/resolution between and among the caudiciform and tuberous *Claytonia* species, which

10 had been classified in different sections [21, 22]. A phylogenomic analysis of 297 loci yielded a relatively

11 highly resolved tree of 77 samples of *Rumicastrum* comprising all 48 described species plus several

12 putative ones [17]. This may indicate that phylogenomic approaches will yield comparable resolution in

13 as yet poorly resolved nodes.

14   Ogburn & Edwards [16] reanalyzed Montiaceae phylogeny with additional DNA sequence

15 markers and more recently developed implementations of both maximum likelihood (ML) and Bayesian

16 phylogenetic estimation (BE). They analyzed two data sets: an 89-terminal three-marker set (plastome

17 *trn*K–*mat*K and *ndh*F; nucleosome *phy*C); and a 142-terminal five-marker set (the preceding plus

18 plastome *ycf*3-*trn*S spacer and nucleosome rDNA-ITS).The latter dataset included earlier data of [19].

19 These markers are more variable than the others at the interspecific level. Not all sequences were

20 available for all samples.

21   Smith et al. [18] included 207 Montiaceae samples in a nearly 5000-taxon phylogenetic analysis

22 of Caryophyllales. They incorporated data from plastome *mat*K, *ndh*F, *rbc*L genes and *trn*H-*psb*A and

23 *trn*L-*trn*F spacers, and nucleosome rDNA-ITS and *phy*C. Again, not all markers were available for all

24 taxa, though this hardly matters for the more highly conserved ones. Smith et al. [18] used an analytical

25 protocol optimized for large datasets [23]. Their protocol uses ML trees derived from bootstrapped data to

26 simultaneously optimize the full data ML tree and estimate edge support via an approximate likelihood

27 ratio test. Under ideal circumstances, these edge support values approximate conventional bootstrap

28 values [23], but these conditions are not met in the case of Montiaceae phylogeny (see below).

29   Hancock et al. [17] included samples of most major Montiaceae clades in their phylogenomic

30 analysis of the thoroughly sampled *Rumicastrum*. They analyzed four datasets extracted from a total 297

31 loci comprising more than 3×10^5 DNA base pairs. The datasets differed according to a criterion of

32 higher/lower proportions of loci/sites shared among higher/lower proportions of sampled individuals.

33 Each dataset was analyzed using two methods, one as in [18] and the other a coalescence-based approach.

34 Thus, the analysis includes a total of 12 data/method combinations. They also performed a Bayesian

1 analysis of phylogenetic concordance among loci, which estimates the proportion of total loci that support

2 conflicting topologies.

3   The present discussion will emphasize especially the results of Ogburn & Edwards [16] and,

4 where conflicting, Hancock et al. [17]. The Smith et al. analysis [18] will not be emphasized, because it

5 was optimized for sampling of all Caryophyllales and not, specifically, Montiaceae, and because of

6 possible methodological artifacts. Hancock et al. [17] might share these artifacts, but their principal

7 results agreed using three very different methods. However, the coalescent and Bayesian concordance

8 methods they applied are relatively new, as are phylogenomic sampling methods generally.

9 Unfortunately, the data and methods themselves become too complex to scrutinize by eye. Current

10 methodological emphasis is on analytical speed and data quantity and the statistical preponderance of

11 recovered clades, with the hope that preponderance alone obviates the need for detailed scrutiny.

12   Using the taxonomy in [1], and with caveats discussed below, current molecular phylogenetic

13 evidence suggests the following [16: *Fig. 2*; 17: *Figs. 3-4*]:

14   1. *Phemeranthus* as the outgroup of the remainder of Montiaceae. This accords with

15   morphological and phylogeographic evidence, as will be discussed in a later section.

16   Hershkovitz [1] classified *Phemeranthus* and *Schreiteria* in Phemerantheae.

17   2. Divergence/diversification of Cistantheae, a principally Chilean (semi-)arid region lineage

18   that includes: (a) *Cistanthe*; (b) *Montiopsis*; and (c) Calyptridinae, comprising *Lenzia*,

19   *Calyptridium*, and *Philippiamra*.

20   3. Monophyly of Montioideae, a morphologically/ecologically more diverse and geographically

21   more broadly distributed lineage comprising the remaining Montiaceae.

22   4. *Calandrinia* and *Rumicastrum* as the successive outgroups of remaining Montioideae. One of

23   the 12 data/method combinations in [17] yielded maximal support for a conflicting topology,

24   in which *Calandrinia* is sister to Cistantheae.

25   5. Hectorelleae as sister to the preceding. Support for this relation degenerates markedly in the

26   five- compared to the three-marker data [17], but no Hectorelleae data were available for ITS

27   of *ycf*3-*trn*S. This suggests that the inclusion in the latter of more rapidly-evolving markers

28   introduced not conflict, but noise that perturbed the BPs and PPs

29   6. Divergence/diversification of Montieae, a principally western North American lineage

30   including *Lewisiopsis*, *Lewisia*, *Claytonia*, and *Montia*.

31   7. The uncontroversial sister relation of *Claytonia* and *Montia*, often classified as Montieae, but

32   here classified as Montiinae.

33   All of the preceding are recovered in all but one of the 12 phylogenomic analyses [9], but there is

34 significant discrepancy in support for these in the three-marker versus five-marker data sets of [16].

1   Backbone branches in the three-marker set are recovered mostly with very high to maximum ML

2   bootstrap proportions (BP) and BE posterior probability (PP) values. These backbone branches are

3   unresolved in [19]. The five-marker data set incorporates data from [19]. Oddly enough, support for most

4   of the backbone degenerates. BP values fall, in several cases to below 70% and, in some, to below 50%.

5   Likewise, PP values decline nontrivially, some to below 50%. The interpretation and/or reliability of both

6   of BPs and PPs in the context of phylogenetic analysis have been a contentious theme (see below). In any

7   case, increasing data size ought to maintain or increase BP/PP values. The observed decreases, even slight

8   ones in the case of PPs, suggests that something is "wrong."

9   Ogburn & Edwards [16] acknowledged, but did not explain, discrepancies between their two data

10   sets. It resembles dataset conflict, where the data reflect different histories, as can occur with

11   hybridization. The possibility might be explored by analyzing the three plastome and two nucleosome

12   markers separately (see also below). Another possible source of discrepancy is methodological.

13   Hershkovitz [19] analyzed the ITS data using maximum parsimony (MP), especially in order to

14   accommodate information from coded indels. Ogburn & Edwards [16] used an ML protocol, which does

15   not accommodate indel data. But these differences do not explain the discrepancy in Ogburn & Edwards'

16   [16] two analyses.

17   It should be reiterated that BP and PP values estimate different aspects of tree reliability.

18   Interpretation of BPs in phylogenetics [24] is not straightforward [25-31]. Theoretically, they are not

19   probabilities, but confidence intervals (but see [29]). However, BPs generally are considered to be

20   conservative predictors of tree reliability. Of course, the bootstrap can be no more consistent statistically

21   than the tree reconstruction procedure it applies. While PPs are considered to represent (estimates of)

22   conventional probabilities of clades, they are known to be severely overestimated in certain circumstances

23   [26, 30-32]. Nonetheless, coincidence of high BP and PP values has been considered to be a reassuring

24   measure of tree reliability [27] - unless, of course, both happen to be coincidentally misleading. The latter

25   possibility emerges in the case where the evolutionary process violates the assumptions of the analytical

26   model or criterion. This can cause BP and PP values to behave inconsistently, i.e., indicate high support

27   for the wrong result. This model/criterion misspecification may be global across all the data, but, as

28   discussed below, more likely it is local, yielding inconsistency in part of a phylogenetic tree but not all of

29   it.

30   It must be stressed also that the mere specification of estimation method (e.g., MP, ML, BE, and

31   alignment methods), credibility measure and values (e.g., BP, PP), and computer programs are not

32   sufficiently informative to judge the reliability of published phylogenetic trees and statistics. Methods are

33   distinct theoretically and their implementations are distinct in practice. All methods make assumptions

34   about the analyzed data, and implementations generally permit considerable user manipulation. BE

methods are the most variable theoretically/methodologically and the most contentious philosophically. To paraphrase Dragicevic [33], computer methods and results should be used to augment-not substitute for-human cognition.

The discrepancy between three-maker and five-marker results in [16] might owe to idiosyncrasies in molecular evolution that violate the assumptions of the statistical phylogenetic analysis methods. However, all of the assumption violations are parametric components of one single assumption: that evolution is a linear process. As elaborated especially in the second part of this work [2], this assumption is questionable and probably wrong. Idiosyncraticity emerges a property of a nonlinear stochastically-perturbed chaos-like process. It yields known or plausible phenomena not predicted by standard statistical analytical methods. Standard methods correct only for certain statistically detectable patterns of substitution bias evident in comparative DNA sequence analysis (e.g., [34]). There are caveats, often ignored in method application (see, e.g., [27]). A few caveats relevant to the present problem include:

1. Commonly implemented methods do not correct for all known sources of substitution bias (e.g., consequent to DNA/RNA secondary structure), nor other idiosyncratic features of DNA sequence evolution not detectable statistically and/or not corrected in existing computational methods. Conventional methods apply a general time-reversible base substitution model with corrections for base compositional bias and among-site rate-heterogeneity [34].

2. Statistical precision in those substitution biases methodologically estimated is contingent upon maximal DNA sequence sampling and maximal DNA divergence among sequences. This sampling-divergence breadth, in turn, increases the likelihood of occurrence of localized idiosyncratic and/or uncorrected substitution biases. But implemented methods estimate and apply uniform (stationary) substitution models over the entire phylogeny, thus ignoring local variation. Nonstationary models exist, but they present both technical and theoretical problems. Most importantly, they converge on branch-specificity of models, which is the same as absolute idiosyncrasy of molecular evolution or, effectively, no statistical model at all [34].

3. ML phylogenetic analysis ignores variance in those substitution biases estimated. BE methods permit but do not obligate incorporation of such variance in PP calculation (but see above).

4. Even if substitution bias were a linear and uniform process, accurate phylogenetic estimation is compromised by inadequate phylogenetic signal along internal branches and algorithmic determination bias [23].

5. Statistical DNA phylogenetic reconstruction restricts analysis to (putatively) aligned substitutions and ignores informative indel characters. The latter can be numerous especially in intron and ribosomal DNA sequences.

6. Under the best of possible circumstances relating to the preceding, accuracy of phylogenetic estimation remains compromised by discrepancies between gene and organism phylogeny (hybridization and lineage sorting; see below), as well as certain extreme branch length-associated artifacts.

The articulation above is not gratuitous (nor exhaustive). Studies of Portulacineae and their DNA sequences [9, 10, 19; Hershkovitz, unpublished data] yielded evidence of such violations of methodological assumptions. Implemented methods may well be robust to most assumption violations and/or in most of the resultant phylogenetic resolution. But no methodology exists to detect localized failures. Conflicts emerging from different analyses provide a clue. Possible causes of this conflict are articulated below.

Hershkovitz & Zimmer [9] illustrated base compositional bias in ITS across Portulacineae. GC content of variable sites varied about two-fold across the order, highest among "anacampseroid" taxa (Anacampserotaceae; [14]) and lowest in the genus *Claytonia*. Among Montiaceae, the difference is about 50%, the highest GC values among Cistantheae, with a phylogenetic trend in Montioideae towards the minimal values in *Claytonia*. Consequently, the base substitution kinetics among *Cistanthe* and Montioideae cannot be the same. Base compositional bias was not examined in plastomic *ycf3-trnS* data [19], although, like plastomic sequences in general, these have <50% GC content.

Considerable overall substitution rate heterogeneity also is evident among Portulacineae, including among Montiaceae (see figures in [9, 10, 19]). Coincident with the change in base composition in Montioideae, their substitution rate increases. Based on phylogram branch lengths, the rate in *Claytonia* appears to be up to five times faster than among Cistantheae. Interestingly, this increase is evident in both the ITS and plastome data, though I have not analyzed base compositional nonstationarity in the latter. This contrast is especially evident in *Lewisiopsis*: its divergences from the root of ITS and plastome trees, as well as phylogenomic trees [17], are far less than for closely related taxa. This lower sequence divergence coincides with lower morphological divergence of *Lewisiopsis*: its morphology resembles that of *Cistanthe* sect. *Cistanthe* species [5, 6, 35, 36]. I explain this further below in the context of a hybrid origin of *Lewisiopsis*. Overall substitution rate heterogeneity per se does not violate assumptions of substitution bias models. Its effect on phylogenetic analysis may emerge as a consequence of localized tree branch length asymmetry.

Another pattern evident from published phylograms especially of Montiaceae [19: *Figs. 1, 2*] is pervasive branch length asymmetry. In particular, there appear to be excess high and low divergences

1 relative to medium divergences. Internal branches along the backbone are short and unresolved, the

2 emerging branches longer, and interspecific level branches again short and unresolved. While sequences

3 of genera cluster, interspecific sequence divergence is extremely low, especially in *Cistanthe*,

4 *Calyptridium*, *Montiopsis*, *Calandrinia*, and (unpublished data) *Lewisia*. These asymmetries have several

5 possible causes, all of which violate analytical methodological assumptions. The pattern renders artifacts,

6 especially using the method applied by [18; cf. 23].

7   The asymmetries might be explained as molecular punctuated equilibria. In particular, especially

8 the ITS sequences apparently are functionally constrained (e.g. to maintain secondary structure and/or

9 genomic-level processes) such that particular sequence "morphologies" are evolutionarily more stable

10 than others. Evolution from one to another molecular morphology may involve a combination of

11 substitutions and insertions/deletions that fix rapidly in the genome. Thus, ITS sequences possess

12 phylogenetic signatures conserved hierarchically at remarkably deep phylogenetic levels [37-39]. But the

13 evolutionary steps between forms are not so conserved, yielding bushy phylogenetic trees.

14   The preceding suggests that ITS violates the single most important assumption of ML DNA

15 phylogenetic analysis: that the DNA sequence evolution process is uniform across the phylogeny (see

16 [23]. Thus, by increasing marker number, [16] may have added "noise" to "signal." This would predict

17 reductions in both the ML BP and BE PP values.

18   The analysis of [19] avoided this problem by employing only MP and incorporating discrete

19 multi-site indel data as characters. This avoided two problems: spurious alignment of length-variable

20 noncoding ITS and *ycf*3-*trn*S and sequence regions, and spurious imposition of locally erroneous

21 substitution models owing to nonstationarity. Relations along the backbone were "unresolved" as opposed

22 to spurious. This point is critical, because the virtue of global ML model s [40] becomes their weakness in

23 the case of nonstationarity. Nonstationarity might yield artifacts with MP, but MP formally is agnostic

24 towards substitution probability, whether stationary or not. At the same time, incorporation of indel data

25 contributed significantly to phylogenetic resolution at lower divergences. Here, divergence often owed

26 primarily or completely to length variation and rather than substitution.

27   Another explanation of the three- and five-marker tree conflict implicates lack of concordance

28 between gene and taxon trees. Hershkovitz [19], I emphasized that apparent rapid bursts of molecular

29 divergence coincided with those of morphological divergence, and suggested that the pattern might owe

30 to both contemporary and ancient factors that might decouple the gene and taxon trees, hybridization in

31 particular. In the case of the backbone, this may reflect rapid diversification within the ancient species

32 dimension. In that dimension, hybridization and lineage sorting would be expected. This also would

33 explain dataset-specific conflict. Whole-genome phylogenetic analyses are beginning to reveal heretofore

34 unappreciated degrees of hybridization and/or lineage sorting during the course of plant phylogeny, not

1　only among recently evolved species, but at what are now deeper cladogenetic levels (e.g., [41]. These

2　results impact not only interpretation of genealogy, but also phenotypic evolution, as elaborated more

3　below and in [2].

4　　　　　Nonetheless, until the conflict between the three- and five-marker trees can be satisfactorily

5　explained, choice between them is arbitrary and must be regarded as provisional. Ogburn & Edwards [16]

6　used the statistically less well-supported five-marker topology for their subsequent evolutionary analysis

7　of phenotype. The latter did, however, include protocols to account for a degree of phylogenetic

8　uncertainty. One would hope that any accommodation of phylogenetic uncertainty helps to avoid spurious

9　conclusions. However, while genotypes and phenotypes indeed are consequent to phylogeny,

10　phylogenetic trees and analytical derivations thereof are not. These are consequent to reconstructive and

11　interpretive methods and data accuracy. As emphasized repeatedly here and in the final section of [2],

12　quantitative methods are valuable heuristically, but they unavoidably canalize the truth that they seek to

13　discover.

14

15　**Phylogeny of Cistantheae**

16

17　　　　　The refutation in [19] of the earlier proposed generic circumscription of *Cistanthe* [5, 6] was

18　confirmed in [16]. In particular, [19] demonstrated that *Lenzia* is the sister taxon of a clade comprising

19　*Calyptridium* and *Philippiamra* (see [1]). Hershkovitz [5, 6] classified these genera in *Cistanthe*. This

20　clade, denominated the "*Philippiamra* lineage" in [16} is classified in [1] as Calyptridinae. But the

21　increased resolution of intergeneric relations in [16] revealed something new: a clade comprising

22　Calyptridinae and *Cistanthe* (*s. str.*) with *Montiopsis* nested therein. This result is strongly supported in

23　all of the phylogenomic analyses in [17]. All molecular analyses [9, 10, 19, 16, 18; but see below] have

24　refuted the inclusion of *Lewisiopsis* in *Cistanthe* [5, 6, 36]. However, phenetic similarity of both DNA

25　and morphology between *Lewisiopsis* and *Cistanthe* remains tantalizing, suggesting their similarity bases

26　on ancient homology rather than convergence (see also below).

27　　　　　The relations of *Lenzia* emergent in [19] were surprising. *Lenzia chamaepitys* is a peculiar plant

28　that bears no resemblance to other Calyptridinae. The plant resembles a small scaly cone, about 2 cm

29　high, the densely packed awl-like leaves markedly scarious and broadly membranous along both margins,

30　with the narrow mesophyll cladodromously vascularized. Reportedly the plants bear solitary, axillary

31　flowers, but I have never seen these. The plants evidently are clonal, connected by delicate rhizomes.

32　Hershkovitz [19] mentions that, if anything in nearby Montiaceae, *Lenzia* most closely resembles

33　acaulescent perennial alpine species of *Calandrinia* and perhaps also *Montiopsis* (subg. *Dianthoideae*)

34　*cistiflora*. Ecologically, *Lenzia* is distinctive in being restricted to the driest sector of the Andean alpine

1   zone, where the "arid diagonal" crosses the cordillera. Here, the high cordillera generally is at the limits

2   of the range of both the (southern hemisphere) summer Atlantic moisture arriving from the north and east

3   and the winter Pacific moisture arriving from the south and west.

4   Significantly, the cladograms in [16, 17] permit deeper-level homology of the morphological

5   traits [5, 6, 35] shared by *Calyptridium* and *Philippiamra* with *Cistanthe*, these being lost in *Lenzia* and

6   *Montiopsis*. These include: (i) succulence; (ii) oblanceolate leaves often differentiated into a more

7   rhombic apical portion and broad linear basal portion; (iii) laminate (ribbon-like) leaf vein anatomy; (iv)

8   an "indeterminate" primary leaf vein; (v) weakly but definitely brochidodromous secondary leaf veins;

9   (vi) brachyparacytic stomata; (vii) cymose inflorescences in the form of a cincinuss; and (viii) markedly

10   unequal inflorescence bracts. This trait complex characterizes no other Montiaceae. *Calyptridium* and

11   *Philippiamra* species differ from *Cistanthe* mainly in having reductions in floral part number, but the

12   genera intergrade [5, 6]. Thus, not anticipating the idiosyncratic evolution of *Lenzia* and evidently

13   *Montiopsis*, the earlier morphological circumscription of *Cistanthe* [5, 6] seemed reasonable. In this

14   sense, the analysis in [16] corroborates the morphological analytical conclusions. However, [16]

15   emphasizes only paraphyly of *Cistanthe sensu* [5, 6] and does not discuss morphological phylogenetic

16   evidence. In Chile, plants of *Philippiamra* and *Cistanthe* also intergrade ecologically. The former are

17   decidedly more xerophytic than the latter, but in many arid locations, species of both groups grow side-

18   by-side. This was circumstantial evidence that the latter derived from among the former.

19   The inclusion of *Montiopsis* in Cistantheae deserves comment, because the morphology can be

20   described as idiosyncratic. Species of *Montiopsis* bear no obvious synapomorphy with other Cistantheae.

21   They are distinctive among all Montiaceae (and Portulacineae) in bearing multiseriate-multicellular

22   trichomes, these sometimes also glandular [3, 6, 42-44]. Otherwise, only short unicellular foliar

23   trichomes/papillae occur among Portulacineae (although some clades are characterized by axil-specific

24   trichomes [3, 6]).

25   Hershkovitz [6] described the *Montiopsis* inflorescence as botryoid or a bostryx are thyrsoid (but

26   solitary in *M. cistiflora*), and the sepals are irregularly dentate-erose. Among Portulacineae, the

27   inflorescence is unique and the sepal trait traits occur only among certain species of *Lewisia*. *Montiopsis*

28   comprises two monophyletic subgenera, *M*. subg. *Montiopsis* and *M*. subg. *Dianthoideae*, these

29   comprising ca. 17 and four species, respectively [44]. Subgenus *Montiopsis* is more diverse and more

30   specialized: perennials (all alpine) and annuals (sea-level to alpine), distributed from southern Bolivia to

31   southern Chile and across broad temperature/precipitation regimes. In addition to the trichome forms

32   shared with *M*. subg. *Dianthoideae*, all species bear unique multiseriate-unicelluar trichomes formed by

33   fusion of long epidermal hair cells. All species have pantoporate pollen. Species of *M*. subg.

1   *Dianthoideae*, by contrast, are all alpine perennials restricted to the central Chilean Andes and all have

2   tricolpate pollen.

3   With some caveats, the inclusion of *Montiopsis* in Cistantheae seems well-supported [16, 17].

4   However, the five-marker cladogram in [16] shows reduced support for Cistantheae monophyly relative

5   to the three-marker cladogram. The BP and PP reduce from 100% to 69% and 1.0 to 0.99, respectively.

6   While these reductions are not as severe as those observed at other nodes, they are not trivial. Edge

7   support for Cistantheae in [18] is <50%; for *Cistanthe + Montiopsis* is 62%; and for Calyptridinae is 64%.

8   All of the analyses in [17] yield maximal support for Cistantheae (though *Lenzia* was not sampled).

9   However, the concordance analysis in [17] manifests nontrivial support for monophyly of *Cistanthe* plus

10 Calyptridinae. In all analyses, *Montiopsis* "sticks out" of Cistantheae, i.e., it is subtended by a long branch

11 and the terminals extend further than the terminals of other Cistantheae.

12   These morphological and molecular data indicate that something has "gone down" during the

13 origin and evolution of Cistantheae. Although there is a small level of conflict regarding the placement of

14 *Montiopsis* within Cistantheae, the support seems to outweigh this. The conflict may be an artifact of the

15 long branch subtending the genus. The result is that Cistantheae includes two genera that are

16 phenotypically very similar in both vegetative and reproductive morphology, differing only in the degree

17 of congestion of the inflorescence and, correspondingly, the size of the flowers. And from this emerge

18 two genera, *Lenzia* and *Montiopsis*, which are morphologically divergent from all other Montiaceae. Is

19 this unusual? My thesis is that idiosyncraticity is the norm. Further scrutiny of morphological and

20 genomic data will help explain mechanically the origins of the peculiar taxa. But the observation itself has

21 broader implications for evolutionary analysis. It is evidence against the monotony of the evolutionary

22 process that evolutionary analytical methods presume and, in fact, impose.

23

24   **Phylogeny and taxonomy within Calyptridinae**

25

26   Hershkovitz [5,6] concluded that the classically conceived genus *Calyptridium* (including

27 *Spraguea*; [45]) pertained to a clade comprising also Reiche's [46, 47] *Calandrinia* section

28 *Amarantoideae* and the genus *Philippiamra*. I refer below to this group as the "CAP" clade. Carolin's

29 cladogram [3], in contrast, split the CAP clade, with *Cistanthe s. str.* arising in between the *Calyptridium*

30 and *Philippiamra*. Still, both cladograms agreed on monophyly of these taxa together. Hershkovitz thus

31 classified classical *Calyptridium*, *Philippiamra*, and *Calandrinia* sect. *Amarantoideae* as sections within

32 the genus *Cistanthe* [5, 6, 48, 49; cf. 3, 4]. Molecular analyses in [16] corroborate [19] with respect to

33 phylogeny within Calyptridinae.

1   Current DNA sequence evidence [19, 50] demarcates two speciose clades in Calyptridinae: (1)

2   *Calyptridium sensu* Hinton [45]; and (2) *Philippiamra*. Support for *Philippiamra* stems from the

3   essentially identical DNA marker sequences of its species, regardless of floral/fruit morphology [19].

4   There are two morphologies: a *Calandrinia*-type, with five petals/stamens, three carpels, and multi-

5   seeded valvate capsules; and a *Philippiamra*-type, with reduced petal/stamen numbers, two carpels, and a

6   one-seeded indehiscent fruit. Based on this floral/fruit morphology, [8] classified these taxa in different

7   genera and in different tribes of Portulacaceae. Yet, their genotypes overlap, some samples of differing

8   morphology sharing identical ribosomal and plastome sequences. From the DNA evidence, it is not clear

9   that the *Philippiamra*-type morphology evolved only once, although a single origin followed by

10   hybridization also is possible.

11   DNA evidence, morphology, and cytology mutually support monophyly of the bicarpellate

12   species of *Calyptridium* (*sensu* Hinton [45]). Likewise the data support monophyly of *C* sect. *Spraguea*

13   [16, 19, 50], but not so convincingly *C*. sect. *Calyptridium*. Species of *C*. sect. *Spraguea* (two perennial

14   and one annual) share three synapomorphies: loss of the smaller of the two unequal inflorescence bracts;

15   loss of laminar leaf venation; and leaves coriaceous rather than succulent [5, 35]. The perennial condition

16   is derived [2]. Species of *C*. sect. *Calyptridium* and *C*. sect. *Thingia* have bracts, leaf veins, and leaf

17   texture the same as species of *Philippiamra*, especially *P. calycina*.

18   Low bootstrap support in [19] for the bicarpellate clade is an artifact of the short branch

19   separating these species from the tricarpellate *Calyptridium ambiguum*. Thus, many bootstrap samples

20   may have missed the supporting data and/or duplicated data that created spurious relations between *C.*

21   *ambiguum* and particular bicarpellate *Calyptridium* species. The collective DNA evidence [16, 19, 50],

22   phylogeography and morphology suggest but do not prove that *C. ambiguum* as sister to the remainder of

23   *Calyptridium*.

24   Returning to taxonomy, an argument could be made for recognizing *C. ambiguum* as a distinct

25   genus, which not only renders the remainder of *Calyptridium* more homogeneous, but also conserves

26   traditional local taxonomic custom. *Calyptridium ambiguum* has *Calandrinia*-type floral/fruit

27   morphology, for which reason [43] included it in Reiche's [46, 47] *Calandrinia* sect. *Amarantoideae*. It is

28   the only species of Cistantheae with basket-forming three-dimensional leaf venation [35; not reported in

29   51].

30   At the same time, an argument can be made for classifying all species of this clade as

31   *Calyptridium*: the consequent overall divergence/diversity is comparable to that in most other Montiaceae

32   genera. Splitting into two genera is justified on the basis that each resultant genus has considerable

33   species diversity in its respective hemisphere, and it maximally conserves prevalent taxonomy. Splitting

34   *Calyptridium* further is no more and probably less justifiable than historical but currently rejected generic

1   segregations within *Lewisia* and *Montia*. Still, in the event that segregation of *C. ambiguum* is preferred, a

2   monotypic genus, *Thingia*, has been erected to accommodate it [1].

3

4   **_Lewisiopsis_ – a living fossil?**

5

6   The phylogenetic relations of *Lewisiopsis* conflict strongly among the various analyses. A sister

7 relation with *Lewisia* was supported by maximal PP and fairly high BP in both the three- and five-marker

8 analyses of [16]. However, a sister relation with remaining Montieae received maximal support in all 12

9 analyses of [17]. But the latter authors did not note this discrepancy. The sister-relation to *Lewisia*

10 received 84% support from MP analysis of *ycf*3-*trn*S data in [19]. The optimal ITS MP tree indicated the

11 sister relation to Montieae, but with <50% BP. However, in the combined MP analysis, BP support for the

12 *Lewisia* relation reduced to 56%, indicating conflict between the nucleosome and plastome. This conflict

13 seems to be corroborated by [16] and [17], as the former included mostly plastome data and the latter

14 presumably overwhelmingly nucleosome data. Also, BP support for the *Lewisiopsis*/*Lewisia* sister

15 relation in [16] declined from 96% in the three-marker dataset to 93% in the five-marker dataset. The

16 latter added proportionally more nucleosome data. As BP maxima in the three-marker data likely were

17 limited at low divergences by lack of informative sites, this difference is more significant than it appears.

18   The data suggest a new hypothesis regarding the evolution of *Lewisiopsis*. This monotype appears

19 to be a "living fossil" of a hybrid between earliest and barely divergent ancestors of *Lewisia* and

20 Montiinae. Further supporting this hypothesis is the high but irregular chromosome number in

21 *Lewisiopsis* [52]. It is approximately octaploid relative to its diploid relatives. As noted above and in [5,

22 6, 19, 35, 36], *Lewisiopsis* is pleisiomorphic in its morphology, plastome, and nucleosome. This pattern is

23 confirmed by broader genomic sampling in [17]. The *Lewisiopsis* branch is markedly less divergent from

24 the ancestor than all other Montieae and, indeed, all other Montioideae. As in previous analyses, the

25 whole-genome divergence from the Montiaceae ancestor approximates that of Cistantheae.

26   *Lewisiopsis* might appear to be an exception to the dogma of the evolutionary consequences of

27 hybridization and/or polyploidy. These processes are regarded widely as catalysts of cladistic

28 diversification and genomic, phenotypic, and ecological diversification [41, 53]. In this case, the parental

29 lineages, Montiinae and *Lewisia* diversified/evolved, but the hybrid offspring did not and its genomic

30 evolution seems to have sequestered. One might conclude that the effect of hybridization/polyploidy has

31 been evolutionarily *inhibitory*.

32   However, as elaborated in [2] in the context of PEI, the dogma is specious.

33 Hybridization/polyploidization are ubiquitous processes during the course of plant evolution. Plant

34 domestication/selection demonstrates that indeed these processes are valuable sources of myriad novel

1   forms—but probably more often failed crosses and uninteresting/undesirable forms relegated to the mulch

2   heap. Nature is less forgiving and its mulch heap much bigger. Hybrids/polyploids are afforded no

3   protected space or special care in Nature's nursery, and likely overwhelmingly die. The dogma also

4   reflects determination bias. Systematists naturally tend to pursue studies of more diversified clades.

5   Hybridization/polyploidy are ubiquitous, frequent, and, effectively, irreversible processes running in

6   parallel to cladistic diversification and phenotypic and ecological evolution. It is to be expected that all

7   taxa will accumulate hybridization/polyploidy footprints in their pedigree, those that subsequently radiate

8   and those, like *Lewisiopsis*, that do not. These observations in no way negate described patterns of

9   hybridization/polyploidy-associated radiations, nor developmental genetic evidence demonstrating

10   associations between hybrid/duplicated genes and novel phenotypes. Rather, it demonstrates that

11   hybridization/polyploidy are neither necessary nor sufficient for such phenomena to occur.

12   Nonetheless, the evidence suggests that *Lewisiopsis* may provide critical evidence for the

13   interpretation of Montiaceae phenotypic evolution. While it is risky to interpret ancestral phenotypes in

14   terms of modern ones (e.g., [54]), the coincidence of both phenotypic and genomic pleisiomorphy in

15   *Lewisiopsis* suggests that the former indeed may be relictual and shared with certain Cistantheae. Yet,

16   *Lewisiopsis* diverged three nodes and as much as 10×10^6 years later than Cistantheae [17: *S18*; cf. 16:

17   *Fig.2*]. Thus, genomic comparison might reveal that *Lewisiopsis* and *Cistanthe* share a developmental

18   bauplan from which phenotypes of other Montiaceae have diverged.

19

20   **Other significant nodes**

21

22   Additional nodes apparently resolved in Montiaceae have significance in terms of phenotypic

23   evolution, especially with respect to life history and life form. This theme is emphasized in [2].

24   1.   All cited DNA analyses demonstrate monophyly of both the perennial and annual clades of

25   *Calandrinia*, which is not mutually supported by independent phenotypic traits [6, 42].

26   Hershkovitz [6] suggested that the perennial group was paraphyletic with respect to the

27   annual.

28   2.   Monophyly of the perennial *Montiopsis* subg. *Dianthoideae*, which lack a phenotypic

29   synapomorphy [6].

30   3.   Monophyly of *Cistanthe* sections *Cistanthe* and *Rosulatae*, each including annual and

31   perennial species.

32   4.   Despite poor overall resolution, monophyly of two subclades within *Cistanthe* sect.

33   *Rosulatae*, each of which is polymorphic for life history. These subclades are recognized as

34   subsections [1].

5. Somewhat ambiguous support for monophyly of two principal groups of *Lewisia*, one comprising the "evergreen" species (*Lewisia* sect. *Cotyledon* [52, 55]). Leaves of these species are coriaceous and persist year to year. Resolution is poor among remaining species of the other subclade, which are morphologically diverse but share ephemerality of their leaves.

6. Monophyly of two subclades of *Phemeranthus*, one comprising the caulescent species, the other the acaulescent [20].

7. Monophyly of three *Claytonia* sections differing in life form/history: annual, rhizomatous perennial, and caudiciform taproot or tuberous [21, 22]. Again, this seems to rule out paraphyly, rendering less certain evolutionary polarities.

Although it may seem trivial to point out, monophyly described above (and in general) refers to existing evidence supporting monophyly of extant clade members. This does not implicate necessarily that the phenotypic differences between the clades originated in a single common ancestor or ancestral species that split into two. Gene trees, species trees, and phenotypic trait trees are presumed to substantially overlay, but they are not the same. Phenotypic synapomorphies can originate before or after molecular marker synapomorphies, and can originate also via lateral transfer. Whole genome analyses (e.g., [22, 41]) just now are scratching the surface of the complexity underlying phylogenies artificially simplified by analysis of few genetic markers. Thus, the sense of monophyly applied in this work and in [1, 2] is simplistic and may be naïve.

Summary: phylogenetic conceptualization of Montiaceae

Beginning with Carolin's [3, cf. 56] seminal work, understanding of evolutionary relations among Portulacineae and Montiaceae transformed radically from ideas persistent and pervasive up to the end of the 20th century. Most critical to this transformation was Carolin's ability to escape from conceptual inertia imposed by prevailing taxonomic order, i.e., to think "out of the box." Based on his extensive field and morphological studies, he applied cladistic reasoning to reconstruct Portulacaceae taxonomy from square one. But neither empirical knowledge nor cladistic reasoning was by itself sufficient. Previous Portulacaceae taxonomic research was empirical, but it was constrained by noncladistic evolutionary dogma. Cladistic methods per se proved their impotence when applied vacuously and conditioned excessively upon classical noncladistic taxonomic order [56; cf. 57, 58]. Carolin understood that existing taxonomic units within classical Portulacaceae were constructed non-cladistically. They had no a priori utility for cladistic analysis except coincidentally. So he completely decomposed Portulacaceae to the

1 species level before reconstructing it as cladistically determined. He also was careful to assure data

2 availability/adequacy for each operational taxonomic unit.

3   Not unexpectedly, much of the refinement of the Carolin-Hershkovitz model of Portulacineae

4 phylogeny owes to analysis of DNA sequence data. But this also benefitted from out-of-box thinking. In

5 particular, the earliest molecular phylogenetic analyses of Caryophyllales [59-62] likewise were

6 essentially mechanical and conditioned by classical taxonomic order. Classical familial circumscriptions

7 evidently were presumed to reflect, if not monophyletic (as argued in [57] on the basis of weak and/or

8 incorrect evidence), then at least homogenous and significantly diverged taxa. Thus, slowly-evolving

9 DNA markers were sampled in one to a few proxy species per classically-conceived family.

10   Hershkovitz argued [6, 56] that classical Caryophyllales familial circumscriptions were unnatural

11 and phylogenetically misleading. Partly to demonstrate this, [9] deliberately analyzed nominally

12 interfamilial Portulacineae relations using a rapidly evolving DNA marker normally applied to

13 infrageneric phylogeny. This demonstrated that some "interfamilial" divergences were less than

14 "infrafamilial." Radical differences between the current phylogenetic and classical familial classification

15 [14, 63] demonstrate that the argument of familial nonmonophyly made years earlier was correct, and that

16 the counterargument for monophyly of classical families [57] was spurious. By the time of [63], this

17 "discovery" was already "settled science" [6, 9, 11, 63, 65].)

18   To be fair, much of the credit for current molecular phylogenetic knowledge is owed to the

19 authors/inventors of the corresponding theory and technology, as well as providers of DNA samples and

20 analytical services. This is because, by the late 1990s, available technology and analytical programs

21 yielded purely mechanically a plausible phylogenetic estimate. This rendered empirical molecular

22 phylogenetics largely an endeavor of "acquisition" more than "inquisition," viz. acquisition of specimens

23 and the material wherewithal to run them through the mill. As Nobel laureate John Watson reportedly

24 said, "any monkey could do it."

25   However, the superficial simplicity of modern genomic/computational systematics is-and must

26 be-illusory. In particular, parametric complexity of evolutionary analysis is *increased*, not decreased. It

27 *adds*, however conveniently packaged, dimensions from molecular genetics, mathematics, statistics,

28 informatics, computation science—and philosophy. It subtracts nothing. More importantly,

29 genomic/computational phylogenetic methods *also* impose order. However accurate is a phylogenetic

30 tree, as ever, it canalizes subsequent evolutionary thinking. That evolutionary thinking must be questioned

31 post-analytically. Much like modern powerful weaponry, powerful analytical methods can make powerful

32 errors, or at least powerful oversights.

33   As an example in the present context, the *Lewisiopsis* morphological and molecular data

34 demonstrate an idiosyncratic but significant result overlooked by linear method-oriented evolutionary

1   thinking. This might reflect a methodologically-reinforced underlying preference to perceive evolution as

2   a monotonic process whose understanding is limited only by data quantity and computational power. The

3   emphasis on automated cladogram resolution possibly biases against consideration of idiosyncratic hybrid

4   origins and other idiosyncratic but informative data behavior. Thus, [16] overlooked the possible

5   significance of among-dataset conflicts. Likewise, [17] applied the "nuclear option" of whole genome

6   phylogenetics in order to maximize cladogenetic resolution. But perhaps in the zeal to maximize data,

7   [17] overlooked the glaring conflict with [16] in the position of *Lewisiopsis*. Branch length asymmetries

8   with respect to *Lewisiopsis* and taxa in general were noted earlier in [9, 10, 19], but not in the more

9   recent, more data-laden , and computationally more sophisticated analyses of [16] and [17]. However, the

10 last did apply methods that "correct" branch length asymmetries for the purpose of chronological dating.

11 This means that branch length differences were perceived, but no evolutionary significance was afforded

12 them. They required computational "correction" to facilitate interpretation. Likewise, [16, 17] did not

13 detail the morphological peculiarities of *Lewisiopsis* or, in [16], taxa in general.

14   The view advocated here and in [2] is that advancing evolutionary knowledge remains an

15 intellectual as much as a technological challenge. It depends upon escaping from conceptual order. This is

16 because evolution itself is idiosyncratic and not constrained by the order that methodological dogma

17 imposes on it. This view in no way dismisses the validity or utility of methods per se, provided that their

18 assumptions and limitations are understood. An example is justification for pattern-based probabilistic

19 phylogenetic reconstructive methods (e.g., [40]). It must be understood that probabilistic methods are

20 restricted to parameters that are truly stochastic and sufficiently variable to be amenable to statistical

21 analysis. It is useful, of course, if the stochasticity of this variation can be validated independently. For

22 example, base substitution biases can be explained by empirical evidence for the biological cause of such

23 bias and its stochasticity.

24   Likewise, it is understood (theoretically) that: (i) existing substitution parameter estimation

25 methods do not account for all known (much less unknown) molecular evolutionary phenomena; (ii) there

26 should be-and is-an inverse relation between the "globality" of evolutionary parameter estimates and their

27 local accuracy; (iii) incidents of "less probable" evolution are, collectively, highly probable; and (iv)

28 phylogeny captures an asymptotically infinitesimal portion of evolutionary natural history. The last

29 statement emphasizes that molecular phylogenies are merely abstract one-dimensional pedigrees of

30 derived from DNA sequences of extant individuals. They (might) corroborate sequential evolution of

31 traits, but document little if anything else of events that transpired during the course of phylogenesis. To

32 appreciate this, merely consider how much of Mesozoic seed plant evolution is documented by molecular

33 phylogenetic analysis of extant taxon phylogeny.

1   The significance of the preceding in the present context is that it likewise is understood-

2   theoretically-that conventional computational phylogenetic analysis (in all of its forms) merely *calculates*

3   phylogenetic order given uniform methodological assumptions, parameter estimates, and algorithm [27].

4   Methodologically unpredictable idiosyncratic evolutionary events are overwritten. For the record, I do not

5   assert that current estimates of Montiaceae are unreasonable or inaccurate. As generalized phylogenetic

6   *descriptions*, much of the resolution probably is accurate. Rather, I assert that phylogenies can be only as

7   accurate as their methods allow. For example, *none* of the essentially *infinite* number of possible

8   phylogenies of 270 species and 20 subspecific taxa of Montiaceae can be true if even *one* of the clades

9   has a hybrid origin [19; cf. 66]. And even if it assumed that half of the nodes now are resolved with

10   reasonable certainty, this leaves correspondingly only less than infinite the number of possible

11   phylogenies among the remainder.

12   However, theoretical and empirical knowledge of genetics and evolution render moot the ideal of

13   fully resolving the phylogenetic tree of Montiaceae, Portulacineae, or life in general. It is known that

14   organismal evolution sometimes is and sometimes is not, hence was or was not, tree-like. Even when tree-

15   like, diversification sometimes occurred too rapidly to recover the cladistic sequence. Here,

16   overindulgence in phylogenetic analysis-beating the phylogenetic bush-cannot help but degenerate into

17   the byzantine. Failure of data and methods to resolve phylogenies is more profitably interpreted as an

18   indication of evolutionary phenomena not anticipated by analytical approaches. In other words,

19   phylogenetic analysis profitably can be directed as a search for evolutionary idiosyncrasy as much as

20   evolutionary order.

21

22   **PERSPECTIVES FROM CURRENT EVIDENCE FOR MONTIACEAE PHYLOGEOGRAPHY**

23

24   Hershkovitz [6] noted that the "portulacaceous alliance" (i.e., Portulacineae) partitioned into two

25   groups whose members distributed mainly on opposing sides of the American cordillera: a western

26   American and Australian group and an eastern American and African group. Carolin [3] derived a

27   "reduced area cladogram" demarcating the same partition. However, in Carolin's phylogeny, the

28   partitioning was repeated, whereas in Hershkovitz [6], it occurred once. Most of the taxa are southern

29   hemisphere, but the east-west pattern maintains in both hemispheres. The phylogeny thus superficially

30   suggested an ancient distribution in Pangaea (at least 180×10^6 ybp), then diversification primarily in

31   Gondwana (at least 100×10^6 ybp), and persisting today in the various break-up products. A further

32   observation was the latitudinal bias between the two partitions. Taxa of the western partition have an

33   almost exclusively temperate to arctic distribution, whereas the eastern partition taxa are primarily

34   tropical to warm temperate.

1   The geographic partitions described above superficially seemed to corroborate the posture of the

2   vicariance phylogeography school, viz., the interpretation of historical land connections in terms of

3   cladistic relations of modern taxa [67, 68]. Vicariance-mediated diversification at least tacitly had been

4   invoked for some southern hemisphere Portulacineae [3, cf. 66]. In this discussion, I use the term

5   phylogeography mainly in the Cartesian coordinate sense, i.e., the interpretation of the transport

6   mechanism of plants from point A to point B across the global landscape. Phylogeography more broadly

7   also encompasses ecological dimensions of spatiotemporal organismal incidence, which will emerge later

8   in the discussion.

9   Hershkovitz & Zimmer [9, 10] corroborated the phylogeographic pattern evident from the

10   morphological analysis, but also interpreted as pure coincidence the correspondence between

11   portulacaceous phylogeny and ancient landmass configurations. In particular, intercontinental

12   disjunctions among modern taxa appeared to be too recent to be explained by ancient landmass

13   connections. Hershkovitz & Zimmer also estimated a remarkably high LDD "rate" for Montiaceae given

14   the apparent lack of a corresponding LDD adaptation [10]. This result further undermined the prevalent

15   vicariance phylogeography philosophy, at least with respect to plants.

16   Antitropical temperate/polar infrageneric disjunctions of Montiaceae and numerous putatively

17   recently-evolved angiosperm lineages conventionally were explained by LDD and/or

18   contraction/expansion during major historical climate change cycles [69, 70; cf. 71]. The latter is

19   plausible for the origin of North American *Calandrinia menziesii* and *C. breweri*, given the current range

20   of *C. ciliata* in the cordillera from southern Mexico to northern Argentina. Cordilleran migration might

21   also explain the origin of northernmost Andean *Montia* forms. Analogous historical latitudinal expansion

22   of aridity [72] emerges as a possible explanation for antitropical disjunctions in *Cistanthe* and

23   Calyptridinae.

24   Otherwise, philosophical aversion to "one-off" LDD explanations of antitropical disjunctions has

25   advanced two alternatives. One is an appeal to hypothetical transitory ancient land bridges [67, 68; cf. 70,

26   72]. The other appeals to hypothetical widespread Pangaean ancestral species that differentiated

27   cladistically following land area separations[73-75]. Concomitantly, [73-75] argue that current clade-

28   dating methods grossly underestimate the true age of clade origins. This view degenerates to tautology not

29   unlike Biblical Creationism. It ignores ample evidence for dispersability inherent in the origin of recent

30   oceanic island floras, and it requires that essentially all plant clades differentiated prior to the Pangaean

31   separation..

32   Hershkovitz [9, 10] argued that Portulacineae diversified as recently as the latest Eocene to

33   Miocene. More recent analyses [15-17] have calculated an eariler mid-Eocene origin. But even these

34   estimates rendered untenable vicariance explanations of Portulacineae intercontinental disjunctions.

1   Moreover, the observed intercontinental and/or transoceanic disjunction divergence dates for different

2   taxa do not coincide temporally. Disjunctions originated repeatedly throughout the Tertiary-Quaternary,

3   most apparently Miocene or later [9, 10; cf. 15, 16; but see 17]. The latter observation is critical.

4   Hershkovitz [10] also emphasized that Montiaceae lack LDD-facilitating morphological

5   specializations, such as winged, fleshy, or adhesive propagules. It is conceivable that the scarious floral

6   apparatus of certain Calyptridinae species (e.g., *Calyptridium monospermum* and *Philippiamra*

7   *celosioides*) could become aloft while still containing a seed. However, the distribution of this trait within

8   these genera and the amphitropical prevailing wind patterns renders unlikely that disjunction of

9   Calyptridinae originated this way. Heads [73] considered lack of dispersal mechanism as problematic in

10   dispersalist explanation. But phylogenetic evidence for dispersal suggests that LDD is common, with or

11   without a morphological mechanism. Hershkovitz [10] also remarked that the observed disjunctions must

12   severely underestimate actual LDD incidence. These data, along with pervasive evidence for LDD-

13   mediated diversification in other angiosperms (e.g., Hawaiian plants and non-anthropogenic

14   intercontinental distributions of many hundreds of species) render infinitely moot the vicariance-LDD

15   question (see below). Thus, Hershkovitz [10] asserted that the evidence affords considerable *a priori*

16   likelihood to LDD even in cases where vicariance is plausible (see below).

17   The inevitable acquisition of Hectorelleae DNA [11, 12] provided an interesting twist on

18   phylogeographic interpretation. Its members occur in two insular terrains ca. 8000 km apart and otherwise

19   lacking native Portulacineae: New Zealand (*Hectorella*) and the Kerguelen Islands in the subantarctic

20   Indian Ocean (*Lyallia*). These terrains were physically connected in Gondwana, though very remotely, via

21   Antarctica as late as the Cretaceous [76]. Applequist et al. [11] remarked that Hectorelleae

22   phylogeography owed to LDD. But apparently they did not appreciate that the mid-Tertiary origin of

23   Portulacineae [9, 10; cf. 15-17] *a priori* rendered vicariance implausible (see discussion of *Rumicastrum*

24   above; note that Hectorelleae diverged later [16]).

25   Wagstaff & Hennion [12] explained the Hectorelleae disjunction in terms of shorter jumps from a

26   widespread ancestor in Antarctica. However, this explanation assumed an extreme estimate of the age of

27   the *Hectorella*/*Lyallia* split at $18\text{-}25 \times 10^6$ ybp. This dating based on an estimated nucleotide substitution

28   rate. Analyses of [14-16] estimated the Hectorelleae/outgroup split age at $20\text{-}30 \times 10^6$ ybp. From

29   likelihood-based phylograms in [12], it appears that Hectorelleae root to terminal divergence is much less

30   than that of other Montiaceae, and that the Hectorelleae stem itself is rather short. Divergence between

31   *Hectorella*/*Lyallia* likewise is minimal, evidently not much more than the stem divergence. Clearly, and

32   perhaps not surprisingly given its slow growth, molecular evolution has advanced less in Hectorelleae

33   than other Montiaceae. The *trnK*/*mat*K sequences from the two taxa differ from each other by five

34   substitutions and one indel in a poly-A repeat. A sequence from a *Cistanthe* species differs from that from

1   *Lyallia* by only seven substitutions and one indel. Still, the divergences are very low and render age

2   dating difficult. One must consider the possibility of a founder effect difference.

3   Based on the older estimate in [12], Heads [74, 75] likewise suggested that *Hectorella* and

4   *Lyallia* separated via shorter dispersals involving Antarctica and subantarctic islands. He also emphasized

5   that this estimated age was much older than the origin of the modern arctic/alpine habitats of these taxa,

6   which he interpreted as evidence of an earlier broader Hectorelleae distribution in Antarctica. Thus,

7   Heads [74, 75] considered the estimate in [12] as evidence supporting his panbiogeographic

8   interpretation.

9   Hectorelleae remain enigmatic phylogeographically and require further study. Hectorelleae

10 diverged following divergence of, respectively, *Rumicastrum* and *Calandrinia* [16; cf. 17] Hectorelleae

11 then are sister to the North American Montieae. These taxa comprise Montioideae [1]. Vicariance of

12 *Rumicastrum* to Australia is doubted not only because of the timeframe, but because of its warm/arid-

13 adapted form, which renders unlikely its presence in southern Patagonia during the latest Eocene [1] (see

14 also below). *Calandrinia* is another matter. It includes two clades, one alpine perennial and the other

15 lowland temperate annual. Which form is derived remains uncertain [2]. But the perennial *C. caespitosa*

16 complex includes cushion plants morphologically similar to Hectorelleae (though alpine cushion plants in

17 many angiosperms share this form) and distributes to Tierra del Fuego [REF.]. And the Hectorelleae is

18 sister to Montieae, whose first-diverging taxa are cold-adapted perennials.

19   These observations create the possibility that, following divergence of *Rumicastrum*, the ancestor

20 of remaining Montioideae was cold-adapted and situated in southern Patagonia, which would have been

21 cold at that time, ca. Oligocene (see below). From here would have diverged *Calandrinia*, which migrated

22 northward as elevation and cooling of the northern Andes permitted [cf. 54, 70], Hectorelleae, and the

23 ancestor of Montieae, which dispersed to North America. Then Hectorelleae would have dispersed to

24 New Zealand and Kerguelen directly or via Antarctica. Whether Hectorelleae became widespread in

25 Antarctica [12, 74, 75] is not clear. Evidently, the plants are slow-growing, flower rarely, and produce

26 few seeds that evidently do not germinate easily [12]. Hectorelleae would have had to migrate a total of

27 about 16,000 km to situate themselves proximal to both New Zealand and Kerguelen. This undoubtedly is

28 possible over the course of many millions of years, but, in this case, intercontinental LDD would seem to

29 be faster and no less likely. There is also the possibility that the LDD vector was glacial.

30   An alternative to the preceding is a scenario whereby the Hectorelleae ancestor was more warm-

31 adapted and dispersed directly to New Zealand, where it evolved its alpine/arctic ecomorphology in situ

32 as this habitat developed more recently in New Zealand [75]. Such a scenario has been argued for the

33 origin of the central Andean alpine genus *Oriastrum* (nee *Chaetanthera*; Asteraceae; Mutiseae [54]).

34 These alternatives might be evaluated with whole genome methods. Estimation of the arrival date to New

1 Zealand and Kerguelen might be possible using coalescent models at the genomic scale. This would

2 require, among other things, not only a reasonable estimate of generation time, but also an assumption

3 that this has been constant over time.

4   Regardless of whether Hectorelleae arrived to New Zealand and Kerguelen via Antarctica or

5 directly, at least two LDD events were required, unless, as [74, 75] argues, molecular dating estimates are

6 grossly erroneous. As it turns out, distance per se does not favor the former over the latter, because the

7 dispersal potential of "nonstandard" mechanisms is fat-tailed and does not deteriorate normally with

8 distance (see below). And, given enough time, nonstandard mechanisms are more likely to result in LDD.

9   More importantly, the Hectorelleae LDD evidence data bolsters the argument in [9, 10] for a high

10 rate of LDD-mediated diversification among Montiaceae. The data add two more instances of LDD while

11 adding only two more species to Montiaceae. Moreover, Hectorelleae appear even less "LDD-disposed"

12 than other Montiaceae. While also lacking dispersal mechanisms, other disjunct Montieae taxa at least

13 produce large numbers of seeds per generation, mostly orders of magnitude more than Hectorelleae. Thus,

14 Hectorelleae emerge among candidates for an angiosperm taxon a priori least apt to disperse 8000 km

15 (see also below). Applequist et al. [11] evidently did not appreciate the broader significance of their

16 Hectorelleae data. They mentioned a few other examples of LDD among Portulacineae, but did not

17 mention the earlier arguments [9, 10] for LDD explanation of essentially all Portulacineae

18 intercontinental/transoceanic disjunctions.

19   Hectorelleae helps demonstrate that the LDD "pattern" transcends phylogenetic level. With

20 Hectorelleae included, Montioideae alone manifest the entire western/southern "pseudo-Pangaean"

21 distribution: North America (most Phemerantheae and Montieae spp.), South America (most Cistantheae

22 and *Calandrinia* spp.), Australia (*Rumicastrum*), and, with Hectorelleae, New Zealand and the Kerguelen

23 Plateau. Other Portulacineae also include endemic taxa in North America and at least two Gondwanan

24 regions (Cactaceae, Anacampserotaceae, Portulacaceae, Talinaceae). Much of the pattern repeats in the

25 genus *Montia* alone, a relatively young clade comprising about 20 species, with endemic taxa in North

26 America, South America, and Australia/New Zealand. (O'Quinn [78] argued that *Montia howellii* in

27 North America originated as a recent human-mediated introduction of a New Zealand species. While

28 phylogenetic evidence strongly supports this interhemispheric disjunction, DNA sequence divergence is

29 considerable and likely would date the separation to 10^6-10^7 years. Alternatively, a true separation on the

30 order of 10^2 years would seriously challenge the validity of molecular dating methods in general.)

31   In 2018, Hancock et al. [17] suggested, with skepticism, that *Rumicastrum* arrived overland to

32 *Australia* from South American via Antarctica. They cited as circumstantial evidence their age-dating of

33 the *Rumicastrum* split to ca. 30 x 10^6 ybp, slightly younger than the final separation between Australia

34 and Antarctica at ca. 33 x 10^6 ybp. Their skepticism is warranted. Their Montiaceae age-dating, while

1   using the identical procedure as [16], yielded a substantially older origin, which the authors did not

2   address. In [17], the first Montiaceae crown dates to ca. 39 x 10^6 ybp; in [16: *Fig. 3*], it appears to be ca.

3   34 x 10^6, with corresponding reductions in the age of *Rumicastrum*. The younger age would prohibit

4   overland migration from Antarctica. As both works note, however, the method applied can be unreliable.

5   Greater plausibility of the estimate in [17] might be argued on the basis of its much larger loci and base

6   sampling.

7   But even with the older estimate, overland vicariance, even if not impossible, is implausible. The

8   timing at the Antarctica-Australia connection cuts very close, and presumably requires establishment of

9   the ancestor in Antarctica at some time prior to the final split. At the same time, it requires the proto-

10 *Rumicastrum* lineage to have entered Antarctica from South America even earlier and migrated to the

11 opposite side of the continent. The shortest distance between these points is a then-unlikely 5000 km

12 migration path across then-cold central Antarctica. A more tolerable route along the continental periphery

13 is approximately 10,000 km.

14   However, the required South America-Antarctica connection itself is more problematic. First, the

15 connection was a narrow isthmus, in contrast to the continent-wide Australia-Antarctica connection.

16 Second, a seaway is believed to have developed over the continental shelves at ca. 55 x 10^6 ybp [79],

17 which is considerably older than the highest estimate of the Montiaceae crown divergence at ca. 40 x 10^6

18 ybp [17]. Short-distance dispersals might have been possible until the Miocene [79], but the narrowness

19 of the connection remains problematic. Third, by 30 x 10^6 ybp, the warm humid Eocene Antarctic climate

20 had degenerated into a cold one [80]. It must be recalled that the earliest-divergent Montiaceae,

21 *Phemeranthus* and Cistanthe, like their nearest Portulacineae outgroups, are warmer and arid-adapted [16:

22 *Fig. 3*]. The Cistantheae distribution centers in northernmost Patagonia, ca. 4000 km to the north. These

23 data suggest the impossibility of overland migration of a warm- and arid-adapted proto-*Rumicastrum*

24 13,000 km to Australia in the timeframe of interest. Moreover, recalling other undisputable LDD events

25 among Montiaceae (especially Hectorelleae), other Portulacineae, and angiosperms in general, a

26 vicariance explanation for *Rumicastrum* does not merit the inherent parsimony advantage that vicariance

27 advocates presume.

28   The evidence for promiscuous LDD-mediated diversification presents a paradox, however.

29 Montiaceae and other Portulacineae present numerous tantalizing examples of disjunction/distribution

30 that resonate with the vicariance narrative. But the promiscuous LDD narrative predicts that distributions

31 should be more cosmopolitan and not manifest their tantalizing patterns. Besides the pseudo-Pangaean

32 patterns within Montiaceae, another is itself the sister relation of Montiaceae to other Portulacineae. This

33 partition separates "core" Montiaceae of cis-cordilleran western America from primarily trans-cordilleran

34 American and African Portulacineae. The basal divergence of Montiaceae separates trans-cordilleran

1   North American *Phemeranthus* from cis-cordilleran South American Montiaceae. The basal split of

2   Portulacineae separates largely east Gondwanan *Didiereaceae* from more central Gondwanan taxa.

3   Evidently, the few isolated and morphologically "primitive" Anacampserotaceae occur in North America,

4   South America, and Australia, separating these from the more diverse and derived African clade [81]. The

5   basal split of *Portulaca* separates a few morphologically "primitive" Australasian relicts from the rest of

6   the genus [82, 83]. Cactaceae are a large almost exclusively American family. Suitability of habitat would

7   not seem to explain these disjunction/distribution patterns, as suitable habitats for members of both the

8   eastern and western Portulacineae groups occur on both sides of the phylogeographic partition. This is

9   especially evident for Montiaceae species habitats: similar montane/alpine, Mediterranean-climate, and

10 desert habitats occur in Europe, southwest Asia, and southern Africa.

11   But a more detailed examination reveals notable exceptions to the Portulacineae phylogeographic

12 pattern. Endemic Cactaceae and *Portulaca* species occur in Chile and California; these are evidently

13 recent colonizations. *Claytonia* diversified westward to northeast Asia and eastward to the eastern North

14 American seaboard. The *Montia fontana* species complex is essentially cosmopolitan. However

15 "primitive," the disjunct Anacampserotaceae and *Portulaca* taxa are of mid-Miocene age, which means

16 that they dispersed to Africa. And several Portulacineae species, including Montiaceae, have expanded

17 more globally anthropogenically. These include species of *Anredera*, *Basella*, *Talinum*, *Portulaca*, many

18 Cactaceae, and, among Montiaceae, *Calandrinia*, *Cistanthe*, *Claytonia*, *Montia*, and *Phemeranthus*

19 [1].The pattern, therefore, does not have a common historical phylogeographic cause-or an obligatory

20 phylogeographic effect. Why, then, does a pattern appear at all?

21   Phylogeographic pattern-sharing might hold clues for explaining the infrequent eastward

22 diversification of Montiaceae. South American Montiaceae genera appear to share a phylogeographic

23 pattern with numerous angiosperm genera: species diversity concentrated in and mostly endemic to Chile,

24 a few species crossing the border into adjacent territories, and few, if any, completely non-Chilean species

25 [70]. But, again, closer scrutiny reveals that the shared pattern is consequent to phylogeographic

26 convergence. Different taxa have attained the "Chilean" pattern in spatiotemporally and phylogenetically

27 different ways [70]. It is not so clear, therefore, that phylogeographic pattern-sharing is strictly a function

28 of phylogenetic pattern-sharing or geographic distance and connectedness. Other factors, such as

29 ecological similarity, may have greater weight.

30   The case of Chile is special, because of its historical ecological isolation and distinctiveness,

31 narrowness, steep ecological gradients across short distances, and instability. This would result in greater

32 extinction, because there is not, as in broader and more uniform continental areas, a nearby pool of

33 germplasm to repopulate local areas devastated by ecological disasters. This, in turn, offers opportunities

34 for LDD invasion. Naturally, the invaders will include the most pre-adapted taxa from ecologically

1 similar habitats, e.g., mediterranean, desert, and alpine. More importantly, this scenario depends upon a

2 high inherent LDD likelihood, which evidence from Montiaceae and other taxa now corroborate. Only the

3 inherent implausibility of LDD afforded by vicariance phylogeographic philosophy [67, 68, 73-75]

4 obligated otherwise implausible or counterevidenced scenarios.

5   The ecological scenario also helps explain the anti-Chilean pattern, i.e., the paucity of Chilean

6 lineages in trans-cordilleran American and the eastern hemisphere. As noted above, habitats may be

7 similar and some taxa indeed have crossed the phylogeographic partition in both directions. However,

8 other land areas do not share Chile's geographic peculiarities. Their ecoregions are larger and/or

9 ecological gradients are not as steep and/or their climatic stability is greater. Accordingly, their vegetation

10 is more stable and more readily repopulated following localized ecological disasters.

11   Coincidentally, Montiaceae appears to be an exception to the rule. Following the split of trans-

12 cordilleran Phemerantheae, the root of the remaining family seems to be present day northern Chile. From

13 here occurred multiple LDD events that established lineages on other remote land areas, evidently

14 involving also secondary LDD events from those areas. One species, *Montia fontana*, eventually made its

15 way back to Chile. I cannot think of another lineage originating in Chile that has been so successful

16 globally. Whether or not this success owes to traits evolved in Chile's challenging ecological conditions

17 is not clear.

18   I interject here that this and similar phylogeographic patterns might be somewhat an illusory

19 artifact of species diversity. In particular Montiaceae diversity is considerable and comparable in North

20 America and South America. Mainly because of *Rumicastrum*, Australasian diversity also is considerable.

21 This disjunct diversity is possibly what calls attention to the pattern. It would be less evident if only single

22 species were so geographically removed. But this diversity is consequent to many factors unrelated to

23 disjunction per se. For example, genetic divergence within South American clades is very low (see

24 above). By whatever mechanism, it appears that Andean region diversity was achieved recently over a

25 relatively short time period [19]. Before that, Chilean Montiaceae diversity may have been much less than

26 that already achieved in North America. In other words, Montiaceae might have been perceive as a

27 primarily North American lineage. It is important to appreciate that diversification of extant Montiaceae

28 occurred at different timescales.

29   Thus, ignoring *Phemeranthus*, the phylogeny suggests that the Andean lineages diverged before

30 North American Montieae, but extant Montieae genera diversified before diversification of the extant

31 Andean genera. Moreover, the Andean lineages apparently diverged 25-32 x 10^6 ybp [15, 16: *Fig. 2*; 17:

32 *S18*], long before the final uplift of the Andes and development of the current Mediterranean climate [54].

33 At that time, geographic and ecological partitioning of South America was far less pronounced. What

34 were these Andean lineages "doing" during the Miocene? How many species were there? What forms did

they have? Were they less arid-adapted? Did they extend to eastern South America? The answers may never be known. All that is known is that some lineages survived and diversified relatively recently into modern Andean habitats that did not exist when the lineages originated. This is circumstantial. The ancestors had not the foresight to plan and prepare for the Andean uplift.

In conclusion, Montiaceae and other Portulacineae demonstrate the significant role of unique rather than concerted events in explaining phytogeographic distributions. Donoghue [71] recognized the contribution of DNA-based phylogenetics towards testing and debunking phylogeographic dogmas. At the same time, he emphasized that the explanatory power of phylogeographic theory rests not in one-off explanations, but in commonality of cause. Sharing phylogeographic cause necessarily manifests in sharing of phylogeographic patterns (non-random distributions). But is the contrapositive necessarily true? Does sharing phylogeographic pattern implicate shared phylogeographic cause?

Moreira Muñoz [70], presumably among others, referred to the philosophical and perceptual bases of phylogeographic pattern recognition. A detailed discussion of the philosophy and psychobiology of pattern perception and pattern explanation is beyond the scope of the present work. Suffice it to say that pattern perception and explanation are default neurobiological processes. The mind looks for and explains patterns not because the patterns and explanations are real, but because the mind needs predictability to function. Humans consciously prefer to perceive patterns, explain them, and believe their explanations, even when aware that these are false. A prime example is "constellations" and the predictive power afforded them. Even university-educated humans in scientifically advanced societies affirm astrology.

Cartesian phylogeographic patterns are not entirely imagined, however. But even when patterns are "true," or at least "statistically significant," their explanation need not reflect a single common cause [84]. Thus, pattern recognition is, at best, only part of the solution in phylogeographic theory, and it also is part of the problem. Humphries & Parenti [67, 68] evidently perceptually favored uniformity of pattern and universality of explanation. Donoghue [71] evidently appreciated the role of idiosyncrasy in falsifying explanatory dogma, but manifests discomfort in the face of consequent pattern degeneration, hence unifying laws.

Notably, interpretation of global phylogeographic patterns has gone full circle in three decades. Prior to development of vicariance phylogeography, plant disjunctions commonly were explained by dispersal [e.g. 85, cf. 71]. The presence of diverse floras on remote young oceanic islands (especially Hawaii) at least validated dispersal as a potent phylogeographic process. Similarity of intercontinentally disjunct plant (as opposed to terrestrial animal) species provided circumstantial evidence.

But by the 1990s, vicariance had become the default explanation in phylogeography (e.g., [67, 68]) and LDD explanations were derided as unscientific. In fact, at that point, vicariance dogma was

1 considered so robust that plant distributions were applied in reverse to develop and adjudicate hypotheses

2 of plate tectonics and ancient land bridges (e.g., [67, 68]). Ironically, unlike LDD in the case of young

3 oceanic islands, it was not LDD, but rather vicariance, that was not corroborated scientifically by

4 chronological evidence.

5   By about 2010, thanks to molecular dating, the tide shifted again, and LDD re-emerged as a

6 principal explanation for plant disjunctions [70, 72]. But much earlier, even paleontologists criticized

7 vicariance dogma. Pole [86] heretically predicted that disjunct elements of the New Zealand flora

8 reflected LDD. Tay [87] summarized molecular evidence showing Pole [86] was correct, documenting

9 about 50 instances of LDD versus about five instances of vicariance. More globally, LDD was deduced to

10 explain disjunctions even in clades old enough to be vicariant [88].

11   Based on the inferred frequency of LDD disjunctions relative to cladogenetic events, [10]

12 conceived of dispersability informally as a likelihood function, comparing it to a DNA base substitution

13 rate: rare, but over time, with a significant cumulative likelihood of occurring. Moreover, [10] noted that a

14 dispersal likelihood is independent of a vicariance (i.e., normal overland migration) likelihood. This

15 suggestion was consequent to the seemingly obvious observation that whatever explained taxon ranges in

16 contiguous lands, this could not explain discontiguous ranges over water. Thus, even disjunct ranges in

17 contiguous lands might owe to LDD. Just as importantly, evidence that essentially all disjunctions among

18 Portulacineae represented LDD effectively discredited the privilege afforded to vicariance explanations.

19   Coincidentally, shortly thereafter, several researchers proposed formal multiparameter likelihood

20 phylogeographic models not unlike complex DNA substitution models [89-93]. All emphasized the

21 significant role of LDD in explaining global phylogeogtraphy. One line of research in particular [91, 92]

22 emphasized that LDD and "standard" plant dispersal functions generally are distinct. In other words,

23 standard dispersal functions reflect the normal dispersal mechanism of a taxon, which may or not

24 facilitate LDD. This is consistent with the proposal in [10]. Standard dispersability likelihood tends

25 towards zero with increasing distance. The LDD function, in contrast, reflects nonstandard and less

26 predictable dispersal mechanisms capable of abruptly dispersing propagules indefinitely long distances.

27 Consequently, the nonstandard function is fat-tailed with respect to dispersal distance. Moreover, by

28 nonstandard dispersal mechanisms, the cumulative probability of LDD increases with cumulative seed

29 load, whereas by standard mechanisms, it does not. This, in turn, offers an explanation of the LDD

30 success of taxa like Montiaceae that lack a standard dispersal adaptation.

31   It may be surprising, given the molecular-based evidence for high LDD frequency even in taxa

32 lacking dispersal adaptation, that as recently as 2011, evidence for a *single* example of amphipolar LDD

33 was touted in the journal Nature as a significant discovery [71]. Moreover, the example was not

34 unexpected, given that it involved a taxon with fleshy fruits known to be dispersed by amphipolarly

1   migrating birds. Donoghue [71] took the occasion to elegantly summarize the history of debate over

2   intercontinental plant disjunction mechanisms, but did not emphasize that there was never *scientific*

3   reason to doubt, and always every reason to believe, that multiple mechanisms occur and that LDD was a

4   common feature of plant phylogeography. In the case of morphologically very similar species whose

5   disjunction matches the migratory flight path of birds that eat their fruits, LDD seems to be a no-brainer.

6   Only earth-shattering fossil and/or molecular evidence could have nudged the verdict in the direction of

7   vicariance. Thus, if the essay in [71] revealed anything noteworthy, it was that obsolete dogma and a

8   long-since germane but now contrived and byzantine debate persisted lime-lighted in systematic and

9   evolutionary biology well into the 21st century.

10   Nonetheless, as in all of science, advancement of phylogeographic theory rests on predictability.

11 This can be accomplished in two ways. One is the blanket approach of comparing fit of empirical data

12 patterns to alternative explanations and accepting the most parsimonious. The other is the destructive

13 approach of falsifying patterns/explanations one data point at a time (i.e., proving one-off explanations). It

14 is true that general explanations make predictions and one-off explanations do not. But exceptions to

15 general explanations should be perceived as troublesome and not swept into the dustbin of residual

16 variance, as demonstrated above and especially in [2]. Alternatively, analysis of one-off explanations may

17 reveal unappreciated commonalities that ultimately yield better general explanations. Thus, [10] argued

18 that the evidence demonstrates that LDD-mediated diversification is not a one-off explanation, but a

19 phenomenon whose empirically determined frequency validates *a priori* its expectation in

20 phylogeographic reconstruction. This is true even if vicariance is plausible and no dispersal mechanism is

21 obvious. Subsequent research on many taxa has corroborated this view and refocused phylogeographic

22 research in new directions (see below).

23   The evidence for LDD as a principal explanation for plant disjunctions left plant phylogeography

24 in a quandary. In particular, vicariance offered a simple and uniform causal explanation of apparent

25 phylogeographic patterns. LDD does not. What other simple and uniform theoretical framework can

26 replace it? Several researchers [89-93] advocate a multi-parameter approach that can be described as

27 epiphylogenetic ecological community assembly (see below). Thus, parameters of plant phenotypes and

28 environments can be incorporated into phylogeography as a way to study simultaneously the evolution of

29 all parameters that effect plant movements. Phenotypic and environmental parameters thus can constrain

30 or relax likelihoods of deduced changes in taxon ranges. In this way, recurring patterns of {phylogeny x

31 phenotype X ecology X movement} patterns can be detected, with the objective of discovering

32 multidimensional commonality of cause. Formal probabilistic models described in [90, 91] incorporate

33 such ideas.

1   In many ways, the approach suggested by [89-93] is an advance over narrative and/or single-
2   parameter explanations of phylogeographic patterns. Instead of focusing on single parameters, it
3   facilitates delimitation of any and all conceivable parameters that might affect phylogeography. These
4   include not only dispersal vectors and adaptations, but suitability of destination habitats given the ecology
5   in the source habitat. Even relatively rare phenomena can be incorporated. Ostensibly, likelihoods of
6   different scenarios can be compared. Such an approach would be useful in the case of the Chilean flora.

7   At the same time, whatever the heuristic value of the approach, it is unlikely to "prove" specific
8   hypotheses in practice. It is prone to statistical artifacts articulated in this work and in [2]. Proposed
9   parameter categories are complex and render parameter evaluation subjective. As parameter richness
10   increases, so do the number of data categories, hence the fewer the number of data points per category,
11   hence the higher the variance and the less precise and accurate the estimate. Phylogeographic histories
12   that are rare or unique cannot be modeled at all. They will be forced to conform to more frequent
13   histories, possibly reinforcing support for the predominance of those histories. In particular,, lumping
14   parameters for statistical expedience distorts data [2|. Finally, as elaborated more in [2] (see also [84, 95]),
15   almost any reasonable pattern-generating model will tend to fit data better than a random pattern null
16   model, such that the pattern-generating model will bias analysis in its own favor. In other words, the
17   model will as much impose as test itself. As a further complication, the parameter-rich likelihood
18   approach necessitates Bayesian methods, which introduces the same hazards discussed above and in [2].

19   Consequently, the model-based approach at best will permit evaluation of general hypotheses
20   about phylogeography, but will not predict unequivocally phylogeographic histories or trajectories. This
21   is especially because of theoretical predictions that individual phylogeographic histories often reflect
22   "nonstandard" (effectively, one-off) dispersal phenomena [90]. Thus, the parameters most precisely
23   estimated statistically may be irrelevant in explaining many individual phylogeographic histories.

24   One can compare statistical phylogeographic explanation with that of a traffic jam along a stretch
25   of a major highway. Can the explanation derive from the commonality of the joint presence of the
26   vehicles? Perhaps, if the vehicles have a proximal origin and a common destination, e.g., a major sporting
27   event. But suppose each departed at a different time from divergent origins and had divergent destinations
28   and unexpectedly converged at the same point at the same time. Or suppose a distressed small aircraft
29   made an emergency landing on the highway, causing a jam that would not have occurred otherwise. How
30   many model parameters are required to test all possible historical causes for a traffic jam? How much data
31   is required? Does increasing parameter richness not converge on "narrative"? Can statistical analysis
32   discriminate between parameter/data-laden complex and non-nested explanations? Is it reasonable to
33   combine similar but distinct parameters/data in order to improve statistical precision? Is the resulting most
34   probable explanation the most accurate? These questions are explored in greater detail in [2].

1   More troublesome, inevitably the multi-parameter Bayesian approach will be applied

2   dogmatically to broad scale phylogeographic analysis that cannot avoid parameter/data

3   oversimplification. To the degree that the application is purely heuristic and a means of merely

4   statistically describing phylogeographic patterns rather than proving phylogeographic hypotheses, this

5   would be useful. Unfortunately, the scientific endeavor spurns the predicate of description and demands

6   the predicate of proof. The result likely will be prominently-published unwarranted conclusions, with as

7   many authors as necessary to insure that all benefit socioeconomically while none bear any responsibility.

8   These conclusions, in turn, will incarnate as highly-cited truth. Ironically, a computational approach

9   developed precisely to supersede a narrative approach ultimately will validate the narrative approach. At

10   the same time, perhaps that validation renders worthwhile the computational effort.

11   To encapsulate, phylogeography, like evolution generally, is not constrained by statistical

12   analytical assumptions and parameterizations imposed upon it. Put another way, assumptions and

13   parameters are requisite for statistical analysis and not evolution. But both methodological and

14   psychobiological tendencies naturally exaggerate pattern simplification and minimize or omit evidence

15   for idiosyncratic evolution. Finally, even statistically significant correlations can be consequent to

16   historical accident [84]. Different accidents might have yielded different correlations. The second part of

17   this work [2] argues that such statistical approaches to evolutionary analysis are useful if applied

18   heuristically, and if inferred correlations are interpreted not as evolutionary laws or explanations, but as

19   statistical descriptions.

20   In summary, the complexity of phylogenetic analysis must be considered trivial compared to

21   epiphylogenetic analysis, including phylogeography. Here, I borrow the term epiphylogenesis from the

22   realm of philosophy of the human condition. The concept is attributed to philosopher Bernard Stiegler,

23   and refers to processes that become parametrically integral to human evolution but are not genetically

24   programmed by it, in particular technology [95]. Epiphylogenetic processes are supposed to facilitate

25   escape from human phylogenetic constraints. Analogously, processes that affect plant distributions

26   (including plate tectonics) are not genetically programmed or phylogenetically preordained. They are

27   epiphylogenetic, yet become integral to plant evolution and facilitate escape from prior phylogenetic

28   constraints.

29   Phylogeny, at least, reduces causally to the processes of mutation and reproduction.

30   Phylogeographic analysis had attempted to reduce phylogeographic pattern explanation to the process of

31   plate tectonics. This having failed, other workers [89-93] suggest an expanded but no less reductionist

32   approach to accommodate any/all conceivable epiphylogenetic processes. But epiphylogenetic processes

33   are infinite and irreducible. Thus, commonality of epiphylogenetic causality is possible but unlikely.

34   More likely, patterns apparent in different parametric dimensions will conflict. In any case, as emphasized

1 repeatedly here and in [2], evolution is not constrained by pattern. Moreover, evolution does not cause

2 organisms to be similar. Axiomatically, it causes them to be different. Thus, phylogeography indeed is a

3 collection of one-off histories. As Moore and Donoghue [96] suggest, phylogeography is a consequence

4 of "[the right organism with the right descendents "being in the right place at the right time. This

5 interpretation applies to all evolutionary phenomena. This is consequent to PEI [2].

6

7 **Full authored names of subgeneric taxa cited in this work**

8

9 *Calandrinia breweri* S. Watson; *Calandrinia caespitosa* Gillies ex Arn.; *Calandrinia ciliata* (Ruíz &

10 Pav.) DC; *Calandrinia menziesii* (Hook.) Torr. & A. Gray; *Calandrinia* sect. *Amarantoideae* Reiche [≡

11 *Philippiamra*]; *Calyptridium ambiguum* (S. Watson) Hershk.; *Calyptridium monospermum* Greene;

12 *Calyptridium* sect. *Spraguea* Hershk., **comb. nov.** ≡ *Spraguea* Torr., Smithsonian Contr. Knowl. 6: 4.

13 1853; *Calyptridium* sect. *Thingia* Hershk., **comb. nov.** ≡ *Thingia* Hershk, Preprints 2018; 2018080496;

14 *Cistanthe* sect. *Rosulatae* (Reiche) Hershk.; *Lewisia* sect. *Cotyledon* Hohn ex B. Mathew; *Montia fontana*

15 L.; *Montiopsis cistiflora* (Gillies ex Arn.) D. I. Ford; *Montiopsis* subg. *Dianthoideae* D. I. Ford;

16 *Philippiamra calycina* (Phil.) Hershk.; *Philippiamra celosioides* (Phil.) Kuntze.

17

18 **Abbreviations**

19

20   BE: Bayesian estimation; BP: bootstrap proportion; LDD: long-distance dispersal; ML:

21 maximum likelihood; MP: maximum parsimony; PEI: Principle of Evolutionary Idiosyncraticity; PP:

22 posterior probability.

23

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25

26   The author declares no competing economic or political interests.

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33

34   MAH executed this work in its entirety.

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