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SYSTEMATICS, EVOLUTION, AND PHYLOGEOGRAPHY OF MONTIACEAE (PORTULACINEAE)

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ABSTRACT

Montiaceae (Portulacineae) comprise a clade of at least 268 species plus ca. 27 subspecific taxa primarily of western North America, the Chilean Floristic Region, and temperate Australasia. This work uses existing phylogenetic metadata to elaborate a new cladistic taxonomic synthesis. A total of 24 taxa are validated, nine new and 15 necessary nomenclatural recombinations. Hypotheses of Montiaceae historical biogeographical, ecological, and phenotypic evolution are evaluated in light of recent metadata and in terms of classical, contemporary, and novel systematic and evolutionary epistemology.

1. Introduction

This work presents a new cladistic taxonomy of Montiaceae (Portulacineae) and a review of their phylogeny and ecological, phenotypic, and biogeographic evolution. Considerable emphasis is placed on theory and epistemology. The work partially is a redrafting of Hershkovitz (2018a) but is highly modified and corrected. The taxonomy includes 24 nomenclatural novelties. The generic circumscriptions and diversity estimates are modified from Hernández-Ledesma et al. (2015). The suprageneric taxonomy is the first proposed since McNeill (1974) and the only phylogenetic one.

This work first summarizes evidence for diversity, phylogeny, ecological, phenotypic, and biographical evolution of Montiaceae. The taxonomy follows. The generic taxonomy supersedes that of Hernández-Ledesma et al. (2015), which superseded that of Carolin (1993) and Hershkovitz (1993a). In addition, I comment on the taxonomy and taxonomic history of selected taxa, especially *Calandrinia* Kunth, *Rumicastrum*, and *Cistanthe* Spach, and also recombine binomials into *Cistanthe*, *Calyptridium* Nuttall and *Philippiamra* Kuntze. I also conclude that *Lewisiopsis* has a hybrid origin and represents a living fossil.

2. Montiaceae Species-Level Diversity

The present synthesis conceives of Montiaceae as comprising ca. 268 species plus ca. 27 additional subspecific taxa, thus ca. 292 (sub-)specific taxa in total. These figures seem substantially higher than the "about 200" species estimated by Hernández-Ledesma et al. (2015). Much of the difference owes to a near doubling of the estimate of species diversity in the Australian genus *Rumicastrum* over the past two decades (Hancock et al. 2018). New species discovery among American taxa has been much less. In these, the modest increase in species diversity estimates owe mainly to additional study of known species, resulting in taxonomic segregation of previously studied and classified individuals and populations.

The estimate of (sub-)species diversity begs the question of the ontological nature of species and the criteria used to diagnose them. Aperture of this Pandora's Box is beyond the scope of this work, but it should not be ignored, either (McDade 1995). Perhaps it is better to emphasize that species diversity estimates and taxonomies applied in this work are *not* intended to reflect the criteria of any of the 30 or so proposed species concepts (Hey 2006), e.g., biological species or phylogenetic species or any other species of "species." This introduces no taxonomic controversy here, because such criteria *generally* have not been applied in developing Montiaceae species taxonomy.

The species diversity estimates and taxonomies applied here derive from subjective seat-of-the-pants typological classification, whereby the arbiters of (sub-)species are type specimens. (Sub-)species thus comprise real or hypothetical individuals considered to be conspecific with type specimens and, perhaps more importantly, to no *other* named or unnamed (sub-)species. It should be emphasized, in this regard, that there is nor shortage of accepted presumed taxa known only from single individuals, e.g., the genus *Schreiteria* among Montiaceae. The present work defers to the experience and "authority" of multiple contemporary and past students of Montiaceae (sub-)species taxonomy, including myself as appropriate.

Most of this taxonomy is based mainly on intuitive interpretation of morphological variability and geography, in a relatively few cases incorporating also cytological and genetic evidence. Not surprisingly, genetic and/or statistical evidence has been applied to species discrimination mainly for certain North American Montiaceae, in particular species of *Calyptridium* (e.g., Simpson et al. 2010), *Claytonia* (e.g., Stoughton et al. 2017a, b), and *Lewisia* (Foster et al. 1997). But especially for southern hemisphere Montiaceae, species discrimination bases mainly on subjective morphological and geographical studies, historically mainly by northern hemisphere botanists, but that is changing. Cytological criteria have been used mainly in *Claytonia* (Miller & Chambers 2006), but also in some *Phemeranthus* spp. (Price 2012).

Stoughton et al. (2017b) claimed to apply the "unified species concept" (De Queiroz 2005) for *Claytonia*. However, the unified species concept and its contemporary companion buzz term "integrative taxonomy" (e.g., Dayrat 2005) amount to old wine in new bottles. These concepts advocate pluralistic "total evidence" approaches to taxon discrimination. But, other than incorporating modern genetic and/or statistical approaches, they otherwise are indistinguishable from 18th century subjective typological taxonomy. No particular objective criterion is applied consistently and/or uniformly. Even under this epistemologically permissive concept, Stoughton et al. (2017a) demonstrated that about 10% of sampled individuals of the *Claytonia lanceolata* Pursh complex could not be classified, and that the number of unclassifiable individuals was the same as the number of recognized species (discussed later).

Montiaceae species as conceived here and historically are references for taxonomic/ biogeographical *diagnosis/description* only, and for filing specimens in herbaria. Most importantly, the species, their reported essential and/or diagnostic traits, and their incumbent trait variation do *not* represent independent and identically distributed observations for purposes of statistical biogeographical or evolutionary analysis. Such analyses presume that species and their traits are tangible entities so distributed. The failure of taxonomic species to conform to this presumption (empirically or epistemologically) undermines or invalidates much of quantitative evolutionary analysis, as discussed later.

Moreover, unappreciated is the fact that operational species technically are diagnosed not on the basis of what they *are*, but, rather, what they are *not*. Technically, what species *are* is *not other* species. This reflects the nomenclatural convention that mandates that every *new* species must be, in principle, not more or less than diagnostically different from *existing* species. Thus, ontologically, species are singularities, unique forms of life. Their uniqueness means that they are not permutations of other forms or draws from a linear distribution (see also below). The onus is on the statistical analyst to demonstrate the statistical properties of analyzed taxa.

One means of skirting the species concept issue might be to apply the term "specioid." This term has been proposed to refer to cultivated plant varieties that are not taxonomic species but share the ontological properties of being recognizable in one or another dimension and named as distinct entities for communication purposes (Jirásck 1964). Thus, the term specioid can be used to also to refer to a species defined by any operational criterion, however arbitrary, completely agnostic towards the nature of species. Montiaceae can be described taxonomically as having ca. 300 morphologically/ geographically distinguishable specioids, or taxonomic reference points (species and subspecific taxa). Parochial species concepts might yield qualitatively/quantitatively different specioids. At the same time, quantitative biogeographic/evolutionary research can emphasize analysis of specioids whose ontology is transcendental and whose taxonomic designations are for reference purposes only. In other words, no particular species circumscription/taxonomy need be implied. The only requisite is the evidential correspondence of analyzed individuals to the types of the named species. In this case, statistical properties, valid or not, can be ascribed to specioids.

As in all taxonomic groups, some Montiaceae species identities/circumscriptions seem clear and uncontroversial, while others are ambiguous. And some taxa have been studied more thoroughly than others. *Lewisia* is a genus that has been relatively well-studied taxonomically compared to certain other Montiaceae (Hershkovitz & Hogan 2002, 2003). Four comprehensive treatments have been published since 1966, as well as several more floristic treatments that include several to most species, especially those covering California. Yet, no two treatments are exactly alike, and even Hershkovitz & Hogan (2002, 2003) noted the inadequacy of their own treatment, especially with respect to the *L. pygmaea* (A. Gray) B.L. Rob. complex (see later discussion). At the other extreme, there is no critical comprehensive taxonomic treatment of *Cistanthe* sensu Hershkovitz (2006). The treatment that is most recent and comprehensive is Reiche (1898), which covers only the Chilean species.

In a privately-circulated unpublished manuscript, I attempted to resolve not the ontology of species, but the intransigence of individuals to sort themselves into taxa. I described a dynamical process of diversification called the "wave model" that predicts variable degrees of instantaneous species discreteness. Using analogies to wavescape features, especially dynamism, complexity, fractal qualities, and the axiom that, instantaneously, not all water pertains to waves, this model, as opposed to a species concept, attempted to describe biodiversity more objectively and without preconceived notions of what species are or ought to be or how they form.

The wave model was inspired by field observations of Atacama Desert Montiaceae. Here, because of low competition and little ecological community structure/stability, the emergence of a specioid entity is mainly a function of chance survival and proliferation of a novel and *viable*, as opposed to *optimal*, form in *transitionally* adequate conditions. In particular, a novel form must occur in a location that permits nothing more than growth and reproduction, without otherwise being more "adapted" than its progenitors. Other organisms are scarce in patches of barren desert, so infraspecific/interspecific biotic interactions have less impact, positive or negative, on survival. The limiting factor is mainly water, in particular its spatiotemporally irregular distribution. And evidently seeds of desert Montiaceae can survive decades without water. Thus, with few growth/reproductive episodes, a novel form can survive for centuries, even millennia.

At some point, change in conditions might permit greater proliferation of the novel form, so that its perceptual status changes from that of an odd mutant to a taxon. A wave. This may owe to changing conditions locally, or the novel form might disperse to different location. The model is applicable to all ecological conditions, not just the desert. Spatiotemporal separation of organisms and generations in the desert simply render it more apparent. The model is corroborated by phylogenomic studies like that of Stoughton et al. (2017a). In particular, in some timeframe prior or posterior to the present – *or* under slightly different historical circumstances – the singular unclassifiable forms might have proliferated and the proliferated classified forms vice versa (see also later discussion of phylogenomics).

Hershkovitz (2006) noted that phylogenetic trees derived using standard species-level phylogenetic markers exhibited long branches subtending several Montiaceae genera and very short, irresolvable interspecific branches (cf. Ogburn & Edwards 2015). This was despite ample morphological and ecological divergence and diversity, e.g., between diminutive, tiny-flowered annual versus suffruticose, large-flowered species, distributed in habitats ranging from sea-level to over 4000 m and hyperarid to subaquatic. Similar lack of interspecific phylogenetic resolution later was found in *Phemeranthus*, the "oldest" genus of the family (Price 2012).

These molecular data suggest recent and rapid species radiation, but Hershkovitz (2006) mused whether the low genetic divergence reflected hybridization. Lineage sorting emerges as another possible cause (Copetti et al. 2017; Stoughton et al. 2017a). Regardless, Hershkovitz (2006) speculated that genomic and phenomic evolution were decoupled, such that the considerable phenotypic diversification actually occurred over a longer period, whereas the sampled DNA loci "surfed" the evolving species without themselves proportionally diverging/diversifying. Both hybridization and lineage sorting could yield such an effect.

3. Montiaceae Phylogeny

a. Relations of Montiaceae and Portulacineae. Formerly, Montiaceae were included in the traditional but paraphyletic family Portulacaceae (Nyffeler & Eggli 2010a). Its conceptual origins trace to Hershkovitz (1993a), who referred to a group denominated Western American Portulacaceae, members of the family diversified primarily westwards of the American cordillera. Molecular analysis (Hershkovitz & Zimmer 1997) showed that Western American Portulacaceae comprised most of a clade they called the PAW clade, comprising: *Phemeranthus* Raf., the Australian genus *Rumicastrum* Ulbrich, and the taxa included in Western American Portulacaceae. The current circumscription of Montiaceae corresponds to the PAW clade and was completed with the addition of Hectorelleae (Applequist et al. 2006; Wagstaff & Hennion 2007).

The modern cladistic generic classification of Montiaceae originated with morphological analyses by Carolin (1987, 1993) and Hershkovitz (1991a, 1993a). Slowly, the new familial and generic concepts began to replace the traditional generic concepts of Pax & Hoffmann (1934) and McNeill (1974). Molecular evidence, beginning with Hershkovitz & Zimmer (1997), stimulated further acceptance of the cladistic classification and fomented several subsequent studies. Here I elaborate a modified cladistic supraspecific taxonomy based on molecular evidence, especially Hershkovitz (2006), Ogburn & Edwards (2015), Hancock et al. (2018), and Goolsby et al. (2018a, b). Most of this evidence was reviewed in Hershkovitz (2018b), which is undergoing revision.

Current targeted-gene phylogenetic and phylogenomic evidence (Ogburn & Edwards 2015; Smith et al. 2017; Goolsby et al. 2018a, b; Hancock et al. 2018; Wang et al. 2018; Yang et al. 2018; Marinho et al. 2019) places Montiaceae as sister to remaining Portulacineae. The latter comprises six families, including several genera of classical Portulacaceae and the classically segregated families Basellaceae, Cactaceae, Didiereaceae, and Halophytaceae. Most analyses place Portulacineae, in turn, as sister to Molluginaceae as currently circumscribed (Hernández-Ledesma et al. 2015; Ogburn & Edwards 2015; Smith et al. 2017; Hancock et al. 2018; Wang et al. 2018). However, one phylogenomic analysis found lower support for this relationship "than predicted" (Moore et al. 2017). Possibly the discrepancy is moot, given the high divergence between Portulacineae and Molluginaceae and, for that matter, any other candidate outgroup .

Consensus on the generalized phylogenetic position of Portulacineae is not absolute, however. Based on anatomy/morphology, Wang (2018) advocates a radically contrasting view of Caryophyllales and Portulacineae relations. Caryophyllales "should be among the most primitive of angiosperm groups" (Wang 2018: *352*). This interpretation resurrects several unorthodox morphological interpretations proposed during the late-19th to mid-20th century. Citing reproductive traits *especially* of certain Portulacineae, Wang (2018) proposes that Portulacineae are derived from Cordaitales, a Carboniferous seed plant lineage.

Wang (2018) does not reconcile his view with ever-accumulating genomic evidence that "core" Caryophyllales comprise the terminal clades of a broader and remarkably diverse Caryophyllales "sensu lato," well-nested within eudicots. Although the consensus position of Caryophyllales has migrated somewhat over the past two decades with increasing gene/taxon sampling, current analyses (Angiosperm Phylogeny Working Group 2016) position Caryophyllales s. l. as sister to asterids, the most "advanced" of angiosperms. Inadequacy of the fossil record duly noted, Wang (2018) does not address the apparent paradox that existing stratigraphic *sequences* correlate well with phylogenetic evidence. To be fair, however, Wang (2018 and cited references) indeed argues that many pre-Cretaceous fossils are angiospermous. Thus, evidently he does believe that Portulacineae and dinosaur footprints, perhaps along with human, eventually might be found side-by-side.

Another conflicting interpretation of Portulacineae relations is presented by Liu et al. (2018). Their phylogenetic analysis of 48 protein-coding chloroplast genes from 35 Caryophyllales (sensu lato) species yielded what can only be described as a "random" – yet highly statistically supported – phylogeny. None of the familial/ordinal level phylogenetic structure of the consensus phylogeny is evident. Samples of multiply-sampled genera, such as *Silene*, *Fagopyrum*, *Salicornia*, and *Drosera* intersperse throughout the tree. The four samples of Portulacineae genera (*Carnegia*, *Cistanthe*, *Portulaca*, and *Talinum*) do also. I make no attempt here to reconcile or explain the results of Liu et al. (2018).

In retrospect, the cladistic position of Montiaceae among Portulacineae might seem unexpected. Compared to the clade comprising remaining Portulacineae, Montiaceae are less diverse morphologically, genetically, and taxonomically (comprising about 15% of Portulacineae species diversity). Moreover, their "centers of diversity" developed geologically relatively recently: mountainous and arid regions of temperate western America. Remaining Portulacineae have a more tropical Gondwanan distribution (discussed below). Molluginaceae are mainly African.

On the basis of morphology, my initial expectation was that Montiaceae would prove to be nested "within" a much older Portulacineae, more or less as indicated in Carolin (1987). This expectation owed to the morphological similarity and biogeographic proximity of herbaceous perennial species of *Talinum* with many species of the grade group *Calandrinia* s. l. (discussed below). Indeed, these taxa classically had been classified in the same tribe (Pax and Hoffman 1934; McNeill 1974), and historically, species of one genus variously had been described and/or classified as species of the other (discussed below). Furthermore, *Phemeranthus* had been included in *Talinum* by all authors since 1828, and its current segregation was resisted for more than a decade following the cladistic conclusions of Carolin (1987). Thus, the intergradations between *Talinum* s. l. and *Calandrinia* s. l., along with geologically recently developed habitats of the latter, suggested nesting of Montiaceae within classical Portulacaceae.

Interestingly, the earlier morphological cladistic analysis of Hershkovitz (1993a) was more or less consistent with Montiaceae being the sister of remaining Portulacineae, even though no particular outgroup was specified. That work noted that "the cladistics results suggest that the western American group [i.e., Montiaceae] is as old as if not older than the eastern American/African group [i.e., remaining Portulacineae]" (Hershkovitz 1993a: *350–351*). It also pointed out that presumably "primitive" tricolpate pollen was widespread among (effective) Montiaceae, whereas among classical Portulacaceae, it was restricted otherwise to *Portulacaria* and *Ceraria* (Didiereaceae). The latter, it turns out, belong to the lineage diverging after Montiaceae. Hershkovitz (1991b, 1993a) also argued that Cactaceae seemed to nest between *Talinum* and a clade of taxa sharing chromosome base number 9, *Portulaca* and the Anacampseroid genera.

The first relevant molecular analysis, based on nuclear ribosomal internal transcribed spacer (ITS) sequences (Hershkovitz & Zimmer 1997), was not far off from the current phylogenetic consensus for Portulacineae. The midpoint-rooted tree showed Basellaceae/Didiereaceae (as currently circumscribed) as sister to remaining Portulacineae, with Montiaceae diverging subsequentially. This appears to be a branch length artifact, i.e., the midpoint occurred along the especially long branch of Basellaceae/Didiereaceae. But no basis for outgroup rooting existed at that time. Re-rooting the midpoint-rooted tree one node up would generate the current view. Hershkovitz & Zimmer (1997) also corroborated the morphologically-based conclusions regarding the position of Cactaceae.

Current molecular/genomic evidence for Portulacineae relations ought to instill appreciation for the morphological cladistic analyses of Carolin (1987) and Hershkovitz (1993a). Carolin's (1987) work was seminal and radically transformed phylogenetic concepts pervasive up to the end of the 20th century. Up until then, phylogenetic studies proceeded taxonomically top-down, using existing classical higher-level taxa as taxonomic units (e.g., Rodman et al. 1984; Rodman 1990; cf. Hershkovitz 1989; see also chapters in Behnke & Mabry 1994). This presumed that higher-level taxa were monophyletic, a notion which Rodman (1990) defended. The first molecular phylogenetic analyses of the order also proceeded top-down (Rettig et al. 1992, Downie and Palmer 1994; Manhart and Rettig 1994). Because these studies sampled classical families sparsely, they failed to discover familial paraphyly/polyphyly.

Carolin's (1987) approach was bottom-up, seeking to discover clades among Portulacineae based on character evidence and not taxonomic prejudice. Hershkovitz' (1993a and cited references) effort began independently of Carolin's and came to similar, but not identical, conclusions. Both works represent the first and only detailed bottom-up computational morphological cladistic analyses of a Caryophyllales family. Hershkovitz (1993a) was the first and only to consider explicitly and analytically the paraphyly of a Caryophyllales family.

By 1993, the phylogenetic paradigm shifted abruptly and decidedly from morphology to molecular. Hershkovitz (1993a) provided the hypothetical template for Hershkovitz & Zimmer (1997, 2000) and subsequent molecular and genomic phylogenetic (and phylogeographic and evolutionary) analyses of Portulacineae. Hershkovitz & Zimmer (1997, 2000) corroborated several ideas of Hershkovitz (1993a), including some but not all novel generic circumscriptions and the relations of Basellaceae, Cactaceae and Didiereaceae. Hershkovitz & Zimmer's (1997) study overcame numerous technical and analytical challenges, as described therein. But just after that point, technological and analytical advances rendered molecular phylogenetics more an endeavor of "acquisition" than "inquisition." In particular, advance depended not so much on knowledge, theory and problem-solving than it did on the acquisition of unsampled taxa and the wherewithal to run them through the largely automated laboratory and computational mill. To paraphrase James Watson, "any monkey could do it." In some cases, e.g., Liu et al. (2018), a monkey could not have done it any worse.

However, when it emerged, the Carolin/Hershkovitz phylogenetic framework was not embraced widely. This is evident partially in the long delay in nomenclatural transfer of species into their currently accepted genera, as discussed later. This delay continues to the present day in the case of *Rumicastrum* species, still incorrectly classified in *Calandrinia* s. l. more than three decades after Carolin's work (e.g., Goolsby et al 2018a, b; Hancock et al. 2018).

Prolonged skepticism towards the conclusions especially of Hershkovitz (1993a) is evident also in Cuenod et al. (2002), who intimated that paraphyly of Caryophyllales families was their own discovery, *especially* nesting of Cactaceae among classical Portulacaceae (see Kew Scientist 2001). At the minimum, the intimation demonstrates that, despite the morphological and molecular evidence advanced by Hershkovitz (1989, 1991a–d, 1993a; Hershkovitz & Zimmer 1997), Cuenod et al. (2002) did not *anticipate* paraphyly of Caryophyllales families. Possibly this was true more broadly in the plant systematics community (but see Brummitt 2002). Other researchers (e.g., Moreira Muñoz 2011) evidently did not appreciate that currently conceived Cactaceae relations were resolved well before their molecular-based corroboration (Hershkovitz 1991b, 1993a), and that similarities between Cactaceae and certain classical Portulacaceae had been noted by multiple researchers since the 19th century (Hershkovitz 1993a; Metzling & Kiesling 2008).

b. Relations among Montiaceae. With caveats, current molecular phylogenetic evidence suggests the following sequence of divergences and intergeneric-level relations (Ogburn & Edwards 2015: *Fig. 2*; Hancock et al. 2018: *Figs. 3–4*; cf. Hershkovitz 2018b).

1. *Phemeranthus* as the outgroup of the remainder of Montiaceae. This accords with morphological and phylogeographic evidence. On morphological bases (elaborated later), I here classify *Phemeranthus* and *Schreiteria* in Phemerantheae.

2. Divergence/diversification of a clade here denominated Cistantheae, a principally Chilean (semi-) arid region lineage that includes: (a) *Cistanthe*; (b) *Montiopsis*; and (c) Calyptridinae, comprising *Lenzia*, *Calyptridium*, and *Philippiamra*.

3. Concomitantly, paraphyly of *Cistanthe* sensu Hershkovitz (1991a, 1993a; cf. Hershkovitz 2006; Ogburn & Edwards 2015). However, Hershkovitz (2018b) argues that morphological similarities shared by members of *Cistanthe* sensu Hershkovitz (1993a) may be symplesiomorphies, historical synapomorphies lost in more recently divergent lineages.

4. Divergence of *Rumicastrum*. Hershkovitz (2018a) included this genus in Montioideae (see below), but ecological divergence compels me to leave it isolated, thus separating Montiaceae into a *grade* of primarily ancestrally warm/arid-adapted succulents (“paleomonts”) from a clade of decidedly more cool/moist-adapted Montioideae.

5. Monophyly, hence, of a clade here denominated Montioideae, comprising remaining Montiaceae.

6. Divergence of *Calandrinia*, although one of the 12 data/method combinations in Hancock et al. (2018) yielded maximal support for a conflicting topology, in which *Calandrinia* is sister to Cistantheae.

7. Divergence of Hectorelleae. Support for this relation degenerates markedly in the five- compared to the three-marker data in Ogburn & Edwards (2015), but no Hectorelleae data were available for the additional two markers, which are more rapidly-evolving (Hershkovitz 2018b). This suggests that the inclusion of more rapidly-evolving markers introduced not conflict, but noise that perturbed the statistical support.

8. Divergence/diversification of a clade here denominated Montieae, a principally western North American lineage including *Lewisiopsis*, *Lewisia*, *Claytonia*, and *Montia*.

9. A hybrid origin of *Lewisiopsis* (see Hershkovitz 2018a, b; see also below). This hypothesis is supported by strong conflict of *Lewisiopsis* sister relations based on plastome and nucleosome data. The former support a sister relation with *Lewisia*; the latter with a clade comprising *Lewisia* and Montiinae. In addition, the root-to-terminal *Lewisiopsis* branch length is exceptionally short in phylograms in all molecular/genome analyses, from Hershkovitz & Zimmer (1997) to Goolsby et al. (2018a, b). The patristic distance between *Lewisiopsis* and *Cistanthe* is about the same as or generally less than that between *Lewisiopsis* and other Montieae. This parallels the morphological data (Hershkovitz 1992). The evidence suggests that *Lewisiopsis*, in conjunction with its hybrid origin, has persisted as a "living fossil" that has retained genomic and phenotypic characteristics of a *Cistanthe*-like ancestor.

10. The uncontroversial sister relation of *Claytonia* and *Montia* (but see trees in Marinho et al. 2019), often classified as Montieae, but here classified as Montiinae.

In addition, existing evidence supports several infrageneric-level phylogenetic relations:

1. Monophyly of two subclades of *Phemeranthus*, one comprising the (sub-)caulescent species, the other the acaulescent (Price 2012).

2. Monophyly of *Cistanthe* sections *Cistanthe* and *Rosulatae*, each including annual and perennial species.

3. Despite poor overall resolution, monophyly of two subclades within *Cistanthe* sect. *Rosulatae*, each of which is polymorphic for life history. These subclades are recognized as subsections here and in Hershkovitz (2018a). Otherwise, genetic divergence is too low to resolve interspecific phylogenetic relations (Hershkovitz 2006).

4. Possible paraphyly of *Calyptridium* sect. *Calyptridium* with respect to *C.* sect. *Spraguea*. The latter includes the only perennial species of the genus.

5. Tentatively, monophyly of both the perennial and annual clades of *Calandrinia* (Hershkovitz 2006; Ogburn & Edwards 2015), which is not supported mutually by independent phenotypic traits (Hershkovitz 1993a). However, Goolsby et al.'s (2018a, b) phylogenomic analyses show paraphyly of the annual *C.* sect. *Calandrinia* with respect to the perennial *C.* sect. *Acaules*. This result is problematic (see below), but is not otherwise implausible. Hershkovitz (1993a) suggested the contrary relationship, *C.* sect. *Acaules* paraphyletic with respect to *C.* sect. *Calandrinia*, evidenced by morphologically intermediate traits of the annual *C. nitida* (Ruiz and Pav.) DC (synonym: *C. axilliflora* Barnéoud). Interestingly, Goolsby et al.'s (2018a, b) analysis shows *C. nitida* as sister to the perennial clade. If correct, Goolsby et al.'s (2018a, b) results provide another example of a transition from annual to perennial life history, as Hershkovitz (2018c; *contra* Carolin 1987, Hershkovitz 1993; Ogburn & Edwards 2015) argued was the predominant polarity among Montiaceae (see also below).

6. Monophyly of the perennial *Montiopsis* subg. *Dianthoideae*, which lack a phenotypic synapomorphy (Hershkovitz 1993a). Genetic divergence among the annual and perennial species of *M.* subg. *Montiopsis* is insufficient to resolve their phylogenetic relations (Hershkovitz 2006).

7. Somewhat ambiguous support for monophyly of two principal groups of *Lewisia*, one comprising the "evergreen" species (*Lewisia* sect. *Cotyledon*; Mathew 1989). Leaves of these species are coriaceous and persist year to year. In agreement with my unpublished data, the section is monophyletic in Goolsby et al. (2018a, b) with the exception of *L. congdonii* (Rydb.) S. Clay.

The latter species shares reproductive morphology of the evergreen species, but has ephemeral leaves (Mathew 1989). The known interfertility among many *Lewisia* species (Mathew 1989; Davidson 2000) raises the possibility that *L. congdonii* has a hybrid origin. Resolution is poor among remaining species of the other subclade, which are morphologically diverse but share ephemerality of their leaves.

8. Monophyly of three *Claytonia* sections differing in life form/history: annual, rhizomatous perennial, and caudiciform taproot or tuberous (O'Quinn et al. 2005). Again, this seems to rule out paraphyly of perennials with respect to annuals, rendering less certain evolutionary polarities.

9. Monophyly of three clades within *Montia* (O'Quinn et al. 2005).

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 imply 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 be colinear, but they are not the same. Phenotypic synapomorphies can originate before or after molecular marker synapomorphies, and also via lateral transfer. Whole genome analyses (see below) 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 more broadly in contemporary systematics is simplistic and may be naïve.

c. Phylogenomic evidence for Montiaceae phylogeny. Within the past few years, now "classical" targeted-gene molecular phylogenetics has ceded significantly to phylogenomics, phylogenetic analysis of thousands of relatively short (> 300 bp) sequence fragments sampled from whole genome DNA or transcriptomes. Using computer programs, the short fragments often are assembled into longer contiguous fragments. Within the past two years, eight phylogenomic analyses have been published that include significant Montiaceae data (Moore et al. 2017; Smith et al. 2017; Stoughton et al. 2017a; Yang et al. 2017; Goolsby et al. 2018a, b; Hancock et al. 2018; Walker et al. 2018; Wang et al. 2018). In some cases, phylogenomic studies are a hybrid between phylogenetics and functional genomics, i.e., emphasize genomic sampling for particular functional genes (e.g., Goolsby et al. 2018). A deluge of phylogenomic data is likely to appear in coming weeks and months.

Phylogenomic analysis currently presents numerous technical, analytical, and epistemological challenges that will be reviewed in greater detail in a revision of Hershkovitz (2018b). One challenge is common to all phylogenetic and, in fact, evolutionary analysis in general. In particular, statistical analyses obligate the assumption that observed data are generated according to models used to reconstruct their evolutionary history. Yet, models are approximations and "are never true in real data analysis" (Yang & Zhu 2018: *1854*; cf. Gunawardena 2014). But phylogenomics adds additional challenges:

1. Genomic-level evolutionary models are more precarious. Model violations are somewhat tractable in analysis of modest-length, well-studied, and broadly sampled phylogenetic markers. Even then, models usually falsely assume molecular evolutionary stationarity across phylogenetic sample space (Hershkovitz 2018b). Model violations are (practically) intractable in the analysis of hundreds to thousands of machine-sampled, machine-assembled DNA fragments summing to more than 100,000 nucleotide base pairs.

2. Phylogenomic analyses generally emphasize multi-species coalescent model reconstruction, which introduces dicey assumptions on lineage effective population size and generation times during diversification over the course of tens of millions of years (Xu & Yang 2016).

3. The size of phylogenomic data sets constrains their analysis to less rigorous "summary methods" (Xu & Yang 2016) and/or problematic Bayesian methods (Yang & Zhu 2018).

4. If applicable, sampling bias for particular functional genes introduces the specter of convergence in phylogenetic analysis.

The analytical and interpretive challenges do not mean that phylogenomic reconstructions are "wrong." In fact, most nodes emerging from phylogenomic analyses seem to corroborate those of targeted-gene phylogenetic estimates. But not always, e.g., in the case of Molluginaceae-Portulacineae monophyly (Yang et al. 2018) and relations within *Calandrinia* (Goolsby, et al. 2018a, b). Such discrepancies can be understood intuitively. A determination that a racehorse can run faster than a turtle may not be especially sensitive to experimental or analytical method or assumptions or measurement error. But determining which was the fastest racehorse ever, if that is possible, is another matter. Here we expect assumption/data sensitivity and, in empirical Bayesian estimation, maximal support for incorrect and conflicting conclusions. But the analytical intractability of phylogenomic data creates an additional epistemological dilemma. Should we incline towards phylogenomic conclusions, because more data is better? Or should we accept that phylogenomic conclusions are generated by machines and remain, at this point, outside of the realm of human intellectual scrutiny and sensibilities?

An illustrative example of the challenge of phylogenomics emerges in the analysis of the *Claytonia lanceolata* complex (Stoughton et al. 2017a). Without doubt, the approach yielded significant discoveries facilitating the recognition of distinct evolutionary lineages in this group and the polyphyly of individuals classified as *C. umbellata*. At the same time, genetic patterns emergent from two different genomic sampling methods exhibit notable differences that would not be apparent had only one method been applied. And graphics derived using each sequence sampling method exhibit notable differences according to two different analytical methods (phylogenetic tree versus split-tree networks). So there is not one result, but four different ones, even as these agree on several points. Moreover, about 10% of sampled individuals could not be classified into a lineage, and the number of unclassifiable individuals was the same as the number of lineages classified. This result will be reconsidered below.

Another illustrative example is the phylogenomic analysis of columnar cacti (Cactaceae; Pachycereeae) by Copetti et al. (2017). The data demonstrated rampant gene tree conflict, which the authors attributed to incomplete lineage sorting dating back to Cactaceae origins. This, in turn, was explained as a consequence of especially long generation times combined with moderate effective population sizes (but see Gorelick 2009). Again, the phylogenomic investigation yielded useful and potentially paradigm-shifting discoveries. The results may offer insights into the (pleisiomorphic) capacity for intergeneric hybridization among some cacti, as well as graft compatibility. The results recall the notion that, indeed, cacti are a hypervariable "big genus" of classical Portulacaceae. But, notwithstanding the massive data, the analysis did not resolve cladistic phylogeny as conventionally conceived.

The phylogenomic data suggests reconceptualization of existing "species concepts." The results of Stoughton et al. (2017a) are consistent with the dynamic "wave model" of species that I developed in a privately circulated manuscript. That work advocated a distinction between "apospecies" and "synspecies," perhaps better termed "synapospecies," though not in the cladistic sense. Synspecies correspond to operational species, or groups of individuals classified as taxa or lineages. Apospecies are individuals that cannot be so classified. "Type specimens" perfunctory to formal taxon recognition, are, by definition, apospecies, because their diagnosis tautologically asserts that they are different from other species, without otherwise ascribing to them species qualities other than as Platonic ideals. But the taxonomic recognition/acceptance of the hypothetical species does not depend per se upon their status as apospecific (unique). After all, no two individuals are exactly alike. Rather, operational specific status depends on the existence of a real or hypothetical class or category of individuals conspecific to the Type individual and apospecific to the Type of any other species. This class comprises the hypothetical synspecies.

To appreciate the preceding, imagine that the ancestors of the individuals classified into eight taxa in Stoughton et al. (2017a) had never proliferated or, alternatively, were surviving individuals of lineages that had proliferated but died out. And imagine that the history/fate of the eight individuals not classified into taxa likewise was reversed, i.e., that each of them had proliferated. No biological or evolutionary law constrains these possibilities. The pattern of taxa evident in Stoughton et al.'s (2017a) figures would be "inverted." The singletons would be the taxa and the taxa would be the singletons

Alternatively, suppose that *no* individuals currently existed *except* the eight Type specimens of the recognized taxa and the eight unclassified individuals. The figures would illustrate parametric relations between 16 apospecific individuals, i.e., 16 individuals not conspecific with any other. Possibly all 16 individuals would be classified as one to up to 16 operational species, depending on taxonomic inclination. In any case, the nonindependence and nonidentical distribution of species should be clear. Operationally, the eight lineages recognized by Stoughton et al. (2017a) are thus synspecies, and their Types and the unclassified individuals apospecies.

The results of both Stoughton et al. (2017a) and Copetti et al. (2017) also suggest reconceptualization of the relation between "gene trees" and "species trees." Although it has been recognized for decades that the former are distinct from the latter (e.g., Doyle 1992), this conceptualization is nuanced. It emerged from the deduction that an individual gene tree might be in conflict with or otherwise misrepresent a species tree. This trivial conceptualization has persisted into the phylogenomics era, in which the species tree evidently is equated with that of a plurality of concordant loci trees (e.g., Copetti et al. 2017). In other words, the "true" species tree is defined mathematically as the phylogenomic consensus.

But the conceptualization of species as gene tree consensus is flawed epistemologically. In particular, the Type of a species ontologically refers to the entirety of its tangible characteristics, including its DNA sequences. The gene trees are irrelevant. If the phylogenetically "minority" genes were excised, even a single lineage-sorted allele, the individual would be different ontologically. This should be self-evident in the case of hybrid species, whose ontological identity precisely specifies their possession of genes of different lineages.

The paradox is resolved if it is appreciated that gene and species trees are *ontologically* distinct: they *neither* agree *nor* conflict with each other. This can be appreciated in the context of hierarchy theory (e.g., Salthe & Matsuno 1995; Yarrow & Salthe 2008; Fábregas-Tejeda &Vergara-Silva 2017). In particular, genes and species are dynamical self-organizing systems separated hierarchically by several levels. But evolution at each hierarchical level is influenced mainly by proximal, less so distal, levels. Systems thus evolve as constrained by a subordinate level, which establishes starting conditions, and a superimposed one, which establishes a (transitory) boundary. The consequence is that, via percolation, different hierarchical levels evolve coordinately but not in lock step. A species tree is the continuous evolutionary history of the ontogenetic phenotypes

(Maturana & Mpodozis 2000) of its individual members. A gene tree is the continuous evolutionary history of a DNA locus. DNA replication provides the initial conditions for sequence evolution; the genome is the upper boundary. DNA sequences provide the initial conditions for genome evolution; a cell is the upper boundary. And so forth, up to the level of species and the environment. Note that each level is free to "improvise" as long as the improvisation is tolerated at adjacent levels. But failure at any level imposes failure at all levels, even though other levels are functioning "normally." Evolution at different levels is decoupled. Levels function interdependently, yet independently, A change at one level does not "cause" change at another level except in the trivial case that it is lethal. Thus, gene and species histories differ not because they differ empirically, but because they differ ontologically and do not directly *impose* common histories on each other.

4. Montiaceae Phenotypic, Cytological, and Ecological Evolution

a. Habitat/niche diversity. Montiaceae species distinguish from other Portulacineae phylogeographically, ecologically, and phenotypically. Their distribution concentrates in the high-relief and climatically diverse temperate zone westwards from the American high cordillera (cis-cordilleran), with lesser additional native diversity east of the American cordillera (trans-cordilleran). The cis-cordilleran diversity extends circum-Pacifically to Siberia, Australia, New Zealand, and the Kerguelen Islands (Hershkovitz 2018a, b). Other Portulacineae are distributed mainly more towards the tropics and from the American high cordillera eastwards (trans-cordilleran) and extending to Africa/Madagascar, with a few taxa in warmer parts of Australasia/Oceania (Hershkovitz 1993a, 2018c; Ogburn & Edwards 2015). While early-diverging Montiaceae share with other Portulacineae a more warm/arid distribution and succulence, later-evolved lineages concentrate especially in cooler/moister (higher altitude and/or latitude) environments and are less or not succulent (Ogburn & Edwards 2015; Hershkovitz 2018c).

Montiaceae niches are diverse. Their habitats range from desert to aquatic and arctic/alpine to subtropical. Considerable habitat diversity characterizes not only the family as a whole, but several of the included genera. Habitats within the genus *Phemeranthus* alone range from conditions as hot or hotter than those of any other Portulacineae, to cool temperate montane, and even bogs (Price 2012; Ocampo 2017). Calyptridinae comprises ca. 23 mostly arid-adapted taxa in three genera: (1) the arid-region high alpine monotypic genus *Lenzia*; (2) *Philippiamra*, which includes arid alpine and hyperarid desert species that possibly are the most drought-resistant of all vascular plants (Hershkovitz 2018c; cf. Bahamondes et al. 2012: *15*; see also below); and (3) *Calyptridium*, which includes ca. 12 taxa whose habitats range from sea-level to alpine, and from the Sonoran and Mojave Deserts to southern Oregon mountains receiving ca. 500 mm mean annual precipitation (MAP). Perhaps a more extreme example is *Claytonia* sect. *Claytonia*, whose 28 taxa distribute disproportionately in cool, moist habitats. Yet, the habitats of the genus range from the Mojave Desert (ca. 5 mm MAP) to Vancouver Island (ca. 5000 mm MAP), and from Arctic vegetation limits to the warm temperate S/SE US and Mexico. In all of these genera, the extremes span relatively low genetic divergences indicative of Pliocene or more recent diversification.

Montiaceae include species that span small to large ranges and rare to common frequencies. As discussed in Hershkovitz (2018b, c; see also below), seven species of Montiaceae have become adventive intercontinentally to varying degrees. These include one species of *Phemeranthus*, one of *Calandrinia*, two of *Claytonia*, and three of *Montia*. An additional species of *Montia* considered adventive by O'Quinn et al. (2005) likely is not (see below). As will be elaborated better in revisions of Hershkovitz (2018b, c), there seems to be no evolutionary or ecological rhyme or reason to explain, much less predict, adventive establishment among Montiaceae or, for that matter, probably among biological organisms in general. Hypotheses and conclusions advanced to explain species "invasiveness" base on statistical fallacies such as those described in Hershkovitz (2018c).

Interestingly, all intercontinentally adventive Montiaceae species are native to the US, which may provide statistical evidence for theories of US imperialism.

Montiaceae diversification has been thought to be related to the diversity of the local habitats in the main range of the family, far-western North America and South America (Hershkovitz 2006; Ogburn & Edwards 2015). But Hershkovitz (2018c) reconsidered this view, pointing out that some Montiaceae lineages in this range never diversified (e.g., the monotypic genera *Lenzia* and *Lewisiopsis*), while *Rumicastrum*, the largest genus in the family, is endemic to less macroecologically diverse/extreme regions of Australia (see below). The same phenomenon characterizes many lineages of angiosperms in macroecologically diverse western America: some have diversified and some have not. Similarly, other angiosperm lineages have diversified exceptionally in relatively macroecologically less diverse regions of South Africa and Australia. Thus, local macroecological diversity is neither necessary, nor sufficient, to explain Montiaceae diversity. The criterion of necessity and sufficiency of evolutionary explanation was emphasized in Hershkovitz (2018c) and emerges again below.

b. Growth form and life history diversity. Montiaceae also differ from other Portulacineae in comprising mostly hemicryptophytic (including acaulescent rosettiform-caudiciform) perennials and therophytes (Hershkovitz 1993a, 2018c; Ogburn & Edwards 2015). Other Portulacineae comprise mostly phanerophytic to chamaephytic herbs, shrubs, trees, and vines, and often stem succulents. However, annuals occur among *Portulaca* (Portulacaceae) species (Ocampo 2012), and most Anacampserotaceae species are hemicryptophytes, a few acaulescent (Carolin 1987, 1993; Rowley 1994). Phylogeny of extant Montiaceae implicates at least 14 life history transitions since the split between Cistantheae and Montioideae, 25–35 million years ago, out of the total ca 16 transitions among all Portulacineae over 50+ million years (Ogburn & Edwards 2015; Hershkovitz 2018c; age estimates of Yao et al. 2019 are rather older, discussed further below).

c. Relation of life history evolution to temperature niche. Ogburn & Edwards (2015) reported a statistically significant higher rate of phylogenetic temperature niche diversification among Montiaceae compared to other Portulacineae. They also reported a phylogenetic correlation between life history and temperature niche, resulting in annual/perennial distributional sorting into, respectively, warmer/cooler habitats. They attributed the distribution bias to the shorter growth season of cooler environments, which they supposed is insufficient for annuals to complete their life cycles. They concluded that the Montiaceae ancestor was an acaulescent rosettiform tap-rooted perennial species that, during phylogenesis, repeatedly gave rise to annual species in response to temperature-mediated. This selection, in turn, was enhanced by the heterogeneity of temperature niches across short geographic distances in mountainous western America. Ogburn & Edwards (2015) also concluded that the evolutionary lability of life history among Montiaceae, which facilitated their temperature niche diversification, was a function of their acaulescent rosettiform growth form. This, they supposed, facilitated evolutionary lability of above-/ below-ground biomass allocation.

Hershkovitz (2018c) rejected Ogburn & Edwards' (2015) interpretations, arguing that these owed to a combination of data, statistical, computational, and epistemological artifacts. Among these:

1. Hershkovitz (2018c) concluded that, while the Montiaceae ancestor likely was perennial, contrary to earlier interpretations, including Hershkovitz (1993a), most perennial Montiaceae species/clades were derived from annuals. Goolsby et al.'s (2018a, b) results for *Calandrinia*, if correct, further support this conclusion.

2. Ogburn & Edwards (2015) lumped perennial life forms that are not homologous, i.e., caudiciform, rhizomatous, and pachycaul forms. This evidently biased their statistical analysis (see also below).

3. Ogburn & Edwards (2015) used global climate temperature data as a proxy for plant temperature niche. Hershkovitz (2018c) pointed out that climate temperature values can depart substantially from plant microenvironment temperature values (Körner & Hiltbrunner 2018).

4. Ogburn & Edwards (2015), used species "mean" climate temperature values in their analysis, these calculated based on database collection localities. The view here is that species are not statistical units (see above), but, even so, their extreme values are more relevant than their means, since they approximate better the realizable niche range. Many factors determine plant incidence, e.g., competition, so that mean observed values might not and probably do not reflect physiological optima. Moreover, the method is subject to multiple sources of error: collection bias, databasing bias, misidentification, and taxonomic classification artifact.

5. Ogburn & Edwards (2015) conclusions fail the test of causal necessity and sufficiency. In multiple instances, annuals occur in cold environments and perennials in warmer ones. Five annual species in three genera (*Calyptridium*, *Montiopsis*, and *Philippiamra*) are strictly (sub-) alpine. Two more are facultatively so. Numerous perennial species of several genera (*Cistanthe*, *Claytonia*, *Lewisia*, *Phemeranthus*, and *Rumicastrum*) are distributed in warm environments, occurring alongside annual Montiaceae species. There are both annual and perennial species having very broad temperature niches.

6. As alluded to above, ecological heterogeneity is neither necessary nor sufficient to promote diversification. Some taxa, e.g., *Lewisiopsis*, failed to diversify under the same geographic/ ecological conditions as co-occurring Montiaceae. As noted, *Rumicastrum* is the most diversified genus in the family, yet distributes across Australia, which is ecologically more homogeneous than western North America or South America.

7. Hershkovitz (2018c) disputed the notion that growth season length restricts annuals to warmer environments, noting that the growing season of the warmer desert habitats of Montiaceae is much shorter than the cold alpine ones. Interestingly, the annual life history evidently is an adaptation to *short* growing season in the C4 species *Portulaca oleracea* L. (Portulacaceae). Among *Portulaca* species, range of the latter extends by far furthest into the cool temperate zone. Here, light/temperature are insufficient to accommodate the physiological requisites of perennial C4 species. But their seeds may be perfectly cold-hardy, so an annual life history is possible.

8. Ogburn & Edwards (2015) presented no evidence supporting their assertion that life history evolution among Montiaceae reflected optimization of above-/below-ground biomass allocation. Hershkovitz (2018c) disputed this notion and presented a more plausible and empirically-evidenced argument that the life history transitions originated consequent to temperature sensitivity of reproductive induction, later differentially fixed by genetic assimilation in different temperature environments.

d. Moisture niche evolution among Montiaceae. The overall phylogenetic trend among Montiaceae has been towards cooler/moister niches. The earliest diverging lineages (Phemerantheae, Cistantheae, and *Rumicastrum*) comprise often warmer and mainly arid- to hyperarid-adapted taxa. Most of these taxa are succulent or, in the case of *Montiopsis* species, (glandular-)pubescent. Nonetheless, some species of these genera evolved into cooler/moister niches, e.g., a subaquatic *Phemeranthus* species (Ocampo 2017), more southerly Chilean (ca. 38S) and northern Chilean coastal fog desert species of *Cistanthe*, more southerly Chilean (ca. 40S) populations of *Montiopsis,* and southern Oregon species of the otherwise xerophytic genus *Calyptridium.* The successively diverging lineages, *Calandrinia*, Hectorelleae, and Montieae, trend to moister niches.

But some species of Montiinae, in particular *Claytonia* sect. *Claytonia*, also have evolved back into more arid niches of the south central and SW US and Mexico (O'Quinn et al. 2005; Stoughton et al. 2017a, b). These taxa thus converge on the geographic range shared by *Phemeranthus* and other arid-adapted Portulacineae, e.g., species of Anacampserotaceae, Cactaceae, Portulacaceae, and Talinaceae.

Below is a description of precipitation/moisture niche extremes that occur among Montiaceae genera and major subgeneric taxa, all approximated from distributional data and general climate maps:

1. *Phemeranthus*: Sonoran Desert (< 100 mm MAP) to SE US (ca. 1500 mm), with one subaquatic species in Mexico (Ocampo 2017).

2. *Cistanthe* sect *Cistanthe*: Hyperarid Atacama Desert (< 50 mm) to seasonally moist south central Chile (500–1500 mm).

3. *Cistanthe* sect *Rosulatae*: Hyperarid Atacama Desert (< 50 mm) to moderately wet south-central Chilean Andes (ca. 2000 mm).

4. *Calyptridium*: Mojave and Sonoran Deserts (< 50 mm) to the Klamath Mountains, southern Oregon (ca. 1500 mm).

5. *Philippiamra*: Atacama Desert vegetation limit ("zero" to < 50 mm) to arid alpine Andes (ca. 500 mm).

6. *Lenzia*: Arid alpine (ca. 300 mm).

7. *Montiopsis* subg. *Montiopsis*: Atacama Desert (< 50 mm) to moderately wet south-central Chilean Andes (ca. 2000 mm).

8. *Montiopsis* subg. *Dianthoideae*: Seasonally dry to moderately wet south-central Chilean Andes (ca. 600–2000 mm).

9. *Rumicastrum*: Arid western Australia (< 50 mm) to moderately wet NE Australia (ca. 2000 mm). Data from Hancock et al. (2018) indicate that arid/wet transitions occurred multiple times.

10. *Calandrinia*: Desert/semi-desert (ca. 100 mm) to more or less persistently wet S Chile and Pacific NW N America (> 5000 mm). Some perennial species are subaquatic, restricted to bogs and streams.

11. Hectorelleae: Persistently wet habitats (1000 to > 5000 mm; see Wagstaff & Hennion 2007).

12. *Lewisiopsis*: Seasonally dry (ca. 1500 mm).

13. *Lewisia* sect. *Lewisia*: Seasonally moist sites of the Sonoran and Mojave Deserts (ca. 200 mm) to persistently wet Pacific NW N America (ca. 5000 mm). Some species occur in bogs or boggy sites (Davidson 2000).

14. *Lewisia* sect. *Cotyledon*: Central Sierra Nevada Mountains (ca. 1500 mm) to persistently wet Pacific NW N America (ca. 5000 mm).

15. *Montia*: Seasonally arid (ca. 1000 mm) to persistently wet (ca. 5000 mm). One species is subaquatic to aquatic.

16. *Claytonia* sect. *Claytonia*: Seasonally moist SW US deserts (ca. 200 mm) to persistently wet Pacific NW N America (ca. 5000 mm). Data of Stoughton et al. (2017a) indicate that the arid/wet transition occurred twice.

17. *Claytonia* sect. *Limnia*: Seasonally moist SW US deserts (ca. 200 mm) to persistently wet Pacific NW N America (ca. 5000 mm).

18. *Claytonia* sect. *Rhizomatosae*: Seasonally moist Mediterranean and Great Basin areas (ca. 1500 mm) to persistently wet Pacific NW N America (ca. 5000 mm). Some species occur in bogs.

Thus, arid/wet precipitation/moisture niche transitions (at least ten-fold precipitation differences) have occurred at least (and probably more than) 10 times in a clade of ca. 300 modern taxa. Subaquatic/aquatic species have evolved at least five times. The low genetic divergence within clades suggest that most of these transitions occurred relatively rapidly, perhaps over the course of < 5 million years.

Meanwhile, Ogburn & Edwards (2015) found no evidence of increased phylogenetic diversification of Montiaceae precipitation niche relative to other Portulacineae and no correlation between precipitation niche and life history diversification. Presumably, precipitation niche was considered to be a proxy for moisture niche. Hershkovitz (2018c) argued that Montiaceae, contrary to Ogburn & Edwards' (2015) conclusions, indeed have experienced a greater rate and degree of moisture niche diversification relative to other Portulacineae.

Although I do not provide a detailed accounting here, moisture niche evolution among remaining Portulacineae has been less and slower. Although the largest family, Cactaceae (1500–1900 spp.), spans considerable moisture niche breadth, the species are restricted overwhelmingly to arid habitats. On a cladogenetic basis, cactus moisture niche evolution has been infrequent and slow. Moisture niche is narrow among Anacampserotaceae and Didiereaceae, but broader among Basellaceae and Talinaceae, and broadest among Portulacaceae. In the latter three families, perhaps significantly, the species occurring in the wet end of the precipitation spectrum (> 3000 mm) are weedy/invasive and/or escapes from cultivation. Thus, while many, probably most, other Portulacineae species evidently are obligate xerophytes, unlike Montiaceae, other Portulacineae include no obligately hydrophytic or subaquatic species. In contrast, while many Montiaceae species are as xerophytic as any other Portulacineae and they include arguably the *most* xerophytic vascular plant species (viz., *Philippiamra* spp.), the family also includes also several hydrophytes.

Hershkovitz (2018b) explained Ogburn & Edwards' (2015) results partially as a consequence of their using precipitation as a proxy for moisture niche. The discrepancy between precipitation climate data and physiological moisture niche is even greater than that for temperature niche. Hershkovitz (2018b) described a well-known summer alpine botanizing locality at a ski resort near Santiago that harbors at least 11 Montiaceae species in four genera. The species share the same precipitation niche but occupy microenvironmental moisture niches ranging from physiologically xerophytic (*Cistanthe* spp.) to more or less mesic (*Calandrinia* and *Montiopsis* spp.) to boggy (*Calandrinia* spp.) to aquatic (*Montia fontana* L.). Also, precipitation obviously ignores evapotranspiration potential, which is a function of humidity and temperature. For example, some Chilean/Peruvian Montiaceae are restricted to desert fog oases, where fog precipitation is not recorded, or, if recorded, amounts to perhaps 10–20% of the equivalent rainfall necessary to support the incident physiognomy. Thus, using precipitation data as a proxy for moisture niche severely distorts the estimated rate and degree of evolution of the latter.

In addition, Ogburn & Edwards (2015) analyzed only resolved cladistic nodes, whereas extreme differences in moisture niche occur within genera whose interspecific relations are poorly resolved (see above). The poor resolution, in turn, is consequent to rapid evolution. They also recorded precipitation niche as a function of the mean of few collecting localities, thus ignoring the extremes of widespread species, which also reflect rapid evolution. Thus, and quite remarkably, Ogburn & Edwards (2015) not only effectively ignored much, if not most evidence of Montiaceae moisture niche diversification, they also overlooked the short evolutionary time with which this diversification had occurred.

e. Succulence and other xerophytic adaptations among Montiaceae. Especially among the earlier-diverging lineages, Montiaceae include many leaf-succulent species. Ogburn & Edwards (2015) hypothesized that succulence should be phylogenetically correlated with low and/or seasonally distributed precipitation, finding only the former relation. As above, presumably they believed that precipitation proxied for moisture niche. Ogburn & Edwards (2010) earlier had noted that not all arid-adapted plants are succulent and not all succulent plants are arid-adapted. Hershkovitz (2018c) pointed out that indeed Montiaceae include several non-succulent but otherwise arid-adapted species (*Montiopsis* spp. and *Lenzia*), and degrees of succulence occur in bog species. Thus, (possibly even mesophytic) succulent ancestors can evolve nonsucculent xerophytic descendents. The analysis of Ogburn & Edwards (2015) lumped arid-adapted with non-arid-adapted taxa and also lumped xeric and moist microhabitats within the same precipitation zone. The premise of the hypothesis that succulence should correlate phylogenetically with precipitation thus is unexplained.

f. Polyploidy and Montiaceae diversification and ecological evolution. This section reconciles evidence for a hypothetical relationship between whole genome duplication (WGD) and phylogenetic/ecological diversification of Montiaceae. Considerable theoretical attention over the past two decades has focused on the historical contribution of WGD, in particular autopolyploidy, to plant phylogenetic and ecological diversification (D. Soltis et al. 2014, 2016 ; P. Soltis et al. 2015; see also Gorelick and Olson 2011; Levin 2019). One premise, among others, is that duplicating all loci facilitates locus subfunctionalization, hence both taxonomic and ecological diversification.

Polyploidy consequent to cytokinetic failure is the prevalent mechanism of WGD. In theory, a genome could duplicate entirely via short infra-chromosomal tandem repeats, or by successive partial chromosome duplications. In a different parametric dimension, polyploidy is an extreme form of DNA sequence duplication, the minimal form being a single DNA base duplication. But the latter is a duplication within the DNA-level hierarchy, which the chromosomal level absorbs. Polyploidy and all other forms of heteroploidy occur within the chromosomal hierarchical level, and subsume the DNA level along with it.

Allopolyploids, consequent to hybridization, share with autopolyploids the feature of duplicated loci and might be expected to manifest the same evolutionary consequences (Hegarty & Hiscock 2008). However, it is difficult to dissect the consequences of polyploidy from those of hybridization per se, as the latter immediately creates a distinctive phenotype, with additional diversity segregating in progeny. More problematic, the distinction between allo- and autopolyploidy can be blurred on both subjective and objective bases. Allopolyploidy presumes hybridization between taxonomically distinct parents, but this distinction is subjective.

While allopolyploids can be diagnosed on positive evidence (allozymes, genomic evidence), the absence of such evidence does not rule out allopolyploidy. The diploid progenitors of a highly divergent allopolyploid might be extinct or otherwise genomically highly modified. Moreover, the effects of allopolyploidy might occur in hybrids between differentiated genotypes within the same taxon, even genomically very similar ones. A single allele in one of two otherwise genomically identical parents might cause polyploidy in the offspring. This "cryptic allopolyploidy" creates "pseudo-autopolyploidy." The consequence is that in phylogenetic time and space, autopolyploidy will tend to be overestimated.

Chromosomal data exist for less than half of Montiaceae species, and most reports represent single or very few sampled individuals. Moreover, the reports are scattered in the literature, some of them in obscure and/or unpublished theses. There exists nothing close to a monographic accounting, a task beyond the scope of the present work. By far, the genus most thoroughly studied cytologically is *Claytonia* (Miller & Chambers 2006), and this genus and its taxonomic species are notoriously heteroploid. Complete species sampling is available for *Montia* (Heenan 2007; Miller & Chambers 2012a) and *Montiopsis* (Ford 1992), with considerable species data available for *Calyptridium* (Guilliams and Miller 2014), *Lewisia* (Mathew 1989; Hershkovitz & Hogan 2002, 2003), and *Phemeranthus* (Price 2012). Few counts are available for *Calandrinia*, *Cistanthe*, and *Rumicastrum* (e.g., Wickramasinghe et al. 2009; Marinho et al. 2019), and apparently none for *Philippiamra, Lenzia*, or *Lyallia*. Polyploidy is reported in *Claytonia*, *Lewisia*, *Montia*, *Montiopsis*, and *Phemeranthus*, and it is the base condition in three genera (*Calyptridium* and the monotypic genera *Hectorella* and *Lewisiopsis*; Hinton 1975; Mathew 1989; Wagstaff & Hennion 2007; Heenan 2007). Aneuploidy/dysploidy are common in all examined polytypic Montieae, i.e., *Claytonia*, *Lewisia*, and *Montia*, and is evident in *Rumicastrum* (Wickramasinghe et al. 2009).

Only two studies have analyzed the evolutionary consequences of polyploidy among Montiaceae in a hypothetico-deductive framework. One is McIntyre (2012), who studied the relation of polyploidy and habitat in 2–6x *Claytonia perfoliata* Donn ex Willd. complex populations. The other is Smith et al. (2017; see also Yang et al. 2018), who attempted to align phylogenetic WGD events with habitat shifts among all Caryophyllales, including some Montiaceae. Both studies were similar to Ogburn & Edwards (2015) in using climate temperature and precipitation data as surrogates for ecological niche. Thus, the same criticism as above applies, as does the epistemological criticism of confounding correlation with cause (Hershkovitz 2018c).

Notably, in this case, different investigations of the same phenomena (phylogenetic and ecological diversification) consider the hypothetically plausible consequences of evolution of one parameter (polyploidy or life history) while mutually ignoring the hypothetically plausible consequences of the other. Hershkovitz (2018c) pointed out this statistical fallacy, which is epidemic in the contemporary evolutionary biology paradigm generally (see below).

McIntyre (2012) noted that both autopolyploidy and allopolyploidy occur in the *Claytonia perfoliata* complex, but did not specify the condition of the study populations. Smith et al., (2017), likewise did not distinguish between allopolyploidy and autopolyploidy. Thus, neither study validly evaluated the effect of ploidy per se. But these points are moot, since neither study yielded evidence sufficiently convincing to attribute phylogenetic or ecological diversification to polyploidy.

Hershkovitz (2018c) disputed the significance afforded autopolyploidy in explaining phylogenetic/ecological diversification, as revision of that work will elaborate. Lack of autopolyploid necessity and sufficiency was emphasized. Two monotypic polyploid Montiaceae taxa, *Hectorella* and *Lewisiopsis*, evidently are octaploids that have diversified much less than their close relatives.

Moreover, *Lewisiopsis* shares the same geography, ecology, and growth form that are supposed to explain Montiaceae diversification in general. Hershkovitz (2018c) suggested that, in this case, polyploidy may have sequestered its diversification (see below). There is no shortage of other examples among plants contradicting the supposed relation between polyploidy and diversification, nor, for that matter, the supposed relation between any two variables in the course of evolution.

Other evidence inconsonant with the supposed polyploidy/diversification relation is more sublime:

1. Soltis et al. (2007) noted that accepted taxonomic species commonly include both diploid and autopolyploids. Possibly or potentially they can be distinguished phenotypically, but evidently not sufficiently to be distinguished taxonomically by excellent taxonomists. Heteroploidy especially of *Claytonia* spp. demonstrates this (Miller & Chambers 2006).

2. Kubešová et al. (2010) reported an *inverse* correlation between genome size and plant species invasiveness (effectively, ecological adaptability). They attributed this to the metabolic cost of DNA/chromosome replication, hence greater reproductive efficiency of genomes with little “junk” DNA. Although polyploidy per se was not addressed directly, one can infer from Kubešová et al.’s (2010) data that polyploidy possibly has a neutral or negative effect on invasiveness. In particular, 20/47 (43%) species they characterized as merely “naturalized” in the Czech Republic are diploid. But a *higher* proportion (20/40; 50%) of diploids were “invasives.”

3. Polyploidy has additional evolutionary disadvantages (see, e.g., Gorelick and Olson 2011). Meanwhile, Smith et al. (2017), Yang et al. (2018), and other WGD researchers, advertise only hypothetical WGD advantages and do not consider, much less model and supercompute its costs.

4. In an analysis of *Castilleja* (Orobanchaceae), Tank and Olmstead (2008) concluded that the deleterious effects of polyploidy promotes the evolution of longer generation times, which, in turn, decreases the rate of phylogenetic and ecological diversification. But Smith et al. (2017) seem to maintain that polyploidy is associated with faster ecological diversification. This seems to be a contradiction.

As an epistemological criticism, Hershkovitz (2018c) emphasized that polyploidization and organismal diversification are concurrent and sequential biogenetic processes operating at well-separated organizational levels. Superimposing the history of one over the other is bound to yield some degree of temporal coincidence, as Smith et al. (2017; Yang et al. 2018) conceded. Arguments for a cause /effect relationship are specious, if not frivolous. This is so especially given the lack of necessity/sufficiency evidence at the infraspecific level, and the axiomatically increasing ambiguity of historical evolutionary/ecological reconstruction at deeper phylogenetic levels. Indeed, organismal diversification might involve subfunctionalized loci duplicated consequent to polyploidization. But this may be exaptation rather than adaptation, and it is not bound to occur. In short, the evolutionary consequence of polyploidy seems to be no more or less than polyploidy itself.

g. Montiaceae leaf morphological/anatomical evolution. One would suppose that the morphology and anatomy of photosynthetic organs figure prominently in ecological adaptation and evolution. As noted, most Montiaceae are rosette-forming annuals and perennials. Their leaves, accordingly, appear superficially similar, even monotonous (Hershkovitz 1991f, 1992, 1993b). The leaf shape most commonly is oblanceolate to spathulate, but ranges from linear to broadly obovate. Sometimes the blades are essentially sessile, but often the blade is tapered basally into a broad petiolar region. In some species, especially among annual *Claytonia*, the petiolar region may be 5–10 cm or longer. Regardless, the leaf base among Montiaceae usually is broad to clasping, in a few species amplexicaul to perfoliate.

The exception to this generalized form is in Phemerantheae and possibly several but not all *Rumicastrum* species (which I have not studied in detail). Phemerantheae species have linear, succulent leaves and an extremely short but more distinct petiole. The basal portion of the blade is flanged and clasps the stem. Some *Rumicastrum* species have succulent, liner leaves that resemble Phemerantheae leaves, but other species have leaves more typical of other Montiaceae.

Commonly, leaves of perennial species are basal or suprabasal on unelongated internodes. However, in suffruticose and pachycaul *Cistanthe* species, the stems are leafy. Meanwhile, leaves of closely related annual congeners commonly are both basal and distributed along the flowering stems, as in annual species of *Cistanthe*, *Calyptridium*, *Rumicastrum*, and *Calandrinia*. In these taxa, the stem leaves are morphologically/anatomically similar to the basal leaves. However, flowering stems of *Claytonia* species have only a single pair of sessile foliaceous bracts. In some species, these bracts resemble the basal leaf blades in size and anatomy. In some *Philippiamra* species, the flowering stem leaves are bract-like and succulent. Nonetheless, they appear to be the principal photosynthetic organs, remaining green long after the basal leaves have senesced. At that point, the shoot system may break from the root and form a sort of tumbleweed. All species of *Montia* have leafy stems, but in the rhizomatous species *M. parvifolia*, these are arranged in rosettes resembling those of caudiciform Montiaceae.

Leaves are entire except for some species of *Lewisia* sect. *Cotyledon* (Hershkovitz 1992). The petiolar region in some species of *Montiopsis* also may be dentate (Hershkovitz 1993b). Leaf serrations may be vascularized or not in *Lewisia*, but apparently are not in *Montiopsis*. In both of these genera, species with both dentate and entire leaves often have dentate sepals.

Given the similarity in gross leaf morphology, Montiaceae leaf anatomy, especially venation ´pattern, is surprisingly diverse (Hershkovitz 1991f, 1992, 1993b). This diversity proved to have taxonomic significance and was critical to the development of the current taxonomy of Montiaceae and Portulacineae generally. In fact, I had interpreted my preliminary Portulacineae leaf morphological/anatomical data in the classical Aristotelian taxonomic framework and according to prevalent notions of orthogenetic trends (Hershkovitz 1986). I realized my error literally days later, and this is what prompted me to change my dissertation focus from Nyctaginaceae to Portulacineae.

Several Montiaceae taxa can be diagnosed on the basis of leaf characteristics alone. For example, leaves of almost all *Calandrinia* species have a distinctive intramarginal vein and also distinctive epidermal morphology (see below). Montiinae leaves also have an intramarginal vein, but its configuration at the leaf apex is very different from *Calandrinia*, and the epidermal characters also are different. Venation and stomata of *Lewisia* are highly variable but very different from its sister, Montiinae. Leaves of *Calyptridium*, *Cistanthe,* and *Philippiamra* have weakly organized brochidodromous venation and brachyparacytic stomata.

Finer leaf veins in many taxa are distinctively sinuous and laminar or “ribbon-like,” a single cell layer thick and up to at least 11 xylem elements broad. Annular protoxylem elements situate on one side, intergrading to scalariform-reticulate metaxylem elements on the other. These laminar veins are characteristic also of Phemerantheae, Cistantheae except *Lenzia*, and many *Rumicastrum* species. Among other Portulacineae, they are evident in certain Anacampserotaceae and Talinaceae. Apparently they occur in no other vascular plants.

Three-dimensional (3D) venation characterizes Phemerantheae, many if not most *Rumicastrum* spp., one species each of *Calyptridium* and *Lewisia,* and at least some portion of veins in the most succulent *Cistanthe* spp. (Hershkovitz 1991f, 1992; Ogburn & Edwards 2013). 3D venation also occurs in Anacampserotaceae and Portulacaceae (Hershkovitz 1991f, Ogburn & Edwards 2013). Hershkovitz (1991f, 1992, 1993b) also reported preliminary data on other venation characteristics, such as branching anatomy of finest veins and veinlet number per smallest vein enclosure.

Current phylogenetic evidence permits only a few insights on the evolution of Montiaceae venation characteristics. For example, the distribution of laminar veins in other Portulacineae and within Montiaceae, suggests that these may represent an ancestral condition in the family. These appear to have been lost in *Lenzia* and *Montiopsis* (Cistantheae), whose leaves are small and have poorly and irregularly structured venation. In fact, the evidence suggests that in the evolution of these genera, leaves became highly reduced and cataphyll-like, as they remain in *Lenzia*. In *Montiopsis*, non-succulent foliage leaves thus re-elaborated with a morphology/anatomy distinct from succulent Cistantheae. In conjunction, distinctive trichomes evolved in *Montiopsis*, and these possibly replace succulence as an adaptation to aridity. 3D venation may have evolved as a developmental by-product of extreme succulence, but apparently succulence is neither necessary nor sufficient to induce 3D venation. In particular, 3D venation characterizes nearly all species of *Portulaca*, including *P. oleracea*, whose leaves are broad, flat, and not especially succulent by Portulacineae standards. Presumably laminar veins function to accommodate leaf expansion/shrinkage in response to water potential fluctuations during development and at functional maturity. They were lost during the evolution of Montioideae and did not reappear in the more succulent/xerophytic taxa, e.g., *Lewisia*.

Leaf histological analyses of Montiaceae evidently are too few and far between to draw systematic and evolutionary conclusions. The data will not be reviewed here. Given the diversity in vasculature patterning and the interest in Montiaceae evolution from the standpoint of succulence and photosynthetic innovation, new systematic histological analysis should be fruitful.

Stomatal morphology distinguishes Montiaceae from other Portulacineae (Hershkovitz 1991f, 1992, 1993b). Montiaceae all have brachyparacytic or similar perigenous forms, in which 1–2(–3) pairs of lateral subsidiary cells divide and differentiate from epidermal cells adjacent to the guard cell mother cell. This form is characteristic of *Phemeranthus*, most Cistantheae, the few examined *Rumicastrum* spp., *Lewisiopsis*, a few *Lewisia* spp., and most Montiinae. Variations include tetracytic stomata in most *Calandrinia* spp. and laterocytic stomata restricted to several *Lewisia* species. Anomocytic stomata (lacking subsidiary cells) have been observed in a few *Calyptridium, Lewisia*, and *Montiopsis* species. All other Portulacineae have anisocytic or parallelocytic stomata with mesogenous devlopment, in which the subsidiary cells and guard cells all develop from the stomatal meristemoid. Hershkovitz (1991f) also reported preliminary data for stomatal index, size, and laminar distribution, but this has not been followed up with detailed analysis.

Most Montiaceae taxa have glabrous leaves: *Phemeranthus*, *Calyptridium*, *Lenzia,* Montieae, and essentially all of *Cistanthe* and *Rumicastrum.* Known exceptions in the last two involve papillate epidermal cells in single species (Hershkovitz 1991f, 1993b). Trichomes are characteristic of *Calandrinia* and *Montiopsis*, but they are structurally distinct in the two taxa. Most *Calandrinia* species have unicellular ribbed trichomes on the leaf and sepal margins (rarely on the laminar surface). *Montiopsis* leaves and sepals all have both glandular and nonglandular multicellular trichomes, and sometimes these are elaborated into echinate appendages. *Montiopsis* subg. *Montiopsis* species have, in addition, multiseriate simple and barbed hairs, these developed from intertwining of long single adjacent epidermal hair cells.

Hershkovitz (1991f, 1993b) briefly reviewed theoretical aspects of leaf development, form, and function, but could draw no conclusions regarding, e.g., why *Calandrinia* and Montiinae species should have an intramarginal vein and other Portulacineae not, or differences in stomatal subsidiary cell development and anatomy. I do not pretend to resolve these questions here. From an evolutionary perspective, two general findings of the leaf morphological research stand out:

1. *The contrast between the relative monotony of Montiaceae gross leaf morphology with the diversity of anatomical structure and, presumably, physiological functioning.* My 1980s preliminary investigations of leaf anatomy of Caryophyllales more broadly (including Polygonaceae and Plumbaginaceae) indicated that Montiaceae diversity was especially high. In other families, leaf venation and epidermal characteristics are relatively monotonous at the familial/subfamilial level.

2. *Evolutionary transitions from xerophytic to mesophytic leaf anatomy.* This occurred in conjunction with the origin of Montioideae. Xerophytic adaptations tend to be considered de facto evolutionarily derived. They are at one level, but Montiaceae are an example of where mesophytic adaptations are derived. Succulence decreased and laminar venation was lost. Mucilagenous cells characteristic of Phemerantheae, *Cistanthe*, *Calyptridium*, and *Philippiamra* also became reduced or lost in derived taxa. Transition back to xerophytic leaves occurred in *Lewisia*, but the vasculature is distinct from that in the "paleomonts."

h. Montiaceae reproductive morphological evolution. Reproductive morphological diversity among Montiaceae genera is described adequately by Carolin (1987, 1993) and Hershkovitz (1993a). There appear to be no particular phylogenetic trends at the familial level, so detailed descriptions will not be repeated here. In fact, the most notable aspect of reproductive morphology of Montiaceae is the degree to which historically it misled phylogenetic and taxonomic interpretation.

Many to most species of most Montiaceae genera have a generalized floral morphology that includes two sepals, usually 5(–9) petals, 5–∞ stamens, 3(–5) carpels, and numerous seeds. That the sepals are an involucre and the petals sepals (Dos Santos & De Craene 2016) is not important in this context. This general morphology characterizes *Phemeranthus*, *Cistanthe*, *Montiopsis*, *Rumicastrum*, *Calandrinia*, *Lewisiopsis*, *Lewisia*, and some *Philippiamra* species. Infrageneric variation in numbers of floral organs often is correlated positively with floral size, but not always, e.g., relatively small-flowered *Calandrinia* species have 6–8 petals and five carpels (Elvebakket al. 2015). Sepal number, however, does not vary except in one species of *Lewisia.* Meanwhile, flowers of Hectorelleae, *Calyptridium*, and certain species of *Philippiamra*, *Rumicastrum*, *Montiopsis*, and *Calandrinia* have small and reduced flowers with fewer than the standard number of petals, stamens, carpels, and/or seeds. Flowers in some *Calyptridium* and *Philippiamra* species occur in dense heads.

Fruits in most taxa are basipetally dehiscent valvate capsules, except *Lewisia*, in which dehiscence is acropetal. Indehiscent or irregularly dehiscent 1-seeded fruits occur in one or more species of *Calandrinia*, *Calyptridium*, *Philippiamra*, and *Rumicastrum*. Seeds in the family *mostly* are similar to those characteristic of all core Caryophyllales: lenticular to subglobose, 1–2 mm in diameter, embryo linear, curved, peripheral, and seed surface smooth to colliculate, black, and lustrous. Variation in all of these traits, as well as size, occurs at the generic and infrageneric level. *Cistanthe* is the most distinctive and variable genus. Most species have pustulate or hirsute seeds, and sculpturing can be tuberculate, granulate, or areolate. Tuberculate sculpturing occurs in species of *Calandrinia*, as well. The exotesta of most *Phemeranthus* species is pelliculate, and seeds of some species are sculptured with arctuate ridges (Price 2012). Several species of *Montiopsis* have brown seeds (Ford 1992). Strophioles occur in most *Cistanthe* and Montiinae species and in *Lewisiopsis*.

Ovule number among Montiaceae presumably is correlated with seed number, but not all ovules develop into seeds. Because most Montiaceae species descriptions at best report numerical seed counts (as opposed to, e.g., "numerous"), ovule numbers at best only can be estimated. An exception is among Montiinae: species of *Montia* and *Claytonia* sect. *Limnia* have three ovules, whereas remaining *Claytonia* taxa have six.

Arroyo et al. (2018, 2019) reported ovule counts in 178 incidental species of the central Chilean Andes, among these nine Montiaceae species. They tested in a Darwinian Modern Synthesis framework a hypothesis that, corrected for phylogeny, flowers of highest elevation species should have more ovules as a form of bet-hedging against pollinator scarcity/unreliability in extreme environments. The hypothesis found some statistically significant support, but in a method/parameter-specific manner. I reject the conclusions on technical but mainly epistemological (see below) bases. Since the study is not Montiaceae-specific, I will not elaborate here a technical critique, except to note the axiom that if enough parameters are tested with enough methods, statistical significance is bound to emerge somewhere. Similarly, in planar view, especially bright light from spatiotemporally remote stars may seem to form patterns.

In any case, the Montiaceae data did not seem to corroborate the hypothesis especially well. One higher elevation *Calandrinia* species had modestly more ovules than a lower elevation one, but a lower elevation *Montiopsis* species had about twice as many ovules as the higher elevation ones. Two incident alpine *Cistanthe* sect. *Rosulatae* species were not analyzed, presumably because both are higher alpine, and there is no lower alpine species in this zone for comparison. But my informal accounting indicates that these alpine species do not have higher ovule numbers than many lower elevation species of the section. Meanwhile, among *Cistanthe* as a whole, seed numbers per fruit and even more so per individual are highest in the numerous lowland *Cistanthe* sect. *Cistanthe* species (e.g., Hershkovitz 2018d).

Superficial examination of seed numbers in floristic descriptions of North American and Australasian Montiaceae species yields no clear pattern relation between ovule number and ecology. A further complication is that many Montiaceae species inhabit the desert, where pollinator scarcity/unreliability is at least as severe as it is in the high alpine. However, pollination biology and other relevant data are not uniformly available for Montiaceae species. Hectorelleae stand out as taxa likely subjected to pollinator scarcity, especially *Lyallia* (Wagstaff & Hennion 2007). Yet their ovule numbers are low by Montiaceae standards. The same is true for several 1–few-seeded *Philippiamra* species of extreme desert habitats. Overall, as with other phenotypic/environmental traits discussed in the present work, pollinator scarcity/unreliability seems to be neither necessary nor sufficient to affect the evolution of ovule number. Ovule numbers among species reflect merely their functional adequacy.

And whatever happened to pollen morphology? The 1960's–1980's were the heyday of palynotaxonomic research, especially because of a then-fashionable newfangled gadget called the electron microscope. The discipline virtually disappeared with the arrival of another fashionable gadget, the PCR machine. In the meantime, Montiaceae and Caryophyllales generally were subjected to numerous palynotaxonomic studies. A few of these include Nilsson (1967), Nowicke & Skvarla (1979), Carolin (1987), and Nowicke (1996). With the advent of molecular phylogenetics, reference to pollen morphology virtually disappeared from the literature.

Montiaceae pollen morphology is considerably diverse. Aperture types include tricolpate, "broad" pantocolpate, "narrow" pantocolpate, and pantoporate (Carolin 1987). All of these forms are shared by other Portulacineae and core Caryophyllales generally (Nowicke & Skvarla 1979, Nowicke

1996), although distinctions might be evident in exine ultrastructure (Nowicke 1996). Generic or subgeneric taxa usually have a single aperture type: Phemerantheae spp. are broad-pantocolpate, Cistantheae spp. are tricolpate except for *Montiopsis* subg. *Montiopsis* spp., which are pantoporate. *Calandrinia* spp. are pantoporate, Hectorelleae and Montieae spp. are tricolpate, except for *Montia* spp., which are narrow-pantocolpate. *Rumicastrum* includes all forms except tricolpate, plus a unique operculate pantoporate form. The individual aperture types phylogenetically are conserved in some subclades of this genus. Thus, aperture type manifests phylogenetic conservation, but also homoplasy. Nilsson (1967) noted the presence of numerous aperture mutants in the normally tricolpate *Claytonia sibirica* L. Tricolpate would seem to be the ancestral form of Montiaceae. The exine surface in Montiaceae pollen mostly is the spinulose-punctate form common throughout core Caryophyllales, but reticulate, psilate, and tholate surfaces occur in particular species.

I do not attempt to explain here Montiaceae pollen evolution and/or its ecological significance. Till-Bottraud et al. (1994) proposed an explanation in the framework of game theory, but I reject this Darwinian Modern Synthesis proposal on epistemological grounds. In fact, I do not propose here evolutionary ecological explanations for any of the variability of Montiaceae reproductive morphology. I call attention to it here for a different reason. As elaborated below, the modern phylogenetic paradigm tends to focus on the supposed evolutionary consequences of single or a few variable phenotypic/ecological traits, e.g., life history, succulence, ploidy level, ovule number, photosynthetic pathway (see below), temperature/precipitation niche, elevation, or, in general, any trait whose disembodiment and oversimplification thus lends itself to correspondingly simplistic and contrived statistical analysis. Such analyses presume that all other phenotypic traits are "equal." The descriptions of Montiaceae phenotypic/ecological trait variability here serve as a reminder that they are not.

i. Montiaceae physiological evolution. Current phylogenetic reconstructions indicate that ancestral and early diverging Montiaceae lineages were warm/arid adapted, manifested today by their distribution, succulence, and other phenotypic characteristics. Evolution of Montioideae coincided with a shift to cooler/moisture habitats, hence loss of warm/arid adaptations. However, cool/moist-adapted species also evolved independently in the warm/arid lineages, and warm/arid-adapted species evolved in Montioideae.

Photosynthesis is challenged under warm/arid conditions, in which carbon assimilation via light-dependent ribose bisphosphate carboxylase/oxygenase (Rubisco) becomes water-use inefficient and/or counterproductive. Thus, many warm/arid-adapted plants possess photosynthetic adaptations that permit them to optimize carbon assimilation under these conditions, i.e., C4 and CAM photosynthesis. Both permit carbon assimilation as transitory C4 acids, one carbon then fed into the universal Rubisco C3 assimilation cycle. C4 plants fix carbon efficiently at high temperatures in daylight and shuttle carbon to a physically/mechanically isolated Rubisco cycle. This prevents oxidative photorespiration. CAM plants use the same C4 biochemistry, but they reverse normal light-sensitive stomatal movements, so that carbon assimilation as C4 acid occurs via open stomata at night. The light-dependent Rubisco C3 cycle then functions in daylight with the stomata closed. While C4/CAM terminology is applied in reference to photosynthetic carbon fixation, its biochemical mechanisms exist in all plants and function in other physiological contexts, e.g., in root tissue carbon metabolism. Thus, C4/CAM operation in photosynthesis is coopted/exapted.

Not surprisingly, C4 and CAM species occur among Portulacineae. However, many Portulacineae lineages are not C4 nor obligately CAM, but rather facultatively CAM or "C3-CAM" (Goolsby et al. 2018a, b). C3 assimilation occurs under certain physiological conditions, CAM under others. There exist also C3-C4 intermediates in other Portulacineae. Evidently, many, if not most, Montiaceae are C3-CAM, and none are C4 or obligately CAM (Goolsby et al. 2018a, b). In phylogenetic reconstruction, C3 and C3-CAM transition multiple times throughout Montiaceae evolution. The Montiaceae basal node reconstructs as C3-CAM, the next split as C3, and the *Rumicastrum* ancestor as C3-CAM, with C3 retained as ancestral in all other examined Montioideae genera except *Calandrinia*, whose ancestral state remains ambiguous because phenotypes remain poorly sampled. Within Cistantheae, only the *Cistanthe* ancestor reconstructs as C3-CAM. Perhaps surprisingly, C3-CAM is not demonstrated in *Calyptridium*, although the most arid-adapted species were not studied. *Philippiamra*, which include the most arid-adapted of vascular plants, were not examined. C3-CAM reverts to C3 several times in *Rumicastrum*. Meanwhile, C3-CAM has evolved at least twice in *Claytonia*. Other polytypic genera are inadequately sampled to affirm monomorphism, especially because negative evidence for facultative trait expression may be unreliable.

However, the objective of Goolsby et al. (2018a, b) was to analyze the relationship between evolution of C4/CAM phenotypes and that of metabolically relevant “carbon concentrating mechanism” (CCM) genes. They hypothesized that “positive selection” in these genes should be enhanced relative to other sampled genes of Portulacineae, a lineage that manifests a high rate of C4/CAM/C3-CAM evolution. The premise itself seems to appeal to an arcane (pre-McClintock) dogma that phenotypic evolution is a linear function of amino acid substitution. Otherwise they would not have considered “surprising” the failure to confirm the hypothesis.

Goolsby et al. (2018a, b) considered possible methodological artifacts that may have affected the results, as well as the possibility that *all* examined genes were under positive selection, but for different reasons. They did not seem to consider the possibility that the CCM genes were already perfectly functionally adequate and/or that factors besides CCM genes affect carbon metabolic expression in vivo. They did find evidence for convergence at particular Portulacineae CCM gene amino acid sites in C4/CAM species, a result paralleling that for other C4/CAM angiosperms. However, convergence is an observation, not a cause nor an explanation.

j. Montiaceae phenotypic/ecological evolution and evolutionary epistemology. Hershkovitz (2018c) emphasized the role of epistemology in the interpretation of Montiaceae evolution. Revision of that work will elaborate its thesis further. Hershkovitz (2018c) criticizes the epistemological basis of contemporary comparative evolutionary analysis, epitomized by Ogburn & Edwards (2015), Goolsby et al. (2018a, b), and similar studies. Even if the statistical correlations are accurate mathematically, evolutionary correlation is confounded with evolutionary cause.

Many contemporary comparative evolutionary analyses purport to analyze the phylogenetic causes/consequences of the evolution of single or few biotic characters. The tendency is to idealize phylogenetic parameter space as comprising discrete, independent, and identically distributed taxa, characters, and cladogenetic events. Characters are idealized as having as few discrete and time-reversible states as possible or, alternatively, a continuous linear distribution. These idealizations precisely underwrite the statistical methodology, in which artificially linearized distributions of idealized trait observations are compared with artificially linearized and idealized null distributions. The folly of the approach is evident in analyses such as Ogburn & Edwards (2015), in which nonlinearly related life forms are reduced to two-state life histories, and niche characteristics are proxied using simplistic but easily acquired macroclimate data. Likewise, C3/C4/CAM once was considered a simple three-state characteristic, but its evolution is more complex than its three idealized phenotypes would suggest.

Goolsby (2016; Goolsby et al. 2017) developed rudimentary methods that facilitate simultaneous phylogenetic comparative analysis of multiple parameters. It remains to be demonstrated whether evolutionary analysis of some tractable number of characters can explain adequately the diversification of large clades. Hershkovitz (2018c) argues that it cannot (see below). Alternatively, increasing parameter space may help demonstrate that evolutionary consequences are unpredictable and evolutionary explanations cannot be generalized. In the meantime, no computational advancement can calculate its way around fundamental theoretical and empirical limitations and flaws, many of which have been delineated in previous sections. These include ambiguities in phylogenetic resolution, nonlinearity/nonstationarity of the phylogenetic process, hybridization and lineage sorting, and the behavior of Bayesian estimation when assumptions inevitably are violated. The problem of statistical nonequivalence and nonindependence of taxa also is not addressed.

But irrespective of whether evolutionary correlations appear to be statistically highly significant, Hershkovitz (2018c) rejected the applicability of the probabilistic paradigm to evolutionary analysis (cf. P. Hershkovitz 1977: *64*). Hershkovitz (2018c) traced the roots of the contemporary hegemonic phylogenetic/ phylogenomic paradigm to the Darwinian Modern Synthesis probabilistic population genetics paradigm and its adaptationist notions. In this interpretation, organismal evolution is conceived as a linear stochastic process, its null trajectory *indeterminate* (i.e., drift) or determined *extrinsically* probabilistically by the interaction of "selective" forces operating at lower (suborganismal) or higher (supraorganismal) hierarchical levels, i.e., traits or environments. In this paradigm, evolution is defined as a statistically significant change in the mean of a trait distribution in a population. Covariation of mean change with some extrinsic parameter evidences "natural selection," evolutionary biology's phlogiston.

Hershkovitz (2018c) discussed how all biogenetic processes, hence evolution, conform better to formal chaotic than to stochastic functions. Chaotic functions are intrinsically *determinate*, not probabilistic. Seemingly paradoxically, they are *unpredictable*, unless the function and initial conditions are known. Which, in the case of evolutionary analyses, they are not. This "epiphany" emerged from the conclusion that evolution of Atacama Desert Montiaceae conformed to the evolutionary model of "natural drift" (Maturana and Mpodozis 2000). Indeed, in this model, organismal evolutionary trajectory is unpredictable and determined not extrinsically, but intrinsically, by organismal enactivity itself. Factors at hierarchical levels below and above the organismal level establish initial conditions and bounds for this trajectory, but they do not determine it (cf. Salthe & Matsuno 1995; Yarrow & Salthe 2008; Fábregas-Tejeda &Vergara-Silva 2017).

The preceding observations led Hershkovitz (2018c) to describe the Principle of Evolutionary Idiosyncraticity (PEI), which models organismal evolution as a determinate chaos-like process that is perturbed stochastically by the collective action of myriad forces operating at suborganismal/ supraorganismal levels. [Although inspired by observations of Atacama Desert Montiaceae, PEI actually was conceived and developed while contemplating Chilean horse racing. Horse racing programs document myriad parameters that bettors might use to estimate race outcome probability. In fact, the parameters establish only limiting conditions and bounds, but the race outcome is determined by no more or less than the idiosyncratic enactivity of the horses.]

The principal consequence of PEI is that, if correct, the hegemonic contemporary probabilistic paradigm of comparative evolutionary analysis is scientifically invalid. Hershkovitz (2018c) provides independently derived conclusions to this effect (e.g., Wenzel & Carpenter 1994; Franz & Engels 2010). A conundrum appears to arise to the degree that scientific conclusions obligate probabilistic analysis. This proves to be a red herring. Hershkovitz (2018c) suggested that, while the outcome of a chaotic process is unpredictable statistically, it should be statistically differentiable from that of any stochastic process. Thus, Hershkovitz (2018c) suggested that this can be accomplished by inverting null hypotheses. For example, Goolsby et al. (2018a, b) explicitly state that their failure to reject the null hypothesis of relative neutrality of CCM gene evolution was "contrary to expectations." The objective of science must be to challenge and not affirm expectations. As "positive selection" clearly is the expectation, it should be the null hypothesis tested. I suspect that invariably it would be rejected. Repeated rejections in specific cases eventually would lead to rejection of positive selection theory generally and a search for a better theory. Hershkovitz (2018c) intimated that most or all of contemporary evolutionary biological dogma would not withstand proper statistical scrutiny.

He noted, moreover, that empirical evidence from Montiaceae already implicates nonstochasticity of evolution. In particular, the genus *Lewisiopsis* possesses the growth form, cytological traits (octaploid), evolutionary history (evidently a hybrid), and geographic range (western North America) that, individually, have been predicated to promote phylogenetic and ecological diversification. Yet, the monotypic genus evidently is an isolated relict, morphologically and genomically similar to its Eocene ancestors. This might be interpreted statistically as a "longshot," but PEI explains the outcome as determined intrinsically by the organisms and not by any particular trait or circumstance.

4. Montiaceae Historical Biogeography

a. Phylogeographic disjunctions among Montiaceae. The native range of Montiaceae includes NE Siberia, the Americas, especially along the cordillera, from Alaska to Tierra del Fuego, Australia, New Zealand, and the Kerguelen Islands. One species, *Montia fontana*, is cosmopolitan in temperate and cool tropical habitats. Hershkovitz (2018a, b) reviewed evidence for Montiaceae phylogeographic history, and a revision of that work will elaborate further on its theses. The principal conclusion was that all transoceanic and perhaps even many terrestrial disjunctions among Montiaceae taxa originated via long distance dispersal (LDD) and not vicariance.

Below is a list of Montiaceae phylogeographic disjunctions of 1000 km or more, both transoceanic and terrestrial. Likely anthropogenically-induced disjunctions are excluded. I attribute all transoceanic disjunctions to LDD and terrestrial ones at least plausibly so.

1. *Schreiteria* (S Am) - *Phemeranthus* root (N Am or C Am)
2. *Phemeranthus* root (N Am or C Am) - *P. punae* (R.E. Fr.) Eggli & Nyffeler (S Am)
3. *Phemeranthus spinescens* (Torr.) Hershk. and *P. sediformis* (Poelln.) Kiger (Pacific NW N Am) - remainder of *Phemeranthus* (N Am, > 1000 km E and S)
4. *Cistanthe* clade (S Am) - *C. guadalupensis* (T.R. Dudley) Carolin ex Hershk. & *C. maritima* (Nutt.) Carolin ex Hershk. (N Am)
5. *Philippiamra* (S Am) - *Calyptridium* (N Am)
6. Montioideae root (S Am) - *Rumicastrum* (Aus)
7. *Calandrinia acaulis* Kunth (S Am) - *C. acaulis* (C Am)
8. *Calandrinia ciliata* (Ruiz & Pav.) DC (S Am) - *C. ciliata* (C Am)
9. *Calandrinia* sect. *Calandrinia* (S Am, C Am) - *C. menziesii* (Hook.) Torr. & A. Gray (N Am)
10. *Calandrinia* sect. *Calandrinia* (S Am, C Am) - *C. bonarensis* Hauman (Buenos Aires Province, ARG; this species currently is identified as *C. ciliata*, but the disjunction exists either way)

11. Montioideae root (S Am) - Hectorelleae (NZ, Kerguelan I)

12. *Hectorella* (NZ) - *Lyallia* (Kerguelan I)

13. Montioideae root (S Am) - Montieae root (N Am)

14. *Lewisia pygmaea* s. l. (lower USA, S Can) - *L. pygmaea* s. l. (N Can, Alaska)

15. *Claytonia* sect. *Claytonia* spp.(lower USA) - *C. ogilviensis* McNeill (Yukon; see Stoughton et al. 2017a).

16. *Montia* root (N Am.) - *Montia* sect. *Australiensis* (NZ, Aus.)

17. *Montia* sect. *Australiensis* (NZ) - *M.* sect. *Australiensis* (Aus)

18. *Montia* sect. *Australiensis* root (NZ or Aus) – *M. howellii* S. Watson (N Am; not anthropogenic contra O'Quinn et al. 2005; see Hershkovitz 2018a, b; see also Mason 1934; cf. Axelrod 1983)

19. *Montia* sect. *Montia* root (N Am) - *M. meridiensis* Friedrich (S Am)

20. *Montia fontana* root (N Am) - *M. fontana* (subcosmopolitan, pre-anthropogenic)

21. *Montia chamissoi* (Ledeb. ex Spreng.) Greene (N Mex - Alaska) - *M. chamissoi* (S Mex)

b. Evidence for pre-Columbian anthropogenic Montiaceae dispersal. I classify the preceding disjunctions as non-anthropogenic. More accurately, in the case of Western Hemisphere Montiaceae and plants in general, I refer to human dispersal beginning in the age of transoceanic global exploration and settlement, ca. 1500 AD and thereafter. Without doubt, massive transoceanic travel initiated the catastrophic phase of the global biotic diaspora. However, anthropogenic dispersals since the dawn of the human evolution have had significant consequences on modern taxon ranges and genetics. This is evidenced in the pre-colonial Western Hemisphere, especially in the case of cultivated taxa (Piperno 2011). But, just as in SW Asia and Europe, presumably New World indigenous migration over several millennia would have influenced also at least passively the distribution especially of useful non-cultivated and weedy plants.

Archeological and anthropological evidence indicates that pre-Columbian migrations may have affected the distribution especially of certain North American *Calandrinia*, *Claytonia*, and *Lewisia* spp., though there is no specific evidence involving South American Montiaceae. However, the evidence does not undermine the thesis that non-anthropogenic LDD explains most major Montiaceae disjunctions.

The most tangible evidence for anthropogenic range intervention among Montiaceae involves the bitterroot plant, *Lewisia rediviva* Pursh. This is considered to have been an important food and medicinal plant in pre-colonial western North America (Bandringa 1999; Davidson 2000). Assuming that the *L. pygmaea* complex is polyphyletic (see below), *L. rediviva* has the most expansive range of any *Lewisia* species (Hershkovitz & Hogan 2003) and among the more expansive among all Montiaceae. Bandringa (1999) described in detail the indigenous people's harvesting of natural populations in Alberta, Canada, and sometimes successful transplanting/cultivation attempts. Wilson et al. (1988) believed that transplantation expanded the range of the species. However, Strong et al. (2003) believed that Hypsithermal warming, ca. 6000–9000 years before present (ybp), explained this and other latitudinal disjunctions in northern North America. But they conceded that LDD and anthropogenic dispersal could not be ruled out. Regardless, the bitterroot harvesting process itself likely transported seed. The limited interfertility among the *Lewisia* spp. (Mathew 1989; Davidson 2000) renders a possibility that anthropogenic dispersal of *L rediviva* may have facilitated gene flow between this and other more range-restricted species.

California indigenous peoples harvested large quantities of the edible seed of the native *Calandrinia menziesii* and/or *C. breweri* S. Watson (Timbrook et al. 1982, Bousman et al. 2012, Reddy 2014). The seeds were stored in large earthen jars and sometimes ceremonially buried. It is not clear whether the plants actually were cultivated, but any degree of deliberate or accidental transport would be sufficient to establish new populations. *Calandrinia menziesii* is especially weedy in California and broadly distributed between Arizona and S British Columbia. Again, Hypsithermal warming might explain the latitudinal distribution (Strong et al. 2003), but other mechanisms cannot be ruled out. The species is human-introduced in Australia, New Zealand, and the Falkland Islands.

The genetically, but apparently not morphologically, distinct species *C. ciliata* (Hershkovitz 2006), is an important non-cultivated harvested leaf vegetable in Mexico (“chivito;” Castro Lara et al. 2011). This suggests a possibility that the California/Mexico connection might be anthropogenic, but circumstantial evidence is not corroborative. The California plants are a seed crop used by a lowland/coastal culture and, indeed, the California plants flower/seed prolifically. The Mexico plants are a leaf crop used by a montane culture and evidently flower/seed more reservedly. The latter I have surmised on the basis of herbarium collections and numerous internet images of Mexican *C. ciliata*, in herbaria, growing, or in markets. In addition, *Calandrinia menziesii* reportedly was present in California during the Pleistocene, ca. 28,000 ybp (Mason 1934; cf. Axelrod, 1983).

Several *Claytonia* species also were used as food by indigenous peoples (Miller and Chambers 2007; Native American Ethnobotany Database 2019). Among these is the widespread and weedy *Claytonia perfoliata* complex, commonly known as “miner’s lettuce,” whose leaves are eaten raw or cooked. Roots/tubers of several species of *Claytonia* sect. *Claytonia* were eaten (Miller and Chambers 2007), and cultivation likely was attempted (Bandringa 1999). Again, even passive anthropogenic dispersal would be sufficient to perturb local gene pools and create some of the taxonomic havoc (Stoughton 2017a, b) in this group.

There is less evidence for anthropogenic dispersal of South American Montiaceae. Many other cultivated species were dispersed anthropogenically between Central and South America along the cordillera by indigenous highland peoples (Piperno 2011). This reflects continuity of the distinctive cordilleran climate and physiognomy, and the development of a corresponding agronomic culture distinct from a forest or coastal culture. But the South American cordillera also circumscribes a natural biogeographic corridor, so natural versus anthropogenic biotic movements during the past ten millennia would be difficult to discern.

South American Montiaceae evidently had little ethnobotanical importance. Unlike important Andean crop species, it is unlikely that their natural ranges were perturbed deliberately. *Calandrinia compressa*, like *C. ciliata*, evidently was a minor leaf vegetable. Multiple internet sources provide a common name, “vinagrillo,” which, like “chivito,” refer to its acidic flavor. Vinagrillo evidently is an ethnobotanical “genus,” as it also is applied to *Oxalis* spp., which, like *Calandrinia* spp., contain considerable oxalic acid. High elevation perennial *Calandrinia* spp. were used for livestock foraging (Aldunate et al. 1981; Jai Vidaurre 2006). *Cistanthe* spp. reportedly had medicinal applications analogous to similarly succulent and mucilaginous aloes (Aldunate et al. 1981; Cecchini & Ticli 2016). Bahamondes et al. (2012) reported that leaves of *Cistanthe* spp. (including

Philippiamra spp.?) afforded solar/heat protection to indigenous desert travelers. Obviously, using plants as sportswear afford an opportunity for anthropogenic dispersal.

An anthropogenic intervention in Andean Montiaceae diversification would have been passive. Such is not unlikely, however. Many Montiaceae have weedy tendencies, and, indeed, certain Chilean species of *Calandrinia*, *Cistanthe*, and *Montiopsis* are especially abundant on disturbed sites, especially along roads and in cultivated fields. It seems unlikely that human migrations in the Chilean region over the course of ten millennia never would have dispersed any Montiaceae species to new sites, and also facilitated gene flow among populations and interfertile species. However, distinguishing between such anthropogenic and non-anthropogenic effects would be difficult, if not impossible.

c. Evidence for Montiaceae age and metastasis. Montiaceae origins/diversification are not preserved in the fossil record (Hershkovitz & Zimmer 2000). Evidence for their age and metastasis is circumstantial, although molecular dating evidence offers a degree of tangibility. Based on what were considered then typical rates of ITS substitution in herbaceous lineages, Hershkovitz & Zimmer (1997) estimated that Montiaceae originated 8–16 million years before present (mybp). They noted that an age of 80 mybp would follow from rates estimated for long-lived trees. These substitution rates had been estimated for other taxa using one or another sort of calibration point. Using a tree-based approach calibrated by Hawaiian island ages, Ocampo & Columbus (2012) estimated Montiaceae age at 13 mybp, which seemed to corroborate Hershkovitz & Zimmer (2000).

However, all subsequent fossil-calibrated tree-based age estimates that sampled Caryophyllales more broadly are much older. Ogburn & Edwards (2015) and Hancock et al. (2018) dated Montiaceae origins at, respectively, ca. 34 and ca. 43 mybp, i.e., late Eocene to perhaps earliest Oligocene. These estimates do not significantly alter the phylogeographic conclusions of Hershkovitz & Zimmer (2000) with respect to LDD. At the same time, all tree-based estimates indicated that diversification of modern species occurred from the Miocene and mostly the Pliocene onwards, much more recently than major lineage origins. However, I speculated above and in Hershkovitz (2006) how molecular markers might underestimate the true age of generic-level diversification among Montiaceae. These ideas must be kept in mind in the following discussion.

The most recent Caryophyllales molecular age analyses (Yao et al. 2019) date Portulacineae and Montiaceae crown divergences at ca. 75 and ca. 60 mybp, respectively. They estimated the Portulacineae-Molluginaceae split at ca. 85 mybp. The authors estimated similar ages for crown divergence of several families throughout Caryophyllales, and argued that this corroborates evidence for massive early Paleogene diversification following Cretaceous mass extinctions. These older estimates affect significantly the phylogeographic interpretation of Montiaceae, as it renders more plausible vicariance of the earliest divergences.

Aligning the 34–43 mybp age estimates with paleoclimatic evidence and the overall phylogenetic trend towards cooler /moister habitats described above, Hershkovitz (2018a, b) proposed that the early diverging arid-adapted Montiaceae lineages Phemerantheae, Cistantheae, and *Rumicastrum* originated in west-central South America during the late Eocene (but see discussion of *Phemeranthus* below). Aridity in this region had established as early as the Jurassic (Hershkovitz et al. 2006a). But both hyperarid and alpine taxa in these first two lineages originated much later with the development of these habitats in, respectively, North America and South America. Given the low genetic divergence within the relevant genera (Hershkovitz 2006, Price 2012), this diversification likely occurred rather recently, perhaps Pliocene (but see below).

Hershkovitz (2018b) suggested that the ancestor of cooler-adapted Montioideae (*Calandrinia*, Hectorelleae, and Montieae) was situated in southern Patagonia during the Oligocene. Both annual and perennial *Calandrinia* taxa spread northward along the uplifting Andes, eventually arriving in Central America and North America via LDD. This presumes that there was never a suitably cool terrestrial connection between the continents. Even so, given the evidential propensity for LDD, the transitory existence of a terrestrial migratory route does not necessarily favor the vicariance hypothesis (see below). Likewise, it is not clear whether the annual *Calandrinia* species of the western US arrived (overland or via LDD) from the most proximal source in Mexico or represent an independent LDD from South America. Meanwhile, Hectorelleae migrated to New Zealand (and/or the Kerguelen Islands) directly or via Antarctica. The Montieae ancestor migrated via LDD to temperate North America.

The 34–43 mybp Montiaceae age estimates remain consistent with Hershkovitz & Zimmer's (1997, 2000) conclusion that the many intercontinental/interoceanic disjunctions among Montiaceae and other Portulacineae owe to LDD. This conclusion is consistent with that speculated on the basis of non-cladistic taxonomy (Raven and Axelrod 1974). The result is significant in that Montiaceae generally have no obvious morphological specialization to facilitate long distance dispersal via zoochory or anemochory. Most *Cistanthe* species are excepted, because their seeds have a short and somewhat sticky pubescence that facilitates passive zoochory. But *Cistanthe* account for only one Montiaceae intercontinental disjunction. Seeds of some *Phemeranthus* spp. have a membranous exotesta (pellicle; Price 2012), and strophioles occur in several genera, but the utility of these in LDD is not confirmed. Some Portulacineae (e.g., Basellaceae, Cactaceae, and *Talinella*) have fleshy fruits, but other taxa, e.g., *Portulaca*, have no obvious LDD mechanism. The pan(sub-)tropical distribution of *Portulaca* has been attributed to LDD (Ocampo & Columbus 2012).

Other researchers (e.g., Carolin 1987; Applequist and Wallace 2001; but see Applequist et al. 2007; cf. Moreira Muñoz 2011: *216*) have explained at least intergeneric Portulacineae distributions in terms of vicariance resulting from the break-up of Gondwana. Some distributional patterns render appealing such explanation, especially African endemism of Didiereaceae. The older divergence dates estimated by Yao et al. (2019) seem to lend some credence to the notion that the oldest intercontinental disjunctions among Portulacineae could owe to vicariance. Older Montiaceae disjunctions could also, but I still doubt it (see below).

An intriguing aspect of the 75 mybp estimate for the Montiaceae split is the reconstructed geography of the western hemisphere during the late Cretaceous (Scotese 2017). At that time, the western American cordilleran region was somewhat disjoint from eastern Laurasia. In North America, the cordilleran region was separated by an interior sea that extended south to include much of Mexico and Central America. And it was closer to South America than it is today. At the same time, the central Andes region formed a peninsula whose arc aligned with the southern end of Central America. A further intriguing observation is that, according to Yao et al.'s (2019) estimate, the split between largely North American *Phemeranthus* and remaining largely South American Montiaceae occurred at ca. 65 mybp (see also below). Thus, the scenario is somewhat suggestive of a late Cretaceous land bridge. Humphries & Parenti (1986, 1999) had proposed that a land bridge explained the repeated pattern of western American antitropical disjunctions (see also below).

While the Yao et al. (2019) chronogram (if correct) would be consistent with a larger role for vicariance in Portulacineae and Montiaceae phylogeographic history, most Portulacineae (including Montiaceae) disjunctions still appear to be too recent to involve vicariance. For example, the chronogram would date the *Rumicastrum*-Montioideae split to ca. 55 mybp. Divergence at this and subsequent nodes largely is responsible for the more "cosmopolitan" distribution of Montiaceae, i.e., phylogenetically successively, *Rumicastrum* in Australia, *Calandrinia* mainly in South America, Hectorelleae in New Zealand and the Kerguelen Islands, and Montieae in North America.

Hancock et al. (2018) suggested that *Rumicastrum* could have arrived from South America vicariously, which would have been highly unlikely given their own divergence age estimate (Hershkovitz 2018b). The Yao et al. (2019) estimate coincides with the separation of South America and Antarctica (Livermore et al. 2007), such that a proto-*Rumicastrum* conceivably could have spanned southern Gondwana terrestrially. However, at ca. 50 mybp, the span from S Patagonia to Australia was cooler and wetter than the ancestral Montiaceae range in NW Patagonia. A vicariance scenario implies that proto-*Rumicastrum* evolved from a warm/arid-adapted ancestor, but was itself more cool/moist-adapted.

Hancock et al. (2018) estimated that the ancestral area of *Rumicastrum* is (currently) warm/arid western Australia, but they also noted that this climate developed in the Miocene. This means that proto-*Rumicastrum* indeed might have been cooler-adapted, which implies that the warm/arid adaptation of *Rumicastrum* is convergent on the ancestral Montiaceae condition. And adaptation of *Rumicastrum* spp. to cooler and moister habitats occurred yet again as species evolved into northern, southern, and eastern Australia. However, Goolsby et al. (2018a, b) reconstructed the *Rumicastrum* ancestral node as C3-CAM, which suggests warm/arid adaptation. There is no empirical evidence for a cool/moist-adapted *Rumicastrum* ancestor, but inference of “unseen” ancestral transformations is not unprecedented, e.g., Hershkovitz et al. (2006a). Possibly empirical evidence will emerge from detailed genomic comparison. In the meantime, the *Rumicastrum* age estimate discrepancy, the ancestral phenotype, and the mode of arrival to Australia require additional investigation.

Although Yao et al.’s (2009) chronogram does not include *Calandrinia* or Hectorelleae, extrapolation would place their age at ca. 50 mybp, well after the South America separation. Even if present in Antarctica at that time, vicarious arrival of Hectorelleae to New Zealand and the Kerguelen Islands still seems doubtful, especially because the taxa evidently grow and migrate extremely slowly (Hershkovitz 2018b). Divergence of Montieae as early as 50 mybp still cannot explain their North American distribution by vicariance. Finally, most of Montiaceae disjunctions involve relatively recently diverged species. This is a point emphasized below: if most Montiaceae disjunctions are too recent to be explained by vicariance, why, especially in the absence of fossil evidence, is vicariance a preferred explanation for the older ones?

At the same time, the discrepancy between the age estimates of Yao et al. (2019) and those of Hancock et al. (2018) and earlier workers beg reconciliation. At the time of this writing, Yao et al. (2019) is not published formally and their data are not available for scrutiny. And molecular dating methods are subject to and incorporate the very same sorts of artifacts as molecular phylogenetic reconstruction generally (see above and Hershkovitz 2018b).

A more trivial geographic aspect of Montiaceae geographic origins relates to Chile. The first phylogenetic divergence separates Phemerantheae from the remainder of the family. The next divergence separates largely Chilean Cistantheae from *Rumicastrum* and Montioideae, and the first split in the latter separates largely Chilean *Calandrinia*. Thus, excluding Phemerantheae, the origin of the rest of Montiaceae appears to have occurred in present day northern Chile. There, it diversified mostly southwards, many descendents dispersing to other lands and diversifying, dispersing, and diversifying further. This appears to be the only intercontinentally diversified plant lineage that originated in present day Chile.

In fact, Chile is known for its high phytogeographic endemism (Moreira Muñoz 2011), indicating that this region has been mainly a phytogeographic sink and not a source. Hershkovitz (2018b) speculated that this may owe to Chile's narrow longitudinal breadth, high relief, and, most of all, historical ecological instability. This may result in high lineage extinction rates, which, in turn, offer more opportunities for colonization. Montiaceae, in turn, are among the few lineages that not only diversified under these circumstances, but evolved their own global colonization capability.

However, the basal split between trans-cordilleran Phemerantheae and cis-cordilleran Montiaceae presents a phylogeographic puzzle. Given the morphological and ecophysiological similarities of *Phemeranthus* and other trans-cordilleran Portulacineae to Cistantheae, why are there not more Portulacineae lineages in Chile? Possibly the question is artificial, as various Cactaceae entered Chile at many different times, presumably since the Miocene (Nyffeler & Eggli 2010b; Moreira Muñoz 2011). However, the other trans-cordilleran taxa, Anacampserotaceae, Basellaceae, and Talinaceae, besides Phemerantheae, are absent in Chile, and only one species of Portulacaceae is native to Chile (Moreira Muñoz 2011).

The cordilleran partitioning of Portulacineae is characteristic of many angiosperm lineages (Luebert & Weigend 2014). Based on present geography, it is tempting to believe that the Andes themselves formed a physical barrier and/or created an indirect ecological barrier against trans-Andean migration (Luebert & Weigend 2014). But popular theory maintains that half or more of the modern height of the central and southern Andes was uplifted relatively rapidly beginning in the Miocene. Before that, the trans-Andean macroecological contrast was less marked and abrupt.

Also, the modern Mediterranean and hyperarid climates are considered to have developed even more recently (Moreira Muñoz 2011). But current estimates place the basal split of Montiaceae in the late Eocene, perhaps 25 million years before the physical/macroecological partition and contrasts developed. Unless the much younger age estimates of Hershkovitz & Zimmer (2000) prove to be correct, the Andes cannot explain the phylogeographic partition. However, some evidence indicates that significant cordilleran height indeed was achieved by the Oligocene (Luebert & Weigend 2014). More recent interpretations of the Andes uplift are nuanced (e.g., Armijo et al. 2015; Quade et al. 2015; Lease et al. 2016; Rodríguez Tribaldo et al. 2017) and do not entirely resolve the question of when the Andes became a phytogeographic barrier.

Among other possible explanations for the phylogeographic partition of Portulacineae in Chile is prior broader cis-cordilleran distribution of currently trans-cordilleran taxa, followed by extinction caused by the drastic changes in climate and/or topography. However, it is not established that the absent trans-cordilleran lineages ever occurred in Chile. Another possibility is that South American cis-cordilleran Montiaceae themselves originated from an ancestor dispersed from North America. The putative phylogeography of *Phemeranthus* (Price 2012; see also Ocampo & Columbus 2012) renders plausible this scenario. As noted above and in Hershkovitz (2018b), the historical ecological instability combined with relatively small geographic area of Chile itself renders its vulnerability to colonization, possibly explaining the tendency of Chile to have become a phylogeographic sink rather than source.

Phylogeny within *Phemeranthus* itself presents a phylogeographic enigma. A basal split separates two clades, and the basal split of each clade defines a major geographic disjunction (Price 2012; cf. Hershkovitz & Zimmer 2000). One clade includes the South American *P. punae* and a small clade of largely Mexican species. The other includes the two Pacific NW US species and a disjunct clade comprising the remaining species, which are distributed >1000 km to the east and south in the central, S, SW, and SE US and northern Mexico. Based on Hershkovitz & Zimmer (2000) and Ocampo & Columbus (2012), Price (2012) presumed a Miocene age for *Phemeranthus* divergence (ca. 13 mybp; see above) and correspondingly more recent ages for these disjunctions. Obviously, the three different older *Phemeranthus* age estimates (respectively, ca. 34, 43, and 60 mybp; see above) would implicate different biogeographic scenarios.

In summary, Montiaceae geographic origins, age, and metastasis remain challenging problems to resolve. The working hypothesis advanced here involves origins in west central South America followed by LDD of ancestors of what became major lineages on other continents, and thereafter continued intercontinental LDD and terrestrial metastasis via migration or LDD. Some evidence is consistent with alternative scenarios of origin and early metastasis, but there seems little evidence countering a significant role of LDD within genera. Much of the resolution rests upon the phylogenetic chronology. None of the age estimates proposed to date are inherently unreasonable. But they are "all over the place" with respect to the actual timing of phylogenetic events.

d. Montiaceae biogeography and biogeographic epistemology. The preceding accounting of Montiaceae historical biogeography is unapologetically a single-taxon narrative. The synthesis is elaborated much like classical taxon-specific phylogeographic narratives, but incorporates cladistic epistemology and molecular divergence-based estimates of taxon ages (such as they are), as well as other epistemological considerations. Both narrative and taxon-specific analysis might be anathema to method- and/or ideologically-oriented biogeographers (Moreira Muñoz: *Ch.* 10). But, in the end, the objective of all approaches ultimately is a narrative. Some evidence presented here indeed was derived methodologically (O'Quinn et al. 2005; Ocampo & Columbus 2012; Price 2012; Hancock et al. 2018), but the methods and their application were not analyzed here critically.

Epistemology and methodology influence interpretation of Montiaceae biogeography, for which reason I elaborate on the theme here. The view taken here is that the number and complexity of parameters, quantity of unknown data, and precariousness of methodological assumptions restrict to heuristics the utility of "objective" computational phylogeography. No attempt is made here to summarize, much less critically review, the myriad philosophies and/or methods conceived and/or implemented during past two decades or so. An eclectic list of references give some idea of the philosophical polemic and parametric complexity: Nathan (2006; Nathan et al. 2008), Upchurch (2008), Heads (2009, 2014), Wallis & Trewick (2009), Crisp et al. (2011), Moreira Muñoz (2011), Ronquist & Sanmartin (2011), Wiley & Lieberman (2011), Gillespie et al. (2012), Matzke (2013), Warren et al. (2014), and Ebach et al. (2017). In addition, molecular dating has spawned a new paradigm, genomic geochronology (Baker et al. 2014). Here, the chronological alignment of cladistic events is used to discover/corroborate paleogeological/paleoclimatological events. This approach underlies the thesis that Montiaceae and other Caryophyllales families originated/diversified coincident with the Cretaceous-Paleogene boundary (Yao et al. 2019).

The challenge of phylogeography can be understood in terms of the parametric complexity of its biotic and abiotic components. Biotic components include taxonomy, spatiotemporal phylogeny, and essentially all components of the biology of organisms. Abiotic components include all aspects of neo- and paleo- geology and climatology, as well as spatial relations (i.e., geography). The two components intersect in neo- and paleo- ecology. Much of the present treatise emphasizes that the complexity of biotic components proscribes analytical simplisticity. But, as Moreira Muñoz (2011: *Ch. 10*) emphasized, the abiotic complement is no less important. Systematists tend to be (at best) more critically analytical of biotic evidence and less of abiotic. They tend to cite geological and climatological dogma uncritically as established fact. This is equivalent to geologists and climatologists uncritically citing taxonomy in a most recent popular floristic reference, e.g., Reiche (1898) in the case of Chilean Montiaceae. So, Moreira Muñoz' point must be well-taken. But a biotic bias in phylogeographic interpretation is justifiable, as concluded below.

The legitimacy of the taxon-specific narrative approach adopted here lies in its flexibility and nonlinearity, in particular its capacity to incorporate singular *nuance*. The present work describes amply the limitation of global quantitative evolutionary analysis that disregards nuance. Examples include statistical nonequivalence of operational taxa, nonstationarity of estimated molecular evolutionary "rates," concomitant order of magnitude differences in estimates of cladistic chronology, and the effect of simplistic global parameterization of plant traits such as life history and ploidy, as well as niche traits. Quantitative historical biogeographical methods inherit these shortcomings and add several parametric dimensions of their own. These include arbitrary and dubious definitions of "areas." Thus, as much or more than described in previous sections, quantitative historical phylogeographic analysis intrinsically is inconsistent: the more taxa and areas added, the more violated become the simplistic assumptions.

i. Biogeography top-down or bottom-up? A more existential debate in historical phylogeography concerns the hierarchical level to which the science pertains. Some researchers evidently or explicitly prefer a top-down approach that searches for the most-to-least inclusive biogeographic regions/patterns evident from higher to lower taxonomic levels. The approach seeks to explain lower level biogeographic incidence in terms of higher level biogeographic cause. The approach adopted here is phylogenetically bottom-up, whereby broader biogeographic patterns emerge (or not) from the sum of parts and have multiple and sequential historical causes. The debate is analogous and probably psychologically equivalent to the Clement/Gleason ("socialist"/"capitalist") polemic on the tangibility of ecology communities.

The present discussion of Montiaceae phylogeography uses phylogenetic evidence to both discover and challenge phylogeographic hypotheses, including those emergent from the top-down paradigm. In fact, this approach was applied in my earliest Portulacineae research (Hershkovitz 1991), yielding diagnosis of the Western American (slash Australasian) and Eastern American/African groups. However, these informal groupings were taxonomic and not per se biogeographic. Their names merely described the areas of predominant diversity and presumed diversification. But each group had species in the alternate area. The Western American group ultimately became Montiaceae, the basal divergence of which separated the biogeographically intermediate *Phemeranthus*. The last is the only nominally "eastern American/African," lineage of Montiaceae, but it is restricted to America and absent in Africa.

Epistemologically and methodologically, the top-down approach incarnates in chorology (e.g., Moreira Muñoz 2011), panbiogeography (e.g., Heads 2014), and, essentially, in the original vicariance biogeography paradigm (e.g., Humphries & Parenti 1986, 1999). These approaches presume that patterns represent tangible and/or historical entities/processes. They therefore subordinate taxon-specific narratives to pattern discovery. Chorology divides regional biodiversity among groupings (provinces, regions, or "elements" in Moreira Muñoz 2011) based on taxonomic distinctiveness and/or similarities with other regions. This creates a biogeographic map "deconstructed" from the physical geographic map (Moreira Muñoz 2011). But it is achronological, viz., it is agnostic towards historical biotic assembly.

Panbiogeographical "tracks" are similar to chorological elements in emphasizing interregional taxonomic similarity, but "tracks" purport to be both historical geographic and phyletic hypothesis. Vicariance biogeography emerged with a panbiogeographic mindset on the nature of past geographic connections between disjunct taxa. It departed from panbiogeography in deriving area cladograms as a function of taxon phylogenies derived independently according to cladistic epistemology. Cladistic epistemology effectively is rejected in panbiogeography. In the latter, the most parsimonious phyletic hypothesis is the one that best explains (purported) geographic relations (e.g., Heads 2014; see also below). More recent derivatives of vicariance biogeography (see Ronquist

& Lieberman 2011) increasingly emphasized taxon-specific cladistic criteria, avoid ad hoc assumptions on the significance of regional geographical taxonomic similarities, and have become more agnostic towards a priori assumptions of historical geographic relations.

Note that panbiogeography (and chorology, more or less) are comparable to clique methods in phylogenetics. In particular, both approaches diagnose biogeographical entities (elements or tracks) as cliques that optimize the distribution of taxa (as traits) among areas. This approach is inherent to an epistemology that predicates that large numbers modern disjunct distributions are borne of fewer ancient continuous ranges. Patterns thus are geographic "symplesiomorphies." This contrasts cladistic epistemology, which diagnoses evolutionary entities based on historically shared evolutionary transitions. Thus, shared distributions can reflect both ancient and recent events.

Moreira Munoz (2011) presented a chorological/panbiogeographic classification of the Chilean flora, which includes seven Montiaceae genera. The work is illustrative of artifacts inherent to the chorological approach. Apparently following Moreira Muñoz & Muñoz Schick (2007), the author classified genera present in Chile into seven floristic elements, some subdivided into generalized panbiogeographic tracks, thus yielding a total of 10 biogeographic entities. Moreira Muñoz did not justify analysis at the generic level. Presumably genera optimize both ease of data gathering and number of inter-area similarities/contrasts. But obviously generic splitting/lumping would (and does) affect the chorological analysis, as does evidence from phylogenetic levels both above and below the generic level (see below). Unless I missed it, Moreira Muñoz (2011) and Moreira Muñoz & Muñoz Schick (2007) did not articulate analytical methods for deriving their floristic elements or tracks or for classifying genera into them.

Moreira Muñoz' (2011) analysis is purely spatial and does not incorporate evidence for phylogenetic chronology. As an example, he delimited an australasiatic floristic element comprising genera shared between Chile and Australasia whose distribution "can be traced to the Gondwana era, as a once-continuous cool-temperate flora, now scattered into a relict distribution by tectonic movements" (Moreira Muñoz 2011: *92–93*). He divided this element into three generalized tracks: austral-arctic, circum-austral, and tropical Pacific, depending upon whether a genus also includes species in, respectively, southern Africa or tropical Australasia.

In his "tropical Australasian track," Moreira Muñoz (2011) included the taxonomically problematic *Hebe* (Plantaginaceae). *Hebe* in its broadest sense segregates most Australasian species of the consequently paraphyletic genus *Veronica* (Wagstaff et al. 2002; Albach et al. 2005; Albach & Meudt 2010). In the strictest circumscription, *Hebe* does not occur in the tropics, thus has no "tropical" track. In the broadest circumscription, *Veronica*, with *Hebe* included, is cosmopolitan. Here we see the problem of biogeographic analysis at arbitrary taxonomic levels.

Two species of *Hebe* (s. str., s. l., or as *Veronica*) each occur in both New Zealand and southern Patagonia. Genetic divergence between disjunct samples is low. Thus, based on genetic and morphological *evidence*, the presence of *Hebe* in *both* Patagonia *and* Australasia has been explained as LDD (Wagstaff et al. 2002; Albach et al. 2005; Albach & Meudt 2010; cf. Winkworth et al. 2002, Wallace & Trewick 2009). (Negative) fossil evidence corroborates this conclusion. The only *evidence* that these disjunct distributions represent relictual vicariance is that Gondwana once existed. Moreira Muñoz (2011) separately addressed the LDD/vicariance polemic generally (see below) and described evidence for a few taxa, but not *Hebe*.

In any case, Moreira Munoz´ (2011) chorological/panbiogeographic categories would seem to corroborate/validate themselves only on the basis of the number of taxa they contain, without elaborating evidence whether the shared distributions of included taxa are homologous or convergent.

Alternatively, Moreira Muñoz' (2011) track classification of *Hebe* may betray his uncorroborated conclusion that these two disjunct modern species of *Hebe* existed and spanned Gondwana in the earliest Eocene. These perspectives are critical to interpret the associated classification of Montiaceae.

Setting aside the cosmopolitan *Montia fontana*, Moreira Muñoz (2011) assigned Chilean autochthonous Montiaceae genera to two floristic elements and a total of three tracks: Neotropical - Central Andean track (*Montiopsis*); Neotropical - Wide Neotropical track (*Calandrinia*); and Antitropical - Pacific track (*Cistanthe*; sensu Hershkovitz 1991, including *Philippiamra*, evidently overlooking Hershkovitz 2006). *Lenzia* was classified in the Neotropical element, but, being monotypic, no track is assigned, as though it generated spontaneously and has no biogeographical relations. Moreira Muñoz (2011) characterized the Wide Neotropical track genera as having diversity concentrated mainly in the intertropics. The Central Andean and Antitropical elements localize at, respectively, tropical and temperate latitudes.

Montiaceae distributions in Chile reveal the limitations of the chorological approach, and this evidently extends to other taxa. Multiple species of *Calandrinia, Cistanthe, Philippiamra*, and *Montiopsis* extend into tropical Southern latitudes in nightly/seasonally cool/cold (i.e., temperate-like) habitats. But only two *Calandrinia* species and none of the last three genera are endemic to tropical latitudes. The diversity of all four genera centers in temperate latitudes. *Calandrinia* extends to Tierra del Fuego, and *Montiopsis* to ca. 40S. *Lenzia*, to my knowledge, does not enter tropical latitudes, yet is classified as Neotropical. Thus, the classification of *Calandrinia*, *Montiopsis*, and *Lenzia* as Neotropical is misleading or incorrect.

Oddly enough, *Cistanthe* and *Philippiamra*, the only genera classified (effectively) as temperate, are the most tropically distributed of Chilean Montiaceae. At least 12 *Cistanthe* species occur at tropical latitudes (Flores Fuentes 2016 and personal data), four of which are are endemic to Peru. *Cistanthe* diversity concentrates in Chile's Atacama and Coquimbo regions, and *Philippiamra* does not occur south of 30S. Segregation of *Philippiamra* and *Calyptridium* significantly affect generic-level analysis in Chile. *Philippiamra* is not antitropical, while its antitropical disjunction with closely related *Calyptridium* is not apparent at the generic level. Likewise not apparent is the Circum-Pacific distribution of Montiaceae as a whole. Ironically, the classical conception of *Calandrinia* s. l. would have been classified as Circum-Pacific. The family's actual Circum-Pacific distribution remains, but it is no longer evident at the generic level. It is ironic that Moreira Muñoz (2011) overlooked this Montiaceae distribution, since it is the one that best indulges his panbiogeographic inclinations.

The inadequacies, inconsistencies, and artifacts of Moreira Muñoz' (2011) chorological/panbiogeographic classification of Chilean Montiaceae extends to other taxa, as well. For example, *Crunckshankia* (excluding *Oreopolis*; Rubiaceae), *Schizopetalum* (Brassicaceae), and *Schizanthus* (Solanaceae) all are genera of northern Chile, and the last extends well into tropical latitudes. Yet Muñoz Moreira (2011) included them in the temperate element, while *Calandrinia* and *Montiopsis* were classified as tropical. *Salpichroa* (Solanaceae) was classified in the Wide Neotropical track, the same as *Calandrinia*. But in contrast to primarily Chilean taxa, at temperate latitudes, *Salpichroa* species occur primarily on the east side of the Andes, with two species crossing the Chilean border. In other words, the phytogeography of taxa classified in the same floristic element and panbiogeographic track is intersecting, not coincident.

Some Andean genera, unlike *Salpichroa*, are diverse in both temperate Chile and east of the Andes. Depending upon species distributions, Moreira Muñoz (2011) classified these in either his Wide Neotropical (e.g., *Tropaeolum*, *Drimys*) or Central Andes – Southeast Brazil track (e.g., *Alstroemeria*). The classification is misleading insofar as it implies Neotropical "origins" of the temperate Chilean taxa. For example, *Tropaeolum* includes two clades, one temperate Chilean, the other Central Andean and S Amazonian. Although congeneric, genetic divergence between the clades is comparable to that separating families (Hershkovitz et al. 2006b). This suggests that *Tropaeolum* is not "Neotropical," but Gondwanan, the temperate Chilean and Neotropical Andean clades diversifying independently after the separation of South America. The same probably occurred in *Alstroemeria* and *Drimys* and perhaps other taxa.

Another peculiarity of Moreira Muñoz (2011) owes not to biogeographic epistemology, but to anthropocentrism. While it is axiomatic that a book on Chilean plant geography emphasizes plants occurring in Chile, Moreira Muñoz (2011) seems to treat geopolitical Chile as natural biogeographic entity. One senses that Chilean plant geography is consequent not so much to a half billion years of biological/geological evolution as it is to Chile's 1870s War of the Pacific and the Treaty of 1881, these respectively extending Chile's northern limit 8° in latitude and relinquishing Chile's claim to currently Argentinean Patagonia.

ii. Montiaceae in Chile versus the Chilean Floristic Region. In contrast to Moreira Muñoz (2011), I use the term "Chilean" only as a global reference point, meaning "thereabouts." I use "Chilean flora" in an adjectival sense to refer to plants distributed/diversified primarily along the ca. 5000 X 150-200 km western slope of southwestern temperate to tropical South America. This includes the Argentinean Andes and southern coastal Peru. Native plant taxonomic representation here is biased, and, independent of taxonomic relations, the plants mostly have morphological/ecological characteristics especially adapted to the biotic/abiotic characteristics of the zone (Luebert & Weigend 2014).

Consequent to recent human political history, this biogeographic region largely coincides with continental geopolitical Chile. But geopolitical Chile intercalates with the biogeographically distinct altiplano in the north and Patagonian steppe in the extreme south. Hence it is convenient to refer to the characteristic (though composite) flora as "Chilean," even though it is not congruent geopolitically and does not include Easter Island. At one time, phytogeographic coincidence in this region with Chilean borders was less, and in pre-Columbian times, the phytogeography existed but Chile did not. At these times, the denomination "Chilean flora" would have been inadequate or inappropriate.

The term "Chilean floristic region" (ChFR, to not confuse with the CFR, the Cape Floristic Region) has been applied by Philip Rundel (pers. comm., 2019) to the phytogeographic region described above (INCOMME 2011). The ChFR is analogous to the California Floristic Province (CFP; Bunge et al 2016), which encompasses most of California and extends into adjacent geopolitical territories. Also, the CFP, like the ChFR, is a composite flora, both ecologically and historically. Both include comparable desert, Mediterranean, and temperate forest elements having distinct spatiotemporal and phylogenetic origins. And both are influenced by similar climatic phenomena.

ChFR floristic composition (like that of geopolitical Chile) diverges more markedly latitudinally than CFP. This is why, historically, Chile's latitudinal floristic belts have been classified into different provinces (Moreira Muñoz 2011). The CFP is, or at least seems, more integrated latitudinally, especially because numerous dominant woody taxa span most or all of its length. Also, the CFP is ca. 50% more diverse than the ChFR, which itself offers more opportunity for latitudinal intergradation and integration. Large woody taxa in Chile have fewer species and they largely disappear from the landscape north of 30S. *Schinus* (Anacardiaceae) is an exception. And, of course, diversity approaches zero towards the maximally hyperarid zone. Nevertheless, the recognizable integrity of the ChFR is maintained, because many taxa span more than 20˚ latitude and two or more recognized floristic zones. Numerous genera present in fog oases at ca. 24S extend to at least central and some to austral ChFR zones (e.g., *Alstroemeria*, *Tropaeolum* sect. *Chilensis*). Meanwhile, more numerous taxa of central Chile extend to austral Chile, while others extend to the desert north. And this is aside from the many genera that are primarily Chilean but cross into the Argentinean Andes.

The ChFR's distinctive flora owes to several historical and modern biotic and abiotic contingencies (Moreira Muñoz 2011; Luebert & Weigend 2014). In modern times, the distinctiveness is corralled by three physical barriers, the Pacific Ocean (obviously), a very high and, just as importantly, steep mountain range, and the "arid diagonal," which extends from Chile's Antofagasta Region southeastward, cutting across Argentina's San Juan Province, towards Patagonia. North/northeast of the diagonal, a tropically-influenced macroclimate allows more Neotropical lineages to enter and intermix with ChFR taxa. But for most of Chile's length, the temperate Pacific macroclimate, aided by strong westerlies, facilitates entry of ChFR lineages into Argentinean territory, but mostly not beyond the High Andes. The consequence of the macroclimatic influence is that much of the southern cone flora endemic to the ChFR is not endemic to Chile. This applies to a majority of nonendemic native Chilean species and perhaps a third of the flora as a whole.

Moreira Muñoz (2011) did not afford a term for the ChFR; only the Flora of Chile and the various supra-Chilean and infra-Chilean regional floristic zones that historically have been described. He applied the term "subendemic," two times in reference to families having the ChFR distribution, but also in reference to Berberidopsidaceae, which has one Chilean and one Australasian genus. Thus, the term is not specific to the ChFR. He referred to one of 878 native genera as "subendemic," but no species. A large proportion of the genera classified in one or another of his nonendemic floristic elements, especially the Temperate element, pertain to the ChFR. In the chorological/panbiogeographic classification, these ChFR genera are lumped with genera not pertaining to the ChFR.

Meanwhile, Moreira Muñoz' "endemic" criterion refers to genera contained within geopolitical Chile, including non-ChFR Easter Island, but not straying a micron into Argentina, Bolivia, or Peru. Even within continental Chile, this endemic "element" includes a biogeographically heterogeneous mix of taxa, some separated by 2000 or more km. No sense of geographical or phylogenetic relations of these genera was offered, not within Chile nor externally. It is as though the taxa evolved autonomously in an historically omnipresent Chile. Yet, the composition of the endemic, and, in fact, all of the elements would have differed according to prior territorial maps. The endemic element would gain taxa in the south and lose them in the north. Numerous taxa would lose Chile-Argentina distributions, while others would gain Chile-Bolivia(-Peru) distributions. Eventual cession of Chile-occupied Bolivia, Peru, and Wall Mapu would reduce Chilean plant generic endemism to close to zero.

Phylogeography of Montiaceae and probably most taxa distorts/disappears in the chorological/panbiogeographic analysis of Muñoz Moreira (2011). The preceding digressions demonstrate how epistemology and Umwelt influence biogeographic interpretation of taxa in general. Classical chorological analysis at arbitrary taxonomic levels might have – or at least have *had* – heuristic value. But as a means to an end, the approach is archaic and arcane. Processes that create chorological patterns are offset by processes that superimpose, intercalate, and erase them. The only way that the collective species of nearly 900 plant genera can be fit neatly into seven floristic elements and/or ten panbiogeographic tracks is with cut-and-paste or a bulldozer.

Meanwhile, the taxon-specific narrative analysis of Montiaceae yielded four major results. One is not only a phylogeographic description, but a hypothesis explaining the predominantly

Circum-Pacific distribution of the family. Another is a description and explanation of the concentration of Montiaceae in Chile. In particular, Montiaceae help diagnose the ChFR. Of six Montiaceae genera in Chile, three are endemic not to Chile, but to the ChFR (*Lenzia*, *Montiopsis*, *Philippiamra*) and a fourth is essentially so, ignoring a pair of sister species in N America (*Cistanthe*). Twelve of 19 *Calandrinia* species are ChFR endemics and probably also the *Calandrinia* ancestor (see above). Yet, at most, only 2/19 species are endemic to geopolitical Chile (cf. Peralta & Ford-Werntz 2008, Elvebakk et al. 2015; see also below). Only the single species of *Montia* in Chile is truly allochthonous. Another conclusion is that Circum-Pacific Montiaceae (i.e., excluding *Phemeranthus*) originated in what is present day Chile (and/or what was not so long ago Bolivia and Peru). Finally, it revealed that Montiaceae evidently comprise the most globally successful plant lineage of ChFR origin.

The chorological/panbiogeographic approach to Chilean phytogeography (Moreira Muñoz 2011) failed to detect these phenomena. This owes to several factors. One is analysis at the taxonomic generic level, which “disappeared” the relations to excluded Australasian and North American Montiaceae. Assumption of generic monophyly is violated in the analyzed *Cistanthe* circumscription (as well as certain genera of other families). At the same time, it is understandable that the scope of the Chilean chorological tabulation logistically challenged analysis of 878 phylogenies. The chorological/panbiogeographic analysis itself was agnostic towards phylogeny, hence towards phylogeographic sources and sinks, hence the role of Chilean territory in Montiaceae diversification. This is not so much oversight as consequent to panbiogeographic epistemology, which focuses not on phylogeography, but on discovery of supposedly formerly continuous ranges. Finally, not consequent to chorology/panbiogeography per se, Moreira Muñoz’ (2011) analyzed not a floristic region, but a geopolitical one, rendering an impression that recent geopolitical processes retroactively determine ancient biogeographic patterns.

iii. Vicariance and LDD – again. The present work emphasizes the role of LDD in explaining Montiaceae distributions. The evidence will not convince those inclined to favor vicariance explanations. Moreira Muñoz (2011) provided a thorough and thoughtful review of the historical debate on the role of vicariance and LDD in explaining modern plant disjunct distributions, including epistemological aspects. There would seem little to add, but a few critical references were overlooked, additional evidence favoring LDD has emerged, and nonlinear evolutionary models offer additional insights.

A principal argument of the vicariance/panbiogeographic school (e.g., Humphries & Parenti 1986, 1999; Heads 2009, 2014) and its apologists (e.g., Moreira Muñoz 2011) is that appealing to LDD is ad hoc, it does not explain shared disjunction patterns globally parsimoniously, and, in any case, events resulting in LDD are rare. Implicit is that vicariance events are adequately frequent to explain the majority of disjunctions. Dispersalism dominated phytogeography until the latter 20th century. Then, abruptly, vicariance/panbiogeographic ideology became embedded dogma. Then a deluge of molecular evidence (including Hershkovitz & Zimmer 1997, 2000 for Portulacineae) began to swing the pendulum the other way, suggesting a frequent role for LDD (Moreira Muñoz 2011). Yet, LDD had become so disparaged that even a decade later, evidence for LDD in a migratory *bird-dispersed* taxon was considered noteworthy/newsworthy (Donoghue 2011), perhaps on a par with the proof of cold fusion.

Much earlier, Hershkovitz & Zimmer (2000) argued that evidence for LDD was sufficiently pervasive to afford it a substantial *prior* likelihood to explain disjunctions in taxa that, like most Portulacineae, lacked LDD adaptations. This viewpoint evidently was novel and overlooked. It was not until Rees et al. (2005) that methods were developed that afforded a *post-analytical* likelihood to

LDD. Lack of LDD adaptation remained a principal stumbling block in acceptance of LDD explanation, e.g., Moreira Muñoz (2011: *120*).

Subsequent theoretical and empirical evidence confirmed the notion of Hershkovitz & Zimmer (2000). Nathan (2006; Nathan et al. 2008) demonstrated that the cumulative probability density functions of LDD frequency and distance for non-LDD-adapted propagules are fat-tailed. In other words, given enough time, LDD is bound to occur. The actual probability is a function of "nonstandard" vector frequency, e.g., hurricanes, tsunamis, or nonstandard zoophily. A nonstandard vector is any vector that is not the one or among those that normally disperse the overwhelming majority of propagules. Thus, lack of LDD adaptation is a red herring in phylogeographic debate.

But nonstandard vectoring is much more frequent than vicariance/panbiogeographic adherents would suggest. A single successful hurricane/tsunami-facilitated LDD per century for 10 million years yields 100,000 LDDs, presumably far more than the number of plant phylogenetic long-distance disjunctions. Yet, the number of strong hurricane/tsunami events is much greater than one per century, and each is capable of facilitating multiple LDDs. The negative correlation between frequency/force of catastrophic events is offset by the positive correlation between event force and number/distance of propagules dispersed. Adding birds to the equation, a single bird-facilitated LDD per year would yield 10 million LDDs, overshadowing catastrophic LDD frequency. But the number of long distance bird migrations annually likely is > 10 billion (Viana et al. 2016; Dokter et al. 2018), yielding 10^{17} LDD opportunities over 10 million years.

The evidence suggests that the supposition of infrequency of LDD vectoring opportunities is, at least, "incompetent, irrelevant, and immaterial," and, at most, patently false and absurd. If anything, the number of observed disjunctions among Montiaceae and Portulacineae generally is not higher, but *lower* than expected via LDD. In the case of Montiaceae, assuming a 50 million year age, it amounts to less than one successful dispersal every two million years. Of course, most observed disjunctions are at the interspecific level (i.e., recent), so the rate obviously must be much higher. In other words, the 50 million year calculation ignores lineage extinction. At the same time, the more recent the disjunction, the less likely it owes to vicariance. But as Nathan (2006; Nathan et al. 2008) notes, the factor limiting successful LDD is not dispersal itself, but the low likelihood of establishment of the propagule.

Upchurch (2008) agued that, because of unseen events such as range expansion, vicariance/dispersal analysis will tend to bias in favor of dispersal. He is correct that unseen events can distort interpretation of historical relations. Correcting for unseen events is the point of probabilistic parametric models in likelihood analysis. However, Upchurch (2008) did not appreciate that bias is a double-edged sword. For example, the evidently recent spread of *Montia* into South America may render more plausible the notion that the Australasian disjunction is vicariant, since these areas were connected in the Cretaceous and separate from Laurasia since the Triassic.

However, a more important overlooked bias is that loss of vicariance approximates Dollo's Law, while loss of LDD disjunction does not. More precisely, a vicariant relationship can occur only once, when connected areas are separated. This relationship is broken when either descendent lineage becomes extinct – which is inevitable. Thereafter, areas rarely become reconnected, e.g., India, Panama, Beringia, but usually long after biota on both sides have evolved substantially. However, reconnection/reseparation of land areas does not recreate vicariance. Ontologically, vicariance relations cannot reestablish

Alternatively, the LDD clock begins ticking immediately after separation. Its probability is highest the soonest after area separation, but the "fat tail" of the LDD probability density function maintains its likelihood thereafter. And possibly the former presence of a taxon in a separated terrain renders more likely the success of related taxa dispersed to that terrain (Thuiller et al. 2010). LDD thus can create "pseudovicariance," or cases where vicariance appears or is actually plausible, yet did not occur. In addition, LDD can distort apparent vicariance relations if there is gene flow between vicariant and subsequently dispersed individuals.

Additional criticisms of molecular phylogenetic and molecular clock-based LDD conclusions include the possibility of lineage sorting and unreliability of molecular dating methods (Heads 2009, 2014). Evidence discussed earlier in this work makes clear that these concerns are valid. But, in the present context, they also are red herrings, because they can bias data in both directions. Moreover, an argument for greater lineage antiquity does not necessarily favor vicariance, because, as noted, the older the lineage, the more likely that it has experienced LDD.

Dismissal of fossil absence as "negative evidence" also is unjustified. Heads (2014) especially attributes broad disjunctions of locally restricted modern species to former widespread ranges, ignoring absence of corresponding fossils. Indeed, vicariance seems to require broad taxon ranges, as taxa with smaller ranges and more locally restricted populations are less likely to span rift zones, and rift zones themselves are not conducive to survival of normally inland species. However, the broader the range and more frequent the taxon, the more likely is its fossil preservation. And the older the lineage, the less likely that its fossil preservation will be delayed tens of millions of years. Thus, the present interpretation of a mainly or completely LDD-mediated Montiaceae distribution is only partly based on phylogenetic and molecular dating evidence. It is based on the logic that the absence of Paleocene/Eocene fossils, if not positive evidence that Portulacineae, including Montiaceae, were absent, is at least positive evidence that the lineage was not broadly distributed across Gondwana.

Thus, the phytogeographic vicariance mentality distributed worldwide during the late 20th century evidently persists relictually only in isolated Gondwanan fragments (e.g., Upchurch 2008; Heads 2009, 2014; Moreira Muñoz 2011). Vicariant disjunctions certainly exists, but the then-blasphemous proposal of high prior LDD likelihood suggested by Hershkovitz & Zimmer (2000) now seems modest. In the case of plant disjunctions, LDD not only should be afforded a prior likelihood, it qualifies as the default assumption. It is vicariance that demands positive evidence in the form of contemporaneous fossils, and in not one, but *both* of the formerly connected areas.

iv. Closing remarks: biology, geology, and biogeography. Moreira Muñoz' (2011) defense and application of chorology/panbiogeography roots in his argument that biogeography is an independent discipline. Biogeographers draw on phenomenologically independent biological and geological events, and, like their astrological brethren, align them, discern patterns, and make predictions. Historically, this approach has "worked" only once, predicting the principle of plate tectonics. A half century ago, chorology, especially in zoology, figured significantly in corroborating plate tectonic theory (e.g., P. Hershkovitz 1969, 1972). But even by then, the utility of panbiogeographic research was questioned (e.g., P. Hershkovitz 1972: *331*), its resonance with plate tectonic theory notwithstanding. And notwithstanding its role in advancing plate tectonic theory, chorology has not yielded since a new, comparably significant discovery. Rather, its role has been limited, and to questionable effect, to the hashing out of consequent biogeographic details.

In theory, biogeography should privilege neither biological nor geological dogma. In practice, this is not always so. Panbiogeographers seem to afford greater predictive power to geology. But in systematics, biology has been privileged. As Moreira Muñoz (2011) and others have noted, most phytogeographic research is undertaken not by card-carrying geographers, but by systematists (i.e., biologists), often as a convenient pretext for justifying mass DNA sequencing projects. The objective generally is to explain the geographical history of particular organisms, not the geographical history of land areas.

Moreira Muñoz' (2011) points are well-taken here, yet I maintain that biological evidence must be privileged in biogeography. Certainly, as demonstrated here, taxonomy and taxonomic relations presumed in biogeographical analysis are theory-laden. The same applies to a priori presumed geographic areas. But the privilege of biology owes to a different factor altogether. Specifically, while geology and biogeographic patterning indeed provide critical and independent data for explaining/predicting particular plant distributions, geology and geographic patterns absolutely *never* have *determined* the distribution of any biological organism. They merely provide boundary conditions. Distributions are determined by the enactivity of the organisms themselves (Hershkovitz 2018c; cf. Maturana and Varela 1992; Varela et al. 1992; Maturana and Mpodozis 2000). Geographical survival and persistence of organisms is not chiseled into (fragmented) stone. Stones cannot force their will on organisms. The "choice" (*not* in a teleological sense) to live and reproduce in a particular location is made by the organism and not the location itself, much less statistics or ideology.

But Hershkovitz (2018a, b) also emphasized the precariousness of evolutionary reconstruction, hence the limitation biology consequently imposes on phylogeographic analysis. However complex is historical geological reconstruction, its processes seem to conform to linear stochastic physical models. Organismal evolution, in contrast, is a nonlinear idiosyncratic process (Hershkovitz 2018c). Modern patterns of Montiaceae phylogeographic distribution developed over the course of tens of millions of years of their biological evolution. Many biologically plausible evolutionary scenarios could generate their present forms and distributions, and no plausible scenario can be falsified unequivocally. Moreover, modern Montiaceae species diversification evidently transpired mainly during the Pliocene and continued up until the Pleistocene. The absence of fossils renders difficult the reconstruction of the morphology and ecology of Montiaceae ancestors between the time of their late Eocene (or earlier) origins and the Miocene/Pliocene. Yet, this unrecoverable history is critical to phylogeographic reconstruction. In phylogenetics, the very existence of these real but disembodied ancestors is reduced to a few sterile, abstract lines on a phylogram. Possibly the complexity of tens of millions of years of biological and terrestrial evolution is so mind-boggling that the mind short-circuits and reduces it conceptually to an instant and attempts to explain it correspondingly simplistically.

5. Synopsis of Subfamilial and Generic Taxonomy of Montiaceae

This work concludes with a summary of a subfamilial to subgeneric level taxonomy of Montiaceae, modified from Hernández-Ledesma et al. (2015) according to current phylogenetic evidence (see above). Each taxon comprises a clade. Numbers/letters in bold denote cladistic rank. Vertically aligned taxon names share cladistic rank. Rank suffixes, when applied, accord with conventional classification (McNeill et al. 2011). But, above the generic level, no conventional nomenclatural ranks are assigned per Cantino and De Queiroz (2007). Thus, missing conventional nomenclatural ranks can be assigned if so desired.

MONTIACEAE Raf.

1. **MONTIOIDEAE**
1A. **MONTIEAE**
1A1. **MONTIINAE**
1A1a. *Montia* L.

1A1b. *Claytonia* L.
1A2. *Lewisia* Pursh
1A3. *Lewisiopsis* Govaerts
1B. *Calandrinia* Kunth
1C. HECTORELLEAE Appleq., Nepokr. & W.L. Wagner
1C1. *Hectorella* Hook. f.
1C2. *Lyallia* Hook. f.
2. *Rumicastrum* Ulbrich
3. CISTANTHEAE Hershk.
3A. *Cistanthe* Spach
3B. *Montiopsis* Kuntze
3C. CALYPTRIDINAE Hershk.
3C1. *Calyptridium* Nutt. in Torr. & A. Gray
3C2. *Thingia* Hershk.
3C3. *Philippiamra* Kuntze
3C4. *Lenzia* Phil.
4. PHEMERANTHEAE Hershk.
4A. *Phemeranthus* Raf.
4B. *Schreiteria* Carolin

The taxonomy below elaborates the synopsis above to the subgeneric level and includes estimated species numbers, distributions, and relevant clarifications and commentary. Conventional ranks are retained at the subgeneric level, because these have somewhat greater application in practice than suprageneric taxa. Monophyly of species is not presumed nor generally in evidence.

MONTIACEAE Raf.

1. MONTIOIDEAE

1A. MONTIEAE

1A1. MONTIINAE

Historically, the generic taxonomy in this clade has been unstable and somewhat confusing, such that most species have homotypic synonyms in multiple genera (O'Quinn et al. 2005), and many in both *Claytonia* and *Montia*. Because taxonomic references are not self-correcting, the problem persists, e.g., in Marinho et al. (2019).

1A1a. MONTIA L., Sp. Pl. 1: 87. 1753. **TYPE**: *Montia fontana* L.

Claytonia sect. *Alsinastrum* Torr. & A. Gray, Fl. N. Amer. 1(2): 201. 1838.

Claytonia sect. *Naiocrene* Torr. & A. Gray, Fl. N. Amer. 1(2): 201. 1838.

Claytonia subsect. *Montiastrum* A. Gray, Proc. Amer. Acad. Arts 22: 283. 1887.

Crunocallis Rydb., Bull. Torrey Bot. Club 33: 139. 1906.

Naiocrene (Torr. & A. Gray) Rydberg, Bull. Torrey Bot. Club 33: 139. 1906.

Montiastrum (A. Gray) Rydberg, Fl. Rocky Mts. 265. 1917.

Claytonia sect. *Australiensis* Poelln., Repert. Spec. Nov. Regni Veg. 30. 1932.

Limnalsine Rydb., N. Amer. Fl. 21 (4): 25. 1932.

Mona Ö. Nillson, Bot. Not. 119: 266. 1966.

Neopaxia Ö. Nilsson, Bot. Not. 119: 469. 1966.

Maxia Ö. Nillson, Grana Palynol. 7: 359. 1967.

Claytoniella Jurtzev, Bot. Zhurn. (Moscow & Leningrad) 57: 644. 1972.

Ca. 19 annual and perennial (rooting at nodes) species; eight in W North America to NE Asia, one in N South America, seven in New Zealand, one in Australia, and one cosmopolitan (O'Quinn et al. 2005; Heenon 2007). How much of the range of the cosmopolitan *Montia fontana* is natural versus anthropogenic is not clear. Polymorphic, more than 30 heterotypic taxa are included in its synonymy (Tropicos.org 2018). Within the past 50 years, *Montia linearis* (Dougl. ex Hook.) Greene has expanded to lower elevations adjacent to its past native range and has become adventive in the central and eastern US and in Europe (Hershkovitz 1998a; Dembicz et al. 2015). *Montia parvifolia* is reportedly adventive in the UK (GBIF Secretariat 2017). *Montia chamissoi* is distributed mainly in W North America, but it has established more recently in midwestern and eastern US states (GBIF Secretariat 2017). Whether or not these occurrences are natural or anthropogenic is not clear. This species also is widely disjunct in S Mexico (GBIF Secretariat 2017).

O'Quinn et al. (2005) recognized three monophyletic sections based on molecular phylogenetic evidence. No attempt will be made here to list all of the synonyms implicated. The sections distinguish in pollen morphology.

1A1a1. M. sect. MONTIA

Ca. six species evidently originally of W North America, including the widespread *M. fontana*, and the apparently adventive *M. chamissoi* and *M. parviflora*. The species share pollen aperture membranes bearing a single row of projections.

1A1a2. M. sect. **AUSTRALIENSIS** (Poelln.) Pax & K. Hoffm., Die Natürlichen Pflanzenfamilien, ed. 2, 16c: 282. 1934. *Claytonia* sect. *Australiensis* Poelln., *Paxia* Ö. Nilss., *Neopaxia* Ö. Nilsson. **TYPE:** *Montia australasica* (Hook. f.) Pax & K. Hoffm. Synonyms: *Claytonia australasica* Hook. f. *Neopaxia australasica* (Hook. f.) Ö. Nilsson. *Paxia australasica* (Hook. f.) Ö. Nilsson.

Nine species, eight in Australia/New Zealand and one in NW North America and SW Canada. The species share pollen aperture membranes with 2–3 rows of projections.

1A1a3. M. sect. **MONTIASTRUM** (A. Gray) Pax & K. Hoffm. Die Natürlichen Pflanzenfamilien, ed. 2, 16c: 259. 1934. *Claytonia* sect. *Montiastrum* A. Gray. *Montiastrum* (A. Gray) Rydb.

TYPE: *Montia linearis* (Douglas ex Hook.) Greene. Synonyms: *Claytonia linearis* Douglas ex Hook., *Montiastrum lineare* (Douglas ex Hook.) Rydb.

Four species of NW North America and NE Asia, including the adventive *M. linearis*. The species share tholate pollen aperture membranes.

1A1b. CLAYTONIA L., Sp. Pl. 1: 204. 1753. *Claytonia* [unranked] *Euclaytonia* Walp., Repert. Bot. Syst. 2: 237. 1843 (*nom. inval.*). *Claytonia* [unranked] *Cormosae* A. Gray, Proc. Amer. Acad. Arts 22: 278. 1887. *Claytonia* sect. *Cormosae* A. Gray ex Poelln., Repert. Spec. Nov. **TYPE**: *Claytonia virginica* L.

Belia Steller ex S.G. Gmel., Fl. Sibir. 4: 88. 1769.

Limnia Haw., Syn. Pl. Succ. 11. 1812. *Claytonia* sect. *Limnia* (Haw.) Torr. & A. Gray, Fl. N. Amer. 1: 199. 1838. *Montia* sect. *Limnia* (Haw.) B.L. Rob., Syn. Fl. N. Amer. 1: 273. 1897. *Claytonia* subg. *Limnia* (Haw.) Holub, Preslia 47: 328. 1975.

Claytonia [unranked] *Caudicosae* A. Gray, Proc. Amer. Acad. Arts 22: 279. 1887.

Claytonia [unranked] *Rhizomatosae* A. Gray, Proc. Amer. Acad. Arts 22: 280. 1887. *Montia* [unranked] *Rhizomatosae* (A. Gray) B.L. Rob., Syn. Fl. N. Amer. 1: 272. 1897. *Claytonia* sect. *Rhizomatosae* (A. Gray) Poelln., Repert. Spec. Nov. Regni Veg. 30: 281, 296. 1932.

Claytonia sect. *Chenopodinae* Poelln., Repert. Spec. Nov. Regni Veg. 30: 280. 1932.

Ca. 33 species with ca. 20 additional recognized subspecific taxa, mostly in W North America and NE Asia, two extending to S Mexico and one to N Guatemala (O'Quinn et al. 2005; Miller & Chambers 2006; Stoughton et al. 2017a, b). *Claytonia sibirica* and *C. perfoliata* are adventive in Europe, Australia, and New Zealand, and the latter also in Argentina (Howell & Sawyer 2006; Miller & Chambers 2006; GBIF Secretariat 2017; Atlas of Living Australia 2018).

With a minor exception, subgeneric cladistic classification of *Claytonia* (O'Quinn et al. 2005) corresponds approximately to the classical classification according to life form (annual, rhizomatous, tuberous, caudiciform), except that the last two form a single undifferentiated clade. None of the three principal life form clades is paraphyletic with respect to any other. O'Quinn et al. (2005) recognized three sections; again, no attempt is made here to elaborate the synonymy. Discrepancies persist in the number of taxa recognized (O'Quinn et al. 2005; Miller & Chambers 2006; Stoughton et al. 2017a, b). The genus is known for variability in karyotype and ploidy.

1A1b1. CLAYTONIA sect. CLAYTONIA

Ca. 16 species plus 12 additional subspecific taxa; tuberous or tap-rooted caudiciform perennials. Although the two growth forms are conspicuously distinct morphologically, their genetic divergence is low, and evidently the tap-rooted form has evolved more than once or species having different growth forms have evolved reticulately (O'Quinn et al. 2005). Whole-genome DNA sequence sampling and analysis has revealed evidence of ancient hybridization and/or genetic lineage sorting among several species (Stoughton 2017a). Evidently, unclassifiable individuals are not uncommon. This section has the broadest climate niche of any Montiaceae taxon, ranging from

Siberia southwards along the cordillera to Mexico and then eastward to Atlantic and Gulf of Mexico states, and with a MAP gradient spanning ca. 5–5000 mm.

1A1b2. CLAYTONIA sect. **LIMNIA** (Haw.) Torr. & A. Gray, Fl. N. Amer. 1: 199. 1838. *Limnia* Haw., *Montia* sect. *Limnia* (Haw.) B.L. Rob. *Claytonia* subg. *Limnia* (Haw.) Holub. **TYPE:** *Claytonia sibirica* L. Synonyms: *Limnia sibirica* (L.) Haw. *Montia sibirica* (L.) Howell.

Ca. nine species plus eight additional subspecific taxa; annuals and two facultatively stoloniferous perennials. One species may behave as a winter annual (Miller & Chambers 2006; Hershkovitz 2017b). Reportedly, subspecific taxa of both the *Claytonia perfoliata* and *C. rubra* complexes intergrade, as do the two species complexes with each other (Miller & Chambers 2006, 2012b). Hybridization is suspected, but lineage sorting also emerges as a cause, especially given the frequency of polyploidy (cf. McIntyre 2012).

1A1b2. CLAYTONIA sect. **RHIZOMATOSAE** A. Gray ex Poelln., Repert. Spec. Nov. Regni Veg. 30: 281, 296. 1932. *Claytonia* [unranked] *Rhizomatosae* A. Gray., *Montia* [unranked] *Rhizomatosae* (A. Gray) B.L. Rob. in A. Gray & S. Watson. **TYPE:** *Claytonia sarmentosa* C.A. Meyer. Synonyms: *Montia sarmentosa* (C.A. Meyer) B.L. Rob. in A. Gray & S. Watson. *Limnia sarmentosa* (C.A. Meyer) Rydb.

Eight species, one annual and seven rhizomatous perennials. The perennials evidently are monophyletic (O'Quinn et al. 2005).

1A2. LEWISIA Pursh, Fl. Amer. Sept. 2: 360. 1813. **TYPE**: *Lewisia rediviva* Pursh.

Erocallis Rydberg, Bull. Torrey Bot. Club 33: 139. 1906.

Oreobroma Howell, Erythea 1: 31. 1893.

Ca. 18 perennial species plus six additional subspecific taxa of W North America, concentrated in California, extending into S Canada and NW Mexico (Hershkovitz & Hogan 2002; Wilson et al. 2005).

Limited molecular/phylogenomic data (Goolsby et al. 2018a, b; Hershkovitz, unpublished) evidence two major clades, one comprising *Lewisia* sect. *Cotyledon* excluding *L. congdonii*. The latter resembles species of this section morphologically, but its leaves are ephemeral like those of the remainder of the genus. The remaining species variously classified into several sections (Mathew 1989; Davidson 2000) also form a clade, but their interrelations remain unresolved and possibly are irresolvable cladistically. Thus, the genus is classified here into two subtaxa.

1A2a. LEWISIA sect. **LEWISIA**

At least 13 (likely more) perennial species plus one commonly accepted subspecific taxon (Hershkovitz & Hogan 2002; Wilson et al. 2005) of W North America, concentrated in California, extending into S Canada and NW Mexico. Taxonomy of the species varies markedly in various treatments, and no attempt is made here to resolve it definitively. Limited molecular/phylogenomic data (Goolsby et al. 2018a, b; Hershkovitz, unpublished) show no correspondence to any proposed sectional taxonomy of the included species. The data confirm the suspected historical complexity of plants conservatively classified as *L. pygmaea* by Hershkovitz & Hogan (2002). The species complex evidently is polyphyletic, but the limited data do not adequately investigate the degree of reticulate evolution likely in this genus, whose species manifest a considerable degree of interfertility (Mathew 1989; Davidson 2000). Available molecular/phylogenomic data indicate that *L. congdonii* is well-nested within this section. Its morphology hints that it may have an intersectional hybrid origin. Perennating structures of this section span the range observed in *Claytonia* sect. *Claytonia*, viz., ranging from deep, sinuous to shorter fusiform taproots to globose tubers.

1A2b. LEWISIA sect. **COTYLEDON** J.E. Hohn ex B. Mathew, The Genus *Lewisia*: 139. **LECTOTYPE** (designated here): *L. cotyledon* (S. Watson) B.L. Rob. in A. Gray. Synonyms: *Calandrinia cotyledon* S. Watson. *Oreobroma cotyledon* (S. Watson) J.T. Howell.

Excluding *L. congdonii*, this section comprises three allopatric species complexes and their variably recognized segregates/subtaxa, plus one interspecific hybrid taxon as follows: **(i)** *Lewisia cantelovii* J.T. Howell (incl. 2–3 subtaxa) of the east slope of the Sacramento River drainage in California; **(ii)** *L. cotyledon* (incl. 3–4 subtaxa) of the Klamath region in NW California, **(iii)** *L. columbiana* (Howell ex A. Gray) B.L. Rob. in A. Gray (incl. 3 subtaxa) of the Pacific NW US and SW British Columbia; and **(iv)** *L. leeana* (Porter) B.L. Rob. in A. Gray of the Klamath region, with an outlying population in central California. The last is believed to be a hybrid between *L. columbiana* and *L. cotyledon*. Subtaxa of the *L. cotyledon* complex are sympatric/parapatric and intergrading. Those of the other two complexes are distinct geographically and morphologically, hence species designation is defensible. Their subspecific status owes to their geographic restriction, rarity, and taxonomic inertia. In terms of biodiversity accounting, regardless of taxonomic preference, I prefer to think of *L.* sect. *Cotyledon* as comprising eight species plus two additional subspecific taxa (two of the three *L. cotyledon* subtaxa).

1A3. LEWISIOPSIS Govaerts, World Checkl. Seed Pl. 3(1): 21. 1999. *Lewisia* subg. *Strophiolum* J.E. Hohn ex B. Mathew, The Genus *Lewisia* 139. 1989. *Cistanthe* sect. *Strophiolum* (J.E. Hohn ex B. Mathew) Hershk., Phytologia 68: 268. 1990. **TYPE**: *L. tweedyi* (A. Gray) Govaerts. Synonyms: *Calandrinia tweedyi* A. Gray. *Lewisia tweedyi* (A. Gray) B.L. Rob. in A. Gray. *Cistanthe tweedyi* (A. Gray) Hershk.

One perennial species of central Washington State, USA, extending into southernmost British Columbia, Canada (Mathew 1989; Davidson 2000).

On morphological evidence, Hershkovitz (1990a, b, 1991a, 1992, 1993a) transferred this taxon from *Lewisia* (Mathew 1989; Davidson 2000) to *Cistanthe*, later retreating from this position based on molecular evidence (Hershkovitz & Zimmer 1997, 2000; Hershkovitz 2006). Hershkovitz (2018a) cites molecular evidence that *Lewisiopsis* originated as a hybrid between early divergent ancestors of *Lewisia* and Montiinae, followed by polyploidization and sequestering of further evolutionary change. This, in turn, explains phenotypic similarities between *Lewisiopsis* and *Cistanthe*.

1B. CALANDRINIA Kunth (*nom. cons.*), Humb., Bonpl. & Kunth, Nov. Gen. Pl. (fol. ed.) 6: 62. 1823. **TYPE**: *C. ciliata* (Ruiz & Pav.) DC. (*nom. cons.*). Synonym: *Talinum ciliatum* Ruiz & Pav.

Cosmia Dombey ex Juss., Gen. Pl. 312. 1789., *obs.*

Baitaria Ruiz & Pav., Fl. Peruv. Prodr. 63. 1794.

Tutuca Molina, Sag. Stor. Nat. Chile, ed. 2. 135. 1810.

Geunsia Moc. & Sessé ex DC, Prodr. 3: 358. 1828, *nom. inval.*

Phacosperma Haw., Philos. Mag. Ann. Chem. 2 (1): 123. 1827.

Monocosmia Fenzl, Nov. Stirp. Dec. 84. 1839.

? *Diazia* Phil., Fl. Atacam. 22. 1860.

Ca. 17 annual and perennial herbaceous species of W North America and W South America (Hershkovitz 2006; Peralta & Ford-Werntz 2008; Elvebakk et al. 2015).

The genus *Tutuca* Molina is recognized here as a synonym of *Calandrinia* based on its original characterization and illustration in Feuillée (1725). The sole species, *T. chilensis* Molina, likely is *C. compressa* Schrad. ex DC. A subsequently published name, *T. fistulosa* Molina, evidently refers to this same type and is superfluous (cf. Gunckel 1972). Hooker and Arnott (1833,1841 [1830]) included "*Tutuca* Feuillée" in synonymy with (effectively) *Calandrinia compressa*, and Philippi (1867) shared this opinion. Gunckel (1972) (mis-)identified *Tutuca chilensis*/*fistulosa* as *Senecio fistulosa* (Molina) Poeppig ex Lessing. The International Plant Names Index (2012) erroneously refers *Tutuca* to Ericaceae.

Hershkovitz (2018a) classified *Diazia* as incertae sedis. Since that work was posted, I obtained and examined an image of the supposed type specimen, *Diaz 87* (SGO!), and found that I had annotated it in 1992 as *Calandrinia ciliata* (Ruiz and Pav.) DC. Indeed the specimen itself pertains to *Calandrinia*, but the identity of the specimen with the type of *Diazia* was questioned in a prior annotation by Rebecca Acevedo. Carolin (1993) included *Diazia* in *Philippiamra* as circumscribed below.

The current cladistic circumscription of *Calandrinia* was proposed in Hershkovitz (1990b), based on intuitive interpretation of morphology. The circumscription differed from the previous (and first) cladistic circumscription (Carolin 1987, 1993), which classified the annual species in this genus, but classified the perennial species in *Baitaria*, along with all species of *Montiopsis*. Monophyly of the current circumscription has been confirmed by all six subsequent molecular analyses cited in this work, including Hancock et al. (2018), who proposed a different circumscription (see below).

Calandrinia s. l. is an example of a classical so-called "evolutionary" taxon. These were conceptually fundamentally Aristotelian (Scala Natural) in that taxa were conceived hierarchically according to their perceived degree of evolutionary specialization. "Higher" or "advanced" taxa emerged from "lower" or "primitive" taxa (e.g., "lower vascular plants"), the latter cladistically paraphyletic. Segregation of perceptually specialized advanced taxa left taxonomic receptacles to which were relegated more perceptually primitive taxa. *Calandrinia* s. l. was such a receptacle. It was not, nor intended to embody, a monophyletic taxon. It was the receptacle for largely western American and Australian species with most or all of the following traits: hemicryptophytic herbs, hypogynous flowers, conspicuous corolla of five petals, five-plus stamens, three carpels, and a basipetally dehiscent valvate capsule with many seeds. Otherwise, the species were morphologically heterogeneous and classified into 12 American and six Australian sections (Carolin 1987, 1993). The traits delimiting *Calandrinia* s. l. were not good indicators of relationship. For example, achenial species segregated into other genera and even classified in different classical tribes (McNeill 1974) proved to be otherwise morphologically and genetically very closely related to certain *Calandrinia* s. l. species (Hershkovitz 1993a, 2000, 2006).

Apparent taxonomic confusion following the cladistic dissection of *Calandrinia* s. l. owes to several factors. One was the historical fact that, at the time, much, if not most, of the plant taxonomic community did not embrace or yet understand the emerging paradigm of cladistics and/or the logic of cladistic taxonomy. Many subsequent research and reference works continued to apply the classical classification.

Another factor was the failure to appreciate that the cladistic realignments divided *Calandrinia* s. l. along existing taxonomic lines. While the sectional taxonomy per se was not cladistic, cladistic partitions coincided with groups of sections. The morphological distinctions between these groups of sections are unambiguous. In fact, the distinctions between these groupings are less ambiguous than the distinctions between *Calandrinia* s. l. and other classical genera. However, in scientific practice, taxonomy emphasizes only genus and species and not intervening ranks. Thus, non-specialists were unfamiliar with the sectional taxonomy, and the cladistic generic classification seemed arbitrary, if not incomprehensible.

Another factor was "taxonomic provincialism." Regional floristic taxonomists historically tended to perceive, hence classify, new taxa in a local rather than global context. Sometimes, workers simply were unfamiliar with global diversity of local genera. For example, a few species of South American and Australian Montiaceae described as *Calandrinia* s. l. proved to be species of *Phemeranthus*, *Talinum* (Talinaceae), or *Anacampseros* (Anacampserotaceae). But regional specialists classified them in the regionally predominant *Calandrinia* s. lato.

A final exacerbating factor may have been the long delay in transferring species to their new genera. Roger Carolin had prepared but never published catalogs of binomial recombinations according to his cladistic classification. These catalogs recombined *all* existing typified binomials, whether or not the corresponding species were taxonomically accepted. I believed that half or more of these recombinations effectively created new taxonomic synonyms. But as I was primarily a higher taxon specialist, I urged my species taxonomy specialist colleagues to assume the recombination effort. For reasons articulated above, the process was delayed for several years. For my part, I had recombined binomials only as necessary to refer to the corresponding (often misidentified) species in my phylogenetic work and, in Hershkovitz (2006), not even then. Consequently, the taxonomy, especially of *Cistanthe*, persisted in a chaotic state, a haphazard mixture of new and old binomials and misidentifications. Naturally, this did not aid in appreciation of the cladistic generic distinctions. In retrospect, Carolin's unilateral shotgun approach was the more prudent.

1B1. CALANDRINIA sect. CALANDRINIA

Calandrinia sect. *Compressae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Axillares* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Monocosmia* (Fenzl) Hershk., Phytologia 70: 223. 1991.

Ca. eight annual species native to western America, distributed along the American cordillera nearly from British Colombia to SW USA and NW Mexico, central Mexico to the Central Andes of N Argentina (except Panama), Buenos Aires Province in Argentina, throughout all but the southernmost

ChFR, and one species possibly native to the Falkland Islands (Hershkovitz 2006; Peralta & Ford-Werntz 2008). *Calandrinia menziesii* is adventive on other continents/islands (Hershkovitz 2006). Most recently it has been collected several times in central Louisiana (GBIF Secretariat 2017), but I am unable to determine whether it is established there. *Calandrinia compressa* has been collected in Europe (GBIF Secretariat 2017), but its establishment status reports are conflicting. Possibly the reports reflect transitory escapes from cultivation. The species is established, however, in New Zealand (Howell & Sawyer 2006). At least one undescribed species occurs in Patagonia, but revision of these taxa is not undertaken here.

Five molecular phylogenetic analyses (Hershkovitz & Zimmer 2000; Hershkovitz 2006; Ogburn & Edwards 2015) indicate that this section is monophyletic, but a more recent phylogenomic analysis (Goolsby 2018a, b) shows this section as paraphyletic with respect to the perennial clade, *C.* sect. *Acaules*, with the annual *C. nitida* (synonym: *C. axilliflora*) as sister to the latter. Hershkovitz (1993a) suggested the reverse relation, with the perennials paraphyletic to the annuals. Interestingly, however, *C. nitida* was cited as the morphologically transitional taxon.

1B2. CALANDRINIA sect. **ACAULES** Reiche, Ber. Deutsch. Bot. Ges. 15: 500. 1897. *Baitaria* Ruiz & Pav. **LECTOTYPE** (designated here): *C. acaulis* Kunth.

Ca. 11 perennial species plus one variety of W South America, mostly of the ChFR, two species of the Central Andes, one extending to Central America and southern Mexico (Hershkovitz 2006; Peralta & Ford-Werntz 2008; Elvebakk et al. 2015).

All molecular/phylogenomic analyses cited in this work indicate that this section is monophyletic (see above). Taxonomy of the central Andean plants (Argentina, Bolivia, Chile, and Peru) remains problematic. Hershkovitz & Ford[-Werntz] (1993) renamed *Baitaria acaulis* Ruiz & Pav. as *Calandrinia carolinii* Hershk. & D.I. Ford. The type collection is mixed and includes individuals identified as *Calandrinia acaulis* Kunth. But Hershkovitz & Ford[-Werntz] (1993) did not resolve definitively the taxonomic identity of *C. carolinii*. Peralta & Ford-Werntz (2008) applied the name *C. carolinii* to plants distinct from *C. acaulis*.

1C. HECTORELLEAE Appleq., Nepokr. & W.L. Wagner, Syst. Bot. 31: 316. 2006. **TYPE:** *Hectorella* Hook. f.

1C1. HECTORELLA Hook. f., Handb. N. Zeal. Fl. 27.1864. **TYPE**: *Hectorella caespitosa* Hook. f. Synonym: *Lyallia caespitosa* (Hook. f.) Nyanyano & Heywood.

One perennial species of New Zealand (Applequist et al. 2006; Wagstaff & Hennion 2007).

1C2. LYALLIA Hook. f., Bot. Antarct. Voy. Antarct. (Fl. Antarct.) 2: 548, t. 122. 1847. **TYPE**: *Lyallia kerguelensis* Hook. f.

One perennial species of the Kerguelen Islands (Applequist et al. 2006; Wagstaff & Hennion 2007).

2. RUMICASTRUM Ulbrich, Engler & Prantl, Nat. Planzenfam. 16c: 519. 1934. **TYPE**: *Rumicastrum chamaecladum* (Diels) Ulbrich. Synonym: *Atriplex chamaecladum* Diels

Calandrinia sect. *Apicales* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Basales* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Tuberosae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Partitae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Pseudo-dianthoideae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Calandrinia sect. *Uniflorae* Poelln., Repert. Spec. Nov. Regni Veg. 35. 1934.

Parakeelya Hershk., Phytologia 84: 101. 1999 [1998].

About 74 annual and perennial species from throughout Australia, about 25 not yet described (Hancock et al. 2018; Thiele et al. 2018). All described species except *R. chamaecladum* (Diels) Ulbrich commonly remain classified *Calandrinia*. Most have combinations in *Parakeelya* (Hershkovitz 1998b, 2002; Thiele et al. 2018).

Hancock et al.'s (2018) analysis reveals partial agreement between phylogeny and classical sectional divisions, but also ambiguous relations in portions of the tree. The work also shows that perenniality evolved 2–3 times in this genus with no reversals.

Thiele et al. (2018) published a proposal to conserve the generic name *Parakeelya* [lectotype: *P. ptychosperma* (F. Muell.) Hershk.; synonym: *Calandrinia ptychosperma* F. Muell.] against *Rumicastrum*. Seddon (2005) described how he first diagnosed *Rumicastrum chamaecladum* (Diels) Ulbrich (synonym: *Atriplex chamaeclada* Diels) as a species of *Calandrinia* s. l. and not, as it had been classified, Chenopodiaceae. The latter classification owes, no doubt, to the fruit, which is achenial rather than capsulate. A fruiting specimen, lacking the ephemeral perianth and stamens and enclosed by its two sepals, indeed would resemble a female *Atriplex* flower, atepalous and enclosed by two deltoid bracts. Roger Carolin corroborated the finding (Carolin 1987, 1993; Seddon 2005) and thus planned to transfer all Australian species of *Calandrinia* s. l. to *Rumicastrum*, and he drafted a manuscript accordingly. He retired in 1986 and sent me a copy of this manuscript.

In my work (e.g., Hershkovitz 1993a), I trusted Carolin's diagnosis of *Rumicastrum*. But I had no need for a taxonomic combination in this genus until submitting my molecular phylogenetic analysis of cactus origins (Hershkovitz & Zimmer 1997) for publication. In the original journal submission, I provided a new combination for the sampled species in *Rumicastrum*. However, the journal editor, Werner Greuter (B), disputed this classification. Although the type specimen is believed to have been destroyed, he insisted that a conspecific specimen in B was "perfectly good Chenopodiaceae" and had "nothing whatsoever to do with Portulacaceae." Greuter, therefore, would not permit me to apply the name *Rumicastrum* in my publication.

I had had no means of verifying Greuter's claim, but I could not delay this publication in order to resolve a peripheral taxonomic question. Therefore, I applied a new generic name, *Parakeelya*. I learned recently that this is the same name Carolin planned to use before diagnosing the identity of *Rumicastrum* (Seddon 2005). In 1999 (nearly 20 years ago), Judy West (CANB) advised me (among other people) that Carolin's diagnosis was correct, and that I had erred in erecting the genus *Parakeelya*.

Judy West and other knowledgeable Australian botanists now long have agreed that *Rumicastrum chamaecladum* is an Australian species of classical *Calandrinia* s. l., and that transfer of the remaining species was inevitable, e.g., (Richardson 1998). But they continued to classify the species in the genus *Calandrinia* – all except for one: *Rumicastrum chamaecladum*, for which no such combination in *Calandrinia* existed and none was proposed. Instead, between 2006–2017, 13 new species were described as *Calandrinia* (Obbens 2006, 2012; Syeda & Carolin 2011; West & Chinnock 2013; Obbens et al. (2017). The generic concept of *Calandrinia* in these works is not clear. Syeda & Carolin (2011) described the genus as comprising "about 100 species." At that time, there were perhaps about 55 recognized species in *Calandrinia* and *Rumicastrum* combined. The inclusion of Carolin as author was surprising, since he had advocated *Rumicastrum*. Carolin himself does not appear to have pronounced on the matter since his 1993 synopsis (Carolin 1993), which was prepared before his retirement in 1986.

Hancock et al. (2018) circumscribed *Calandrinia* as comprising this genus sensu Hershkovitz (1993a) plus *Rumicastrum*. This circumscription, which the same work rejects, appears to be *ad hoc*. It has no precedent and was not supported (though not unequivocally refuted) by prior evidence (e.g., Applequist et al. 2007; Ogburn & Edwards 2015). Hancock et al. (2018) argued that existing evidence did not prove that *Rumicastrum* was not sister to *Calandrinia*. A sister relation would justify, on phylogenetic taxonomic criteria, the continued classification of *Rumicastrum* species as *Calandrinia*. Another possibility was that the peculiar *R. chamaecladum* would figure outside of this clade. Hancock et al. (2018) rejected both possibilities.

Hancock et al. (2018) evidently knew that their ad hoc circumscription of *Calandrinia* was not monophyletic and that *Rumicastrum* was the correct name for the Australian plants. But they preferred to not apply the name *Rumicastrum*, seeking instead to conserve the name *Parakeelya*, (Thiele et al 2018), which, pending proposal resolution, remains incorrect. Unable to use *Parakeelya* and unwilling to use *Rumicastrum*, they continued to use *Calandrinia*. It is for this reason that the authors committed themselves to an a posteriori ad hoc circumscription of *Calandrinia* that they knew a priori was incorrect.

But even if these genera indeed form a clade, existing molecular evidence indicate that strong support was unlikely. Moreover, their demonstrated morphological, genetic, and biogeographic divergence rendered senseless, even misleading, their merging. To appreciate this, had the Australian plants been described initially as a new genus (and never classified in *Calandrinia* s. l.), there would seem to have been no reasonable basis (or motive) for then merging said genus with *Calandrinia*, even if the resulting genus were monophyletic, and much less so in a paper that proved that the thusly merged genus is not monophyletic.

The preceding clarified, the importance of Hancock et al. (2018) and their collaborators' research cannot be understated. Study of this genus had been badly neglected, as evidenced by the large number of new species described and predicted. Aside from their value in study of succulence, several species have ornamental value, especially with the trend towards water conserving garden plants.

3. CISTANTHEAE Hershk., **tax. nov. LECTOTYPE** (designated here): *Cistanthe* Spach.

3A. CISTANTHE Spach, Hist. Nat. Veg. 5: 229. 1836. **LECTOTYPE** (designated here): *Cistanthe grandiflora* (Lindl.) Schltdl. Synonym: *Calandrinia grandiflora* Lindl. (*nom. cons.*).

Tegneria Lilja, Fl. oefver Sver. Odl. Vext.76. 1839. **LECTOTYPE** (designated here): *Tegneria discolor* (Schrad.) Lilja. Synonyms: *Calandrinia discolor* Schrad. *Cistanthe discolor* (Schrad.) Spach. *Rhodopsis discolor* (Schrad.) Lilja. Lectotypification here of *Tegneria* Lilja is for clarification. Lilja (1841) included in this genus *Calandrinia discolor* Schrad. and, apparently erroneously, *Calandrinia speciosa* Lindley, 1833, *nom. illegit.* [synonyms: *Calandrinia elegans* Spach. *Calandrinia menziesii* (Hook.) Torr. & A. Gray. *Cistanthe speciosa* Lilja ex Heynh. (cf. Reiche 1897, 1898; Rydberg 1928.] and not *Calandrinia speciosa* Lehm., 1831. It is the latter that pertains to *Cistanthe*, hence *Tegneria.* Lilja evidently did not appreciate that the homonymous plants were distinct (see Steudel 1840: *253*; cited by Lilja 1841). Thus, the lectotypification here establishes that *Tegneria* (hence *Rhodopsis* Lilja) are taxonomic synonyms of *Cistanthe* and not *Calandrinia*. Peralta & Ford Werntz (2008) and Hershkovitz (2018a) erroneously used the combination "*Cistanthe speciosa* (Lehm.) Lilja ex Heynh." as a synonym for *Calandrinia speciosa* Lehm. This combination does not exist. Adding further confusion is an additional homonym, *Calandrinia speciosa* Hooker, 1835, *nom. illegit.* Taxonomically, this plant is *Cistanthe laxiflora* (Phil.) Peralta & Ford-Werntz.

Rhodopsis Lilja, Fl. Sverig. Suppl. 1: 42. 1840.

At least 38 species of succulent annual and perennial herbs, a few perennials being suffruticose/pachyform, of the ChFR (Chile, 18S–40S, Argentinean Andes, southern coastal Peru), with two species in SW North America (Ford[-Werntz] & Peralta 2002; Peralta & Ford-Werntz 2008; Hershkovitz 2018a).

Current acceptance of the generic segregation of *Cistanthe* from *Calandrinia* s. l. stems from Carolin's (1987, 1993) work. Combinations for these taxa transferred from *Calandrinia* s. l. are provided in Hershkovitz (1991b), Ford-Werntz & Peralta (2002), and Peralta & Ford-Werntz in Zuloaga et al. (2007) and below.

The current cladistic circumscription of *Cistanthe* was proposed in Hershkovitz (2006), based on molecular analysis. This work demonstrated that the circumscriptions of Carolin (1987, 1993) and (Hershkovitz 1990a, 1991a, 1992, 1993a), based on morphology, were paraphyletic. Ogburn & Edwards (2015) subsequently confirmed paraphyly of the 1990 circumscription. They did not note that their circumscription of *Cistanthe* was identical to Hershkovitz (2006).

Hershkovitz (2018a) considers that current molecular evidence demonstrates that the numerous morphological similarities shared among sections of the paraphyletic *Cistanthe* in the Hershkovitz (1990a) circumscription are symplesiomorphies, not convergences. This is supported by low genetic divergence among these taxa. Thus, these shared traits appear to reflect morphology prevalent in among "paleomonts," from which other genera have diverged markedly.

Taxonomy of *Cistanthe* remains problematic. The most recent and most comprehensive taxonomic treatment is Reiche (1898), which is more than 120 years old, and covers only the Chilean species. It was based substantially on work of Philippi, especially Philippi (1893a, b). Reiche (1898) clearly was frustrated by this genus, combining diverse related forms as polymorphic species and manifesting uncertainty regarding the status of others. Also, numerous species have been described since Reiche's (1898) treatment.

The taxonomic difficulty is understandable. The plants are succulent and, unless carefully prepared, make poor herbarium specimens. Especially older collections, including type specimens, often are degraded and/or fragmentary and incomplete. Another problem is that most described species are endemic to the arid zone of Chile, especially between Regions II–IV. Because of the ENSO effect, periodicity of rains ranges from about 10 years to almost literally forever. This renders difficult plant exploration across this 1000 km tract. Moreover, species distributions in this area behave differently from areas of denser vegetations, which create local biotic communities and niches. Also, the stressful environment presumably induces mutation, such that odd phenotypes might be collected once and never again. The principal constraint on growth is not so much morphological phenotype as it is adequacy of moisture in the location where a seed happens to germinate. Finally, the strong moisture gradients across relatively short distances probably creates an unusual germplasm pool. In particular, in especially rainy years decades apart, the emerging plants represent correspondingly separated generations. Over historical time, the generational difference between plants emerging in a single wet year can accumulate to thousands or more years.

Hershkovitz (2018a) discussed in greater detail the taxonomy of the Chilean species. This discussion is not repeated here; it will be the subject of a spin-off work that revises and corrects errors in the account in Hershkovitz (2018a).

3A1. CISTANTHE sect. **CISTANTHE**. *Calandrinia* sect. *Cistanthe* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897.

At least 10 and perhaps 12 species of the ChFR, all but one perennial, primarily in Chile, one extending into San Juan Province, Argentina, and two endemic to Peru (León 2006; Peralta & Ford-Werntz 2008; Hershkovitz 2018a, d).

Circumscription of this section corresponds almost completely to Reiche's (1898), except that Reiche referred *Cistanthe cachinalensis* (Phil.) Peralta and D.I. Ford [in my opinion, conspecific with *C. grandiflora* (Lindl.) Schlect] to his *Calandrinia* sect. *Rosulatae* (Hershkovitz 2018d). Smith et al. (2017) and Hancock et al. (2018) demonstrated that the Peruvian *C. paniculata* (Ruiz & Pav.) Carolin ex Hershk. pertains to this section. Some taxonomically necessary combinations are lacking and provided here. As in Hershkovitz (1990a, 1991b), I attribute authorship to Roger Carolin, based on an unpublished manuscript he sent me in 1986. This recognizes especially Carolin's contribution to modern Montiaceae taxonomic and phylogenetic concepts.

For expedience, I provide below taxonomically necessary combinations per Hershkovitz (2018a).

CISTANTHE AEGITALIS (F. Phil.) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia aegitalis* F. Phil., Anales Univ. Chile 85: 184. 1893. **LECTOTYPE**: **CHILE. Region IV**. Limarí Province: "Fray Jorge, litt. maris," *F. Philippi s.n.* (SGO!).

CISTANTHE CRASSIFOLIA (Phil.) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia crassifolia* Phil., Anales Univ. Chile 85: 180. 1893. **LECTOTYPE**: **CHILE. Region III**. Huasco Province: Carrizal, *F. Philippi s.n.* (SGO!).

CISTANTHE MUCRONULATA (Meyen) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia mucronulata* Meyen, Reise Erde 1: 314. 1834. **TYPE**: not located. The species was described from Chile, Region VI, Colchagua Province, in the vicinity of San Fernando. Only one species of the section grows in that region, so its identity is not in doubt.

3A2. CISTANTHE sect. **ROSULATAE** (Reiche) Hershk., **comb. nov.** Basionym: *Calandrinia* sect. *Rosulatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897. **LECTOTYPE** (designated here):

Cistanthe longiscapa (Barnéoud) Carolin ex Hershk. Synonym: *Calandrinia longiscapa* Barnéoud.

Calandrinia sect. *Arenarie* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Andinae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

At least 26 annual and perennial species, primarily of the ChFR, mainly Chile, four extending into Argentina (Peralta & Ford Werntz 2008; Hershkovitz 2018a), one primarily in Peru but now collected in Chile, one endemic to Peru (León 2006), and two in SW North America (Hershkovitz 1991a). I have collected but not described five forms that probably represent distinct species.

Taxonomy of *C.* sect. *Rosulatae* species is woefully inadequate, especially for reasons cited above. Also, I have observed in the field three "smoking gun" cases of interspecific hybridization, i.e., where the distinct parental species and their hybrid offspring occur together (Hershkovitz 2006 and unpublished observations).

Hershkovitz' (2006) analysis indicates that *C.* sect. *Rosulatae* comprises two clades, which are recognized here as subsections.

3A2a. CISTANTHE sect. ROSULATAE (Reiche) Hershk. subsect. ROSULATAE, subsect. nov.

Based on Hershkovitz (2006), the discussion above, and personal communication from other researchers, I estimate that there are at least 20 species in this subsection. It includes all species of Reiche's (1897, 1898) *Calandrinia* sect. *Andinae*. These species are mainly Chilean, with a few extending into Argentina. This section also includes several species pertinent to Reiche's *Calandrinia* section *Rosulatae* and all species pertinent to section *Arenarie*. Into the former, Reiche (1898) included *Calandrinia longiscapa* Barnéoud [synonym: *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk.], "pata de guanaco;" the most conspicuous species that essentially defines the Atacama Desert's occasional "desierto florido" phenomenon.

Hershkovitz (2018a) described taxonomic problems in *C.* sect. *Rosulatae* subsect. *Rosulatae*, in particular consequent to his assertion that *Cistanthe arenaria* (Cham.) Carolin ex Hershkovitz is a perennial herb of south-central Chile, rather than, as had been believed, an annual species of north-central Chile. This, in turn, creates havoc with the taxonomy of the many annual forms that commonly are classified as *C. arenaria*.

The discussion in Hershkovitz (2018a) will be elaborated and corrected in a separate work. For expedience, necessary recombinations are provided below.

CISTANTHE CHAMISSOI (Barnéoud) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia chamissoi* Barnéoud in Gay, Fl. Chil. 2(4): 497–498. 1846 [1847]. Synonym: *Calandrinia arenaria* Cham. var. *chamissoi* Reiche, Fl. Chile 2: 346. 1898 and An. Univ. Chile 100: 350. 1898. **LECTOTYPE** (designated here): **CHILE. Region V**. Quillota Province. Quillota: "in petrosis sterilibus calidisque collium," *Bertero 1348,* (G: G440496, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303418&lang=en> [image!]. **ISOTYPES**: G: G440495, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303417&lang=en> [image!], G440494, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303416&lang=en> [image!], P!, P01903300, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p01903300> [image!]). **SYNTYPE**: **CHILE. Region V**. Cachapoal Province. Rancagua. *Bertero 683* (P! P01903301,

<http://coldb.mnhn.fr/catalognumber/mnhn/p/p019033001> [image]. NOTE: *Bertero 683* evidently is a mixed collection that includes the type of *Talinum trigonum* Colla (see below).

CISTANTHE OBLONGIFOLIA (Barnéoud) Carolin ex Hershk., **comb. nov.** Basionym: *Calandrinia oblongifolia* Barnéoud in Gay, Fl. Chil. 2(4): 482–483. 1846 [1847]. **HOLOTYPE**: **CHILE. Region IV**. Elqui Province. Llanos de Guanta: "croissant dans les endroits sablonneauxde cordilleres," *Gay 316* (P! <http://coldb.mnhn.fr/catalognumber/mnhn/p/p019033008>).

CISTANTHE TRIGONA (Colla) Hershk., **comb nov.** Basionym: *Talinum trigonum* Colla, Mem. Realle Accad. Torino 37: 71. 1834. **TYPE**: **CHILE. Region VI**. Cachapoal Province. Rancagua: "in arenososque secus flumen Cachapual," *Bertero 683* (isotypes: G, G00440471, G00440472, G00440473, G00440474, <http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=303323&lang=en> [etc.; images!]). **NOTE**: *Bertero 683* evidently is a mixed collection that includes a syntype of *Calandrinia chamissoi* Barnéoud (see above). The G sheets are annotated by I. Peralta (MERL) as isotypes, but I have not located a specimen designated as a holotype or lectotype.

CISTANTHE VICINA (Phil.) Carolin ex Hershk., **comb. nov**. Basionym: *Calandrinia vicina* Phil., Anales Univ. Chile 85: 301. 1893. Synonym: *Calandrinia arenaria* Cham. var. *vicina* (Phil.) Reiche, Fl. Chile 2: 346. 1898 and An. Univ. Chile 100: 350. 1898. **Holotype**: **CHILE. Region Metropolitana.** Santiago Province. Renca Municipality: Cerro Renca, *Philippi s.n.* (SGO!).

3A2b. CISTANTHE sect. ROSULATAE (Reiche) Hershk. subsect. THYRSOIDEAE Hershk., subsect. nov.

LECTOTYPE (designated here): *Cistanthe thyrsoidea* (Reiche) Peralta and D.I. Ford. Synonym: *Calandrinia thyrsoidea* Reiche, Fl. Chile 2: 342. 1898 and An. Univ. Chile 100: 342. 1898.

Five annual and one perennial species, including the Chilean *C. thyrsoidea* and *C. cephalaphora* (I.M. Johnst.), the North American *C. guadalupensis* and *C. maritima*, and probably the Peruvian *C. lingulata* (Ruiz & Pav.) Hershk. and *C. weberbaueri* (Diels) Carolin ex Hershk.

This section includes the remaining unaccounted species of Reiche's (1898) *Calandrinia* sect. *Rosulatae* except *C. cachinalensis* (see above). Monophyly of the subsection is documented in Hershkovitz (2006). Inclusion of *C. guadalupensis* is based on inspection of an ITS sequence in Genbank (FJ614057.1). In the range of ITS1 base positions 70–80, all samples of this clade share a five-base motif, "C]TCCCT[C." This aligns with a three-base motif, "C]-CTC-[C," shared by all other samples of both sections of *Cistanthe*. I refer *C. lingulata* and *C. weberbaueri* to this clade based on morphological resemblance to *C. thyrsoidea*.

The South American species are relatively small herbs with very small flowers, and I have observed cleistogamy in *C. thyrsoidea*. The North American species have larger and showier flowers, and *C. guadalupensis* is a pachycaul shrub.

3B. MONTIOPSIS Kuntze, Rev. Gen. Pl. 3(2): 14. 1898.

TYPE: *Montiopsis boliviana* Kuntze. Synonyms: *Calandrinia cumingii* Hook. & Arn., *Montiopsis cumingii* (Hook. & Arn.) D.I. Ford.

Ca. 18 annual and perennial species of the ChFR, primarily in Chile, several extending into Argentinean Andes, one annual extending also into the Central Andes in Bolivia (Ford 1992; Peralta & Ford-Werntz 2008).

Hancock et al.'s (2018) 297-loci phylogenomic analysis confirms the results of Ogburn & Edwards (2015) in placing *Montiopsis* within Cistantheae. The relations of *Montiopsis* were unresolved in Hershkovitz (2006). Interestingly, Hancock et al.'s (2018) Bayesian analysis of phylogenetic concordance among loci showed significant residual support for monophyly of *Cistanthe* with Calyptridinae, as in morphological analyses of Carolin (1987) and Hershkovitz (1991a, 1993a). I hypothesize that this residual support reflects loci related to the morphological similarities of these taxa.

Hershkovitz' (1993a) cladogram shows *Montiopsis* as sister to *Calandrinia*. However, he noted that this was supported only by the shared presence of trichomes, and that the trichomes were structurally very different. He also noted the gross similarity between the acaulescent *Montiopsis* (subg. *Dianthoideae*) *cistiflora* (Gillies ex Arn.) D.I. Ford and species of *Calandrinia* sect. *Acaules*. The former has a 1–3-flowered axillary inflorescence, and the latter are 1-flowered, although I have seen a rudimentary second flower on a single specimen of *Calandrinia acaulis*. However, Hershkovitz (1993a) noted that inflorescence development and form of *Montiopsis* (bostryx or botryoid) otherwise was distinct from *Calandrinia* (solitary/axillary and so-derived) and *Cistanthe* (cincinnoid). Thus, current molecular evidence confirms that the distinctive morphology of *Montiopsis* reflects its marked evolutionary divergence, as evident in branch lengths in molecular phylograms of Hancock et al. (2018).

3B1. MONTIOPSIS subg. MONTIOPSIS

Calandrinia sect. *Hirsutae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.

Calandrinia sect. *Condensatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 503. 1897.

Calandrinia sect. *Parviflorae* Reiche, Ber. Deutsch. Bot. Ges. 15: 503. 1897.

Calandriniopsis Franz, Bot. Jarhb. Syst. 42, Beibl. 97: 19. 1908.

Ca. 15 annual and perennial species, of the ChFR, primarily in Chile, several extending into Argentina, one extending also into Bolivia (Ford 1992; Peralta & Ford-Werntz 2008).

Existing molecular data show (Hershkovitz 2006) show no phylogenetic structure among these species.

3B2. MONTIOPSIS subg. DIANTHOIDEAE (Reiche) D.I. Ford, Phytologia 74: 277. 1993. *Calandrinia* sect. *Dianthoideae* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897. **LECTOTYPE**: *Montiopsis cistiflora* (Gillies ex Arn.) D.I. Ford. Synonym: *Calandrinia cistiflora* Gillies ex Arn.

At least three perennial species of the ChFR, apparently all three in Chile and the adjacent Argentinean Andes (Ford 1992: Peralta & Ford-Werntz 2008).

Molecular evidence (Hershkovitz 2006; Ogburn & Edwards 2015) demonstrates that this subgenus is monophyletic, defusing a suggestion by Hershkovitz (1993a) that it might be paraphyletic with respect to *M.* subg. *Montiopsis.*

3C. CALYPTRIDINAE Hershk., **tax. nov. TYPE**: *Calyptridium* Nutt. in Torrey & A. Gray.

Except for the sister relation between *Lenzia* and remaining Calyptridinae, phylogenetic relations among the other two or three genera remain poorly resolved (Hershkovitz 2006; Guilliams 2009). Morphology and DNA weakly support monophyly of the bicarpellate species of *Calyptridium*. Monophyly of 2–3-carpellate *Philippiamra* is not well supported, but this owes to lack of molecular divergence among the taxa. Biogeography provides circumstantial evidence for monophyly of both *Calyptridium* and *Philippiamra*. The problematic taxon is the three-carpellate species currently classified as *Cistanthe ambigua* (S. Watson) Carolin ex Hershk., which, on biogeographic grounds, seems to be most likely sister to the two-carpellate *Calyptridium*. Existing molecular data cannot confirm this. The present work offers two solutions: classify this species in *Calyptridium* or segregate it into its own genus. The former seems preferable, because the divergence between these taxa evidently is much less than between other Montiaceae genera and even subgeneric taxa. Preference for the latter option conserves existing usage in the sense that the species conventionally was classified in *Calandrinia* s. l. or, more recently, in *Cistanthe*., i.e., always in a genus separate from *Calyptridium*.

On the basis of morphology, both Carolin (1987, 1993) and Hershkovitz (1990a, 1991a, 1993a) classified *Calyptridium* and *Philippiamra* as separate sections of *Cistanthe*. Clarification of relations of the relations of *Lenzia* (Hershkovitz 2006) and *Montiopsis* (Ogburn & Edwards 2015; Hancock et al. 2018) defused this classification. As described above, however, the morphological similarities between these genera and *Cistanthe* appear to be symplesiomorphies and not convergences. Morphologically, *Lenzia* and *Montiopsis* are unique and highly divergent. Thus, the cladistic interpretation based on morphology is not surprising and, in a sense, is confirmed.

3C1. CALYPTRIDIUM Nutt. in Torr. & A. Gray, Fl. N. Amer. 1(2): 198. 1838. *Cistanthe* sect. *Calyptridium* (Nutt. in Torr. & A. Gray) Hershk., Phytologia 68: 267. 1990. **TYPE**: *Calyptridium monandrum* Nutt. in Torr. & A. Gray. Synonym: *Cistanthe monandra* (Nutt. in Torrey & A. Gray) Hershk.

Spraguea Torr., Smithsonian Contr. Knowl. 6: 4. 1853.

Thingia Hershk., this paper.

Current classifications recognize nine annual and perennial species plus three additional subtaxa of W North America (Hinton 1975; Guilliams 2009; Simpson et al. 2010; Guilliams et al. 2011; Guilliams & Miller 2014). All but one subspecific taxon occur in California. Simpson et al. (2010) argued for retaining subspecific status for four taxa of *C. parryi*, but given their allopatry and morphological distinctions, specific recognition may be warranted (see below). This would bring the species total to 12.

Molecular data (Hershkovitz 2006, 2018a; Guilliams 2009; Ogburn & Edwards 2015) evidence two clades in the genus corresponding to the morphological distinctions of the species referable to the segregate genus *Spraguea* and the remaining species of *Calyptridium* (Hershkovitz 1991a, b). Thus, *Calyptridium* here is divided into three sections.

3C1a. CALYPTRIDIUM sect. CALYPTRIDIUM

Six to nine annual species of SW USA and NW Mexico.

The species share the derived two-carpellate condition with *C*. sect. *Spraguea* and otherwise the pleisiomorphic vegetative and reproductive traits of other Calyptridinae and species of *Cistanthe* (Hershkovitz 1991a, b, 2018a). Simpson et al. (2010) argued for retention of subspecific status for three traditionally recognized varieties of *C. parryi*. Nonetheless, the varieties are distinguished easily geographically, ecologically, and morphologically. In current Montiaceae taxonomies, subspecific taxa seem to be eschewed in all genera except this one, *Claytonia*, and *Lewisia*. Subspecific taxa have been named in other genera, but current taxonomists seem to prefer to lump with or split from their species. Subspecific taxa of *Claytonia* generally manifest intergradation and or gene flow (Miller & Chambers 2006, 2012; McIntyre 2012, Stoughton et al. 2017a, b), as do those of some *Lewisia* species (Hershkovitz & Hogan 2002a, b). But I have recommended that allopatric and distinct entities be recognized as species, and by that criterion, all *Calyptridium parryi* subtaxa qualify. The main argument against this is in the interest of conserving well-established usage. As ever, much of taxonomy is aesthetics and ergonomics.

I provide here in brief form recombinations as species for remaining *Calyptridium parryi* subtaxa.

CALYPTRIDIUM HESSAE (J.T. Thomas) Hershk., **comb nov., stat. nov.** Basionym: *Calyptridium parryi* A. Gray var. *hessae* J.T. Thomas, Leafl. W. Bot. 8: 10. 1956. Synonym: *Cistanthe parryi* (A. Gray) Hershk. var. *hessae* (J.T. Thomas) Kartesz & Ghandi, Phytologia 71: 62. 1991.

CALYPTRIDIUM MARTIRENSE (Guilliams, M.G. Simpson & Rebman) Hershk., **comb nov., stat. nov.** Basionym: *Calyptridium parryi* A. Gray var. *martirense* Guilliams, M.G. Simpson & Rebman, Madroño 58: 260. 2012 [“2011”].

CALYPTRIDIUM NEVADENSE (J.T. Howell) Hershk., **comb nov., stat. nov.** Basionym: *Calyptridium parryi* A. Gray var. *nevadense* J.T. Howell, Leafl. W. Bot. 4:216. 1945. Synonyms: *Calyptridium parryi* A. Gray subsp. *nevadense* (J.T. Howell) Munz, Fl. S. Calif. 711. 1974. *Cistanthe parryi* (A. Gray) Hershk. var. *nevadense* Kartesz & Ghandi, Phytologia 71: 62. 1991.

3C1b. CALYPTRIDIUM sect. SPRAGUEA (Torr.) Hershk., **comb. nov., stat. nov.** *Spraguea* Torr., Smithsonian Contr. Knowl. 6: 4. 1853. **LECTOTYPE** (designated here): *Calyptridium monospermum* Greene. Synonym: *Cistanthe monosperma* (Greene) Hershk.

Three species, two perennial (one may behave as a winter annual) and one annual of SW USA.

Morphological evidence for sectional monophyly includes nonsucculence of the leaves, absence of planar leaf venation, and absence of the smaller of the two bracts subtending the flowers in other species (Hershkovitz 1991a, b). Molecular evidence confirms that perenniality is derived in *Calyptridium*. Although less clear, it is possible that the lower elevation and more ephemeral condition of *C. monospermum* represent an evolutionary reversal from the alpine and longer-lived condition of *C. umbellatum* (Torr.) Greene. The reduction of seed number to one in *C. monospermum* suggests that this species is derived. The two species hybridize and introgress in at least some locations along their ca. 1000 km contact zone (Hinton 1975).

3C1c. CALYPTRIDIUM sect. THINGIA (Hershk.) Hershk., **comb nov., stat. nov.** Basionym: *Thingia* Hershk., present paper. **LECTOTYPE** (designated here): **CALYPTRIDIUM AMBIGUUM** (S. Watson) Hershk., **comb. nov.** Basionym: *Thingia ambigua* (S. Watson) Hershk., present paper. Synonyms: *Claytonia ambigua* S. Watson, Proc. Amer. Acad. Arts 17: 365(–366). 1882. *Calandrinia ambigua* (S. Watson) Howell, Erythea 1: 34. 1893. *Cistanthe ambigua* (S. Watson) Carolin ex Hershk., Phytologia 68: 269. 1990.

One annual species of SW USA and NW Mexico.

In this paper, as explained above, I classify this species two different ways, allowing users to elect their preference.

3C2. THINGIA Hershk., **gen. nov., stat. nov.** Basionym: *Calyptridium* sect. *Thingia* Hershk., present paper. **LECTOTYPE** (designated here): **THINGIA AMBIGUA** (S. Watson) Hershk., **comb. nov.** Basionym: *Claytonia ambigua* S. Watson, Proc. Amer. Acad. Arts 17: 365(–366). 1882. Synonyms: *Calandrinia ambigua* (S. Watson) Howell, Erythea 1: 34. 1893. *Cistanthe ambigua* (S. Watson) Carolin ex Hershk., Phytologia 68: 269. 1990. *Calyptridium ambiguum* (S. Watson) Hershk., this paper.

Diagnosis: Plants annual, rosettiform with branched inflorescences, leaves succulent with three-dimensional leaf venation, the marginal veins connecting to form a “basket,” inflorescence a sub-umbellate cincinnus, flowers many, pedicellate, subtended by a pair of markedly unequal scarious bracts, sepals 2, petals 5, stamens 5, carpels 3, fruit capsulate with 3 valves, dehiscence basipetal, seeds several, black, smooth, shiny, embryo peripheral, nearly circular.

One species of the Mojave and Sonoran Deserts, Arizona, California, and adjacent northwestern Mexico (Guilliams 2009).

Justification for this segregation is explained above. The generic name metaphorically refers to one of the colloquial names for the type species, “dead man’s fingers” (SEINet 2018). Thus, the genus is named for the literary figure, Thing, of the Addams Family cartoon, television series, and movie. “Thing” is an animated but (at least in the movie) disembodied human hand. This suggests that the hand derives from a deceased human, hence possesses “dead man´s fingers.” Hershkovitz (1991c) described the three-dimensional leaf venation. The generic combination also suggests an appropriate vernacular name, “ambiguous thing,” reflecting the ambiguity of the status of this species following cladistic classification of Montiaceae.

3C3. PHILIPPIAMRA Kuntze, Rev. Gen. Pl. 1: 58. 1891. *Silvaea* Phil., Fl. Atacam. 21. 1860 (*non Silvaea* Hook. & Arn., Bot. Beech Voy. 211. 1837). *Cistanthe* sect. *Philippiamra* (Kuntze) Hershk., Phytologia 68: 269. 1990. **LECTOTYPE** (designated here): *Philippiamra pachyphyllum* (Phil.) Kuntze. Synonyms: *Silvaea pachyphylla* Phil. *Cistanthe pachyphylla* (Phil.) Carolin ex. Hershk.

Calandrinia sect. *Amarantoideae* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897.

Cistanthe sect. *Amarantoideae* (Reiche) Hershk., Phytologia 68: 269. 1990.

Perhaps 10 annual species of ChFR Atacama Desert region, Chile, 18S–28S, extending to adjacent Argentinean Andes (Hershkovitz 1991a; Peralta 1999; Peralta & Ford-Werntz 2008).

Taxonomy of *Philippiamra* is even more difficult than that of *Cistanthe*, for the reasons cited above and more. The genus is distributed mainly in the hyperarid zone of Chile's Regions II and III, extending to the northern province of Region IV. The exploration difficulty posed by infrequent rain thus is exacerbated. Also, the flowers are much smaller than those of *Cistanthe*. Because of their succulence, herbarium specimens often break and crumble.

Philippiamra includes both three-carpellate, capsulate, multiple-seeded species formerly classified in *Calandrinia* s. l. and two-carpellate achenial species classified in *Philippiamra*. Existing molecular data do not discriminate between these groups (Hershkovitz 2006). Both ribosomal and plastid genotypes are shared indiscriminately among both forms.

I have observed that in El Ñino "desierto florido" years, *Philippiamra celosioides* (Phil.) Kuntz is the last plant encountered when approaching the driest and rain-free sector of the Atacama Desert in Region II of Chile, E/SE of Antofagasta. Retreating from here, other *Philippiamra* species appear along with species of *Cistanthe* sect. *Rosulatae*. Bahamondes et al. (2012) described a desolate habitat N/NE of Antofagasta harboring only *P. salsoloides*. Thus, *Philippiamra* may include the world's most drought-tolerant vascular plant species.

According to Brummit (1993), *Philippiamra* replaced *Silvaea* Phil., which had been deemed a homonym with an earlier generic name, *Silvia* Benth. (Scrophulariaceae). Brummit reported that the nomenclatural committee deemed the two names distinct and concluded that "*Silvaea* should be adopted in Portulacaceae and *Philippiamra* should be regarded as a superfluous substitute." Strangely, no reference was made to another earlier generic name, *Silvaea* Hook. & Arn. (Euphorbiaceae). The latter appears to be legitimate and valid (Webster 1994), hence *Silvaea* Phil. remains homonymous and should be considered illegitimate.

Carolin (1993) included the genus *Diazia* in *Philippiamra* as circumscribed here. I have referred *Diazia* to *Calandrinia* (see above).

I provide here taxonomically necessary combinations in brief format:

PHILIPPIAMRA ARANCIOANA (Peralta) Hershk., **comb. nov.** Basionym: *Cistanthe arancioana* Peralta, Gayana Bot. 52: 45. 1995.

PHILIPPIAMRA CALYCINA (Phil.) Hershk., **comb. nov.** Basionym: *Calandrinia calycina* Phil., Fl. Atacam. 21. 1860. Synonym: *Cistanthe calycina* (Phil.) Carolin ex Hershk., Phytologia 70: 220. 1991.

PHILIPPIAMRA DENSIFLORA (Barnéoud) Hershk., **comb. nov.** Basionym: *Calandrinia densiflora* Barnéoud in Gay, Fl. Chil. 2(4): 503. 1846 [1847]. Synonym: *Cistanthe densiflora* (Barnéoud) Carolin ex Hershk., Phytologia 70: 220. 1991.

PHILIPPIAMRA MINUSCULA (Cullen) Hershk., **comb. nov.** Basionym: *Calandrinia minuscula* Cullen, Bol. Soc. Arg. Bot. 5: 12. 1953. Synonym: *Cistanthe minuscula* (Cullen) Peralta in Kiesling, Fl. San Juan 1: 163. 1994

PHILIPPIAMRA SALSOLOIDES (Barnéoud) Hershk., **comb. nov.** Basionym: *Calandrinia salsoloides* Barnéoud in Gay, Fl. Chil. 2(4): 502–503. 1846. Synonym: *Cistanthe salsoloides* (Barnéoud) Carolin ex Hershk. in Phytologia 68: 269. 1990.

3C4. LENZIA Phil., Linnaea 33: 222. 1864. **LECTOTYPE** (designated here): *Lenzia chamaepitys* Phil.

One perennial species of the ChFR: Chile, Regions III and IV, and adjacent Argentinean Andes, above 3000 m (Hershkovitz 2006).

As noted in Hershkovitz (2006), this peculiar acaulescent and evidently finely rhizomatous plant bears no obvious morphological similarity to other Calyptridinae (Reiche, 1898). The plant appears as a ca. 2 cm long cone of scarious-margined awl-shaped leaves. The mesophyll occupies only a thin central portion of the leaf. Flowers are axillary, solitary, with scarious bracts. Found between 3000–4000 m on Andean slopes, it evidently is resistant to extremes of both high and low temperatures and high (i.e., snowmelt) and low moisture.

4. PHEMERANTHEAE Hershk., **tax. nov. TYPE**: *Phemeranthus* Raf.

Molecular/phylogenomic analyses show *Phemeranthus* as sister to remaining Montiaceae (see above), but *Schreiteria*, here included in Phemerantheae, has not been sampled and possibly is extinct.

4A. PHEMERANTHUS Raf., Specchio Sci. 1: 86. 1814. *Talinum* sect. *Phemeranthus* (Raf.) DC., Prodr. 3: 356. 1828. **TYPE**: *Phemeranthus teretifolium* (Pursh) Raf. Synonym: *Talinum teretifolium* Raf.

About 25 perennial species, mainly in North American, one in Argentina (Ferguson 2001, Price 2012). *Phemeranthus confertiflorus* (Greene) Hershk. is adventive in Europe (Nagodă et al. 2013).

The largely North American distribution of the species intriguing. All Portulacineae outgroups of Montiaceae appear to have southern hemisphere origins, as do other early diverging Montiaceae. Thus, *Phemeranthus* may have waifed to North America prior to the diversification of remaining Montiaceae. Alternatively, as noted above, it is not inconceivable that South American Montiaceae arrived by dispersal from North America. Phylogenetic relations among *Phemeranthus* species remain poorly resolved (Price 2012). Interestingly, the Argentinean species diverges early in the cladogram. Resolution of *Phemeranthus* origins may be contingent upon the relations of the Argentine-endemic *Schreiteria* (see below).

4B. SCHREITERIA Carolin, Parodiana 3: 330. 1985. **TYPE**: *Schreiteria macrocarpa* (Carolin) Speg. Synonym: *Calandrinia macrocarpa* Speg.

One species of Tucumán Province, Argentina.

As far as I can determine, the species is known only from the type collection. Carolin's (1987) morphological analysis found the monotype to be sister to *Talinum* s. stricto. But the leaf venation is three-dimensional and the leaf base is pseudo-clasping, as in all species of *Phemeranthus* (Hershkovitz 1991c; Ogburn & Edwards 2013). The essentially sessile leaf is prominently constricted at the base into a miniscule petiole. A false clasping leaf base is formed by basal extension of the succulent leaf blade.

Abbreviations. CCM, carbon concentrating mechanism; CFP, California Floristic Province; ChFR, Chilean Floristic Region; CPR, Cape Floristic Region; ITS: nuclear ribosomal DNA internal transcribed spacer; LDD: long-distance dispersal; MAP: mean annual precipitation; WGD: whole-genome duplication

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