Synopsis of a new taxonomic synthesis of Montiaceae (Portulacineae) based on rational metadata analysis, with critical new insights on historically poorly understood taxa and a review of ecological evolution and phylogeography

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Abstract: Montiaceae (Portulacineae) comprise a clade of at least 280 species and ca. 30 subspecific taxa primarily of western America and Australia. This work uses existing phylogenetic metadata to elaborate a new cladistic taxonomic synthesis, and clarifies morphological circumscriptions of several poorly known species. A total of 20 taxa are validated, seven new and 13 necessary nomenclatural recombinations. Hypotheses of Montiaceae historical biogeography and phenotypic evolution are evaluated in light of recent metadata.
Key words: Montiaceae, taxonomy, phylogeny, ecology, phylogeography, evolution.

1. Introduction

This work presents a new cladistic taxonomy of Montiaceae (Portulacineae) and several of its included taxa, along with notes on the diagnostics of certainly poorly known species and a summary of new interpretations of phylogeography and phenotypic and ecological evolution. The present work includes 20 nomenclatural novelties. However, the whole of the novelty is greater than the sum of these parts. 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. Critical reevaluation of certain common and usually misidentified Chilean taxa is the first since Reiche (1898). Existing metadata are interpreted as evidence for a hybrid origin of a genus. And existing metadata are interpreted as evidence for decoupling of cladogenesis with phenotypic evolution.

Montiaceae comprise a clade of at least 280 species plus ca. 30 additional accepted subspecific taxa, primarily of western America and Australia (Hernández-Ledesma et al. 2015; Ogburn & Edwards 2015). The species diversity estimate (calculated from the taxonomic treatment) is almost 25% greater than that reported in Hernández-Ledesma (2015) and reflects more recent and ongoing research.

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

The modern cladistic generic classification originated with morphological analyses of Carolin (1987, 1993) and Hershkovitz (1991a, 1993). Slowly, the new familial and generic concepts began to replace the traditional 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), and Hancock et al. (2018). This evidence is reviewed in Hershkovitz (2018a).

This work first summarizes information on the ecology and phylogeographic history of Montiaceae. The taxonomy follows. The generic taxonomy supersedes that of Hernández-Ledesma et al. (2015), which superseded that of Carolin (1993). In addition, I comment on the taxonomy and taxonomic history of selected taxa, especially *Calandrinia* Kunth, *Rumicastrum*, and *Cistanthe* Spach and recombine binomials into *Cistanthe*, *Calyptridium* Nuttall and *Philippiamra* Kuntze. I conclude that *Lewisiopsis* has a hybrid origin and represents a living fossil. Finally, I offer detailed observations on taxonomically troublesome Chilean taxa.

2. Montiaceae ecology and ecological evolution

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), Siberia, Australia, New Zealand, and the Kerguelen Islands (Hershkovitz 2018a, b). Correspondingly, Montiaceae species concentrate especially in cooler/moister (higher altitude and/or latitude) and warmer/drier Mediterranean and desert environments (Ogburn & Edwards 2015; Hershkovitz 2018b). They also differ from other Portulacineae in comprising mostly hemicryptophytic (including acaulescent rosettiform-caudiciform) perennials and therophytes (Hershkovitz 1993, 2018b; Ogburn & Edwards 2015)

Other Portulacineae are distributed mainly more towards the tropics and from the American high cordillera eastwards (trans-cordilleran) and Africa/Madagascar, with a few taxa in warmer parts of Australasia/Oceania (Hershkovitz 1993, 2018b; Ogburn & Edwards 2015). They are mostly phanerophytic herbs, shrubs, trees, and vines, and often stem succulents. However, most *Portulaca* (Portulacaceae) species are monocarpic annuals (Ocampo 2012) and most Anacampserotaceae species are hemicryptophytes, a few acaulescent (Carolin 1987, 1993; Rowley 1994).

Montiaceae niches are diverse, including desert to aquatic habitats and arctic/alpine to subtropical habitats and everything in between. This 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 (2018b) reconsidered this view, pointing out that some Montiaceae lineages in this range never diversified, while *Rumicastrum*, the largest genus in the family, is endemic to less macroecologically diverse regions of Australia (see below). The same phenomenon characterizes many lineages o f angiosperms in macroecologically diverse western America: some have diversified and some have not. Similarly, other angiosperm lineages have diversified exceptionally in relatively less macroecologically 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 (2018b).

Montiaceae include species that span small to large ranges and rare to common frequencies. Several species, as noted in the taxonomy discussion, are adventive outside of their original native ranges. These species concentrate among the genera *Claytonia* and *Montia*, and most are annuals. Otherwise, there appears to be no particular correlation between species range/frequency and other obvious possible phenotypic or genetic factors.

Using various methods of statistical phylogenetic comparative analysis, Ogburn & Edwards (2015) studied ecological evolution of Montiaceae, especially the relation between life history and temperature and moisture niche. They reported an increased rate of phylogenetic diversification of temperature niche and life history relative to other Portulacineae. Montiaceae have incurred ca. 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 2018b).

Ogburn & Edwards (2015) concluded that the ancestral growth form of Montiaceae was acaulescent rosettiform-caudiciform and tap-rooted, with little annual above-ground growth. This growth form characterizes, e.g., certain species of *Calandrinia* sect. *Acaules* and *Lewisia*. This conclusion was more or less in agreement with mor5phological cladistic conclusions (Carolin 1987; Hershkovitz 1993). However, Montiaceae also include rhizomatous and tuberous perennials, as well as perennials with substantial above-ground growth, including pachyform shrubs (Hershkovitz 2018b). Ogburn & Edwards (2015) determined that perennials generally were more cold-adapted than annual, and concluded that the annual life history evolved many times as an adaptation to transition to warmer environments. They also concluded that annuals were absent in cold environments because of the shorter growth season, which did not permit annuals to complete their life cycle.

Ogburn & Edwards (2015) attributed phylogenetic life history lability of Montiaceae to their ancestral herbaceous and, in particular, acaulescent rosettiform-caudiciform growth form. Phylogenetic niche breadth lability itself had been ascribed previously to herbaceous more than woody growth forms (Smith & Beaulieu 2009). Ogburn & Edwards (2015) argued that the rosettiform-caudiciform form of Montiaceae permitted phylogenetic lability in relative above- versus below-ground biomass allocation. This, in turn, permitted Montiaceae to adapt phylogenetically to a broader range of climate conditions.

Hershkovitz (2018b) concluded that in many, if not most, cases, the phylogenetic transition in life history among Montiaceae has been from annual to perennial. He also disputed the conclusion that the tap-rooted acaulescent rosettiform-caudiciform growth form was ancestral. It appears to have been derived from either a tuberous or rhizomatous form at least once and from annuals several times. Moreover, while Hershkovitz (2018b) agreed that annuals generally occur in warmer environments than perennials, there were significant exceptions. Five annual Montiaceae species are alpine, and several perennials occur in warm environments alongside annual species.

Hershkovitz (2018b) also disputed that growing season length restricted annuals to warm environments, pointing out that many Montiaceae annuals occur in hyperarid deserts, where the growing season is exceptionally short, and that some annuals indeed grow in the alpine zone. He also pointed out that, while the distantly related genus *Portulaca* (Portulacineae; Portulacaceae) is fundamentally tropical/subtropical, two annual species have become invasive in the cool temperate zone. Hershkovitz (2018b) hypothesized that life history transitions among Montiaceae more likely reflected temperature per se and involved genetic assimilation of developmentally plastic traits that delayed annual flowering in cold temperatures. Finally, appealing to non-Darwinian evolutionary theory and epistemology, he disputed the notion that environmental traits “caused” life history evolution at all.

Finally, Hershkovitz (2018b) pointed out that climate temperature was not the same as plant microenvironment temperature, and described cases where Montiaceae species at given locality and sharing the same climate data differ markedly in temperature niche. For this and many technical and epistemological reasons, Hershkovitz (2018b) rejected the conclusions of Ogburn & Edwards (2015).

Ogburn & Edwards (2015) found no evidence of increased diversification of Montiaceae precipitation niche relative to other Portulacineae and no correlation between precipitation niche and life history diversification. Again, Hershkovitz (2018b) pointed out precipitation niche was a misleading indicator, because the discrepancy between precipitation and physiological moisture niche is even greater than that for temperature niche. He described a locality in the Andes near Santiago that harbors ten Montiaceae species in four genera, sharing the same precipitation niche but occupying local moisture niches ranging from xerophytic to aquatic. For this and otherwise the same reasons elaborated as above for temperature niche, Hershkovitz (2018b) rejected the conclusions of Ogburn & Edwards (2015).

Moreover, Hershkovitz (2018b) argued that indeed Montiaceae, contrary to Ogburn & Edward's (2015) conclusions, indeed have experienced a greater rate of moisture niche diversification than other Portulacineae. They have evolved multiple times into (cooler and) moisture niches rarely or ever accessed by the remaining 75% of Portulacineae species. The overall phylogenetic trend among Montiaceae has been towards more cooler/moister niches. The earliest diverging lineages (Phemerantheae, Cistantheae, and *Rumicastrum*) comprise often warmer and mainly arid- to hyperarid-adapted taxa. Most species are succulent or, in the case of *Montiopsis* species, (glandular-)pubescent. The successively diverging lineages (*Calandrinia*, Hectorelleae, *Lewisia*/*Lewisiopsis*, *Claytonia*, *Montia*) trend to cooler/moister to hydric niches. But some species of Montieae also have evolved back into warmer and/or more arid niches of the south central and SE United States and Mexico. These taxa thus converge on the niche range of other Portulacineae.

Especially among the earlier-diverging lineages, Montiaceae include many 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, they did not distinguish between precipitation and moisture niche. Moreover, Ogburn & Edwards (2010) earlier had noted that not all arid-adapted plants are succulent and not all succulent plants are arid-adapted. Hershkovitz (2018b) pointed out that indeed Montiaceae include several non-succulent but otherwise arid-adapted species (*Montiopsis* spp. and *Lenzia*), and even degrees of succulence in bog species. Thus, the analysis of Ogburn & Edwards (2015) lumped arid-adapted with non-arid-adapted taxa and also lumped xeric and moist habitats. The premise of the hypothesis that succulence should correlate phylogenetically with precipitation is thus unexplained and puzzling.

In the meantime, McIntyre (2012) and Smith et al. (2017) used approaches similar to Ogburn & Edwards (2015) to evaluate the prediction that ecological diversification among Montiaceae is (alternatively) consequent to whole genome duplication (polyploidy). Again, climate temperature and precipitation data were surrogates for ecological niche. Thus, the same criticisms as above apply. But Hershkovitz (2018b) pointed out that polyploidy and diversification are parallel growth functions, thus a degree of autocorrelation is expected. He likewise demonstrated that polyploidy is neither necessary, nor sufficient, to explain ecological diversification. Two polyploid taxa, the ditypic Hectorelleae and the monotypic *Lewisiopsis*, are octaploids that have diversified much less than their close relatives. *Lewisopsis* is endemic to the same western North

American region where other Montiaceae have diversified. Hershkovitz (2018b) suggested that, in this case, polyploidy may have sequestered diversification (see below).

Hershkovitz (2018b) also pointed out that Smith et al. (2017) did not distinguish between autopolyploidy and the more common allopolyploidy, the latter consequent to hybridization. However, hybridization also has been considered to be a driver of ecological diversification in its own right. By not discriminating between auto- and allopolypoidy, Smith et al. (2017) failed to test their hypothesis of the consequences of polyploidy alone. However, even if they had, Hershkovitz (2018b) rejected the premise of this work for other reasons.

Finally, Smith & Beaulieu (2009) earlier had presented evidence that genomic evolution is faster in plants with shorter generation times, and believed that this correlated with faster ecological diversification. Hershkovitz (2018b) commented on this and other evidence relating polyploidy to longer generation times, and consequently slower ecological diversification. But Smith et al. (2017) proposed that polyploidy is associated with faster ecological diversification. If polyploidy, in turn, is correlated with longer generation time, and longer generation time with slower ecological diversification, the proposals of Smith & Beaulieu (2009) and Smith et al. (2017) become diametrically opposed.

3. Montiaceae phylogeographic origins and evolution

Hershkovitz (2018a) reviewed evidence for Montiaceae phylogeographic history. Montiaceae are sister to remaining Portulacineae, an order comprising several families that subsume the classical circumscription of Portulacaceae (Ogburn & Edwards 2015). Montiaceae origins are not preserved in the fossil record. Current cladogram molecular clock-based estimates date the diversification of modern Montiaceae to between ca. 34 million to ca. 43 million ybp, i.e., late Eocene to perhaps earliest Oligocene (Ogburn & Edwards 2015; Hancock et al. 2018). These estimates are rather older than those of (Hershkovitz & Zimmer 1997), but do not significantly alter the phylogeographic conclusions of that work. At the same time, clock-based estimates indicate that diversification of modern species occurred from the Miocene onwards, much more recently than major lineage origins.

Based on the overall phylogenetic niche trend towards cooler and moisture habitats described above, Hershkovitz (2018a) proposed that the early diverging Montiaceae lineages Phemerantheae, Cistantheae, and *Rumicastrum*, originated towards northern Patagonia, and the ancestor of the remaining taxa was situated in southern Patagonia during the Oligocene.

The Montiaceae age estimates corroborate Hershkovitz & Zimmer's (1997, 2000) view that the many intercontinental/interoceanic disjunctions among Montiaceae and other Portulacineae owe to long distance dispersal. The result is significant in that Montiaceae have no obvious morphological specialization to facilitate long distance dispersal via zoochory or anemochory. Carolin (1987) and earlier workers attempted to explain Portulacineae distributions in terms of vicariance resulting from the break-up of Gondwana.

However, Moreira-Muñoz (2011) and researchers cited therein, seem to maintain that vicariance/panbiogeographic patterns intrinsically favor a vicariance/panbiogeographic explanation. On the basis of phytogeographic patterns, some researchers in this school have concluded that molecular dating methods severely underestimate true lineage ages. Meanwhile, Hancock et al. (2018) proposed, with skepticism, that *Rumicastrum* could have arrived to Australia vicariantly. This proposal is evaluated and rejected by Hershkovitz (2018a). The latter also discusses newer theoretical evidence demonstrating why long-distance dispersal might be especially likely in plants like Montiaceae that lack dispersal adaptations.

In any case, below is a list of Montiaceae phylogeographic disjunctions of 1000 km or more, both transoceanic and terrestrial. Anthropogenically-induced disjunctions are excluded.

1. *Schreiteria* (S. Am.) - *Phemeranthus* root (N. Am. or C. Am.)
2. *Phemeranthus* root (N. Am. or C. Am.) - *Phemeranthus punae* (S. Am.)
3. *Cistanthe* clade (S. Am.) - *Cistanthe guadalupensis* & *C. maritima* (N. Am.)
4. *Philippiamra* (S. Am) - *Calyptridium* (N. Am.)
5. Montioideae root (S. Am.) - *Rumicastrum* (Aus.)
6. *Calandrinia acaulis* (S. Am.) - *Calandrinia acaulis* (C. Am.)
7. *Calandrinia ciliata* (S. Am.) - *Calandrinia ciliata* (C. Am.)
8. *Calandrinia* sect. *Calandrinia* clade (S. Am., C. Am.) - *Calandrinia menziesii* (N. Am.)
9. Montioideae root (S. Am.) - Hectorelleae (NZ, Kerguelan I.)
10. *Hectorella* (NZ) - *Lyallia* (Kerguelan I.)
11. Montioideae root (S. Am.) - Montieae root (N. Am.)
12. *Lewisia pygmaea* s. l. (N. USA, S. Can.) - *Lewisia pygmaea* s. l. (N. Can., Alaska)
13. *Montia* root (N. Am.) - *Montia* sect. *Australiensis* (NZ, Aus.)
14. *Montia* sect. *Australiensis* (NZ) - *Montia* sect. *Australiensis* (Aus.)
15. *Montia* sect. *Australiensis* root (NZ or Aus.) - *Montia howellii* (N. Am.; not anthropogenic contra O'Quinn & Hufford 2005; see Hershkovitz 2018a)
16. *Montia* sect. *Montia* root (N. Am.) - *Montia meridiensis* (S. Am.)
17. *Montia fontana* root (N. Am.) -*Montia fontana* (subcosmopolitan, pre-anthropogenic)
18. *Montia chamissoi* (N. Mex.- Alaska) - *Montia chamissoi* (S. Mex.)

A more trivial geographic aspect of Montiaceae origins relates to Chile. The first phylogenetic divergence separates Phemerantheae from the remainder of the family. The next divergence separates the largely Chilean Cistantheae from Montioideae, and the first split in the latter separates the largely Chilean *Calandrinia*. Thus, excluding Phemerantheae, the origin of rest of Montiaceae appears to have occurred in present day northern Chile. There, it diversified, many descendents dispersing to other lands and diversifying, dispersing, and diversifying further. This appears to be the only intercontinentally diverse 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 (2018a) speculated that this may owe to Chile's narrow latitudinal breadth, high relief, and historical ecological instability. This may result in high lineage extinction rates, which, in turn, offers more opportunities for colonization. Montiaceae, in turn, are among the few lineages that not only diversified under these circumstances, but evolved a colonization capability.

However, the late-Eocene 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 did not other Portulacineae lineages early in Portulacineae history enter and diversify in the warm/arid cis-cordilleran region?

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 a popular theory maintains that half or more of the height of the Andes was uplifted relatively rapidly beginning in the Miocene. Before that, the trans-Andean macroecological contrast was less marked and abrupt. Also, the Mediterranean and hyperarid climates are considered to have developed even more recently. But the basal split of Montiaceae dates to the late Eocene, perhaps 25 million years before the physical/macroecological partition and contrasts developed. In this scenario, 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 evidence is nuanced and does not entirely resolve this question (e.g., Armijo et al. 2015; Quade et al. 2015; Lease et al. 2016; Rodríguez Tribaldo et al. 2017).

Another possibility in the case of Montiaceae is that South American cis-cordilleran Montiaceae themselves originated from an ancestor dispersed from North America. The phylogeography of *Phemeranthus* (Price 2012) renders plausible this scenario. As noted above, and in Hershkovitz (2018a), the historical ecological instability combined with relatively small geographic area of Chile itself renders its vulnerable to colonization, possibly explaining the tendency of Chile to have become a phylogeographic sink rather than source.

But Hershkovitz (2018a,b) also emphasized the precariousness of evolutionary reconstruction. Evolution, including phylogeographic evolution, is a nonlinear idiosyncratic process. Modern patterns of Montiaceae phylogeographic distribution developed over the course of tens of millions of years. Many plausible scenarios could yield their present forms and distributions, and plausible scenario can be unequivocally falsified. 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 origins and the Miocene. The very existence of these ancestors reduces to a few 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.

4. Synopsis of subfamilial and generic taxonomy

Below is a summary of a subfamilial to generic level taxonomy of Montiaceae, modified from Hernández-Ledesma et al. (2015) according to current phylogenetic evidence (Hershkovitz, 2018a). Each taxon comprises a clade. Numbers/letters in bold denote cladistic rank. Rank suffixes accord with conventional classification (McNeill et al. 2011) but no nomenclatural ranks are assigned per Cantino and De Queiroz (2007). Thus, missing ranks and 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.
- **1D.** *Rumicastrum* Ulbrich

2. Cistantheae Hershk.
- **2A.** *Cistanthe* Spach
- **2B.** *Montiopsis* Kuntze
- **2C. Calyptridinae** Hershk.
  - **2C1.** *Calyptridium* Nutt. in Torr. & A. Gray
  - **2C2.** *Thingia* Hershk.
  - **2C3.** *Philippiamra* Kuntze
  - **2C4.** *Lenzia* Phil.

3. Phemerantheae Hershk.
- **3A.** *Phemeranthus* Raf.
- **3B.** *Schreiteria* Carolin

5. Detailed and annotated subfamilial taxonomy

The taxonomy below elaborates the synopsis above to the subgeneric level and includes estimated species numbers and distributions. Additional commentary is provided regarding phylogenetic and other taxonomic evidence. 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 nomenclatural synonyms in multiple genera (O'Quinn & Hufford 2005).

1A1a. *Montia* L., Sp. Pl. 1: 87. 1753; type: *M. 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 western North America to NE Asia, one in northern South America, seven in New Zealand, one in Australia, and one cosmopolitan (O'Quinn & Hufford 2005; Heenon 2007). How much of the range of the cosmopolitan *Montia fontana* L. 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 & Hufford (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 western 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. *Montia* sect. *Australiensis* (Poelln.) Pax & K. Hoffm.

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. *Montia* sect. *Montiastrum* (A. Gray) Pax & K. Hoffm.

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: *C. 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 & Hufford 2005; Miller & Chambers 2007; 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 2007; GBIF Secretariat 2017; Atlas of Living Australia 2018).

With a minor exception, subgeneric cladistic classification of *Claytonia* (O'Quinn & Hufford 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 & Hufford (2005) recognize three sections; again, no attempt is made here to elaborate the synonymy. Discrepancies persist in the number of taxa recognized (O'Quinn & Hufford 2005; Miller & Chambers 2007; Stoughton et al. 2017a, b).

1A1b1. *Claytonia*sect. *Claytonia*

Ca. 16 species plus 12 additional subspecific taxa; tuberous to tap-rooted caudiciform perennials. Whole-genome DNA sequence sampling and analysis has revealed evidence of ancient hybridization and/or genetic lineage sorting among several species (Stoughton 2017b).

1A1b2. *Claytonia*sect. *Limnia* (Haw.) Torr. & A. Gray

Ca. nine species plus eight additional subspecific taxa; annuals and two facultatively stoloniferous perennials. One species may behave as a winter annual (Miller & Chambers 2007; Hershkovitz 2017b).

1A1b2. *Claytonia*sect. *Rhizomatosae* A. Gray ex Poelln.

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

1A2. *Lewisia* Pursh, Fl. Amer. Sept. 2: 360. 1813; type: *L. 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 western North America, concentrated in California (Hershkovitz and Hogan 2002; Wilson et al. 2005).

Limited molecular data (Hershkovitz, unpublished) suggest that at least five species of the evergreen *Lewisia* sect. *Cotyledon* J. E. Hohn ex B. Mathew may be monophyletic, but there appears to be otherwise little phylogenetic structure in available data. The remaining species are tap-rooted (one tuberous) acaulescent perennials with ephemeral leaves. The problematic, polymorphic, and widespread *L. pygmaea* (A. Gray) B. L. Rob. probably is polyphyletic, and interspecific gene flow involving several species may have taken place (Hershkovitz, unpublished). Most species have been intercrossed in cultivation, with varying degrees of hybrid fertility (Mathew 1989; Davidson 2000).

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 ≡ *Lewisia tweedyi* A. Gray.

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

On morphological evidence, Hershkovitz (1990a, 1991a, 1992, 1993) 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* (Ruíz & Pav.) DC. (*nom. cons.*) ≡ *Talinum ciliatum* Ruíz & Pav.
= *Cosmia* Dombey ex Juss., Gen. Pl. 312. 1789., *obs.*
= *Baitaria* Ruíz & Pav., Fl. Peruv. Prodr. 63. 1794.
= *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.

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, which classified the annual species in this genus, but classified the perennial species in *Baitaria*, along with all species of *Montiopsis* (Carolin 1987, 1993). Monophyly of the current circumscription has been confirmed by all five subsequent molecular analyses cited in this work, including Hancock et al. (2018), who proposed a different circumscription (see below). But because *Calandrinia* was the conserved name for the classical concept of *Calandrinia* s. l., some confusion has persisted. The generic name was bound to persist. If the cladistic classification included NO species in *Calandrinia*, its assimilation would have been faster and easier.

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 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 1993).

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 sectional lines. Clusters of sections were segregated and/or integrated into other genera. Thus, the cladistic classification, while not conserving existing genera, did conserve existing *taxa*. In fact, on morphological bases, the cladistic taxonomy was far more self-evident than the prior taxonomy, because several sections intergraded morphologically within their cladistic clusters. Cladistically classified, the morphological distinctions among the sections were unambiguous. However, in scientific practice, taxonomy emphasizes only genus and species and not intervening ranks. To non-specialists unfamiliar with the sectional taxonomy, the cladistic classification seemed less comprehensible than the one they had memorized.

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 higher taxa. 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 with 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 recombined binomials only as necessary to refer to the corresponding (often misidentified) species in my phylogenetic work. 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.

Reflecting on the history of the transition between *Calandrinia* s. l. and the cladistic taxonomy, one can appreciate that the purpose of scientific taxonomy is purely informatic, i.e., to help assure that names map to the same type and to promote understanding that types, and not taxa, are the reference point for all taxonomic usage. Thus, taxonomic nomenclatural codes regulate only the nomenclatural validity of scientific names, but not the ontological validity of taxa. The latter is supposed by a very few specialists. In broader usage, scientific names are learned and effectively common Latin names, their ontology not verified by the users. And, of course, one cannot "unpublish" older but still consulted references. Much like fixation of new alleles in populations, only with time do newer taxonomic names become fixed in the vernacular. Perhaps not coincidentally, this transition in Montiaceae has taken approximately a human generation time.

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.

Ca. seven annual species native to western America, distributed along the American cordillera nearly continuously from British Colombia to Tierra del Fuego (Hershkovitz 2006). *Calandrinia menziesii* (Hook.) Torr. & A. Gray 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* Schrad. ex DC 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).

1B2. *Calandrinia* sect. ***Acaules*** Reiche, Ber. Deutsch. Bot. Ges. 15: 500. 1897 ≡ *Baitaria* Ruíz & Pav.; lectotype (designated here): *C. acaulis* Humb., Bonpl. & Kunth *non Baitaria acaulis* Ruiz & Pav. ≡ *Calandrinia carolinii* Hershk. & D. I. Ford.

Ca. 10 perennial species of western South America, one extending to Central America and southern Mexico (Hershkovitz 2006; Elvebakk et al. 2015).

All five molecular analyses cited in this work indicate that this section is monophyletic, disproving the suggestion that it may be paraphyletic with respect to *C.* sect. *Calandrinia* (Hershkovitz 1993).

1C. Hectorelleae Appleq., Nepokr. & W. L. Wagner, Syst. Bot. 31: 316. 2006.

1C1. *Hectorella* Hook. f., Handb. N. Zeal. Fl. 27.1864; type: *H. caespitosa* Hook. f.

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

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

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

1D. *Rumicastrum* Ulbrich, Engler & Prantl, Nat. Planzenfam. 16c: 519. 1934; type: *R. chamaecladum* (Diels) Ulbrich ≡ *Atriplex chamaeclada* 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 of Australia, about 25 not yet described (Hancock et al. 2018; Thiele et al. 2018). All described species except *R. chamaecladum* (Diels) Ulbrich are currently erroneously classified as *Calandrinia* Kunth, most also with 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. ≡ *Calandrinia ptychosperma* F. Muell.] against *Rumicastrum*. Seddon (2005) described how he first diagnosed *Rumicastrum chamaecladum* (Diels) Ulbrich (≡ *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 mature 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 1993), 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. That work sampled an Australian calandrinia. 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 use 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 (i.e., nearly 20 years ago), Judy West (CANB) advised me that Carolin's diagnosis was correct, and that I had erred.

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 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. The circumscription appears to reflect nomenclatural expedience. In particular, the authors evidently knew that *Rumicastrum* was the correct name for the Australian plants.

But they argued that existing evidence did not prove that *Rumicastrum* was not sister to *Calandrinia*. A sister relation would justify, on phylogenetic taxonomyic criteria, the continued classification of *Rumicastrum* species as *Calandrinia*. Another possibility was that the peculiar *R. chamaecladum* would figure outside of this clade. Their analysis rejected both possibilities. They thus sought to conserve the name *Parakeelya*, 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 formed a clade, 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.

2. Cistantheae Hershk., ***tax. nov.***; lectotype (designated here): *Cistanthe* Spach, Hist. Nat. Veg. 5: 229. 1836.

2A. *Cistanthe* Spach, Hist. Nat. Veg. 5: 229. 1836; lectotype (designated here): *C. grandiflora* (Lindl.) Schltdl. (*nom. cons.*) ≡ *Calandrinia grandiflora* Lindl. ≡ *Cistanthe grandiflora* (Lindl.) Carolin ex Hershk. (*nom. superfl.*) ≡ *Claytonia grandiflora* (Lindl.) Kuntze

= *Tegneria* Lilja, Fl. oefver Sver. Odl. Vext.76. 1839 ≡ *Rhodopsis* Lilja, Fl. Sverig. Suppl. 1: 42. 1840; lectotype (designated here): *Calandrinia discolor* Schrad. ≡ *Cistanthe discolor* (Schrad.) Spach.

Current acceptance of the generic segregation of *Cistanthe* 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 1990, 1991a, 1992, 1993), based on morphology, were paraphyletic. Ogburn & Edwards (2015) remarked that their molecular analysis demonstrated paraphyly of the1990 circumscription. But they failed to note that Hershkovitz (2006) had demonstrated this, and that their own 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 *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 earliest Montiaceae, from which other genera have diverged markedly.

Taxonomy of the Chilean species of *Cistanthe* is problematic. The most recent taxonomic treatment is Reiche (1898), which is more than 120 years old. 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, seasonal periodicity of rains ranges from about 10 years to 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 in a single wet year can accumulate to thousands or more years.

Some problematic taxa are discussed below. No intention is made here to provide a revision, much less a monograph. The intention is merely to improve upon the existing, very old, and otherwise inadequate taxonomic references and to facilitate future investigation. Any taxonomic clarification at all will aid in conservation efforts and in studies of phenotypic and ecological evolution, e.g., similar to Ogburn & Edwards (2015).

2A1. *Cistanthe* sect. ***Cistanthe*** ≡ *Calandrinia* sect. *Cistanthe* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897.

About 12 species, all but one perennial, primarily in Chile, one extending into San Juan Province, Argentina, and one endemic to Peru (Peralta 1999; León 2006).

Circumscription of this section corresponds almost completely to Reiche's (1898), except that Reiche included *Cistanthe cachinalensis* (Phil.) Peralta and D. I. Ford in his *Calandrinia* sect. *Rosulatae* (see below). Smith et al. (2017) and Hancock et al. (2018) demonstrated that the Peruvian *C. paniculata* (Ruíz & 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.

Lectotypification here of *Tegneria* Lilja is for clarification. Lilja (1841) included in this genus *Calandrinia discolor* Schrad [= *Cistanthe discolor* (Schrad) Spach] and "*Calandrinia speciosa*," evidently *Calandrinia* speciosa Lehm. [= *Cistanthe* speciosa (Lehm.) Lilja ex Heyn.]. Both of these species are included in Reiche's (1897, 1898) *Calandrinia* sect. *Cistanthe* as possible taxonomic synonyms of *Cistanthe grandiflora* (see below). But Lilja also included a later homonym, *Calandrinia speciosa* Lindley (≡ *Calandrinia elegans* Spach = *Calandrinia menziesii* (Hook.) Torr. & A. Gray; cf. Reiche (1897, 1898). Lilja evidently did not appreciate that the homonymous plants were distinct [see (Steudel, 1840: 253), cited by (Lilja, 1841)].

I provide below taxonomically necessary combinations:

Cistanthe aegitalis (Phil.) Carolin ex Hershk., ***comb. nov.*** ≡ *Calandrinia aegitalis* Phil., Anales Univ. Chile 85: 184. 1893.

Cistanthe crassifolia (Phil.) Carolin ex Hershk., ***comb. nov.*** ≡ *Calandrinia crassifolia* Phil., Anales Univ. Chile 85: 180. 1893.

Cistanthe mucronulata (Meyen) Carolin ex Hershk., ***comb. nov.*** ≡ *Calandrinia mucronulata* Meyen, Reise Erde 1: 314. 1834.

Although taxonomically troublesome, several Chilean species of *C.* sect *Cistanthe* seem to be morphologically diagnosable, especially the high altitude and more southerly taxa. Taxonomy of plants of the Atacama Desert of Regions II-III of Chile remains more problematic. Nominally species-level DNA sequence markers failed to aid in species diagnostics (Hershkovitz 2006). Genotypes were shared haphazardly among multiple morphologically distinct and geographically divergent forms.

Below is an annotated descriptive list of putatively distinct species in Chile, with the distinguishing features italicized. The list in no way is intended as a formal taxonomic/floristic revision. Nonetheless, evidently it provides the only attempted summary of the Chilean species since Reiche (1898). It is intended to assist further investigation.

1. ***Cistanthe mucronulata*** (Meyen) Carolin ex Hershk. (?= *Calandrinia spectabilis* Otto & A. Dietr.; see below): *the only species of the precordillera and coast ranges of Chile Regions VI-VII*, often found along roadcut cliffs. The type locality is the vicinity of San Fernando (Region VI). Perennial, inflorescence/flowers similar to *C. discolor* but *leaves not correspondingly coriaceous or bicolored*, blades often rotund. An especially large and more succulent form occurs on the beaches at Constitución. Vegetatively, it superficially resembles *C. laxiflora*, but otherwise conforms to the species.

2. ***Cistanthe discolor*** (Schrad.) Spach: *the only precordillera species of Chile Regions IV, V, northernmost VI, and Metropolitana*, approaching the coast at higher elevations in Region IV, e.g., near Andacollo. Perennial, *plants not glaucous*, leaves coriaceous, *green abaxially, paler along the major veins, purplish adaxially*, inflorescence *culms terete*, stamens about 50, style and stamen height equal. The type was cultivated from seed. The original description of the leaf coloration provides its principal diagnosis.

3. ***Cistanthe grandiflora*** (Lindley) Schltdl., *nom. cons.* [= *C. glauca* (Schrad.) Lilja]: coastal regions from Chile Region III-V, possibly also in Region II, extending as a ruderal to the precordillera from northernmost Region V to southern Region III, possibly naturalized elsewhere in Chile and Argentina. Weedy, *usually glaucous* perennial (sometimes annual?) up to 2 m in height; erect, strict (smaller plants) to highly branched, larger plants somewhat suffruticose; branches leafy below, terminating in usually 2-3-branched inflorescences, *culms becoming sharply angular or fasciated distally*, stamens about 50, style and stamen height equal. Plants I carelessly misnamed *C. discolor* in Hershkovitz (2006) are actually *C. grandiflora* as described here, as might be evident from their collecting localities.

The size of larger plants suggests the plants are perennial (as indicated in the original diagnosis), but I have not verified this by perennial monitoring tagged individuals. I have observed small plants flowering in their first year. In drought conditions, these may behave as annuals. Alternatively, *C. grandiflora* might be a species complex with otherwise similar perennial and annual forms.

Perennial, more suffruticose plants with more coriaceous and only (supra-)basal leaves of coastal and interior Region III Atacama Desert flats have the angled inflorescence and floral traits of *C. grandiflora.* I believe that they represent a distinct species (or hybrid), but I cannot confirm their identity. *Cistanthe speciosa* emerges as a candidate, but its diagnosis indicates terete culms (see also below).

I suspect that both *Cistanthe cachinalensis* (including *Calandrinia taltalensis* I. M. Johnst.) of Region II fit within the range of variation of *C. grandiflora*. It has been considered distinct and endangered (Rosas and Estévez 2010), but I emphasize that the species is morphologically variable even in the Mediterranean climate zone, hence this plasticity ought to manifest even more so in the hyperarid zone. Reiche (1898) described *C. cachinalensis* as annual or biennial. It is probably for this reason and the relatively small size of the Philippi's specimen that Reiche (1898) included this species in his *Calandrinia* sect. *Rosulatae*. As noted, I have observed facultatively annual individuals of *C. grandiflora* throughout its range. Given the description, photos, and ecology of *C. cachinalensis* (Rosas and Estévez 2010), I suggest these represent simply stunted forms of *C. grandiflora* occurring at the physiological limit of this species. However, as noted above and in Hershkovitz (2018b), mechanisms exist that might facilitate evolution of a distinct species under these extreme ecological circumstances. Genetic and cultivation experiments could resolve this question.

Veldcamp (2015; cf. Applequist 2016) presented evidence that, contrary to what historical literature would suggest (Schlectendal, 1831), *Calandrinia glauca* Schrad. [≡ *Cistanthe glauca* (Schrad.) Lilja], was validly named prior to *Calandrinia grandiflora* Lindley [≡ *Cistanthe grandiflora* (Lindley) Schltdl. Because these names generally are considered heterotypic synonyms, *C. glauca* should have priority. Conservation of the name *C. grandiflora* is based on historical preponderance of its application.

4. ***Cistanthe sp. n.***: coastal range valleys, coastal terraces, and beaches, Chile Regions (II? -)IV-V; *annual*, leaves (supra-)basal, strict to sparsely branched bracteates inflorescences less

than 50 cm high; *culms terete*; petals 1-3 cm long, stamens about 30, *stigma much lower than to about the same height as the stamens*. This taxon includes the plants described and illustrated as *C. grandiflora* in Villagrán et al. (2007), based on my erroneous diagnosis. My identification of the annual plants as *C. grandiflora* based purely on deduction. As I could account for the identities of *C. glauca* and *C. laxiflora*, *C. grandiflora* was the only remaining name for plants from this geographic range. I failed to verify the diagnosis of *C. grandiflora*, which indicates suffrutescence. Yet, there clearly is a distinct and definitely annual species in the range shared with *C. grandiflora* and *C. laxiflora*.

There are three forms of the annual species. Whether this variation represents plasticity is not clear. One is an uncommon and more or less prostrate and more succulent form that occurs among herbaceous beach vegetation, e.g., at Zapallar and Huaquén [illustrated in Villagrán et al. (2007)]. Another is a more erect and less succulent form with identical flowers very uncommonly found in low drier sites from the coast to interior valleys of Region V and the Metropolitana Region. Collections 99-945 and 99-977 misidentified as *C. grandiflora* in Hershkovitz (2006) are of this form. The third form comprises somewhat larger plants common during rainy years on the sandy coastal plains between Ovalle and Coquimbo (Region V). Collection 00-144 misidentified as *C. grandiflora* in Hershkovitz (2006) is this form. The flowers are larger and stigma height equals the stamens. These plants are absent drought years, but in rainy years, some populations rival in aspect the carpets of *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk. of the "desierto florido."

As noted above, Reiche (1898) formally recognized only a polymorphic *C. grandiflora* in his *Calandrinia* sect. *Cistanthe* (≡ *Cistanthe* sect. *Cistanthe*). He briefly discussed other named species informally. For a century thereafter, many authors and collectors worldwide, including myself (Hershkovitz 1991a, 1991b,1992), commonly identified any/all individuals of *C.* sect. *Cistanthe* as *C. grandiflora*. The confusion mainly owes to the poor preservation of herbarium specimens, these often just an inflorescence branch and a few moldy or broken leaves. In the field, the species of *C.* sect. *Cistanthe* are remarkably distinct, since they range from annuals to pachycaul shrubs.

It is remarkable that a locally common and conspicuous annual species of *C.* sect. *Cistanthe* has been overlooked throughout two centuries of Chilean botanical exploration. Possibly, as in Hershkovitz (2006), the plants were known but misidentified because of the historical taxonomic ambiguity/confusion within *C.* sect. *Cistanthe* and poor specimen preservation. The oversight probably owes also to its infrequency in the moister southern portion of its range, and the infrequency of adequate precipitations sufficient to spawn the larger and more conspicuous Region IV populations.

5. ***Cistanthe laxiflora*** (Phil.) Peralta & D. I. Ford: *coastal cliffs and outcrops*, Chile Regions IV-V (ca. Cartegena to just south of Fray Jorge); perennial with leafy erect to scandent stems to 2 m, *culms terete*, petals 3-5 cm long, usually magenta but ranging from rose to violet in some populations, *stamens about 75, style prominently exserted, about twice as high as the stamens*. Because of its large size and unique coastal niche, this is perhaps the most conspicuous and recognizable species of *C.* sect. *Cistanthe*. Based on the original description, type locality (Concón; Region V, Chile), and the type specimen in SGO, its identity is not in doubt.

6. ***Cistanthe aegitalis*** (Phil.) Carolin ex Hershk.: *beaches in the vicinity of Fray Jorge and Talinay*, Chile Region IV; perennial, *suffruticose* with (supra-)basal coriaceous leaves, stem leaves markedly reduced to bracteate, overall similar to *C. crassifolia* 200 km to the north but *corollas with magenta centers and pale rose margins*. The identity is not in doubt, as it is the

only *Cistanthe* species at the type locality. The original description and type specimen in SGO match. I did not find *C. laxiflora* or *C. glauca* here.

7. ***Cistanthe crassifolia*** (Phil.) Carolin ex Hershk.: *beaches and coastal bluffs of Chile Region III*, Huasco to Totoral; perennial, *suffruticose on beaches, but on bluffs developing into a pachycaul (sub-)shrub*; corollas pink (southern populations) or white (northernmost populations). The original description, type locality, and type specimen in SGO render diagnosis unequivocal. My suggestion that the species grades into and includes low chamaephytic beach forms is novel and requires confirmation.

8. ***Cistanthe cabrerae*** (Cullen) Peralta: *cordillera, Chile Region III to San Juan Province, Argentina*; perennial with prominently *amplexicaul leaves*. The species is illustrated in Peralta (1993). Its diagnosis is not in doubt.

In addition to the above, there probably exist at least two other forms that will prove to merit acceptance as species. Muñoz (1985) illustrated a plant that she diagnosed as (effectively) *Cistanthe speciosa* (Lehm.) Lilja ex Heyn. Collection 00-91 in Hershkovitz (2006) is this form. Its distinctive features are its very large size and, especially, its bowl-shaped corollas (resembling peonies) with pale pink petals and about 80 stamens. However, I cannot confirm its identity as *C. speciosa*. As noted above, in desert valleys of southern Region III (e.g., along the Panamerican Highway between Cuesta Pajonales and Cuesta Buenos Aires), there occur large suffruticose perennials with coriaceous basal/suprabasal leaves with angled inflorescence culms. The last trait characterizes *C. grandiflora*, but the vegetative form is distinctive.

2A2. *Cistanthe* sect. ***Rosulatae*** (Reiche) Hershk., ***comb. nov.*** ≡ *Calandrinia* sect. *Rosulatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897; lectotype (designated here): *C. longiscapa* (Barnéoud) Carolin ex Hershk. ≡ *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 in Chile, four extending into Argentina (Peralta 1999), one primarily in Peru but now collected in Chile, one endemic to Peru (León 2006), and two in North America (Hershkovitz 1991a). I have collected but not described five forms that probably represent distinct species..

Taxonomy of *Cistanthe*, especially *C.* sect. *Rosulatae*, species is woefully inadequate and the most unsatisfactory and neglected of that of any Portulacineae genus, 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.

2A2a. *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*. In the former, Reiche (1898) included *Calandrinia longiscapa* Barnéoud [= *Cistanthe longiscapa* (Barnéoud) Carolin ex Hershk.], "pata de guanaco;" the most conspicuous species that essentially defines the Atacama Desert's occasional "desierto florido" phenomenon.

In *Calandrinia* sect. *Arenarie*, Reiche (1898) recognized three species, one annual and two perennials. The annual species he recognized as a polymorphic *Calandrinia arenaria* Cham. These annual forms are low elevation plants distributed in Chile's Regions IV-VI. They are found in natural vegetation, but also are weedy, often encountered along roadsides and on cultivated or otherwise disturbed lands. Reiche (1898) included therein eight synonyms, three of which he recognized as distinct varieties. Difficulty of distinguishing between these annual forms was discussed by Philippi (1893a). Reiche (1898) indicated that part of the taxonomic difficulty owed to the incompleteness of the type specimens. The other two species Reiche (1898) recognized were perennials from Chile's Regions VIII-IX, *Calandrinia fenzlii* and *C. solisii* Phil.

However, the type locality of *Calandrinia arenaria* is in fluvial sands of coastal Region VIII. While the life history and root morphology were not described by Chamisso (1831), the short, obviously shriveled caudex/root fragment of the type specimen [*Chamisso s. n.*, "II./III. 1816," "Concepción," Chile [holotype (designated here**)**: HAL!; isotype: K, photo!)] is ca. 3-5 mm broad. I have seen corresponding plants from this area: the root is succulent , ca. 1 cm broad when fresh, and the plant appears to be perennial. Apparently, Reiche had no access to the type specimen, so he would not been able to evaluate its life history. The consequence is that *none* of the central/northern Chilean annual plants commonly currently identified as *Cistanthe arenaria* (Cham.) Carolin ex Hershk. pertain to this species.

A further twist is that the type specimen morphology and locality of *Calandrinia arenaria* otherwise are in good agreement with Philippi's (1893a) description of *Calandrinia solisii* Phil. While Philippi had no access to the type specimen of *C. arenaria*, it is difficult to believe that he did not have Chamisso's (1831) publication in Linnaea. Philippi published in this same journal, had maintained a close correspondence with its editor, Schlectendal, and deposited many of his duplicates in HAL.

A final twist is that Philippi (1893b) was perplexed by herbaceous plants he found and described at the type locality of *Calandrinia spectabilis* Otto & A. Dietr., fluvial sands in coastal Region VIII. From Philippi's account, these also correspond to both *Calandrinia arenaria* and *Calandrinia solisii*. *Calandrinia spectabilis* was described as suffruticose with a 30 cm high stem, as well as its large organ dimensions (Otto & Dietrich, 1833). It seems to belong to *Cistanthe* sect. *Cistanthe*. There is no type specimen. Reiche (1898) listed it in synonymy with *C. grandiflora*, but the only plants of *C.* sect. *Cistanthe* that conceivably could extend to Region VIII are the coastal succulent forms of *C. mucronulata* (see discussion of this species above).

Although perplexed, Philippi evidently believed that the herbaceous plants were *Calandrinia spectabilis*, lest, no doubt, he would have described them as a distinct species. Philippi (1893a) did not mention these plants in his description of *C. solisii*, which he described from a herbarium collection, not his own. Thus, it seems that Philippi (1893a, b) overlooked the type locality of *Calandrinia arenaria*, lest he would have realized that it was the same as the locality of the plants that puzzled him and also the type locality of *Calandrinia solisii*.

In any case, this information is sufficient to diagnose *Cistanthe arenaria* as a somewhat succulent perennial from Chile's Region VIII. It differs from its latitudinal perennial neighbor *C.*

fenzlii (Barnéoud) Carolin ex Hershk. in its less woody caudex and lower elevational range (< ca.200m versus > ca. 500 m). Additional investigation may reveal greater intergradations between these taxa. *Calandrinia lancifolia* Phil. from Angol (Region IX; base elevation ca. 200 m) was described in the same publication as *C. solisii*, but it was described as being more woody at the base (Philippi, 1893a). Reiche (1898) included *Calandrinia lancifolia* in synonymy with *C. fenzlii*. Additional research may indicate that all of these forms are best treated as *C. arenaria*, possibly distinguished as varieties.

Thus, the taxonomy of the highly variable and relatively common annual plants of this affinity in Chile's Regions IV-VI remains completely in limbo. Hershkovitz (2006) briefly comments on two common forms in Region IV identified as *C. arenaria*. Both have the distinctive leaf form described by Reiche (1898), oblanceolate, differentiated into a rhombic blade portion apically, and tapering basally. One is "large," with stems extending ca. 40 cm and leaves ca. 5 cm long and up to 2 cm broad. The other is "small," all vegetative dimensions about one half those of the large form. The floral dimensions of the large form are similar to but somewhat smaller than those of the small form, and the flowers also differ in petal color and stigma color/morphology. However, in precordilleran Region Metropolitana, I have found only a single annual form highly variable in size, spanning the extremes demarcated above. I do not doubt the specific distinction of the Region IV plants. The Metropolitan plants may be a plastic form of one of them.

Unfortunately, all of my research collections (1998-2006), including all vouchers cited in Hershkovitz (2006), were removed from their storage in the University of Chile a total of five times. I recovered the specimens four times, but the final time, I was unable to rescue them from the trash. These collections contained at least ten undescribed species, whose descriptions now await recollection. This will be difficult to accomplish, because these mostly annual plants were collected during the very occasional rainy years in northern Chile, and are absent during the intervening drought years.

In the meantime, however, it is possible to revalidate two of the taxa that Reiche included in synonymy with *C. arenaria*. The forms are very different from each other and from the common annual *C. arenaria* form described by Reiche (1898). But neither can pertain to *C. arenaria*, based on the diagnosis and distribution of the latter described above. I provide necessary recombinations below.

Cistanthe chamissoi (Barnéoud) Carolin ex Hershk., ***comb. nov.*** ≡ *Calandrinia chamissoi* Barnéoud in Gay, Fl. Chil. 2(4): 497-498. 1846 [1847] ≡ *Calandrinia arenaria* var. *chamissoi* Reiche, Fl. Chil. 2:346. 1898 ≡ *Claytonia chamissoi* (Barnéoud) Kuntze, Rev. Gen Pl. 1 56: 1891; holotype: *Bertero 1348,* "Quillota," Chile (P!).

Reiche (1898) recognized this taxon as a variety of *C. arenaria*, distinguished by its sublinear leaves merely dilated at the apex and its smaller flowers bearing fewer stamens. My extensive field observations indicate that it is a distinct species from the larger-flowered annual forms with larger flowers, though the point is moot given that these forms are unnamed, also. The flowers bear five stamens and the stigma is not much broader than the style, subcapitate, and pale. The larger-flowered and broader-leaved plants usually have more than ten stamens and the stigma is larger and prominently lobed/sulcate and deeply colored. The plants grow together with large-flowered forms on disturbed ground. On less disturbed ground, the two species also tend to segregate, *C. chamissoi* preferring gray, limey substrate and the large-flowered forms brownish, granitic substrate.

Cistanthe venulosa (Hook.& Arn.) Carolin ex Hershk., ***comb.nov.*** ≡ *Calandrinia venulosa* Hook. & Arn., Bot. Misc. 3: 336. 1833, holotype (designated here): *Cuming 514*, "Valparaiso" (K, photo!); syntype: *Bridges s. n.*, "Valparaiso" (K, photo!).

Among the synonyms Reiche (1898) included in *C. arenaria* is *C. venulosa*. Given the characteristics of the evidently annual *C. venulosa*, along with the confused taxonomic identity of the evidently perennial *C. arenaria*, I revalidate its name. In my travels in Chile's Regions IV-V, I have found that annual plants of this complex generally are of the so-called annual *C. arenaria* form (rhombic leaf blades, large flowers) or the *C. chamissoi* form (linear leaves, small flowers). As evident from the type and description, *Cistanthe venulosa* has large flowers but narrowly linear leaves, hardly or at all dilated at the apex. I have seen such plants rarely, e.g., south of Chincolco, Region V (formerly Valparaiso Province), Petorca Province.

Cistanthe oblongifolia (Barnéoud) Carolin ex Hershk., ***comb. nov.*** ≡ *Calandrinia oblongifolia* Barnéoud in Gay, Fl. Chil. 2(4): 482-483. 1846 [1847].

This species pertains to the Andinae group of Reiche (1898). As I described in Hershkovitz (2006), I observed in the Cordillera Doña Ana (Region IV, Chile) fertile annual hybrids between the perennial *C. oblongifolia* and the annual *C. humilis* (Phil.) Peralta. The hybrids appear at the altitudinal border of their ranges. These hybrids thus present the potential for establishing a new hybrid species.

2A2b. *Cistanthe* sect. ***Rosulatae*** (Reiche) Hershk. subsect. ***Thyrsoideae*** Hershk., ***subsect. nov.***; lectotype (designated here): *C. thyrsoidea* (Reiche) Peralta and D. I. Ford ≡ *Calandrinia thyrsoidea* Reiche.

Six annual and one perennial species, including the Chilean *Cistanthe thyrsoidea* and *C. cephalaphora*, the North American *C. maritima* (Nutt.) Carolin ex Hershk. and *C. guadalupensis* (T.R. Dudley) Carolin ex Hershk., and probably the Peruvian *C. lingulata* (Ruíz & Pav.) Hershk. I have seen an unaccessioned specimen from Region I of Chile.

This section includes the remaining unaccounted species of Reiche's (1898) *Calandrinia* sect. *Rosulatae* except *C. cachinalensis* (see above). Relations of most of the species are 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* 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 rather larger and showy flowers, and *C. guadalupensis* is a pachycaul shrub.

2B. ***Montiopsis*** Kuntze, Rev. Gen. Pl. 3(2): 14. 1898; type: *M. boliviana* Kuntze ≡ *M. cumingii* (Hook. & Arn.) D. I. Ford ≡ *Calandrinia cumingii* Hook. & Arn.

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, 1993). I hypothesize that this residual support reflects loci related to the morphological similarities of these taxa.

Hershkovitz' (1993) 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. However, he 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).

2B1. ***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. 18 annual and perennial species, primarily in Chile, several extending into Argentina, one extending also into Bolivia (Ford 1992).

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

2B2. ***Montiopsis*** subg. ***Dianthoideae*** (Reiche) D. I. Ford, Phytologia 74: 277. 1993 ≡ *Calandrinia* sect. *Dianthoideae* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897; type: *M. cistiflora* (Gillies ex Arn.) D. I. Ford ≡ *Calandrinia cistiflora* Gillies ex Arn.

At least four perennial species in Chile and Argentina (Ford 1992).

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

2C. Calyptridinae Hershk., ***tax. nov.***; type: *Calyptridium*.

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. lato 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, 1993) classified *Calyptridium* and *Philippiamra* as 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.

2C1. *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: *C. monandrum* Nutt. in Torr. & A. Gray ≡ *Cistanthe monandra* (Nutt. in Torr. & A. Gray) Hershk.
= *Spraguea* Torr., Smithsonian Contr. Knowl. 6: 4. 1853.

About 12 annual and perennial species of western North America, mainly California, *C. parryi* A. Gray having four recognized allopatric varieties (Hinton 1975; Guilliams 2009; Guilliams et al. 2011; Guilliams & Miller 2014).

Given the allopatry on morphological distinctions among the varieties of *C. parryi*, possibly these varieties are better classified as distinct species. Molecular data (Hershkovitz 2006, 2018a; Guilliams 2009; Ogburn & Edwards 2015) evidence two clades in the genus corresponding to the morphological distinctions (Hershkovitz 1991a,b) between the species referable to the segregate genus *Spraguea* and the remaining species of *Calyptridium*. Thus, *Calyptridium* here is divided into three sections.

2C1a. *Calyptridium* sect. *Calyptridium*

Eight 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).

2C1b. *Calyptridium* sect. *Spraguea* (Torr.) Hershk., ***comb. nov.*** ≡ *Spraguea* Torr., Smithsonian Contr. Knowl. 6: 4. 1853; lectotype (designated here): *C. monospermum* Greene.

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. 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. These species hybridize and introgress in at least some locations along their ca. 1000 km contact zone (Hinton 1975). However, the reduction of seed number to one in *C. monospermum* suggests that this species is derived.

2C1c. *Calyptridium* sect. *Thingia* (Hershk.) Hershk., ***comb nov.*** ≡ *Thingia* Hershk., lectotype (designated here): ***Calyptridium ambiguum*** (S. Watson) Hershk., ***comb. nov.*** ≡ *Claytonia ambigua* S. Watson, Proc. Amer. Acad. Arts 17: 365(-366) ≡ *Calandrinia ambigua* (S. Watson) Howell, Erythea 1: 34. 1893 ≡ *Cistanthe ambigua* (S. Watson) Carolin ex Hershk., Phytologia 68: 269. 1990 ≡ *Thingia ambigua* (S. Watson) Hershk.

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.

2C2. *Thingia* Hershk., ***gen. nov***.; lectotype (designated here): ***Thingia ambigua*** (S. Watson) Hershk., ***comb. nov.*** ≡ *Claytonia ambigua* S. Watson, Proc. Amer. Acad. Arts 17: 365(-366) ≡ *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.

Diagnosis: Plants annual, rosettiform with branched flowering branches, leaves succulent with three-dimensional leaf venation, the apical 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, seeds several, black, smooth, shiny, embryo 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 name 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 a "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.

2C3. *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): *P. pachyphyllum* (Phil.) Kuntze ≡ *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 the Atacama Desert region, northern Chile, and adjacent San Juan Province, Argentina (Hershkovitz 1991a; Peralta 1999).

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, Chile's Regions II and III, extending to the northern province of Region IV. The exploration difficulty posed by infrequent rain thus is exacerbated most. 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. The specimens in Argentina have been identified as *Cistanthe densiflora* (Peralta 1999), but I have cultivated a specimen from seed. It is a distinct species, differing from *C. densiflora* in having leaves with firm texture, sharp-angled margins, deltoid shape, acute apex, and glossy luster, these traits similar to those of certain *Echeveria* DC (Crassulaceae) species. Leaves of *C. densiflora* have a spongy texture, oblanceolate shape, rounded apex, and matte luster.

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. Retreating from here, other *Philippiamra* species appear along with species of *Cistanthe* sect. *Rosulatae*. Thus, *Philippiamra celosioides* may be the world's most drought-tolerant ephemeral vascular plant.

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.

I provide here taxonomically necessary combinations:

Philippiamra arancioana (Peralta) Hershk., ***comb. nov.*** ≡ *Cistanthe arancioana* Peralta, Gayana Bot. 52: 45. 1995.

Philippiamra calycina (Phil.) Hershk., ***comb. nov.*** ≡ *Calandrinia calycina* Phil., Fl. Atacam. 21. 1860 ≡ *Cistanthe calycina* (Phil.) Carolin ex Hershk., Phytologia 70: 220. 1991.

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

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

Philippiamra salsoloides (Barnéoud) Hershk., ***comb. nov.*** ≡ *Calandrinia salsoloides* Barnéoud in Gay, Fl. Chil. 2(4): 502-503. 1846 ≡ *Cistanthe salsoloides* (Barnéoud) Carolin ex Hershk. in Phytologia 68: 269. 1990.

2C4. *Lenzia* Phil., Linnaea 33: 222. 1864; lectotype (designated here): *L. chamaepitys* Phil.

One perennial species of Chile, Regions III and IV, above 3000 m (Hershkovitz 2006).

As noted in Hershkovitz (2006), this peculiar acaulescent and evidently finely rhizomatous plant (Hershkovitz 2006) bears no obvious morphological similarity to other Calyptridinae. I have never seen a flowering individual of this taxon, hence cannot verify the reported reproductive morphology (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. Found between 2500-3500 m on Andean slopes of Chile's Region IV, it evidently is resistant to extremes of both high and low temperatures and high (i.e., snowmelt) and low moisture.

3. Phemerantheae Hershk., ***tax. nov.***; type: *Phemeranthus* Raf.

3A. *Phemeranthus* Raf., Specchio Sci. 1: 86. 1814 ≡ *Talinum* sect. *Phemeranthus* (Raf.) DC., Prodr. 3: 356. 1828; type: *P. teretifolium* (Pursh) Raf. ≡ *Talinum teretifolium* Raf.

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

Phemeranthus is sister to remaining Montiaceae (Ogburn & Edwards 2015; Hancock et al. 2018). Its largely North American distribution is 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. The question of *Phemeranthus* origins may rest upon the relations of the Argentine-endemic *Schreiteria* (see below).

3B. ***Schreiteria*** Carolin, Parodiana 3: 330. 1985; type: *S. macrocarpa* (Carolin) Speg. ≡ *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) analysis found the monotype to be sister to *Talinum* s. stricto. 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. These traits characterize species of *Phemeranthus*.

Incertae sedis

Diazia Phil., Fl. Atacam. 22. 1860, lectotype (designated here): *D. portulacoides* Phil.

Based on the protolog and illustration, I cannot diagnose the genus or even family of *Diazia* [cf. Reiche (1898: *499*)].

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