

CONFOUND IT! The taxonomy of plants mistaken for *Cistanthe arenaria* (Cham.) Carolin ex Hershk. [MONTIACEAE, *Cistanthe* sect. *Rosulatae* (Reiche) Hershk.]

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ABSTRACT

Cistanthe arenaria (Cham.) Carolin ex Hershk. is a species of Montiaceae distributed from Chile's Maule to Araucanía Regions. But the name historically and currently has been applied also to readily distinct species distributed from the Libertador Bernardo O'Higgins to Coquimbo Regions: *C. chamissoi* (Barnéoud) Carolin ex Hershk., *C. trigona* (Bertero ex Colla) Carolin ex Hershk., *C. vicina* (Phil.) Carolin ex Hershk., and *C. subverticillata* (Phil.), ined. (\equiv *Calandrinia subverticillata* Phil.). The source of this confusion traces to two 1833 works by Hooker & Arnott and Lindley. Here, the taxonomy and diagnostic characteristics of these species are clarified.

Key words: *Cistanthe*, Montiaceae, Chile

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Introduction

The name *Cistanthe arenaria* (Cham.) Carolin ex Hershk.¹ [*C. sect. Rosulatae* (Reiche) Hershk.; Montiaceae] currently is applied to herbaceous plants distributed broadly in Chile from the Atacama Region to the Araucanía Region (Rodríguez et al., 2018). The limits of these regions span 25.3–39.6°S, or ca. 1580 km. However, HersHKovitz (2018a) reported that the identity of *C. arenaria* had become confused historically, and that this species, described from Concepción, Chile (ca. 36.5°S; Biobío Region), was restricted to the southern portion of the range reported by Rodríguez et al. (2018).² Plants from the more northerly portion of the distribution pertain to *C. trigona* (Bertero ex Colla) Carolin ex Hershk.³ (Fig. 1), *C. chamissoi* (Barnéoud) Carolin ex Hershk. (Fig. 2), *C. vicina* (Phil.) Carolin ex

¹ HersHKovitz (1991a) published the combination erroneously as "*Cistanthe arenaria* (Diels) Carolin ex Hershk.," a copy-paste error. However, the basionym *Calandrinia arenaria* Cham. and its citation were given correctly, hence it seems to fall in the realm of "correctable error" per ICN (Turland et al., 2018). The error is not mentioned in the International Plant Names Index (www.ipni.org), which gives the same citation but the correct combination.

² In addition, the Flora Cono Sur database (Zuloaga et al., 2008) indicates that *C. arenaria* also occurs in Argentina, and it cites a specimen (*N.M. Bacigalupo 11617*), though without indicating the herbarium or Argentinean provenance. The Flora Argentina database (Anton & Zuloaga, without year) likewise lists this otherwise undocumented specimen. Especially given the confused taxonomy of *C. arenaria*, I will not consider further the possible occurrences in Argentina.

³ HersHKovitz (2019a) validated this combination as "*Cistanthe trigona* (Colla) Carolin ex Hershk." This was based on the basionym as listed in International Plant Name Index (www.ipni.org), *Talinum trigonum* Colla. However, Colla (1833 ["1834"]) attributed the authorship to Carlo Bertero "in sched." Stafleu & Cowan (1976: 201) consider Colla's work as "composite," to which Bertero contributed posthumously. Per Article 46 of the ICN, the combination is valid with or without the "ex" designation.

Hershk. (Fig. 3), and *C. subverticillata* (Phil.), ined. (\equiv *Calandrinia subverticillata* Phil.; Fig. 4). These were considered by Rodriguez et al., (2018) to be synonyms of *C. arenaria*. But their combinations thence existed only in *Calandrinia* and *Talinum*, for which reason HersHKovitz (2019a) transferred all but *Calandrinia subverticillata*⁴ to *Cistanthe* Spach.

The present work documents the history of the taxonomy of *C. arenaria*, the cause of its historical confusion, and the distinguishing characteristics of the other species. The first two sections summarize the systematics, distribution, and critical taxonomic characteristics of the genus *Cistanthe*. Then the taxonomy, characteristics, and distribution of species confused with *C. arenaria* are detailed. This articulation permits pinpointing the historical cause of the confusion. Finally, I present a diagnostic key to *C. arenaria* and the species which with it has been confused. The presentation is light years shy of a true systematic revision, but it provides a foundation for such.

The Taxonomic Milieu: The Genus *Cistanthe* Spach

1. Subgeneric taxonomy of *Cistanthe*.

The genus *Cistanthe* sensu HersHKovitz (2019a) comprises ca. 40 species of succulent annual and perennial herbs or, in two cases, pachycaul shrubs. Carolin (1987) and HersHKovitz (1990, 1991a, b; 1993) had circumscribed the genus more broadly, but subsequent DNA analyses found these circumscriptions to be polyphyletic (HersHKovitz & Zimmer, 1997, 2000; HersHKovitz, 2006; Ogburn & Edwards, 2015). Thus, the current circumscription is restricted to the species that Kelley (1973) classified in *Calandrinia* sect. *Cistanthe* Reiche (nom. superfl., = *C. sect. Grandiflorae* Philippi), *C. sect. Andinae* Reiche, *C. sect. Arenarie* Reiche, and *C. sect. Rosulatae* Reiche. Reiche (1897, 1898a, b) established these sections to classify the Chilean species, and Kelley (1973) expanded their circumscriptions to include the species outside of Chile.

Cistanthe is most diverse and abundant in northern Chile, in particular the Coquimbo and Atacama Regions. Including the taxa described here, my current estimate of the number of species of *Cistanthe* in **total** [and in Chile] is “about” **40** [34]: **12** [10] in *C. sect. Cistanthe*, **21** [21] in *C. sect. Rosulatae*, and **6** [3] in *C. sect. Thyrsoidae*. Rodriguez et al. (2018) recognized only 17 species of *Cistanthe* in Chile, my estimate reflecting more recently described and additional undescribed taxa and otherwise taxon “splitting.” Of the 34 species in Chile, 28 (one of these “probable”) occur in the combined Coquimbo and Atacama Regions: 9 in *C. sect. Cistanthe*, 16 in *C. sect. Rosulatae*, and 2 in *C. sect. Thyrsoidae*. Two *Cistanthe* species occur in Chile only to the north of the Atacama/Coquimbo Regions and four only to the south. The remaining species occur in Argentina, Peru, Mexico, and the US.

HersHKovitz (2006) found that chloroplast and nuclear DNA sequences of *Cistanthe* species sorted among three clades (or monophyletic groups, whichever one prefers; see HersHKovitz, 2021a). This structure also is evident in the analysis of Ogburn & Edwards (2015). HersHKovitz (2019a) classified the clades in two sections, *C. sect. Cistanthe*, equivalent to *Calandrinia* sect. *Grandiflorae*, and *C. sect. Rosulatae*, comprising the other three of Reiche’s *Calandrinia* sections. HersHKovitz (2019a) divided the latter section into two subsections. However, a subsectional name proved to be improper per the International Code of Nomenclature for Plants, Algae, and Fungi (ICN; Turland et al., 2018), hence HersHKovitz (2020a) simply recognized the subsections as sections, adding the name *C. sect. Thyrsoidae*.

⁴ At that time, I had not seen the Type of *C. subverticillata*, and relied on Philippi’s (1894) description, which suggested to me *Cistanthe chamissoi*. John McNeill (E) kindly sent me the Type image, and now I appreciate that it is a distinct species.

Thus, the current circumscriptions of *C. sect. Rosulatae* and *C. sect. Thyrsoidae* do not coincide with those of Reiche's (1897) sections.

Otherwise, the DNA data for *Cistanthe* revealed essentially no significant phylogenetic structure at all. This is to say that observed DNA sequence variation appeared to be essentially “random,” whether the samples represented the most similar or least similar or even the very same *morphological* species. The DNA data for *Cistanthe* and, in fact, other Chilean Montiaceae proved problematic for both theoretical and practical reasons. On the theoretical side, the data did not help in clarifying either species taxonomy or interspecific phylogenetic relationships. This was entirely unexpected given that, in studies of countless other genera, these same DNA markers had routinely contributed significantly to resolution of these problems. So much so, in fact, that they had acquired an international reputation as being “species barcodes” (Hershkovitz, 2021b).

2. Some characteristics of *Cistanthe* species

The genus *Cistanthe* is characterized by distinctive morphological traits. Some of these vary within the genus and can be diagnostic at the interspecific level. I highlight below traits that vary among the species discussed in this work.

Bract/sepal markings. *Cistanthe* species bear black (sometimes purple) lines and blotches on the inflorescence bracts and sepals⁵ (“mottled” according to Watson et al., 2020). These are unique to this genus. The purple color in some species presumably owes to betacyanin pigment. It is not clear whether the black coloration owes to some other compound alone or in combination with betacyanin. Nor, for that matter, it is clear in which cells the coloration is produced/localized.

Leaf morphology. Hershkovitz (1991c) described leaf morphology of *Cistanthe* and Calyptridinae, especially leaf venation. The leaf veins typically are sinuous, and the finest veins have an anatomy that, among foliaceous vascular plants, appears to be unique to *Cistanthe* and certain other Portulacineae genera. They are “ribbon-like,” viz. numerous vascular elements positioned side-by-side in a ribbon one element thick (Fig. 5). The xylem vessel elements distal to the procambium have annular secondary wall thickenings and thus are protoxylem. The elements proximal to the procambium have reticulate thickenings, viz. metaxylem. In between the extremes are elements with somewhat flexible helical thickenings.

The anatomy indicates that the vasculature of the fine veins of *Cistanthe* and Calyptridinae develops/matures relatively slowly, similar to that in primary growth stems, probably over the course of several days. Thus, as the mesophyll cells (i.e., “ground tissue”) expand, the vein xylem elements with annular thickenings stretch. Later-formed vein xylem elements mature after the mesophyll has expanded. Their thickenings are reticulate and cannot expand. In other plants, multiple elements in vascular plant leaf veins are more or less isodiametrically bundled, and the secondary wall thickenings usually are uniform. This indicates that the xylem elements matured simultaneously after adequate mesophyll expansion.

Hershkovitz (1991c) was undertaken using only rehydrated leaves from herbarium specimens, and he thus suggested that the sinuous veins could be an artifact of specimen preparation. But live plants

⁵ Functional sepals of Montiaceae and related Portulacineae are considered to be homologous to inflorescence bracts of related Caryophyllales, Molluginaceae in particular. Montiaceae petals are considered homologous to Molluginaceae sepals. This notion is not “new.” But for this reason, floristic/taxonomic literature has referred to the organs variously as sepals, sepaloids (e.g., Watson et al., 2020), or involucre bracts (see Hershkovitz, 2021b). Personally, I like the more “woke” term “psepals” (“pseudo-sepals”), but I doubt this will catch on.

manifest a possible correlate to the sinuous venation. Living leaves may have a flat/smooth surface relief or the relief may be “wrinkled,” variously termed rugose, bullate (e.g., Fig. 1D) and/or, in the extreme state, gibbous to the point of appearing lobed, as in *C. celedoniana* J.M.Watson & A.R.Flores (Watson et al., 2020).

Leaf surface relief may vary among leaves within individuals and among individuals within species, as noted in HersHKovitz (2022a). This suggests that the sinuous venation may relate, as HersHKovitz, (1991c, 2022a) also suggested, to the hydrological state of the leaf during development. Thus, if leaf water content abruptly increases/decreases during development, the mesophyll would expand/retract. And so would the veins. The early-formed xylem elements, with annular or helical thickenings, would stretch/retract with the mesophyll easily. But the later-formed elements, with scalariform or reticulate thickenings, cannot stretch/retract. If leaf size decreases (“wilts”) with decreasing water content, the veins would *buckle*. This buckling would create surface relief. In the meantime, continued maturation of the leaf epidermis fixes the final leaf dimensions, because the epidermis is not elastic. If maturation occurs in the wilted state, the vein buckling and associated surface relief becomes the final phenotype.

The preceding characterizes variation in leaf surface relief as developmentally plastic. This does not mean that different phenotypic states cannot become “fixed” in a lineage and therefore no longer developmentally plastic. To the contrary, fixation of nominally developmentally plastic phenotypes is a frequent mechanism lineage diversification (West-Eberhard, 2003; cf. HersHKovitz, 2020b), and this mechanism is consistent with Natural Drift evolution as described by Maturana & Mpodozis (2000; Vargas et al., 2020; cf. HersHKovitz, 2019b). In this view, life is defined as an autopoietic condition, and physical living organisms as autopoietic “machines” whose behavior (ontogenetic phenotype) is self-determined *epigenically* (including “epigenetically;” Vargas et al., 2020).

Thus, phenotypes are not determined by “genes,” nor environment, as neo-Darwinian dogma would have it. But genes and environment do constrain the broad range of ontogenetic possibilities manifested by phenotypic plasticity consequent to epigenesis. Phenotypic plasticity, in turn, demonstrates the range of phenotypes that are viable, viz. that do not terminate autopoiesis such that the organism, by definition, dies. However, the genome itself evolves, and may evolve in a way that effectively reduces the range of ontogenetic possibilities, such that plasticity is constrained and a particular phenotypic state becomes at least transitorily “fixed” in a lineage. This is genetic assimilation.

In the present case, this process explains how plastic leaf surface relief variation in some *Cistanthe* species could become a fixed phenotype in others. Evidently, in developmentally plastic species, plants with rugose/bullate/gibbous leaves are perfectly viable, lest the plants would die. This establishes that fixation of this phenotype is permissible. Fixation (genetic assimilation) would be a consequence of permissible changes in genetic architecture that restrict variability in vein length and leaf size, yielding “short leaves” with “long veins” that inherently buckle. This would be the case for *Cistanthe celedoniana*.

Seed morphology. Many *Cistanthe* species have pubescent seeds, either pusticulate-tomentose (PT) or distinctly hairy (H; Kelley, 1973). Carolin (1993) called the pustules of the PT type “polypiform trichomes.” Watson et al. (2020) described the PT type as “papillose” and also described the seed pubescence in greater anatomical detail. For example, under the lupe, PT pustules appear stellate, but in the SEM photos of Watson et al., they manifest complex branching. Watson et al. (2020) also noted that the PT form may appear brownish or whitish. They also described a new phenotype in *Cistanthe*

celedoniana J.M.Watson & A.R.Flores that would be equivalent to PT/H in Kelley's (1973) terminology.⁶ The individual seeds are "mottled" in their words, with PT and H patches.

In any case, seeds of all species of *Cistanthe* sections *Cistanthe* (except one⁷) and *Thyrsoideae* have H seeds, while those of *C. sect. Rosulatae* can be H, PT, or glabrous. The testa surface of glabrous forms betrays additional variation perhaps occluded by pubescence, ranging from smooth and shiny to "granular" opaque to reticulate to tuberculate (Kelley, 1973; Hershkovitz, unpublished; see also Watson et al., 2020). The species considered here vary in seed surface morphology: seeds in two species are glabrous, in one species H, and in three species PT. The systematic significance of this variation is discussed later.

Stem morphology and movements. Another trait of *Cistanthe* species that now impresses me, one not evident from the herbarium material I studied exclusively as a grad student, is the swollen succulent base of flowering stems (Figs. 1D–E), which is reminiscent of a ball joint. I mentioned this trait in my description of *Cistanthe philhershkovitziana* Hershk. (Hershkovitz 2018b). The stem base is swollen whether the flowering stem arises terminally from the basal rosette or in basal leaf axils. The mature flowering stems often diverge at an angle oblique to the axillary or terminal bud angle from which the stem emerges. In higher order branches, the swollen base is less prominent, but it is evident even in the pedicels. Prominently swollen stem/branch bases seems to be nearly universal among *Cistanthe* species. But the feature is notably absent in *Cistanthe floresiorum* J.M.Watson, a feature I noticed in the field 20 years ago and evident in photos in Watson (2019).

The swollen stem base may be associated with tropic/nastic stem movements.⁸ Watson et al. (2020) reported that flowering stems of *C. celedoniana* are prostrate from late afternoon to noon the next day but raise themselves during mid-day to late afternoon. They attributed this to tropic and/or nastic movement. In other taxa, such movements often are effected by adjustment of general or anatomically localized turgor pressure in specialized cells/tissues. The swollen stem base would be the obvious candidate for turgor adjustment in the case of *C. celedoniana*, but this implies mechanical flexibility that ought to manifest by manual manipulation.

I have not followed diurnal stem movements in *Cistanthe* species and have not studied *C. celedoniana* at all. But I have found that, in other species, the stem angle *seems* generally more or less fixed and unyielding when mechanical pressure is applied, and that the established angle varies among plants within a population. This was the case I found for plants in a microenvironmentally heterogeneous

⁶ While Watson et al.'s (2020) description and illustrations of *C. celedoniana* seeds are illuminating in the above respect, I find their other data to be problematic. In particular, they indicated in both the text and figure captions that their scanning electron micrographs in Figs. 53–61, which seem to show four *different* seeds with *different* pubescence morphology, *all* pertain to *C. celedoniana*. Indeed their Figs. 53–54 resemble the seeds in the light micrograph of *C. celedoniana* seeds in their Fig. 52. These manifest the described patches of distinct hairs and smaller papillae or pustules. But their Figs. 55–59 show two different seeds having pure H pubescence, while their Figs. 60–61 show a seed with "classic" PT pubescence. However, Watson et al. (2020) reported that they examined seeds in *three* species besides *C. celedoniana*, viz. *C. crassifolia* (Phil.) Carolin ex Hershk., *C. grandiflora* (Lindl.) Schldtl., and *C. arenaria*.⁶ And they described the pubescence in these as, respectively, *effectively* H, H, and PT, with the last characterizing the pubescence as having "coralloid branching." And these are *exactly* the morphologies illustrated in their Figs. 55–61. It seems possible, therefore, that these figures illustrate seeds from these three species and are mislabeled.

⁷ *Cistanthe lamprosperma* (I.M.Johnst.) Peralta & D.I.Ford has glabrous seeds (Johnston, 1929).

⁸ Tropic and nastic movements are influenced environmentally. Tropic movements are directional in relation to the environmental stimulus, e.g., light direction. Nastic movements are nondirectional, e.g., flowers opening relative to light quantity/quality.

population of *C. trigona*. The flowering stem of an especially prostrate individual growing on packed substrate on a road shoulder seemed to be fixed in the horizontal position (Fig. 1D–E), whereas flowering stems of nearby plants growing in other circumstances were held more erect. Days later, in the comfort of my rented room, I found that the stem of the prostrate individual seemed permanently horizontal. I cannot imagine that it would have levitated at night. But I could be wrong. I did not make the observation in the field.

But there is no reason why a *different* species or even different stems of the same species cannot have more flexible stems that change position tropically/nastically. Indeed, I have observed this, again in the comfort of my rented room, where I put in my windowsill live collections of *Cistanthe vicina* and “*C. sp. nov.*” The flowers of these species are oriented at a positive angle relative to the horizontal, viz. lateral to upwards. After flowering, and much to my dismay, the young fruits become oriented to a negative angle, viz. pendent to eventually vertically downward. I was concerned that the seeds would dehisce into the water of the containers. Much to my surprise, as the capsules became nearly mature, the pedicels reoriented absolutely vertically upwards (Figs. 3K–L, 6). The capsule valves split, forming an erect cup, and the seeds awaited my harvest. An identical movement series also was reported and illustrated for *Cistanthe floresiorum* (Watson, 2019: Fig. 45).

However, the behavior of the pedicels in fruit in these species contrasts markedly with that in *Cistanthe philhershkovitziana* and to a lesser extent in other species of *C. sect. Cistanthe*. In *C. philhershkovitziana*, the pedicels in fruit become oriented vertically *downward* (Hershkovitz, 2018b). In *C. chamissoi* and *C. chrysantha* (I.M.Johnst.) Peralta & D.I.Ford, the fruits retain more or less the same horizontal orientation as the more or less prostrate flowering stems that bear them. A similar infrageneric contrast occurs in *Calandrinia*. In *Calandrinia jompomae* Hershk., the flowers are oriented laterally, but the distal portion of the pedicel becomes curved vertically upward in fruit (Hershkovitz, 2020c, 2022b). In contrast, in the closely related *C. nitida* (Ruiz & Pav.) DC, the contrary, the pedicels curve downward and, in prostrately-oriented plants, are suggestive of violet fruits.

The variation in stem movements within individuals, among individuals, and among species is another example of evolution mediated by developmental plasticity, as described above.

“Weediness.” Hershkovitz (2019a) noted that species of several Montiaceae genera tend to be weedy, although Hershkovitz (2020b) cautioned that weediness per se does not predict the circumstances under which a species actually colonizes new territory. Hershkovitz (2020b) attributed this unpredictability to *idiosyncraticity*, a consequence of organismal *self*-determination, in turn a consequence of autopoiesis (see above).

Several species of *Cistanthe* might be considered “weedy,” and these include the four species of north-central Chile discussed here, viz. *C. chamissoi*, *C. subverticillata*, *C. trigona*, and *C. vicina*. I consider them weedy because they occur commonly and abundantly on human-disturbed sites, such as roadsides, grazed pastures, cultivated lands, and “waste places” near constructions. But the historical *cause* of colonization is difficult to establish.

In the case of “weedy” Chilean Montiaceae, it is important to note that they are “native weeds,” i.e., autochthonous. They are good colonizers in a landscape that inherently favors good colonizers. Landscapes in north-central to northern Chile are not only *relatively* open overall, their ecological instability constantly creates local landscape patches that are transitorily unoccupied by plants. This is a consequence of the combination of high year-to-year fluctuation in precipitation and high relief that potentiates the destructive power of water flows during periodic wet El Niño years. Meanwhile, the Pacific Ocean nibbles its way into the fragile coastal landscape.

In this context, evidently many Montiaceae species, including *Cistanthe* species, have performed well, holding their own in anthropogenically disturbed habitats even against globally notorious alien invaders. But plants cannot discriminate per se between “natural” disturbances and anthropogenic ones. Hershkovitz (2022a) remarked that, during rainy years in the Coquimbo Region, *Cistanthe philhershkovitziana* is abundant in roadcuts along the shoulder of the Pan American Highway, which runs along the coast west of the coast ranges in the Coquimbo Region. This highway originally was constructed in the 1960s as a narrow two-lane road. Before that, there was no road here. The Pan American highway replaced was a largely dirt road that ran *east* of the coast ranges. The current highway is a freeway that was constructed in ca. 2000 along partly the same and partly different alignment as the former highway. The current roadbed is about four times wider. Thus, the presence of *C. philhershkovitziana* along the Pan American Highway, especially along the more recently excavated roadcuts, *must* be anthropogenic. Hershkovitz (2022a) suggested that this was because, during rainy years, the roadcuts actually simulate a natural habitat of this species, viz., fluvial margins.

The significance this natural weediness is that it renders difficult, if not impossible, to infer the original “natural” distribution of all four of the species of north-central Chile discussed here. Clearly the species are capable of colonizing *recently* anthropogenically disturbed habitats. But, as Hershkovitz (2019a) pointed out, habitats in north-central Chile have been anthropogenically disturbed for many thousands of years. Moreover, the presence of species on anthropogenically disturbed sites does not demonstrate anthropogenic *introduction*. In other words, the plants may have spread into such sites by natural means.

Taxonomy of *Cistanthe* species pertinent to Reiche’s *Calandrinia* sect. *Arenarie*⁹

As its name indicates, *Calandrinia* sect. *Arenarie* is the autonomous section for its consequently default Type, *C. arenaria*, the species of central interest here. Hershkovitz (2006) found no evidence for a clade corresponding to *Calandrinia* sect. *Arenarie*, hence Hershkovitz (2019a) submerged it into *Cistanthe* sect. *Rosulatae*. Rodriguez et al. (2018) referred all species names pertinent to *Calandrinia* sect. *Arenaria* to two species: *Cistanthe arenaria* and *C. fenzlii* (Barnéoud) Carolin ex Hershk., each with multiple synonyms. These species thus proxy for *Calandrinia* sect. *Arenarie*. However, *C. fenzlii* reportedly is restricted to the Biobío and Araucanía Regions (Rodriguez et al., 2018) and evidently is not common. And, indeed, sometimes specimens of *C. fenzlii* have been identified as *C. arenaria*. Thus, *C. arenaria* alone as currently classified nearly proxies for the entire section.

⁹ Though 125 years old, and already inadequate then, Reiche (1897, 1898a, b) remains the most recent and therefore the *current* taxonomic revision of Chilean species of *Cistanthe*. Nonetheless, Reiche’s work represented a milestone advance over earlier work that emphasized descriptions of new species of *Cistanthe* as *Calandrinia* sensu Candolle (1827, 1828; see Hershkovitz 2021b). Earlier, Philippi (1893, 1894) attempted to recognize sections within Chilean *Calandrinia*, and, as Hershkovitz (2019a) noted, Philippi’s *Calandrinia* sections *Amarantoideae*, *Caespitosa*, and *Grandiflorae* have priority over Reiche’s (1897) *Calandrinia* sections *Amarantoideae* (= *Philippiamra*), *Acaules*, and *Cistanthe* (≡ *Cistanthe* sect. *Cistanthe*). Philippi (1894), however, seriously goofed in the case of the species Reiche classified in *Calandrinia* sect. *Arenarie*, which Philippi referred to an unnamed group effectively “typified” by *Calandrinia axilliflora* Barnéoud [= *Calandrinia nitida* (Ruiz & Pav.) DC; *Calandrinia* sect. *Calandrinia*; Hershkovitz, 2019a]. Moreover, Philippi (1894) included in this group *Calandrinia glauca* Schrad. ex DC [= *Cistanthe glauca* (Schrad. ex DC) Lilja, = *Calandrinia grandiflora* Lindl., nom. cons. ≡ *Cistanthe grandiflora* (Lindl.) Schltd.]. But he propagated Barnéoud’s erroneous *description* of *C. glauca*, which refers to *Calandrinia jompomae* Hershk. (*Calandrinia* sect. *Calandrinia*; Hershkovitz, 2020b, 2022a). If you were able to follow this, you get an “A” in taxonomy.

1. Characteristics of species pertinent to *Calandrinia* sect. *Arenarie*

Species pertinent to *Calandrinia* sect. *Arenarie* are rosetiform and mostly spreading herbs rather smaller and/or less conspicuous than the more familiar “patas de guanaco,” species of *C.* sect. *Cistanthe* and *C. longiscapa* (Barnéoud) Carolin ex Hershk. Their flowers are similar, but usually are ca. 5–20 mm broad, rather than the 20–40 mm broad of other species. The leaves commonly have a peculiar morphology, differentiated into an apical laminar portion that often is *rhombic* in shape, and a basal broad petiolar portion. Because of their smaller size, plants referred to *C. arenaria* sometimes have been called “patitas de guanaco.”

Like most other *Cistanthe* sect. *Rosulatae* species, those pertinent to *Calandrinia* sect. *Arenarie* commonly have secondary leaf rosettes at some point along the length of the axillary flowering stems, the latter arising from basal leaf axils. The secondary rosette recapitulates the basal rosette and, similarly, terminates in a cyme. This trait occurs in all species but not all individuals. In particular, in some instances, the plant matures precociously, such that the basal rosette itself terminates in a cyme, and there are no axillary flowering stems (Figs. 3P, 4H, J). These forms are thus caespitose. Thus, the rosette itself can be conceived of as a “module” that reiterates on axillary branches as an imperfect “fractal.” Whether or not axillary flowering stems with secondary rosettes develop is a consequence of developmentally plastic variability in the growth of the primary rosette. Via genetic assimilation, there might be a potential for the evolutionary fixation of a completely caespitose form, but this does not seem to have occurred among *Cistanthe* species.

The relative and absolute distance between the secondary rosette, the flowering stem base (i.e., the proximal portion), and the cyme (i.e., the distal portion) is variable. Also variable is the quantity of nodes along the proximal and distal portions of the flowering stems and the quality of foliar appendages that appear at the nodes. At one extreme, nodes may be absent. When they are present, the foliar appendage may be a bract or a leaf, and both bracts and leaves might occur along the same flowering stem. Leaves tend to develop along the proximal portion of the flowering stem, but they also may occur along the distal portion.

2. “Materials and Methods:” the taxonomic analytical approach

HersHKovitz (2018a) noted that the taxonomy of *C. arenaria* is problematic. In fact, consequent to discrepancies/ambiguities dating back to Hooker & Arnott (1833) and Lindley (1833), taxonomic designations as *C. arenaria* in all modern scientific and popular publications, databases, and other internet documents, including my own (HersHKovitz, 1991a, b; 2006) are confused and substantially incorrect. For this reason, this work provides a *preliminary* clarification of the taxonomy of plants identified as *C. arenaria*. The summary is somewhat simplistic given the complexities/subtleties I have observed, but it establishes a new taxonomic scaffold that represents a significant advance over the existing taxonomy.

For purposes of the present work, original species descriptions and images of Type specimens were obtained for all taxa pertinent to *Calandrinia* sect. *Arenarie* and one additional pertinent taxon that Reiche classified in *Calandrinia* sect. *Rosulatae*. This information was tabulated according to original names. Using general (Google) and specialized (e.g., iNaturalist¹⁰) search tools, the internet was screened for images and locality data of live plants of pertinent taxa. The information, supplemented by my extensive unpublished field notes, was synthesized using the time-honored “intuitive” taxonomic method in order to generate a revised scheme of the taxonomy and geography of Reiche’s (1898a, b) *Calandrinia* sect. *Arenarie*.

¹⁰ <https://www.inaturalist.org>

Table 1 lists the names, references, homotypic synonyms, Type material, and Type localities of all taxa pertinent to *Calandrinia* sect. *Arenarie*, along with certain critical comments, especially with regard to growth form and seed surface morphology. The data in Table 1 form the basis for the analysis below.

Here I must interject a commentary about the “species concepts” I apply in the present analysis. This topic is far too broad to address in any detail here. I have offered comments elsewhere (HersHKovitz, 2019a, b, 2021b). Here I simply speak to the critique of Luckow (1995), who lamented that, in the wake of endless proposed theoretical and/or empirical criteria for species recognition/delimitation, the criteria applied in *actual* taxonomies of the world’s biota generally is unspecified. This is certainly the case for Montiaceae, so the question of species ontology becomes a red herring (HersHKovitz, 2019a).

In the analysis that follows, I derive *operational* species using the *typological* species concept. I do not address per se the *ontology* of species. By operational, I mean *heuristic*, e.g., for discrimination/identification in taxonomic/floristic references, for discovery of new forms, and for scientifically *valid* derivative studies. The latter would include, for example, phylogenetic, geographic, and ecological analysis, but *excluding* those that defer to unscientific anthropocentric parameters, such as the Flora of an area arbitrarily delimited by 17–18th Spanish kings and, thereafter, late 19th Century geopolitical treaties (HersHKovitz, 2019a: 38).

As another example of an invalid operation upon the operational species is any ecological/evolutionary analysis that assumes tacitly or explicitly that species are statistical units (cf. HersHKovitz, 2019a: 2), or that assume incorrectly that the ecological/evolutionary behavior/trajectory of species is a function of statistical means of their traits, including ecological traits, such as incident temperature or rainfall (HersHKovitz, 2019a, 2020a). Statistical ecological/evolutionary analyses may have certain heuristic value, but autopoiesis dictates that life itself is a determinate process. It is influenced by stochastic processes, but organismal behavior/evolution itself is *not* a stochastic process. Organisms behave and evolve *idiosyncratically* (HersHKovitz, 2019a, 2019bm 2021b).

The *typological* species concept is inherent in the ICN, which many naïve taxonomists consider anachronistic and obsolete. Yet, it is philosophically brilliant. The nature, or *ontology*, of biological “species” remains one of the great unresolved questions of all of science, and there are “countless” species definitions/concepts, none of which “work” in practice. Yet the typological concept *always* works. The reason that it works is that it is the “natural” constitutive taxonomic algorithm that we all express and apply not only to classification of organisms, but to all objects. We focus on and analyze whether axiomatically infinitesimally small but observable points in space are the *same* points or *different* ones. In the case of organismal classification, the smallest point is the organism itself. Hence we have the Type, something that the brain files in a unique place. Because humans tend to perceive and process knowledge similarly, our brains tend to file raw perceptions similarly. Typological taxonomy thus is inherently more stable than taxonomy based on species concepts that require additional learning, myriad additional observations and *inferences*, and more complex cognitive processing. In this case, taxonomy is bound to diverge and become broadly incomprehensible to the point of being useless.

Per ICN, the typological concept specifies that the name of a species corresponds to the name of its physical Type specimen, here denoted Type with a capital “T.” The Type specimen represents a single individual that is purported to not belong to the same species as any other thus named Type. HersHKovitz (2019a, 2021b) used the term “apospecies” to refer to the Type. The ICN requires that one or more differences between each Type be explicitly stated in its *diagnosis*.¹¹ Thus, regardless of what taxonomists

¹¹ Naming of a new species requires designation of a Type and a prosaic diagnosis or description, but the latter need not be accurate. Only the Type itself has currency.

believe to be the cause of species or the underlying basis of species, when classifying an individual, per ICN, they are doing nothing more or less than deciding whether that individual is conspecific (“synspecific” sensu HersHKovitz, 2019a, 2021b) to a Type or, alternatively, is apospecific. There is no escaping this.

For neurobiological reasons, we tend to confuse the species defined by Types, whose identities are fixed and permanent, with operational *taxonomic* species, whose identities are arbitrary and not fixed (nor even “real,” for that matter), manifestly not permanent, and in no way regulated by the ICN. These two notions occupy adjacent hierarchical levels that overlap via the Type. But *both* are called “species.” Maybe that is the problem. Operationally, all but well-trained taxonomists tend to perceive/conceive of species at the level of the group rather than the Type, and likewise perceive/conceive individuals in the group as “the same.” This is consequent to constitutive cognitive processing. The eyes capture photons, the brain sorts their quantity/quality, and “files” them in a location in “physical” memory according to the similarity with prior perceptions. In this location resides the cumulative “image.” So in “real time,” we do not actually “see” what we *think* we see. We see a composite *virtual* image constructed in *memory*. This inherently reflects a “group” of prior perceptions of identical or merely *similar* objects, and not an image “typified” by a single instantaneous perception of a single object. This, then, is the taxonomic species, and generally it comprises perceptions of multiple individuals, viz. a group rather than a Type.

Another feature of the typological system is that in no way is the Type purported to be representative of the taxonomic species that it is supposed to typify. A taxonomist might construct the taxonomic species such that the Type itself is an exceptional or “abnormal” member. Again, the only criterion of the typological concept is whether individuals classified in a species are considered to belong to the “same taxonomic species as” the Type, and not their material similarity to or difference from that Type.

Thus, the present work focuses first on those Types that proxy for species pertinent to *Calandrinia* sect. *Arenarie* and then secondarily on the collective set of individuals. Then intuitive/subjective decisions are made regarding *operational* synspecificity/apospecificity. The decisions reflect a variety of criteria: primarily morphological similarity/difference, locality of individuals in populations, geographic distributions, intuitively inferred “genetic” and “evolutionary” relationships, etc. And these all reflect my prior “education.” This, in turn, overlaps with the education of other taxonomists, but is nonetheless unique to me. To quote my friend, the late great Arthur Cronquist, “...my intuition may differ from yours” (Cronquist, 1987: 17).

At the cognitive level, my “intuition” as to whether individuals are the same/different as/from a Type presumably is derived using one or another constitutive cognitive algorithm. I suggest two analogies. One can be described as “three-item analysis.” Thus, if I consider that *any two* among three individuals pertain to the same species as *each other*, then *all three* must pertain to the same species. This process is reiterated, connecting the triplets, until a Type is included. Alternatively, one can conceive of individuals as pieces in a jigsaw puzzle in which one or more of the pieces are Types. The pieces are fit together until Type pieces are included. Pieces that cannot be connected in this way to a particular Type piece do not pertain to the same species as that Type piece. Two Type pieces that can be connected via nontype pieces can be considered to belong to the same taxonomic species and reduced per ICN. It is possible also that during piece assembly, no Type piece is encountered. Per ICN, a new Type can be selected from among these pieces, creating a new species. Young children could play this game. Scientists seem to have difficulty.

3. Currently accepted taxonomy of species pertinent to *Calandrinia* sect. *Arenarie*

Reiche (1897) indicated that *Calandrinia* sect. *Arenarie* included ca. four species of “herbae annuae (vel perennes?),” but he did not there name them. Rodolfo Philippi (1864, 1893, 1894) described seven additional species pertinent to this section. Reiche (1898a, b) later listed only three species in this group, *C. arenaria* (including three varieties that had been named as species), *C. fenzlii*, and *C. solisii* Phil.

Ford[-Werntz] & Peralta (2002) recognized two species, *C. arenaria* and *C. fenzlii*, with no varieties. But they remarked (p. 381) that *C. arenaria* was an “extremely polymorphic species, closely related to *C. fenzlii*,” and that “the intergradation in this group warrants further study.” Ford[-Werntz] & Peralta’s (2002) work did not mention the names of seven of the ten typified taxa in Table 1.

Rodriguez et al.’s (2018) catalog of “accepted” Chilean species seems to have followed Ford[-Werntz] & Peralta (2002), accepting the same two species. They assorted among these all but one of the heterotypic taxa in Table 1, referring six (including *Calandrinia solisii*) to *C. arenaria* and two to *C. fenzlii*. The Flora Cono Sur database (without year; based on Zuloaga et al., 2008) currently accepts four species, effectively *C. arenaria*, which it lists erroneously as a taxonomic synonym of the later name *C. chamissoi*, *C. fenzlii*, and, apparently following Hershkovitz (2019a), *C. trigona* and *C. vicina*.

Reiche (1898a, b) and Navas Bustamante (1976) described *C. arenaria* as an annual distributed in Chile’s “central provinces,” which conventionally includes the area between Chile’s Valparaíso Region (ca. 33°S) and Biobío Region (ca. 36.5–37°S). Ford[-Werntz] & Peralta (2002) listed the range as the Coquimbo Region (ca. 30–32°S) to Malleco Province (ca. 37–38°S) of the Araucanía Region. As noted above, Rodriguez et al. (2018) gave its distribution as spanning from the Atacama Region to Araucanía Region.

Reiche (1898a, b) did not specify the growth form of *C. fenzlii*, though he remarked that it has a thick root. He listed its distribution as only in the Biobío Region. Rodriguez et al. (2018) listed it also for the Araucanía Region. Thus, according to Rodriguez et al. (2018), the range of *C. fenzlii* is the same as the southernmost range of *C. arenaria*. Of course, this work and the databases above are merely catalogs; they do not diagnose the taxa or document the distribution data.

4. The “true” identity, characteristics, and distribution of *Cistanthe arenaria*

Hershkovitz (2018a) proposed that the taxonomic identity of *C. arenaria* had been confused historically, and that the type material, from Concepción (Biobío Region; Fig. 6), was a perennial rather than an annual. This conclusion was an eventual consequence of my 2003 observation of plants that I believed to be *C. fenzlii* on a beach north of Concepción. This diagnosis was based on the thick taproots of the plants, perhaps 15–20 mm broad when fresh (cf. Reiche, 1898a, b). In fact, a decade earlier, I had annotated a very similar herbarium specimen from Concepción, *C. Joseph 4015* (US 03613605; Fig. 7), as *C. fenzlii*. But my diagnosis was mistaken.

Only relatively recently have I appreciated that both *C. Joseph 4015* and the plants I observed in 2003 correspond in every way to Chamisso’s (1831) description of *C. arenaria*. In fact, *C. Joseph 4015* serves as an epitype of *C. arenaria*, because it is very similar to Chamisso’s Type, but it possesses the entire taproot, which is missing in both the holotype and isotypes. As evident in *C. Joseph 4015*, inflorescence branches emerging from the basal rosette produce a secondary rosette some 5 cm from the base. The leaves of *C. Joseph 4015* have the “*arenaria*” morphology described above, viz. differentiated into an apical more or less rhombic laminar portion and a basal broad petiolar portion. Both of these traits distinguish *C. arenaria* from *C. fenzlii* (see below).

Another trait I observed in 2003 was the distinctive petal coloration of the Biobío plants compared to the annuals from the more northerly Regions that have been referred to *C. arenaria*. The petals were rose-colored¹² apically (betacyanin pigment) and yellow at the base (betaxanthin pigment). But in the middle region, there appeared an orange hue, certainly a mixture of the others. In contrast, petals of annual plants from the more northerly Regions seem to have only betacyanin pigmentation, and typically are rose apically and darker red-magenta basally. Certainly they lack the orange hue.

The petal coloration I observed in 2003 also was evident in an image of a live plant sent to me on 10 August 2022 for my taxonomic opinion. This plant was growing in the vicinity of the town of Cabrero (ca. 37°S), some 60 km east of Concepción. I replied to the consultation, sending also a screenshot of an image of another plant posted on Instagram, which was identified as *C. arenaria*, also from Cabrero.¹³ The plant has the rosette, stem, and leaf characteristics of *C. arenaria*, but the petals are entirely orange, though yellow at the very base. Another photo of an orange flower is from the Maule Region,¹⁴ evidently from the vicinity of the Río Achibueno (ca. 35.8°S; Linares Province), which extends ca. 100 km in the central valley between the coast ranges and the Andes.

Images of two other plants from the Maule Region (Cauquenes,¹⁵ 36°S; San Javier de Loncomilla,¹⁶ ca. 35.5°S) show the *C. arenaria* petal color scheme. However, another photo of a plant from the Maule Region shows flowers that seem to lack yellow centers or orangish hue.¹⁷ This would implicate *C. trigona* rather than *C. arenaria* (see below). However, the precise location in this Region is not given.

The rosette, stem, and leaf characteristics of the coastal *C. arenaria* also characterizes an interior form, *Calandrinia solisii* Phil. (Philippi, 1894; Table 1), described from Chillan (ca. 36.5°S; formerly Biobío Region, now Ñuble Region). Reiche (1898a: 346, 1898b: 350) considered this plant to be perennial “judging from the thick root.” The above data, though meager, suggests that these thick-rooted forms all pertain to *C. arenaria*, and that the distribution of this species spans latitudinally at least 35.5–37° and from the coast to valleys as much as 100 km inland.

Reiche (1898a, b) described the seeds of *C. solisii* as “punteadas, opacas,” which probably indicates PT. This differs from the glabrous seeds of *C. arenaria* described by Chamisso (1831). However, Reiche gave the distribution as including effectively the Metropolitana Region. Plants from here are *Cistanthe trigona* (see below), which has PT seeds. Philippi (1893) did not describe the seeds of *C. solisii*, which suggests that the specimen had no mature seeds. Thus, Reiche’s (1898a, b) seed description of *C. solisii* probably refers to misidentified *C. trigona* from the Metropolitana region. Since Reiche listed the latter, which has PT seeds, as a synonym of *C. arenaria*, which has glabrous seeds, and Rodriguez et al. (2018)

¹² According to Wikipedia (. https://en.wikipedia.org/wiki/Shades_of_rose), rose is the color halfway between red and magenta, the latter including a purple component, and purple, in turn, a mix a red and blue. Thus, rose is a shade of pink (pale red) that includes a blue component. I apologize if this does not jibe with RHS.

¹³ Photo: <https://www.instagram.com/p/BvmqzOFhtJL/> (identified as *C. arenaria*; sometime between 10 August and 14 September, the words “Cabrero, Chile,” were deleted, so that there is now no locality information. Fortunately, this is conserved on my screenshot.

¹⁴ Website: <http://apuntesbotanicos.blogspot.com/2009/01/hierbas-y-flores-chilenas.html?m=1>; photo: https://3.bp.blogspot.com/-8ODCpgoMR-U/WmOzZ2eoa-I/AAAAAAAAAKyo/dGHI2c_K9sI512wO-zyU_73LoHf-yEu9gCLcBGAs/s1600/Calandrinia%2Bsp%2BAchibueno%2Bene16%2Bcc.jpg (species not identified).

¹⁵ Photo: <https://www.inaturalist.org/observations/125869096> (species not identified at this writing).

¹⁶ Photo: <https://www.inaturalist.org/observations/102846345> (species not identified at this writing).

¹⁷

https://m.facebook.com/photo.php?fbid=3269809106570771&id=100006251407371&set=gm.1539337499840340&eav=AfaNBGv7VBHLTuCVG40akhKZMzymHuiNfLveXI_FbtsOLnrexP03AsrRNtTcy4BFN0U&paipv=0&source=48

listed both *C. solisii* and *C. trigona* as *C. arenaria* synonyms, it becomes easy to see how species in this group became confounded and incorrectly described.

5. The relation between *Cistanthe arenaria* and *C. fenzlii*

Cistanthe arenaria and *C. fenzlii* share their distribution and two morphological traits: thick roots and lustrous black glabrous seeds (see also below). The thick roots suggested a perennial life form, but the life form in these species (and their heterotypic synonyms) has been questioned and evidently not confirmed empirically. Barnéoud (1847 [“1846”]) characterized both *C. arenaria* and *C. fenzlii* as having “annual roots.” But Barnéoud did not see Chamisso’s plant and he did not refer to the obvious thickness and woodiness evident in the original material of *C. fenzlii* (Fig. 8). And obviously he did not see live plants. So there was no basis for qualifying the roots in either species as “annual.”

As for the species Rodriguez et al. (2018) included in *C. fenzlii*, Philippi characterized *Calandrinia sanguinea* Phil. as perennial (Philippi, 1893), and *C. lancifolia* Phil. as perennial but possibly annual (Philippi, 1894). As for the latter, Philippi (1894: 301) commented that the root was 3 mm thick and somewhat woody, but that it seemed annual.

Philippi (1894) described the flower color of *C. sanguinea* as blood red, as the epithet implies. This seems to be the only description of flower color of *C. fenzlii* and its synonyms. The “default” flower color of most *Cistanthe* species, including *C. chamissoi*, *C. trigona*, and *C. vicina* (described below) is rose, though typically more magenta towards the center. Blood red formally is a brownish red formed from magenta and yellow,¹⁸ and it may have an orange hue. Thus, the flower color in *C. fenzlii* seems consistent with that in *C. arenaria*, though obviously additional observation is desirable.

In his discussion of *C. fenzlii*, Philippi (1894) also suggested that *Calandrinia polyclados* Phil. pertained to *C. arenaria*. Philippi (1864) had characterized this species from (effectively) the Libertador O’Higgins (LBO) Region as annual to biennial. But for reasons not clear, Reiche (1898a, b) later included *Calandrinia polyclados* in *C. fenzlii*. I presume that Reiche did not see the Type or even read carefully the description of *C. polyclados* (cf. Table 1), which hardly resemble the descriptions and Type of *C. fenzlii*. For example, Reiche described the seeds of *C. fenzlii* as shiny, whereas Philippi (1964) described the seeds of *C. polyclados* as opaque and, effectively, PT.

I suspect that Reiche (1898a, b) was confused by Philippi’s (1894) discussion of *C. polyclados* within his discussion of *C. lancifolia*, which pertains morphologically to *C. fenzlii*. Rodriguez et al. (2018) did not mention *C. polyclados*. Based on overall and seed morphology and geography, *Calandrinia polyclados* clearly pertains to *C. trigona* (see below).

The question of life form might be a red herring as far as the taxonomy is concerned. Based on root thickness and not empirical study, HersHKovitz (2018a) characterized *C. arenaria* as perennial. But evidently this criterion is not inviolate, e.g., the case of *C. philhershkovitziana* (HersHKovitz, 2018b). However, it seems safe to say that both *C. arenaria* and *C. fenzlii* have relatively thick and woody roots.

Cistanthe fenzlii differs from *C. arenaria* in three traits (Philippi, 1894). The Type of the former appears more caespitose, and the suprabasal flowering stem rosettes, although architecturally the same as in *C. arenaria*, appear closer to the basal rosette and near ground-level. The leaves of *C. fenzlii* are more linear and apetiolate. And the sepals supposedly are proportionally much smaller. The last trait requires

¹⁸ https://en.wikipedia.org/wiki/Blood_red

confirmation with live plants, because sepals tend to shrink after anthesis and/or during herbarium specimen preparation.

6. The identity, characteristics, and distribution of annual plants CONFOUNDED with *Cistanthe arenaria*

Regardless of life form, Hershkovitz (2018a) thus considered untenable the application of the name *C. arenaria* to the thinner-rooted annuals distributed from the LBO Region northward. For this reason, Hershkovitz (2019a) resurrected and recombined in *Cistanthe* the later-published names of three species whose types originated in the north: *Cistanthe trigona*, *C. chamissoi* (Barnéoud) Carolin ex Hershk., and *C. vicina*. To these, I add *Cistanthe subverticillata* (Phil.), ined. (= *Calandrinia subverticillata* Phil.)

a. *Cistanthe trigona*. *Cistanthe trigona*¹⁹ (Fig. 1) is superficially similar to *C. arenaria* in overall vegetative and reproductive morphology, notably including the rhombic leaf blade shape. It is easy to see how the species might be considered the same or confused upon superficial examination. But *C. trigona* lacks the thick root and the yellow and orangish hue on the petals, and it has PT rather than glabrous seeds. The description of *C. arenaria* in Navas Bustamante's (1976) flora of the Metropolitana Region corresponds to *C. trigona* and not to the other three species present in this Region, viz., *C. chamissoi*, *C. vicina*, and "*C. subverticillata*," nor, for that matter, to *C. arenaria*.

The plants of *C. trigona* from the population I studied from the northeastern Valparaíso Region manifest an unusual trait absent or at least not evident in photos of plants from other areas, nor in other species discussed here or other *Cistanthe* species. The sepals are distinctly *keeled* (Figs. 1J–M). This called my attention, because this trait is among the *diagnostic* characteristics of the genus *Calandrinia* Kunth. In fact, it was the characteristic that prompted Spach (1836) to segregate *Cistanthe* from *Calandrinia* in the first place.

Cistanthe trigona is biogeographically distinct from *C. arenaria*. It often forms extensive dense carpets that "paint" hillsides²⁰ mainly in the precordillera of the Metropolitana, O'Higgins, and Valparaíso Regions. But two records are from well to the west in the LBO Region coastal ranges, and one is from an unspecified locality in the Maule Region. I cannot document here the comprehensive distribution of this species. But its ubiquity and abundance in the vicinity of Chincolco (Valparaíso Region, Petorca Province; pers. obs., 25 Sept 2022) seems to render likely that it extends across the Coquimbo Region border, a mere 20 km to the north.

I add to the above the observation that a species of *Cistanthe* sect. *Cistanthe*, *C. mucronulata* (Meyen) Carolin ex Hershk., described from San Fernando (LBO Region), distributes from the LBO precordillera southwesterly across the Maule Region²¹ and then south along the coast to the Biobío Region. This approximates the tract of the transition between *C. trigona* and *C. arenaria*. But the distribution is not identical: *C. trigona* extends along the precordillera up to and probably into the Coquimbo Region, and *C. arenaria* extends well inland in the Biobío Region. Moreover, *C. mucronulata* is more or less morphologically constant across this range, although plants growing on the ocean shore

¹⁹ More photos: <https://www.inaturalist.org/observations/100745829>, <https://www.inaturalist.org/observations/96303249>, <https://www.inaturalist.org/observations/99227389>, <https://www.inaturalist.org/observations/98017836>, <https://www.instagram.com/p/CU7NEoaL205/>, <https://www.inaturalist.org/observations/98848060> (all at this writing identified as *C. arenaria*).

²⁰ Photo: <https://www.instagram.com/p/CVWku5pL44F/> (at this writing identified as *C. arenaria*).

²¹ In 2004, I traced the Maule Region trajectory of *C. mucronulata* from the precordillera near Los Cipreses (Curicó Province, Romeral Community) to the coast at Constitución (Talca Province, Constitución Community), finding this species more or less continuously present along the roadside.

itself are larger, shrubbier, and more succulent, superficially resembling *C. laxiflora* (Phil.) Peralta & D.I.Ford.

The identity of plants from the Maule Region requires confirmation. It is possible that *C. trigona* and *C. arenaria* “intergrade” in this zone. Possibly there is gene flow. However, any uncertainty regarding identification in this zone does not alter the taxonomy of *C. trigona* and *C. arenaria* proposed here. This is based on three trait differences besides distribution. Moreover, circumstantial evidence suggests that *C. arenaria* represents a distinct evolutionary trajectory. In particular, *C. sect. Rosulatae* would seem to have originated in the arid zone. Thus, *C. arenaria* seems to represent a derived *lineage* that established in a cooler, wetter environment.

The distinction between *C. trigona* and *C. arenaria* thus can be justified not only in terms of traits, but also *causally* via genetic assimilation under the model of Natural Drift, described above. I have described above developmental plasticity of seedlings of species of *C. sect. Rosulatae*, which can transition precociously from vegetative to reproductive growth. This change presumably is triggered by an environmental parameter that, in turn, alters the physiological condition of the individual, e.g., cellular water potential, which, in turn, triggers the ontogenetic trajectory.

But this is a two-way street. Cool, moist conditions seem to promote vegetative (including primary root) growth, and *delay* transition to reproduction phase. Despite the relatively short distance (ca. 362 km) between the Type localities of *C. trigona* (ca. Rancagua, Cachapoal Province, LBO Region) and *C. arenaria* (Concepción, Concepción Province, Biobío Region), the climate of the latter is much cooler and wetter, with 2–3X the “average” annual rainfall and a longer “effective” winter from a plant physiological standpoint. However, “average” is misleading because rainfall in central Chile is a function of the “El Niño Southern Oscillation,” whose effects are exaggerated in Rancagua relative to Concepción. The result is that the “average” Rancagua rainfall includes few extremely wet years with more frequent exceptionally dry ones.

Thus, the conditions of Concepción *permit* (but do not “select for”) genetic changes that restrict ancestral developmental plasticity to the phenotypic range *constitutively* induced in such a cool, wet environment. This is because, in this environment, the developmental plasticity becomes irrelevant to the realized ontogeny. The plasticity can persist or be lost. It is all the same to the plant itself. But with passing time, the cumulative probability of loss increases towards unity. Once the plasticity is lost, the lineage can be considered distinct.

Based on geography, I suspect that *Calandrinia nana* Phil. (Table 1) pertains to *C. trigona* rather than *C. chamissoi* (cf. Reiche, 1898a, b). The type (from the precordillera of the Valparaiso Region) seems to be a precociously reproducing seedling, as I have described above. This illustrates how developmental variability may mimic trans-specific differences and, in turn, blur the taxonomy.

I “cultivated” some plants of *C. trigona* and *C. subverticillata* in my residence – actually, just plants I collected in the field and put in water in order to follow their flowering and fruiting. I noticed that, as the fruit matures, the sepals become completely dry, spread out from the receptacle, and sometimes abscise. This seems like a trivial detail, but in HersHKovitz (2021c), a still incomplete treatise on perianth persistence among Portulacineae, I included *Cistanthe* among those genera of Montiaceae whose sepals were patently persistent in fruit. These are exceptions. If I live long enough to complete HersHKovitz (2021c), I will add this detail.

b. *Cistanthe chamissoi*. As noted above, *C. trigona* historically has been confused with *C. arenaria*. But the two species indeed share several traits and have similar “Gestalt.” So the confusion is not entirely

surprising. *Cistanthe chamissoi* (Fig. 2) also has been confused with *C. arenaria*, or, more accurately, with *C. trigona*, which has been confused with *C. arenaria*. Some photos of plants of *C. chamissoi* have been posted as “*Cistanthe* sp.,” i.e. not identified, hence not positively misidentified, either.²²

Yet, *C. chamissoi* is strikingly different from both of these species. In some ways, *C. chamissoi* suggests an “underdeveloped” *C. trigona*: (1) it is usually much smaller, the flowering stems of the largest plants extending to perhaps 20 cm versus the typical 40 cm of larger *C. trigona* plants;²³ (2) the leaves are narrower and shorter and linear to linear-oblongate rather than differentiated into a lamina and broad petiole, although the apicalmost portion of the leaf often is dilated, and this small dilation is suggestive of the apical half of the rhombic blade of *C. arenaria* and *C. trigona*; (3) the inflorescence remains congested after anthesis through fruiting, whereas in *C. trigona* and *C. arenaria*, the inflorescence internodes and pedicels elongate after anthesis, so that the inflorescence is more open in fruit; and (4) the flowers are much smaller, the petals scarcely exceeding the sepals, and the stamen number is maximally ca. 5 rather, whereas well-developed flowers of *C. trigona* have 20–30 stamens in two whorls.

However, the most distinctive characteristics of *C. chamissoi* relative to *C. trigona* and *C. arenaria* pertain to sepal morphology: (5) the sepals are thinner and they become scarious by anthesis, whereas in *C. trigona* they remain more foliaceous at anthesis and, in my own collection, even up to fruiting; (6) the lines on the sepals appear to be dark magenta or purple rather than the jet black of the other species; and, most notably (7) the lateral abaxial sepal margins are merely curved about the adaxial in bud and become spread/splayed outwards at anthesis, becoming somewhat winged, whereas in *C. trigona* and in *C. sect. Rosulatae* in general, the lateral abaxial sepal margin is sharply folded inwards in bud, tightly clasping the margin of the adaxial sepal, and it continues to enclose the flower/fruit, not spreading/splaying outwards after anthesis (e.g., in *C. trigona*, Figs. 1G, M–N; and *C. vicina*, Fig. 3C). The spreading sepal margins are shared with and more easily seen in “*C. subverticillata*” (Fig. 4: C–D).

The plants of *C. chamissoi* I observed in Puerto Oscuro and Illapel (Choapa Province, Coquimbo Region) were prostrate. However, evidently plants from the western Valparaiso Region may be more ascending and also have somewhat larger flowers.²⁴

Cistanthe chamissoi also is distributed somewhat differently than *C. trigona*, although I cannot document here the complete distribution of either species. *Cistanthe chamissoi* occurs from the Valparaiso to (at least) the northern Coquimbo Regions and, therein, most frequently towards the humid coast, then

²² <https://www.inaturalist.org/observations/136659598>,
https://m.facebook.com/groups/floresnativasdechile/permalink/1551709715269785/?m_entstream_source=group&anchor_composer=false&paipv=0&eav=AfbFZUjQMxDdsSadsb8a4RjAhsgYIAEEE2fVngq7UCVQRt0QB7ib8DU8zpo7QvzVLFc,
<https://m.facebook.com/photo.php?fbid=10220359500032395&id=1076774777&set=gm.1036864646754297&eav=AfYfSWBjFw0uXG8AcPSA7hP1QVNwbUh1B7xViNnBDqM56u8dU-1TX8TMNJ8QZNht0eM&paipv=0&source=48>.

²³ I have seen a herbarium specimen with flowering stems ca. 30 cm, but the stems in all plants I have seen in many localities in the Coquimbo Region are 20 cm or (usually much) less. In Puerto Oscuro, such smaller plants co-occur with plants of two other species, *C. vicina* and *C. sp. nov.* that have stems in the range of 30–40 cm. Thus, the small size of the *C. chamissoi* stems cannot be attributed to some “limiting” environmental parameter.

²⁴ Photos:

<https://m.facebook.com/photo.php?fbid=10220359500032395&id=1076774777&set=gm.1036864646754297&eav=AfYfSWBjFw0uXG8AcPSA7hP1QVNwbUh1B7xViNnBDqM56u8dU-1TX8TMNJ8QZNht0eM&paipv=0&source=48> (species not identified);
https://m.facebook.com/groups/floresnativasdechile/permalink/1551709715269785/?m_entstream_source=group&anchor_composer=false&paipv=0&eav=AfbFZUjQMxDdsSadsb8a4RjAhsgYIAEEE2fVngq7UCVQRt0QB7ib8DU8zpo7QvzVLFc (species not identified).

becoming less frequent towards the interior areas. I have located a record for the western Metropolitana Region.²⁵ I cannot document its presence towards or in the precordillera. In contrast, *Cistanthe trigona* concentrates further east in the Andes precordillera of these Regions and evidently is far less common or absent in the western portions.

I have observed an “ecological bias” in the distribution of *C. chamissoi*, but this requires confirmation with additional field study. *Cistanthe chamissoi* commonly co-occurs with *C. vicina* (see below) in the western part of the distribution of the latter, especially on disturbed or cultivated substrates. At a few localities in the central Coquimbo Region between Combarbalá (Limarí Province) and Illapel (Choapa Province), on less disturbed substrate, I noticed that *C. chamissoi* was abundant on calcareous substrate, whereas *C. vicina* was abundant on granitic substrate. This possibly associates with the distribution of *C. chamissoi* from mainly from coastal ranges towards the coast, where the substrate commonly is uplifted calcareous deposits formed from mollusk shells thoughtlessly discarded by prehistoric summer tourists. *Cistanthe trigona* and *C. subverticillata* (see below) are mainly precordilleran, where the substrate is more granitic, while *C. vicina* is abundant in both habitats.

C. chamissoi does share traits with *C. trigona*, and both of these, in turn, with *C. arenaria* and *C. fenzlii*. Like *C. trigona*, *C. chamissoi* has PT seeds, and in all four of these species: (1) the sepals are: (a) slightly translucent at anthesis, (b) paler green than the leaves and appearing “greenish-white,” evidently because there are fewer chloroplasts in the tissue, (c) conspicuously glossy at anthesis, (d) conspicuously reticulately marked with dark red to black lines and spots, and (e) more or less chartaceous in fruit; (2) the style is distinct in all of these species, equaling or exceeding the length of the ovary; and (3) the stigma is yellow-green, lobed to subcapitate. But a caveat is that the traits that bridge these taxa also are common among other, in fact *most*, species of *C. sect. Rosulatae* in the more northerly Regions. But these species are differentiated by other characteristics, e.g., they do not have rhombic leaf blades.

c. *Cistanthe vicina*. In contrast to the four species above, *C. vicina* (Fig. 3) is a different beast altogether, so different that its inclusion by Reiche (1898a, b) in *Calandrinia* sect. *Arenarie* is peculiar. *Cistanthe vicina* is similar to *C. coquimbensis* (Barnéoud) Carolin ex Hershk., but larger in all respects, and, logically, with more stamens. Indeed, precocious individuals of *C. vicina* in (Fig. 3P) might be diagnosed as *C. coquimbensis*. The flowers of *C. coquimbensis* were described as being white (Barnéoud, 1847 [“1846”]), but Reiche (1898a, b) surmised that they can be rose.

Thus, the difference between these species seems to be mainly size or size-related, and this might raise doubt as to whether *C. vicina* is even a different species than *C. coquimbensis*. But in the population of *C. coquimbensis* that I have studied several times, a hillside along the Panamerican Highway a few km north of La Serena, the size difference itself seems to loom large. There, even under what I would consider optimal moisture and light conditions, the plants of *C. coquimbensis* are uniformly small and, besides, rather delicate. None attained even half the size of “typical” *C. vicina* plants growing in comparable conditions. The size of the Type of *C. coquimbensis* [*C. Gay* 1332-30 (P01903299!)] is not really outside of the range for “small” *C. vicina*.²⁶ However, this specimen was described as having 6–8 stamens, which is no more than half the number I would expect for a comparably-sized specimen of *C. vicina*.

²⁵ <https://www.inaturalist.org/observations/95912504> (as *C. arenaria*);

²⁶ Interestingly, in the course of the present investigation, I discovered on GBIF specimens of *C. vicina* in US that I had annotated in 1992 as *C. coquimbensis*. I would not have considered *C. vicina*, because I had not seen the Type, and because this taxon was considered as either a variety or synonym of *C. arenaria*. Whatever were the specimens of *C. vicina*, my annotations demonstrate that even 30 years ago, and even without ever having seen live plants of Chilean *Cistanthe*, I already did not consider *C. vicina* to be *C. arenaria*. And my annotations have proven to be damn close to correct. I hasten to add that, at that time, my scientific efforts focused on phylogeny and morphological evolution of all of Portulacineae and not at all on species taxonomy. Notwithstanding, my work was

The differences between *C. vicina* (\pm *C. coquimbensis*) and the other “*Arenarie*” species are illuminating: (1) The sepals have an opaque rather than glossy luster, and they remain foliaceous throughout fruiting rather than becoming chartaceous; (2) the seeds are patently hairy rather than PT or glabrous; (3) the inflorescence branches and pedicels are thicker and more elongate more after anthesis, so that in fruit, the cyme is more expanded; (4) the style is sessile or nearly; (6) the stigma is magenta rather than pale green and more distinctly branched rather than merely lobed; (7) the fruits are larger, the capsule exceeding the sepals somewhat to markedly; and (8) the capsule walls are woodier.

As will be described in a separate work, *Cistanthe* sp. nov. also has a short style and magenta stigma and also a woody capsule. However, I believe that this species is a hybrid species, and that *C. vicina* is one of the progenitors. I found that plants of *C. vicina* from Petorca Province (Valparaíso Region) have short styles rather than sessile stigmas (Figs. 3G–H; cf. Fig. 3F), but I believe that this also reflects introgression, perhaps from *C. trigona*.

The sharing of traits between *C. vicina* and *C. sect. Cistanthe* has *systematic* significance. Two of these traits (opaque non-glossy foliaceous sepals, hairy seeds) are shared also with *C. sect. Thyrsioideae*. In the latter, black markings on the sepals are scant (see below) except in the derived North American species *Cistanthe maritima* (Nuttall) Carolin ex Hershk. Thus, while current DNA data (Hershkovitz, 2006) give no hint of phylogenetic structure within *C. sect. Rosulatae*, the morphological data suggest that *C. vicina* and *C. coquimbensis* retain the archetypal morphology of the entire genus, and that the species of *C. sect. Rosulatae* with pusticulate-tomentose seeds and more congested inflorescences with flowers with shiny sepals that become chartaceous in fruit pertain to a later evolved group within the section. Another species of *C. sect. Rosulatae* having glaucous and hardly marked/streaked (“mottled” sensu Watson et al., 2020) sepals that remain foliaceous in fruit is *C. floresiorum* (Watson, 2019). As noted above, this species also shares with *C. vicina* identical pedicel nastic movements during flowering and fruiting. Although the seeds in this species are glabrous, this is evidence that it pertains to this “basal grade” of *C. sect. Rosulatae*.

It is notable that, up until the present investigation, morphological evidence for phylogenetic relations among *Cistanthe* species was obscured by... *bad taxonomy*, in particular, the historical and persistent confusion of *C. vicina* with *C. arenaria*, or rather, with *C. trigona*, which has been confused with *C. arenaria*. Thus, the confusion of *C. vicina* with *C. arenaria* created a taxonomic hodgepodge, a hypervariable species that stymied any effort to sort species of *C. sect. Rosulatae* into coherent categories.

Meanwhile, the identity and distinctiveness of *C. vicina* possibly was obscured by the reported incompleteness of the Type specimen (Fig. 3Q; Philippi, 1894, Reiche, 1898a, b). Nonetheless, Philippi’s (1894) description and the Type are perfectly adequate to diagnose the species. The floral and seed characters cannot be inferred, but the distinctive structure of the cyme is evident, and Philippi (1894) more or less accurately described the sepals and fruit. I find it difficult to believe that, upon side-by-side inspection, anybody would confuse the flowers of *C. vicina* with *C. trigona* (Fig. 3H) or any other “*Arenarie*” species

Philippi (1894) noted that, unlike other *Cistanthe* species, sepal markings/streaks may be scant to nearly lacking in *C. vicina*. This is the condition I found in populations from Puerto Oscuro (Figs. A, C–D) and also in Illapel. However, sepals of plants of the Chincolco vicinity are marked/streaked extensively (Figs. 3I–M). Plants of *C. vicina* from Llay Llay (Valparaíso Region, San Felipe de Aconcagua Province)

fruitful in that it formed the basis for the current Portulacaceae and Montiaceae taxonomy. For species taxonomy, I relied on the experience of my so-oriented colleagues in Chile and elsewhere. That confidence proved to be the mistake *fundamental* to my many specimen misidentifications.

have sepals with dense reticulate black markings/streaks.²⁷ Some plants of *C. vicina* from Puerto Oscuro, described later, have sepals that are jet black throughout the lower half to two-thirds of the sepals (Figs. 3N–O). As I will discuss elsewhere, this phenotype – and possibly the reticulate markings in other populations – may be consequent to hybridization and introgression.

Cistanthe vicina has a geographic range similar to that of *C. chamissoi*, and not uncommonly the two species occur together. But I have found no records of *C. vicina* from the coastal ranges of the Valparaiso Region. I found, besides the Type from Cerro Renca, four additional (and recent) records from the eastern half of metropolitan Santiago.²⁸ *C. vicina* occurs most abundantly in the coastal and central areas throughout the Coquimbo Region. In September 2022, I found the species to be simply ubiquitous, if not “weedy,” in two localities in Choapa Province: north-facing cow-grazed hillsides overlooking the city of Illapel (semi-desert ca. 60 km inland) and throughout numerous hectares of horse-grazed and ungrazed scrub on the hills between the Panamerican Highway and coastal cliffs at Puerto Oscuro. In both localities, this native species held its own in the company of aggressive exotic herbs. Hershkovitz (2006) identified four collections²⁹ as being either *C. arenaria* or affiliated with this species. In fact, all four collections are *C. vicina*.

“*C. subverticillata*.” In Hershkovitz (2019a), I validated combinations in *Cistanthe* for the three species discussed above, but I did not provide a combination for *Calandrinia subverticillata*. This was because Philippi’s (1894) description of this species suggested to me that it pertained to *C. chamissoi*. Most notably, Philippi (1894) described the basal leaves of “*C. subverticillata*” as linear and 1 mm broad, but at the apex, dilated and 2.5 mm broad. I had not seen the Type or its image, as this was available on the commercial and poorly curated JSTOR Global Plants database (<https://plants.jstor.org/>), but not in the freely accessible and far superior GBIF database (GBIF Secretariat, 2017).

On 22 September 2022, I collected annual plants near Chincolco, Chile (Petorca Province, Valparaiso Region) that pertained to *Calandrinia* sect. *Arenarie*, but that were morphologically distinct from the three species described above (Fig. 4). Unable to assign it to a Type, I elaborated a description as a new species, which I intended to validate promptly. Fortunately or unfortunately as it was or would have been, John McNeill (E) kindly supplied me with an image of the Type of *Calandrinia subverticillata* (Fig. 4K). This showed that Philippi’s (1894) description of the basal leaves was inaccurate. They are not narrowly linear with a dilated apex and with the dimensions of leaves of *C. chamissoi*. They are petiolate with patently rhombic blades, ca. 5 mm broad in the shriveled dry state and thus somewhat broader in the fresh state. They are identical to leaves of *C. trigona*. More importantly, the plants I collected pertain to the same species as this Type. Thus, the combination “*Cistanthe subverticillata* (Phil.) Carolin ex Hershk.” will be validated in a publication now accepted, barring the interregnum intervention of taxonomic “ambulance chasers” (e.g., Watson & Flores, 2020).

Plants of “*C. subverticillata*” manifest a peculiar intermediacy between the morphology of *C. trigona* and *C. chamissoi*. In particular, the plants appear to “start out” as *C. trigona* and ontogenetically “transform” into *C. chamissoi*. Thus, the petiolate leaves with rhombic blades suggest *C. trigona*. The flowering and fruiting cymules are much more congested than in *C. trigona*, but less so than in *C.*

²⁷ <http://www.chileflora.com/Florachilena/FloraSpanish/LowResPages/SH1181.htm> (at this writing, the species is not identified by the publishing author).

²⁸ Photos: <https://www.inaturalist.org/observations/134096080> (as *C. arenaria*);

<https://www.inaturalist.org/observations/134948368> (as *C. arenaria*);

<https://www.inaturalist.org/observations/131148927> (as *C. arenaria*);

<https://www.inaturalist.org/observations/96632393> (as *C. arenaria*; a patch of mostly *C. chamissoi*, but an individual of *C. vicina* (with a beetle foraging the flower) is evident in two of the photos).

²⁹ Samples 99-870, 99-910, 00-213, and 00-215 in Hershkovitz (2006).

chamissoi. Often the pedicels and sometimes the sepals are deciduous in fruit, as in *C. trigona*. But the morphology of the floral organs is the same as *C. chamissoi*. The size of the floral organs of the plants examined here (Fig. 4) is about 25% larger than the plants of *C. chamissoi* that I found in Puerto Oscuro (Fig. 3) and Illapel, but perhaps the same size as plants of *C. chamissoi* from the Valparaiso and Metropolitana Regions. Most notably, as in *C. chamissoi* and distinct from *C. trigona* (see above), the abaxial sepal margin is not inrolled and does not clasp the adaxial sepal. Rather, the margin is spread/splayed and becomes somewhat winged (Fig. 4C–D).

Near Chincolco, an “albino” phenotype of “*C. subverticillata*” co-occurs with the rose-flowered and otherwise pigmented form (Fig. 4H–I). These plants have white flowers and sepals with golden-brown rather than purple markings. The stems are completely green, whereas they are partially or completely reddish in the pigmented form. This color polymorphism in “*C. subverticillata*” has been recorded elsewhere, but without geographic locality.³⁰

I have found additional records of “*C. subverticillata*” from the eastern Metropolitana and Valparaiso Regions, viz. towards the precordillera.³¹ I have not located records for the central to western portions of these Regions. Here, I have found only records of *C. chamissoi*. I have located also two records from the Coquimbo Region, both along the road connecting the towns of Vicuña (Elqui Province) and Hurtado (Limarí Province).³² I collected the species from this same road in 2000, collection 00-251 in HersHKovitz (2006; as *C. arenaria*). The description in my field notes renders evident the identification as “*C. subverticillata*.”

The evolution of “*Cistanthe subverticillata*” may be interpreted in different ways. It could be derived from an ancestor pertaining to *C. trigona* and itself ancestral to *C. chamissoi*. This scenario is parsimonious, because the inflorescence and floral traits that “*C. subverticillata*” shares with *C. chamissoi* seem to be derived. Much less parsimonious is an origin from *C. chamissoi* and convergence upon *C. trigona* in vegetative form. The vegetative form itself clearly is ancestral in this species group. The other possibility is that “*C. subverticillata*” is a nothospecies (hybrid species) derived from *C. chamissoi* and *C. trigona*. I will elaborate on this possibility in a subsequent publication.

7. *Cistanthe chrysantha*

Cistanthe chrysantha never has been considered as a synonym of *C. arenaria* or any other species discussed in this work. Remarkably, however, plants of *C. chrysantha* commonly have been misidentified as *C. arenaria*, although also as other species. HersHKovitz (2022c) located eleven online images of *C. chrysantha*, four of which had been identified as *C. arenaria* and none as *C. chrysantha*. Also remarkably, only one plant was identified as the very similar *C. cymosa* (Phil.) Carolin ex Hershk., from which smaller plants of *C. chrysantha* cannot be distinguished except on the basis of seed surface morphology, viz., PT in *C. chrysantha* and glabrous in *C. cymosa*.

³⁰

https://m.facebook.com/groups/floresnativasdechile/permalink/1549189862188437/?m_entstream_source=contextual_profile_feed&anchor_composer=false&ref=m_notif¬if_t=feedback_reaction_generic&paipv=0&eav=AfZJJ_btI5dipzWd7EW6E5T82nE6nC8vtki4szVNprBxvXnKif81_VhH_Hwz_NJUHY (as *C. arenaria*).

³¹ <https://www.inaturalist.org/observations/138251509> (as *Cistanthe* sp.),

<https://www.inaturalist.org/observations/138179272> (as *Cistanthe* sp.),

<https://www.inaturalist.org/observations/137358873> (as *C. arenaria*),

<https://www.inaturalist.org/observations/138146084> (as the North American species *C. maritima*!)

³² <https://www.inaturalist.org/observations/136565811> (as *C. arenaria*),

<https://www.inaturalist.org/observations/137115968> (as *Cistanthe* sp.).

Since posting HersHKovitz (2022c), I have located numerous additional images of *C. chrysantha* identified as *C. arenaria*, mostly from Huasco Province (Atacama Region).³³ In their book on the Atacama Region's flowering desert, Cerda Medina & Mercader Arriagada (2020) misidentified a photo of *C. chrysantha* as *C. arenaria*. Thus, it seems possible that the occurrence of *C. arenaria* in the Atacama Region indicated by Rodríguez et al. (2018) reflects the same misidentification, but I cannot confirm this without seeing the actual voucher material. Mistaking *C. chrysantha* for *C. arenaria* or even any of its "synonyms" seems a bit surreal, since none of the other species discussed here have broadly elliptical to orbicular leaves often found in this species.

8. The historical cause of the taxonomic confusion of *Cistanthe arenaria*

Having clarified the differences between the species confused with *C. arenaria*, it is possible to address the historical cause of the confusion. This owes first to Hooker & Arnott (1833) and Lindley (1833). Hooker & Arnott (1833) listed the *unpublished* name "*Calandrinia venulosa*" as a *synonym* of *Calandrinia arenaria*. Per ICN Art. 36.1 (Turland et al., 2018), therefore, this name is not validly published. The name itself referred to collections from Valparaíso that pertain to *C. chamissoi* (Table 1). Hooker & Arnott (1833) cited Chamisso's plant, but evidently decided that these comparatively anorexic Valparaíso collections were the same species. They did not emphasize there that the Type locality of *C. arenaria* was Concepción, not Valparaíso. Interestingly, Hooker & Arnott (1833) described the seeds in *C. arenaria* as glabrous, the same as Chamisso (1831). As they had at their disposal the isotype of Chamisso's plant (Table 1), presumably they confirmed this. However, the seeds of the Valparaíso collections (viz. *C. chamissoi*) ought to be PT. But I cannot confirm this at the present time.

Lindley (1833) subsequently cited Hooker & Arnott (1833) and described and illustrated what the latter two called *C. arenaria*. He copy-pasted Hooker & Arnott's (1833) description, including the characterization of the seeds as glabrous. But the plant that he illustrated was the Valparaíso "*Calandrinia venulosa*" form (i.e. *Cistanthe chamissoi*). This he cultivated from seed. Again, these seeds ought to have been PT. Regardless, Lindley (1833) effectively expanded the concept of *C. arenaria* to include the diminutive *C. chamissoi* and thus likely every form intermediate between this and the much larger and thick-rooted "true" *C. arenaria*. Like Hooker & Arnott (1833), Lindley (1833) gave the provenance of this so-called *C. arenaria* as *only* Valparaíso, with *no mention* of Concepción.

More accurately, Lindley's (1833) work *transformed* the operational taxonomic identity of *C. arenaria*. This was *transferred* from Chamisso's Concepción plant to a catch-all for diverse annual plants distributed from the LBO Region *northward*. An aggravating factor likely was the infrequency of *C. arenaria* relative to ubiquitous and abundant northern species. The relative infrequency of *C. arenaria* owes to its distribution in a more forested region. The abundance and ubiquity of the northern species, in turn, owes to the more open matorral and semidesert vegetation.

Thus, the name *C. arenaria* has been applied correctly to the southern plants and, because of Lindley (1833), incorrectly to the northern plants. But in *practice*, the name was *applied* much more frequently to the northern plants, because these are far more ubiquitous and abundant. Consequently, over many decades, the true identity of *C. arenaria* became ever more obscured.

³³ I have located one image identified as *C. chrysantha*, <https://www.inaturalist.org/observations/135675221>, but the original ID was *C. arenaria*. I suspect that the change owes an earlier posted version of HersHKovitz (2022c). However, this particular specimen is a small plant with flowers bearing only five stamens. I suspect that it is a "precocious" *C. chrysantha*, but in this case, the ID cannot be confirmed with the seed.

To appreciate the consequence of Lindley (1833), one need look no further than Barnéoud (1847 [“1846”]). Barnéoud cited Chamisso (1831), Hooker & Arnott (1833), and Lindley (1833). But evidently ignoring (or not seeing?) Chamisso (1831), Barnéoud followed Lindley (1833) and gave the provenance of *C. arenaria* as Valparaiso, also not mentioning Concepción. And most notably, he described the seeds not as glabrous, per Chamisso (1831) and Hooker & Arnott (1833), but as “rugulosis” in the Latin description and, effectively, as PT in the Spanish discussion. Meanwhile, he described the seeds in *C. chamissoi* as, correspondingly, “rugulosis” and “muy rugosas.” Thus, Barnéoud consummated the transfer of the identity of *C. arenaria* from Chamisso’s plant to, effectively, *C. chamissoi*. This is remarkably ironic, since Barnéoud in the same work described *C. chamissoi* as a new species. Did he not see the resemblance with Lindley’s (1833) illustration (or did he cite the latter, but not actually see it?).

HersHKovitz (2019c, d, 2020c) commented on Barnéoud’s (1847 [“1846”]) interpretations of species based only on their original description and not on examination of the Types that were not available to him in Paris. He seemed to guess their identities and tended to guess wrong. An example is his accurate description of the Type of *Calandrinia jompomae* Hershk., a Claudio Gay collection (HersHKovitz, 2020c, 2022b). But, based on Candolle’s brief protolog, Barnéoud apparently guessed that this plant was *Calandrinia glauca* Schrad. ex DC [= *Cistanthe glauca* (Schrad. ex DC) Lilja, = *Calandrinia grandiflora* Lindl., *nom. cons.* ≡ *Cistanthe grandiflora*]. He had not seen the Type. He goofed. In the present case, Barnéoud saw neither Chamisso’s plant, nor the specimens that Hooker & Arnott cited. If he had seen the latter, he would have appreciated that these were the same species as *Cistanthe chamissoi*.

I cannot confirm at this point on what material Barnéoud based his description (especially the seeds) of his *C. arenaria*. There are in P two Claudio Gay collections, P04582971 (!) and P04582973 (!) identified as *C. arenaria*. The first of these has a boilerplate label that reads “Herbier du Chile Austral envoyé par M. Gay (3me. envoi.)” The handwritten notation indicates *Calandrinia arenaria* and also gives the citation and page number of Barnéoud’s (1847 [“1846”]) work. Clearly this specimen was annotated after the fact, so it is not clear whether or not Barnéoud saw it when preparing his treatment. No locality or date is indicated. But the individuals are thin-rooted, and, despite my 1992 annotation, I would classify them now as *C. trigona*. The other specimen has a boilerplate label typical of Gay’s oldest collections in P, indicating only “Chili” and “M. Cl. Gay.” Again, no locality or date is indicated, and, again, the specimen is *C. trigona*, not *C. arenaria*. The annotation “*Calandrinia arenaria* (Chamisso)” is indicated in different handwriting than the other specimen. This seems a better candidate for the specimen that Barnéoud examined. If so, this would explain Barnéoud’s characterization of the seed as, effectively, PT.

Barnéoud also mentioned as a problematic species *Talinum trigonum* Colla (≡ *Cistanthe trigona*), but he did not divine its taxonomic affinities, except to question whether this or any other species in Chile pertained to the genus *Talinum* Adans. (see HersHKovitz, 2021c). It is not certain that Barnéoud had seen the highly duplicated original material of *T. trigonum*, Bertero 683. There are now four isotypes in P, but in the time of Barnéoud, the only specimen in Paris (city) was in the private herbarium of A. Richard (see HersHKovitz, 2020d). Had Barnéoud seen this or any other duplicate, he would have appreciated its similarity to (as opposed to identity with) *C. arenaria*. But Barnéoud did not see the latter, either. Barnéoud supposed that the Chilean species that Colla (1833 [“1834”], 1834) classified in *Talinum* actually pertained to *Calandrinia* s. lato. In fact, Colla (1833 [“1834”], 1834) rendered quite clear that the Chilean species he classified in *Talinum* pertained to *Calandrinia* sensu Candolle (1827, 1828; see also HersHKovitz, 2021c). At any rate, the evidence suggests that Barnéoud did not see any of the *Talinum trigonum* specimens, lest his uncertainty would have been resolved.

Reiche (1898a, b) more or less followed Barnéoud’s (1847 [“1846”]) treatment, but he listed *T. trigona* as a *C. arenaria* synonym, and he considered *C. chamissoi* as a variety. He vacillated on the seed surface morphology of *C. arenaria*, describing it as glabrous and shiny (probably per Chamisso’s

description), but then he suggested that possibly the seeds were (effectively) PT when young. Reiche presumably did not see the Type of *C. arenaria* and likely based his seed surface description on plants pertaining to *C. trigona* and/or *C. chamissoi*, the only species that have PT seeds. He also may have been confused by Barnéoud's description.

Note that Barnéoud (1847 ["1846"]) and Reiche (1898a, b) both and independently seem to have mistakenly attributed seed surface morphology of *C. trigona* to another species, the former to *C. arenaria* and the latter to *C. fenzlii* (see above). These errors compounded and reinforced the original errors of Hooker & Arnott (1833) and Lindley (1833). Characterization of the seeds of the southern species as PT blurred the distinction between the southern and northern species.

Following Reiche (1898a, b), three-quarters of a century passed before the question of *C. arenaria* taxonomy reemerged in Navas Bustamante's (1976) flora of what is essentially the Metropolitana Region. According to the present taxonomy, four species (but not *C. arenaria*) occur in this region and the Type localities of two of them. According to Reiche's (1898a, b) taxonomy, the Region would include *C. arenaria* and three varieties. But Navas Bustamante (1976) recognized only *C. arenaria* and listed no synonyms,³⁴ not even the taxa described from this Region. Navas Bustamante's (1976) description of *C. arenaria* reflects *only* the characteristics of *C. trigona* and no other species discussed in this work.

As the first regional-scale flora published in Chile since the time of Reiche, the work of Navas Bustamante (1976) presumably reflected the taxonomic perceptions of Chilean botanists at the time and also presumably was influential in subsequent research. Thus, in this case, the effect of Navas Bustamante (1976) would have been to "cement" the reduction of five species to one. Notably, Navas Bustamante (1976) described the seeds of *C. arenaria* as (essentially) PT, even though Reiche (1898a, b) followed Chamisso (1831) in describing them as glabrous, though he also mused whether they might be (essentially) PT when young.

Whether the influence was direct or indirect, Navas Bustamante's (1976) hyper-reduced (relative to Reiche) *C. arenaria* concept emerged in all subsequent floristic inventories at the national and regional scale (Marticorena & Quezada, 1985; Marticorena et al., 2001; Squeo et al., 2008;³⁵ Zuloaga et al., 2008; Rodríguez et al., 2018; Anton & Zuloaga, without year). Likewise, the reduced synonym-free *C. arenaria* taxonomy has been reproduced in numerous species inventories at the local scale and in more "popular" guides to the flora at the regional and national scale. Unfortunately, contemporary "authority" afforded such works likely influences taxonomic identification more than Reiche's work and infinitely more than original literature. Such works lack the scientific and bibliographic taxonomic information/documentation needed for scientific evaluation and, in this sense, they are *retrogressive*, actually *inferior* to Reiche (1898a, b).

³⁴ Taxonomic synonymy in Navas Bustamante (1976) is incomplete and inconsistent: some but not all taxonomic synonyms are listed for some but not all taxa.

³⁵ This work listed *C. arenaria* for Chañaral Province of the Atacama Region; possibly this is the record reflected in Rodríguez et al. (2018), since the authors of both works are largely the same. Was this identification based on comparison with the Type and/or similar plants from the Type locality, a few km from the offices of five of the authors?

9. Summary: tentative diagnostics of the species associated with *C. arenaria*

The analysis above can be summarized into the following diagnostic key to the species of *Cistanthe* treated in this work.

- 1A. Plants with thickened and somewhat woody taproot, seeds glabrous and lustrous; Maule to Araucanía Region..... 2
- 1B. Plants with herbaceous taproot, seed surface pusticulate-tomentose or distinctly hairy; Atacama to Maule Regions 3
- 2A. Flowering stems with secondary rosettes > 5 cm from their base, leaves differentiated into apical ± rhombic blade and broad decurrent petiole; Maule to Araucanía Region *C. arenaria*
- 2B. Flowering stems with secondary rosettes near their base, leaves linear; Biobío to Araucanía Region..... *C. fenzlii*
- 3A. Seed surface pusticulate-tomentose 4
- 3B. Seed surface distinctly hairy; interior valleys to the coast, Valparaíso and Metropolitana to Coquimbo Regions, but also precordillera of northeastern Valparaíso and perhaps southeastern Coquimbo Regions.....*C. vicina*
- 4A. Leaves differentiated into apical ± rhombic blade and broad decurrent petiole 5
- 4B. Leaves linear, dilated or not dilated at the apex 6
- 5A. Abaxial sepal margin inrolled in bud, clasping the adaxial sepal, petals > 10 mm long, stamens > 10; interior valleys and precordillera (Maule?) LBO, Metropolitana, and Valparaíso Regions and probably also Coquimbo Region*C. trigona*
- 5B. Abaxial sepal margin spreading in bud, not clasping the adaxial sepal, petals > 10 mm long, stamens 10 or fewer; interior valleys to precordillera, Metropolitana, Valparaíso and Coquimbo Regions "*C. subverticillata*"
- 6A. Flowering stems usually < 20 cm long, cymes remaining congested in fruit, sepals ca. 5 mm or less long, the adaxial sepal margins in bud spreading and not clasping the adaxial sepal, membranous in flower, becoming chartaceous in fruit; interior valleys to the coast, Valparaíso, Metropolitana, and Coquimbo Regions *C. chamissoi*
- 6B. Flowering stems usually > 20 cm long, cymes opening in fruit, sepals ca. 10 mm, the adaxial sepal margin infolded and clasping the adaxial sepal, foliaceous in flower, becoming shriveled but persistent in fruit; western Choapa Province, Coquimbo Region *Cistanthe sp. nov.*

Discussion

This work represents the first critical taxonomic reanalysis of any polytypic *group* of Chilean *Cistanthe* in 125 years. I believe that the work demonstrates adequately that Reiche's *Calandrinia* sect. *Arenarie* includes six previously described species rather than two, and that four species considered to be taxonomic synonyms of *C. arenaria* are readily distinct from that species and from each other. Moreover,

these four species are distributed mainly (three completely) from the LBO to Coquimbo Regions, where *C. arenaria* does not occur.

But the present taxonomy, like all taxonomies, is provisional and, again, for heuristic purposes. This is because, as the saying goes, systematics is a “never ending synthesis.” And it is also because organisms are alive and are not bound by anthropocentric notions of taxonomy. They and only they determine their form and distribution. The taxonomy presented here explains *most* of the actual *observed* forms so-determined, but it cannot be expected to explain all past, much less future, observations. Life continues to *evolve*. Indeed, many of my observations do not fit the taxonomy presented here. I have not discussed these, pending further investigation. But the taxonomy explains the sum total of my observations *much better than* the *existing* taxonomy, which claims that the four species that I recognize in north-central Chile do not exist as such, viz. that all of the plants of this zone pertain to the same species as *C. arenaria*. I hope that the illustrations presented in this work suffice to discredit this notion.

Every now and again in recent years, Santiago newspapers and other media have reported on newly discovered plant species in Chile or, in at least one case, the discovery of an extant population of a species presumed to be extinct. With this in mind, I had considered as an alternative title of the present work something to the effect of “Four ‘new’ species of *Cistanthe* from north-central Chile.” Or, perhaps, “...in Metropolitan Santiago, Chile,” literally under the feet of eight million inhabitants. Of course, per ICN, the present work described no “new” species. The Types of the four species here recognized in north-central Chile were named 128–175 years ago.

But is this a matter of semantics? The purpose of the ICN is not per se to track taxonomic species discovery, nor to identify the person who discovered them. Its purpose is to regulate the authorship and application of *names* of taxa. It establishes priority of names/authors according to historical priority of validly published names of Types, which, again, are individuals considered by the author to belong to *no other* typified taxonomic species, i.e., it is designated as an apospecies. As discussed earlier, ICN does not regulate acceptance or validity of *taxonomic* species or any supposed scientific knowledge thereof. It does not adjudicate whether or not any individual other than the Type pertains to the hypothetical taxonomic species that the Type effectively defines.

So in the case of the species *C. chamissoi*, *C. subverticillata*, *C. trigona*, and *C. vicina*, yes, they had been typified, but they never became established as *taxonomic* species distinct from *C. arenaria*. As discussed above, Reiche (1898a, b) relegated one to synonymy with *C. arenaria* and the other three to varietal status within this species. Thereafter, it seems that their existence as taxa became expunged from collective human conscience. This is evident in Navas Bustamante (1976) and subsequent references, which do not even *mention* the names of Types of these taxa in synonymy. Today, numerous photos of individuals of these species available online are classified as *C. arenaria* or *are not identified*. The last instance means that, in the mind of the observer, the individual pertains to the same species of no *known* Type. This is to say that, in the mind of such observers, the species has *not* been typified or described.

The formal floristic literature has not completely expunged the names, hence existence, of these species. Rodriguez et al. (2018) and others have included the names as *taxonomic* synonyms of *C. arenaria*. This seems to corroborate the notion that, no, the species are not newly discovered here. But there is another way to think about this. ICN rejects the validity of new names, such as “*Calandrinia venulosa*” (Table 1), when they are first published as taxonomic synonyms of other species. In this case, there is no recognized Type (apospecies), hence there cannot be a corresponding taxonomic species (synspecies), either. In other words, when a new name is published as a taxonomic synonym, ICN stipulates rejection/denial of its very *existence*.

ICN logically treats differently the case of a name reduced to synonymy *after* it has been validly published. Its existence is not and cannot be denied...ever. But from a *taxonomic* standpoint, synonymy is synonymy: it makes an identical taxonomic assertion. Whether the name considered by the taxonomist is a validly published name or an invalidly published designation makes no difference. In the present case, for example, Rodriguez et al. (2018) *perfunctorily* accepted ICN validity of the names and Types of *C. chamissoi*, *C. subverticillata*, *C. trigona*, and *C. vicina*. But, from a scientific perspective, they *reject/deny/falsify* the existence of the *taxonomic* species associated with these names, as though they were so many Loch Ness Monsters. Now, what are science and society actually concerned with...the nomenclatural validity of a name?...or the existence, characteristics, and distribution of a species as a unique form of life?

Thus, the present work is conceptually no different from, e.g. other papers that validly publish a new species name. The purpose is not to publish a new name. This is a perfunctory prerequisite to recognition and characterization of the taxonomic species associated with the name. In fact, in the case of *Calandrinia jompomae* Hershk. (HersHKovitz, 2020c, 2022b), I pointed out that this species was recognized and characterized *twice* in the 19th Century. In one case, an individual specimen (collected in 1832) was annotated as “*Calandrinia valdiviana*.” The annotator effectively recognized that the individual pertained to no known/named *Calandrinia* species. But this name never was published, so this researcher’s *discovery* is not recognized. The specimen cannot be a Type, hence it is afforded no nomenclatural attention. Even though it *is* a specimen of an undescribed species and is annotated as such.

In the other case, Barnéoud (1847 [“1846”]) accurately described the species based on an 1835 collection by Claudio Gay. But he mistakenly believed, perhaps by elimination of all other named possibilities, that the specimen pertained to the same species as the Type of *Cistanthe glauca* (see above). Yet he had not seen the Type of the latter, and Candolle’s (1828) brief description of *C. glauca* does not match especially well the characteristics of the Gay specimen. Indeed, Reiche (1898a, b) later commented that *C. glauca* likely was a species of, effectively, *Cistanthe* and not *Calandrinia*, and that Barnéoud’s plant (which Reiche did not see) must pertain to some *other* species. But Reiche did not venture to guess which species. Finally, HersHKovitz (2020c) thoroughly characterized *C. jompomae*, but the species *still* was not validly published per ICN. It *still* had not been “discovered,” not until valid publication in HersHKovitz (2022b).

So the above are a few of innumerable examples of what might be perceived as historical distortion of scientific discovery by ICN. In fact, this is consequent to the confusion of nomenclature with taxonomy. The purpose of ICN, again, is to standardize and stabilize the use of names, and nothing else. And for this purpose, the rules work amazingly well. But in order to make heuristic use of taxonomy, it is important to appreciate that nomenclatural history and scientific taxonomic history are not the same thing.

Returning to the tantalizing title of this section, what exactly was “discovered” in the present work? Before addressing this, I want to comment on heuristic approach behind my recent work, here and in HersHKovitz (2018b, 2019d, 2020c). All of these works began with *empirical* observations of plants in the field or in the herbarium. An alternative approach would have been monographic, assembling first all of the literature and Types.

In the case of HersHKovitz (2018b), I had collected/observed *C. philhershkovitziana* on numerous occasions, but I misidentified it. Only years later did I realize that the plants pertained to no published species. And only after publishing HersHKovitz (2018b) did I realize that the species had been collected several times beginning in 1829 (HersHKovitz, 2018d).

Likewise, in the 1980s, believed that herbarium specimens of *Calandrinia jompomae* were *C. ciliata* (Ruiz & Pav.) DC, not realizing until more than ten years later that they pertained to a distinct

species. I realized only three years ago that Barnéoud (1847 [“1846”]) had described but misidentified this species.

In the case of *C. vicina*, I had encountered this species numerous times in the years 2000-2004. And like everybody else, I misidentified it as *C. arenaria*, though I appreciated that another co-occurring species, *C. chamissoi*, also confused with *C. arenaria*, was distinct. I also collected *C. trigona* from Chincolco and realized that it was distinct from *C. vicina*, which I had been calling *C. arenaria*. It was not until within the past three years that I studied the literature and Types of this group that yielded the present interpretation. The difference between the present case and the two above is that it turned out that names and Types *existed*. But I did not know this at the time that I had drawn my principal taxonomic conclusions based on specimens.³⁶

Note that in all of these cases, the heuristic approach is the same. None of the species I “discovered” in this way were accepted or otherwise contemporaneously “known.” It just turned out that no Types existed for two of the species and existed for the other four. A mere technicality from the standpoint of my approach. Names and Types might have existed for all of the species or none of them.

Thus, I find almost surreal the notion that no “new” species were discovered when no botanist in at least the past half century has recognized the *existence* of *C. chamissoi*, *C. subverticillata*, *C. trigona*, and, especially, the markedly divergent *C. vicina*. The names themselves are virtually unknown or, at best, merely acknowledged as having been validly published. It seems to me even more surreal that three of the species (*C. subverticillata*, *C. trigona*, and *C. vicina*) grow abundantly and intimately *intermingled* in at least one locality near Chincolco. There simply is no confusing these three species in the field. Thus, even if *one* of them were to be considered the same as the absent *C. arenaria*, simple visual inspection would demonstrate that the other two *must be* different species.

And the fact that *all four* species occur in Chile’s most populous metropolitan area demonstrates that, unlike new species found in remote and poorly accessible localities, there never has been a logistical barrier to the broader recognition of these species. For God’s sake, they have been *named* and *described*. It is as though their existence was advertised with neon lights. So, if there has been any obstacle at all, it certainly must be a cultural and/or cognitive one. And it is precisely for such mental obstacles that I do *not* expect that *discovery* of the *existence* in Chile’s largest city of not one, not two, not three, but *four* typified but currently *unrecognized* plant species would be considered “newsworthy.”

³⁶ In fact, had I or anyone else used the monographic approach, studying first the literature and Types and discovered Lindley’s error, the present conclusions would have resulted.

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Table 1. Type data for *Cistanthe* taxa pertinent to Reiche's (1897) *Calandrinia* sect. *Arenarie*.

BASIONYM	REFERENCE	HOMOTYPIC SYNONYMS	TYPE	TYPE LOCALITY	COMMENT
<i>Calandrinia arenaria</i>	Chamisso 1831: 345	<i>Cistanthe arenaria</i> (Cham.) Carolin ex Hershk.	LECTOTYPE (designated here): <i>Chamisso s. n.</i> , without date (HAL0070919!; ISOLECTOTYPES: G 00440498 [image!]; K 000424759 [image!]).	Biobío Region, Concepción, sandy soil along the Río Biobío	All specimens lack the root, but a short portion is conserved in the HAL and K specimens. Life form not described. Seed described as black and lustrous, but later described by Barnéoud (1847 ["1846"]), presumably based on different material, as finely aspirate.
<i>Calandrinia chamissoi</i>	Barnéoud 1847 ["1846"]: 497	<i>Cistanthe chamissoi</i> (Barnéoud) Carolin ex Hershk.	LECTOTYPE (designated here): <i>Bertero 1348</i> , Oct-Nov 1829, (P 01903300! [top of three individuals]; ISOLECTOTYPES: P 01903300! [bottom two of three individuals], P 04582976! [without collection number], P 04582981! [specimen image covered with paper], G 00440494 [image!], G 00440495 [image!], G 00440496 [image!])	Valparaíso Region, Quillota	Seeds described as "very wrinkled."
<i>Calandrinia fenzlii</i>	Barnéoud 1847 ["1846"]: 493	<i>Cistanthe fenzlii</i> (Barnéoud) Carolin ex Hershk.	LECTOTYPE (designated here): <i>C. Gay 1415</i> , 2 Jan 1839 (P 01903297!, bottom row, third individual from the left; SYNTYPES: P 01903297!, remaining individuals; ISOLECTOTYPE: SGO [low image resolution!]).	Biobío Region, Angol, Antuco	Root described as annual, though those of the specimens appear to be woody and relatively thick. Seeds described as glabrous and shiny.
<i>Calandrinia glaucopurpurea</i>	Reiche 1898a: 342; 1898b: 346		Not found, possibly destroyed.	Coquimbo Region	The description is similar to <i>C. chamissoi</i> . Seeds described as black, opaque, and finely aspirate.
<i>Calandrinia lancifolia</i>	Philippi 1894: 300		LECTOTYPE (designated here): <i>R. A. Philippi s. n.</i> , 1877 (SGO 000001843; ISOLECTOTYPES?: SGO 000001844, SGO 000001845 [low resolution images!]).	Araucanía Region, Angol, Los Moncoles	Described as "perennial but possibly annual." Seeds not described. Possibly the isolectotypes sheets are fragments of the lectotype individual.

Table 1, continued.

BASIONYM	REFERENCE	HOMOTYPIC SYNONYMS	TYPE	TYPE LOCALITY	COMMENT
<i>Calandrinia nana</i>	Philippi 1894: 304		LECTOTYPE (designated here): <i>Philippi s. n.</i> , 1860 (SGO 000001834 {low resolution image!}); ISOLECTOTYPE: SGO 000001835).	Valparaiso Region, San Felipe de Aconcagua Province, Catemu.	Evidently a precociously flowering seedling of <i>C. trigona</i> .
<i>Calandrinia polyclados</i>	Philippi 1864: 77		Type: <i>Landbeck s. n.</i> , (not found); potential NEOTYPE: <i>Philippi s. n.</i> , 1862 (F; negative [!]) ex Candolle Herbarium, original not located in G database).	Former "Colchagua Province" (~ LBO Region)	Described as annual with seeds opaque granulated, white-marbled. The image, description, and locality correspond to <i>C. trigona</i> . Not mentioned in Rodriguez et al. (2018).
<i>Calandrinia sanguinea</i>	Philippi 1893: 190		LECTOTYPE (designated here): <i>R. A. Philippi s. n.</i> , 1886 (SGO 000001838; ISOLECTOTYPES: SGO 000001836, SGO 000001837, HBG 508125 [low resolution images!]).	Biobío Region, Talcahuano, San Vicente, sandy soil along the Río Itata.	Described as perennial, similar to <i>C. arenaria</i> but differing in its thicker root (and apparently more upright habit, forming a "lawn"). I doubt that Philippi actually saw type material of <i>C. arenaria</i> . Seeds described as "opaque."
<i>Calandrinia subverticillata</i>	Philippi 1894: 302	<i>Calandrinia arenaria</i> var. <i>subverticillata</i> Reiche	HOLOTYPE: <i>F. Philippi s. n.</i> , without date (SGO 000001841 [IMAGE!]).	Metropolitana Region, Santiago	
" <i>Calandrinia venulosa</i> "	Hooker & Arnott 1831: 336		Reference specimens: <i>H. Cuming 514</i> , without date (K 00424760 [image!]); <i>T. Bridges 425</i> , 1832 (K 00424761 [IMAGE!]).	Valparaiso Region, Valparaiso	This name is cited as a valid synonym of <i>C. arenaria</i> in Rodriguez et al. (2018) and other references. But it was published as a <i>synonym</i> and not an accepted species, and therefore it is invalid (Art.36.1). The cited specimens can be diagnosed as <i>C. chamissoi</i> .

Table 1, continued.

BASIONYM	REFERENCE	HOMOTYPIC SYNONYMS	TYPE	TYPE LOCALITY	COMMENT
<i>Calandrinia vicina</i>	Philippi 1894: 301	<i>Cistanthe vicina</i> (Phil.) Carolin ex Hershk.; <i>Calandrinia arenaria</i> var. <i>vicina</i> Reiche	HOLOTYPE: <i>R. A. Philippi s. n.</i> , Nov 1877 (SGO 000001842 [IMAGE!]).	Metropolitana Region, Cerro Renca	Described as annual. Seeds not described.
<i>Talinum trigonum</i>	Colla 1834: 71	<i>Cistanthe trigona</i> (Colla) Carolin ex Hershk.	HOLOTYPE: <i>Bertero 683</i> , "1830" [1828!] (TO [image!]). ISOTYPES: G 00440471 [image!], G 00440474 [image!], L 1687708 [image!], NY 02065853 [image!], MO-1939567 [image!], P 04582974! [without locality, without date], P 04583977!, P 05482978! [without date], P 05482979! ["Nov 1829"], P 04582980! ["1829"], P 04582982!).	O'Higgins Region, Rancagua, Río Cachapoal Other locality data of specimens labeled " <i>Bertero 683</i> ": "La Quinta, Río Claro" (G00440472 [image!]), "Rancagua" (L 1687704 [image!]), without locality (G 00440473 [image!])	Described as annual. Seeds not described. See Hershkovitz (2020d) regarding the reliability of specimen data on Bertero collections.

Figures

Fig. 1. *Cistanthe trigona*. **A–N.** Plants from Cuesta de Alicahue al Sobrante (Petorca Province, Valparaiso Region). **A.** Partially pressed specimen. Note the secondary leaf whorl on the flowering stem towards the bottom of the image. **B.** A large plant emerging from rosette stage from a moist microsite early in inflorescence development. Five flowering stems are visible, and probably more will develop from a rosette this size. Note the secondary leaf whorl on the flowering stem on the left side. **C.** Small plant in full flower after ten days in the dark in a balled up black plastic bag. Scale hashes are 1 mm. **D.** Plant collected from compacted road should matrix with prostrate inflorescence and showing enlarged stem base. **E.** Close-up of enlarged stem base. Such characterize all stems (including pedicels, though not so pronounced) of essentially all *Cistanthe* species. **F.** Flower near full anthesis. Note the relative sizes of the petals and sepals. **G.** Open flower with incurved stamens. Note the style length and small ovary size. The unopen flowers show the inrolling of the abaxial sepal margin, clasping the adaxial sepal. **H.** Fully open flower with spreading stamens. The ovary is occluded by the dilated and pubescent stamen bases. **I.** Lateral view of flower showing stamen and style length. **J–K.** Two oblique views of a flower near anthesis highlighting the dorsal wing/keel of the sepals. **L–M.** Two views of a flower bud highlighting the dorsal wing/keel of the sepals and the inrolling of the abaxial sepal margin and clasping of the adaxial sepal. **N.** Maturing cymule showing capsule development. Note the absence of the calyx on the most mature fruit. Scale hashes are 1 mm. **O.** Lectotype (cf. Table 1).

Fig. 1, continued.



Fig. 1, continued.

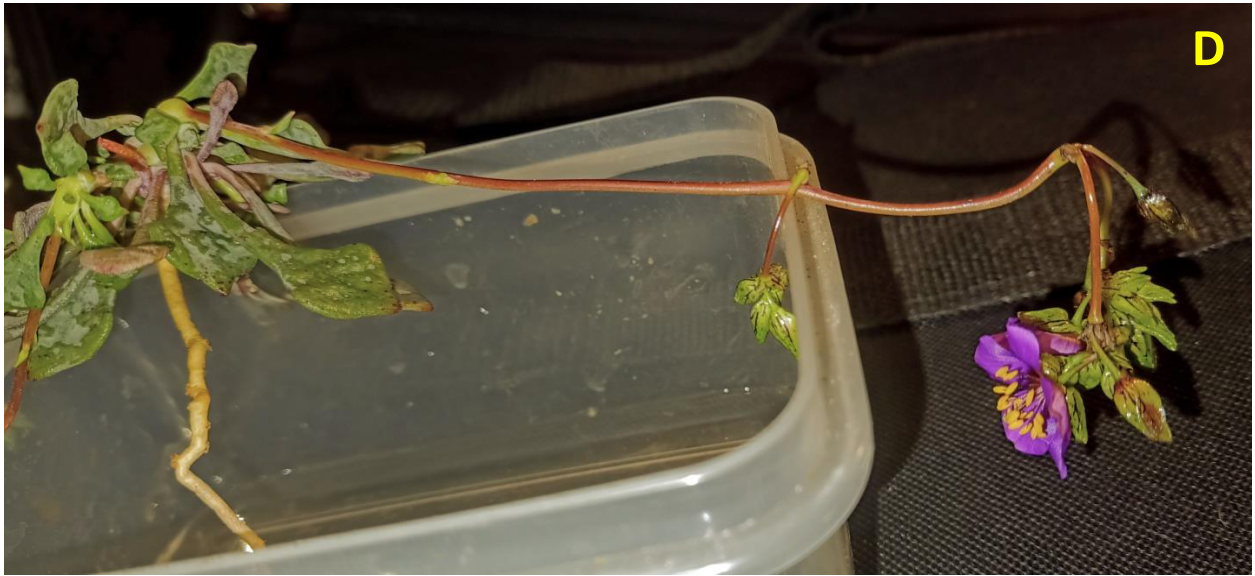


Fig. 1, continued.



Fig. 1, continued.



Fig. 1, continued.



Fig. 2. *Cistanthe chamissoi*. **A–E.** Plant growing at Puerto Oscuro, Choapa Province, Coquimbo Region, Chile. **A.** Whole plant, among the largest in the population. **B.** Side view of multiple branches with flowers. **C.** Terminal cymule of a flowering branch. The scale hashes are 1 mm. **D.** Open flower, ca. 7.5 mm broad. **E.** Gynoecium (sorry, best dissection I can do with a sewing needle and best photo I can take with my cell phone). Even though the gynoecium is small, note that the style length equals the ovary length. The scale hashes are 1 mm. **F.** Illustration of *C. chamissoi* from Lindley (1833), there identified as *C. arenaria*. Evident is the morphology of the abaxial sepal with its spreading margin, enclosing but not clasping the adaxial sepal. Lindley’s misidentification of this plant (following Hooker & Arnott, 1833) proved to be pivotal to the confusion of the taxonomy of *C. arenaria* for the succeeding 190 years (Hershkovitz, 2022a). **G.** Lectotype (cf. Table 1).



Fig. 2, continued.



Fig. 2, continued.



Fig. 2, continued.



Fig. 3. *Cistanthe vicina*. **A–F.** Plants from Puerto Oscuro (Choapa Province, Coquimbo Region). **A.** A relatively large individual growing along the dirt road. **B.** Putative hydathode at leaf apex. This feature characterizes all *Cistanthe* species. **C.** Terminal cymule of a flowering branch. Note the opaque luster and comparatively scant black markings in the sepals. The infolded margin of the abaxial sepal is evident. The scale hashes are 1 mm. **D.** Open flower, side view. Note that the petals are not much longer than the sepals. Scale hashes are 1 mm. **E.** Open flower, top view. The stamen number in the largest flowers typically is greater, 15–20. Scale hashes are 1 mm. **F.** Gynoecium showing sessile magenta stigma. The scale hashes are 1 mm. **G–M.** Plants from Cuesta de Alicahue al Sobrante (Petorca Province, Valparaiso Region). **G.** Flower showing marked/streaked sepals and short style. **H.** Side-by-side comparison of flowers of *C. trigona* and *C. vicina*. **I.** Flowering stem showing expansion following anthesis and during fruit maturation. The secondary leaf whorl shows at the bottom. Note the petiolate leaf on the cyme. Otherwise flowering stems and cymes of *C. vicina* range from essentially naked to bracteate to leafy and bracteate. **J.** Enlargement of 5l. **K.** Cymule in immature fruit stage. The horizontal orientation is natural. Note that the immature fruits exceed the calyx just slightly. **L.** Fruit nearly at anthesis, ca. 0900h. The vertical orientation is natural; pedicel reoriented vertically. Note that the sepals have shriveled somewhat, rendering the impression that the fruit is rather longer. **M.** The same fruit as in K but at 1700h, now dehiscent. **N–O.** Black-sepaled plants from Puerto Oscuro. **N.** Plants growing along the dirt road. **O.** Close-up of cymule. Scale hashes are 1 mm. **P.** Precociously flowering seedlings from a population near Illapel, Chile (Choapa Province, Coquimbo Region). The plants were growing in a large population near Illapel, Chile. Note the peculiar divergence angles of the flowering stems. The angle is “regulated” by the swelling at the stem base. The largest plants at that time in this population had flowering stems ca. 20 cm long and petiolate leaves ca. 10 cm long. **Q.** Holotype (cf. Table 1).

Fig. 3, continued.



Fig. 3, continued.

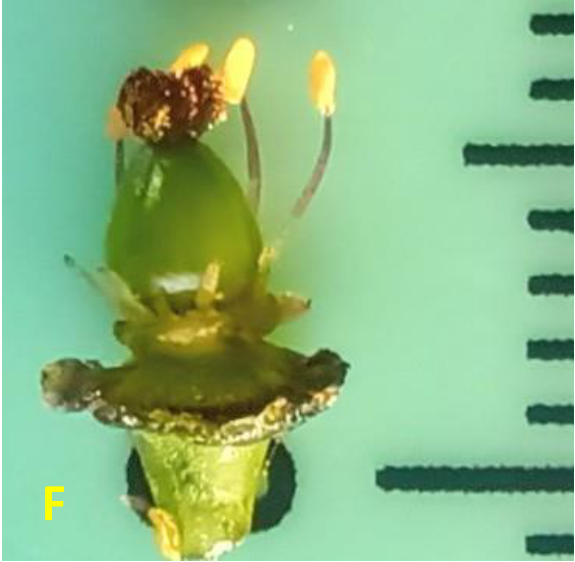


Fig. 3, continued.



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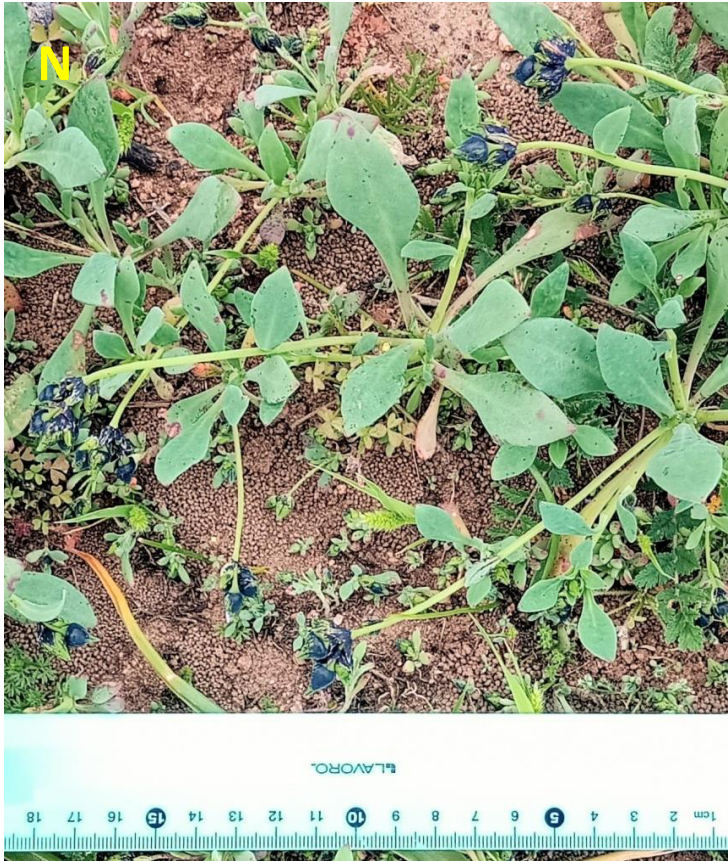


Fig. 3, continued.



Fig. 3, continued.

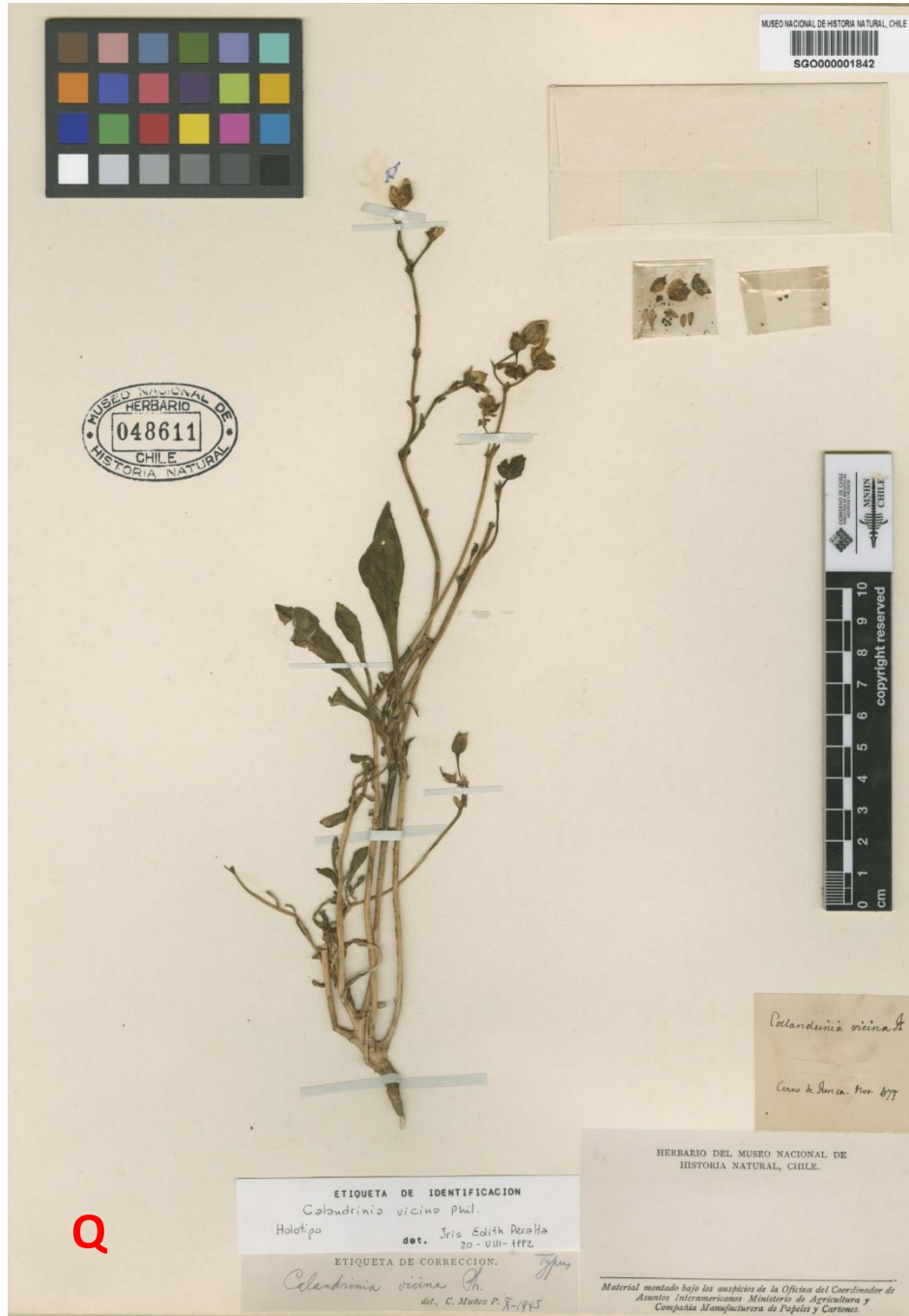


Fig. 4. “*Cistanthe subverticillata*.” **A–F.** Plants from Cuesta de Alicahue al Sobrante (Petorca Province, Valparaiso Region) with rose flowers and otherwise pigmented. **A.** Whole plant. **B.** Portion of inflorescence. **C.** Lateral view of a single flower showing outward splaying of the more or less membranous abaxial sepal margin. The rest of the flower is fully contained within the inflated central portion. **D.** View of abaxial sepals in the inflorescence, showing outward splay of the margins. The adaxial sepals can be seen in the vertically-oriented flowers at the bottom. It can be seen that the abaxial sepal margins do not clasp the adaxial **C.** Close-up of flower. **E.** Portion of inflorescence in fruit. Note the coloration and the absence of sepals on receptacles with mature capsules. **F.** Ovary. **G–H.** Small precociously-flowering white-flowered and otherwise nonpigmented individual from the same locality. **H.** Close-up of the inflorescence showing the brownish rather than dark purple lines on the sepals characteristic of this species or black lines characteristic of other *Cistanthe* species. **I.** Close-up of flowering stem secondary rosette showing bullate leaf surface. **J.** Holotype (cf. Table 1; <https://plants.jstor.org/stable/10.5555/al.ap.specimen.sgo000001841>).



Fig. 4, continued.



Fig. 4, continued.



Fig. 4, continued.

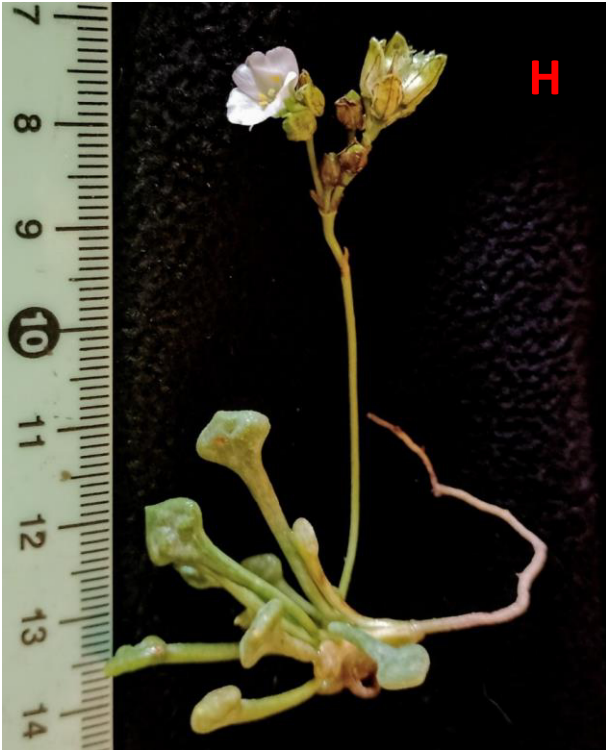


Fig. 4, continued.



Fig. 5. Ribbon-like fine vein anatomy of species of *Cistanthe* and Calyptridinae (from HersHKovitz, 1991b: 1055, Figs. 73–79; see caption details in that work. Reproduced with permission from the Annals of the Missouri Garden Press). The vessel element thickenings are abbreviated as follows: A = annular, H = helical, S = scalariform, S-R = scalariform-reticulate. “Fig. 76” documents a vein eleven elements broad. This vein is not from a *Cistanthe* species, but from *Thingia ambigua* (Calyptridinae).

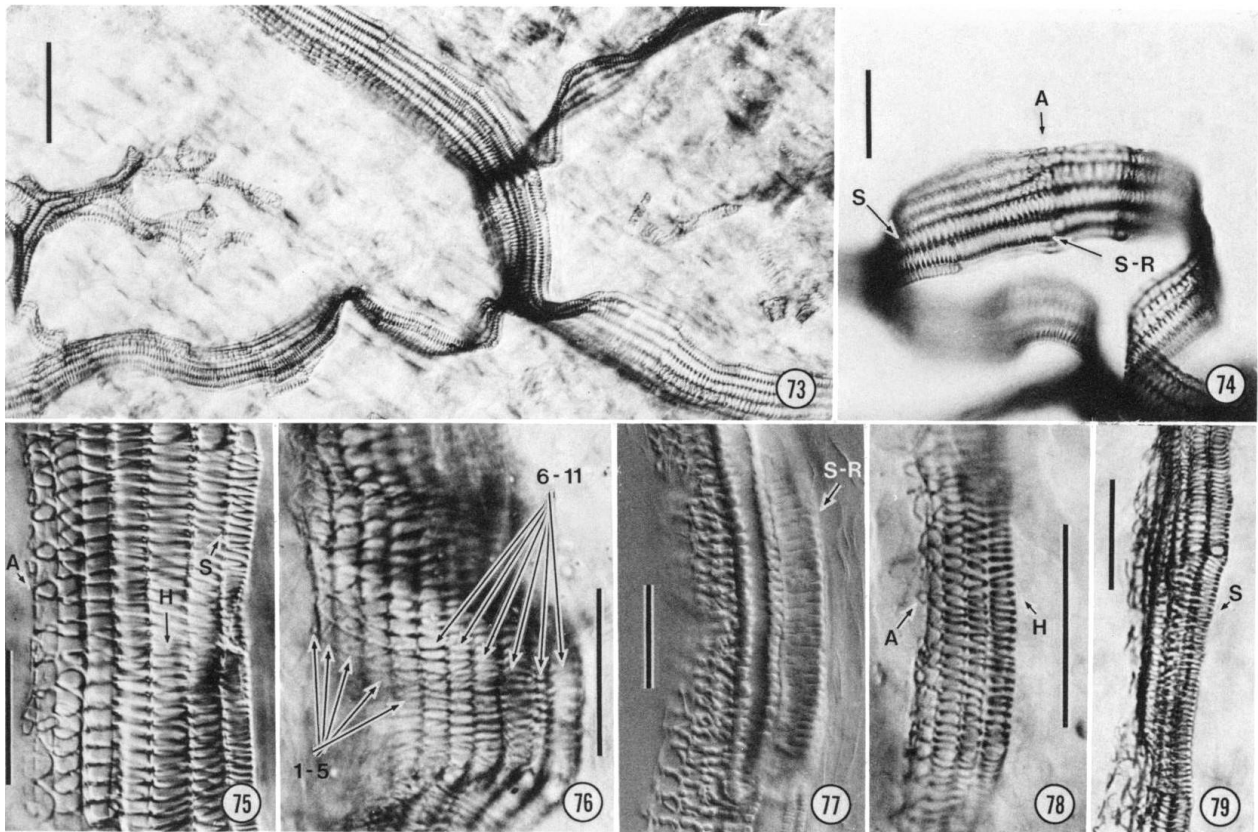


Fig. 6. Upward reorientation of mature fruits of "*Cistanthe sp. nov.*" **A.** Close-up showing the pedicel of a senescent but unpollinated flower oriented upward (center), of an immature fruit bent laterally and slightly downward (left), a maturing fruit reoriented more upward (left-center), and a mature and dehiscent fruit bent vertically upward (right). **B.** Some vertically oriented dehiscent fruits of a single cymule. **C.** Top view of the cymule in B showing the seeds inside the capsule.



Fig. 7. *Cistanthe arenaria*. C. Joseph 4014 (US). <http://n2t.net/ark:/65665/m310f0db94-ac89-4644-89bf-b483a65691ea>

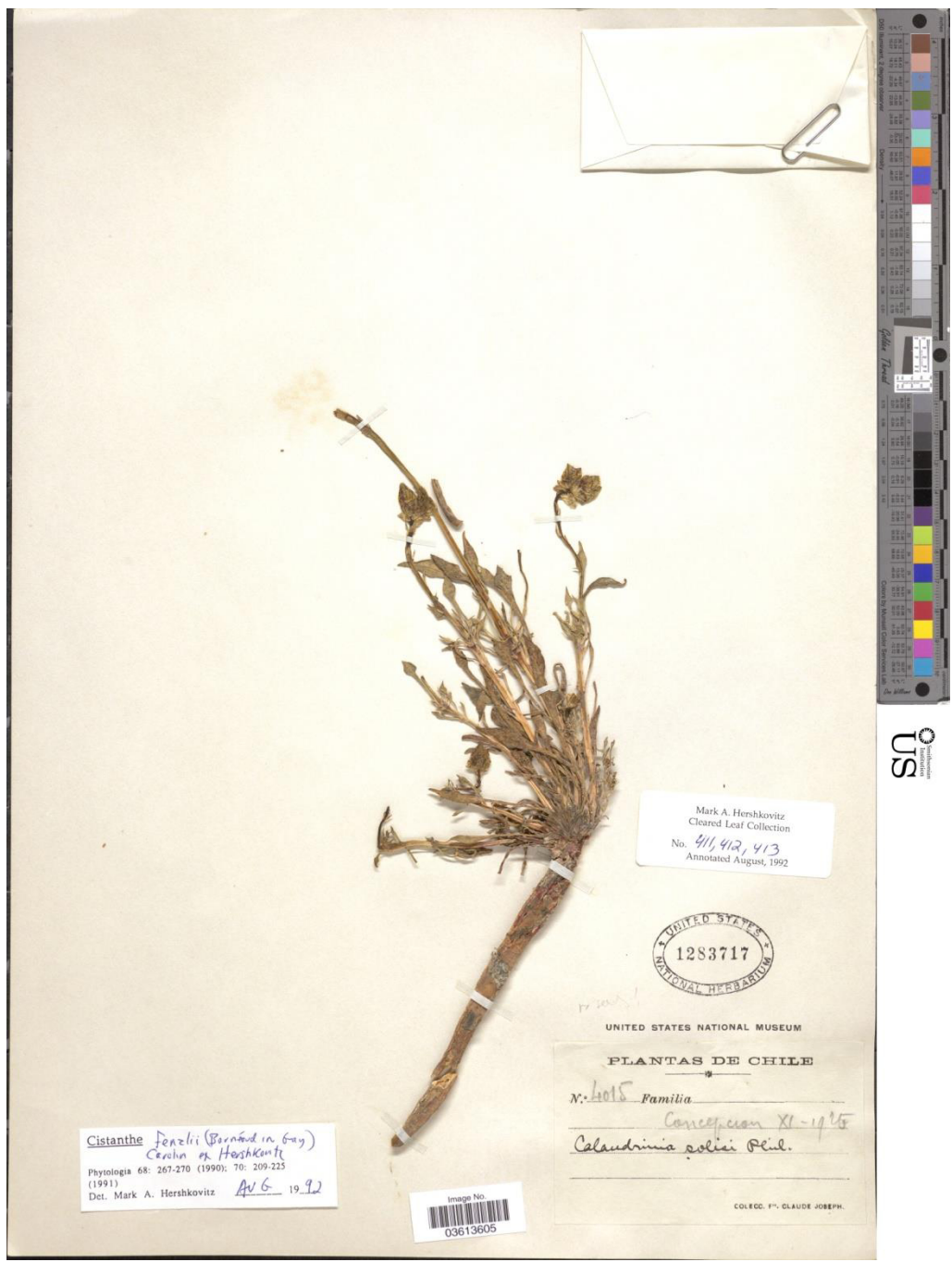


Fig. 8. Type of *Cistanthe fenzlii*. (<http://coldb.mnhn.fr/catalognumber/mnhn/p/p01903297>). Note that the taproots have been partially cut. Compare with Fig. 9.



Fig. 9. Specimen of *Cistanthe fenzlii*. Biobío Region, Concepción Province, Concepción, 13 Nov 1945, E. Junge 2637 (US 03613550). Note the thickness of the taproots. (<http://n2t.net/ark:/65665/3663c2f86-6c53-456c-843b-65b1e0cb945a>)

