Calandrinia jompomae (MONTIACEAE), another overlooked species in the Chilean flora

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ABSTRACT

Calandrinia jompomae Hershk. is described as a distinct species of *C*. sect. *Calandrinia* from south-central Chile. The species was described by Barnéoud, but he erroneously identified it as *C*. *glauca* Schrad. ex DC. *Calandrinia jompomae* is similar to *C*. *bonariensis* Hauman endemic to Buenos Aires Province, Argentina, here recognized as distinct from *C*. *ciliata* (Ruiz & Pavon) DC. But the habitat/ecology of *C*. *bonariensis* is distinct, rendering prudent the recognition of *C*. *jompomae* pending genetic analysis. *Calandrinia jompomae* also is morphologically similar to an unidentified annual calandrinia from the Falkland Islands. *Calandrinia jompomae* is another example of a species easily distinguished and historically well-collected, yet overlooked in the taxonomy of the Chilean flora.

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Hershkovitz (2006: 42) reported identification of a possibly distinct species of annual calandrinia (*Calandrinia* sect. *Calandrinia* sensu Hershkovitz, 2019a) in Chile's Bío-Bío to Los Ríos Regions (Fig. 1). The plants resembled somewhat the allopatric and disjunct *C. ciliata* (Ruiz & Pav.) DC (Fig. 2), but also manifested intermediacy between the two locally sympatric species *C. pilosiuscula* DC (incl. *C. compressa* Schrad ex DC; Hershkovitz 2020a; Fig. 3) and *C. nitida* (Ruiz & Pav.) DC (incl. *C. axilliflora* Barnéoud; Fig. 4). A hybrid origin thus was suggested. In fact, different herbarium specimens of these distinctive plants (see below) had been identified (or not!) by myself and others variously as *C. axilliflora*, *C. ciliata*, *C. compressa*, *C. glauca* Schrad. ex DC, *C. pilosiuscula*, and "*C. valdiviana*" (nom. nudum.). This diversity of opinions themselves suggests that these plants pertained to none of the above.

Hershkovitz (2020a) intimated that the similarity to *C. ciliata* possibly confounded the distinction between *C. ciliata* and *C. pilosiuscula* and also underlies the spurious interpretation of the distribution of *C. ciliata* in Chile as reported by Peralta and Ford-Werntz (2008) and Rodriguez et al. (2018). In fact, the Chilean specimen of *C. ciliata* cited by Peralta and Ford-Werntz (2008), Hicken s. n. (SI; not seen), is from Puerto Montt, Chile (ca. 41.30°S 72.50°W), the southern end of the range of the distinctive plants described here.

Here, I describe these distinctive plants as *Calandrinia jompomae*. Their most distinctive feature is the striking length and apical deflection of the pedicels in fruit, especially in the apical portion of the inflorescence (Fig. 1). In *C. pilosiuscula* (Fig. 2) and *C. ciliata* (Fig. 3), for example, the pedicels in the apical portion of the inflorescence are very short and erect to somewhat reflexed in fruit. The pedicels of *C. nitida* are long but notably reflexed and recurved in fruit (Fig. 4). However, the pedicels of *C. jompomae* also characterize the plant described as *Calandrinia bonariensis* Hauman (Fig. 5) from eastern Argentina. This has been considered a synonym of *C. ciliata* (Añon Suarez de Cullen, 1953: 19–20; Hershkovitz, 2006: 41; Peralta & Ford-Werntz, 2008: 2798).

However, Hauman and Irigoyen (1923) listed *C. ciliata* (as *C. caulescens* Kunth) as distinct. The pedicel trait also characterizes an unidentified annual calandrinia from the western Falkland Islands (FI; Fig. 6; cf. Hershkovitz, 2006; Falklands Conservation, 2007: 15).

Further study revealed that Barnéoud (1847 ["1846"]: 487–488; cf. Reiche, 1898a: 354; 1898b: 358).) described these lengthy pedicels in plants he erroneously identified as *Calandrinia glauca* [\equiv *Cistanthe glauca* (Schrad. ex DC) Lilja, = *Cistanthe grandiflora* (Lindl.) Schltdl., nom. cons.]. In fact, the specimen described by Barnéoud, *C. Gay 104* (P), is designated here as the holotype of *C. jompomae*. Another specimen collected in 1832, *Bridges 738* (E), was labeled originally as "*Calandrinia valdiviana*" (nom. nudum), probably by W. J. Hooker (cf. Johnston, 1928). Regardless of their identifications, both Barnéoud's work and (likely) Hooker's annotation reveal early historical appreciation that these plants represented a species distinct from other annual calandrinias.

The present work compares *C. jompomae* with related *Calandrinia* species and discusses its ecology, biogeography, and evolution. The work also comments on the incidence of species in the Chilean flora that have been overlooked historically despite being easily distinguished and well-collected.

Calandrinia jompomae Hershk., sp. nov. TYPE: CHILE: Los Ríos Region, Valdivia Province, Valdivia, January 1835, *C. Gay 104* (HOLOTYPE, P! [P05276741 {det. *Calandrinia glauca* fide C. Gay and/or F. N. Barnéoud; "*Calandrinia ciliata* complex" fide Hershkovitz, 1992; image!}]; Fig. 1).

Diagnosis. Plants similar to species of Calandrinia sect. Calandrinia (sensu Hershkovitz, 2019a), differing from C. bonariensis in distribution and associated ecology in humid forest vegetation of south-central coastal Chile rather than the shrubby steppe-like vegetation of Buenos Aires Province, Argentina; differing from C. ciliata (Ruiz & Pay.) DC, C. menziesii (Hook.) Torrey & A. Gray, C. pilosiuscula DC, and C. breweri S. Watson in having longer pedicels and shorter leaves (or merely bracts) in the apical portion of the inflorescence, lacking distinct cilia along the sepal keel and margins, and having pale purple rather than pink to deep rose flowers; differing also from C. *pilosiuscula* in having more ovate rather than deltoid sepals that are basally nearly free rather than connate; differing also from C. breweri in having mature capsules ca. 1.5X rather than ca. 2X the length of the sepals and also being intercontinentally disjunct; differing from C. alba (Ruiz & Pav.) DC and C. nitida (Ruiz & Pav.) DC in having only bracteate nodes in the apical portion of the inflorescence rather than leafy sterile and fertile nodes throughout, and relatively smooth rather than deeply sculptured seeds; differing also from C. nitida in having ovate sepals and capsules rather than nearly orbicular, and pedicels deflexed rather than reflexed in fruit; differing from C. monandra (Ruiz and Pav.) DC in having a (superficially) racemose rather than a highly and irregularly branched inflorescence and also much larger flowers with greater numbers of petals, stamens, carpels, and ovules.

Annual herbs growing and flowering in spring, ca. September to December. Roots fibrous, branching from a slender taproot. Basal leaves in a rosette, narrowly spathulate, differentiated into an apical deltoid to rhombic blade and a basal winged petiole, 2-4 cm long, < 1 cm broad, ciliate along the margin. Stems several from the axils of basal leaves, 0-1-branched, ascending, sterile and leafy in the basal half, fertile and bracteate in the apical, resembling a raceme, up to ca. 30 cm long. Stem leaves similar to the basal leaves basally, becoming more linear and eventually merely bracteate towards the stem apex. Flowers 5–10, solitary in the axil of the smaller of two leafy and approximately opposite bracts; pedicels 1–2 cm in flower, elongated, deflexed apically, and somewhat sclerified in fruit, 2–3 cm. Sepals 2, broadly ovate, keeled, glabrous (or papillate along the

margins?), free to nearly the base, imbricate, up to 7 mm long. **Petals** 5, flabellate, 'pale purple with darker purple markings, up to ca. 10 mm. **Stamens** ca. 7. **Ovary** simple, stigmas 3. **Fruit** capsulate, 3-valved, ca. 10 mm long. **Seeds** numerous, black, smooth.

Distribution and habitat. *Calandrinia jompomae* is distributed in Chile, extending northsouth ca. 600 km between ca. Concepción (Bío-Bío Region) to at least Valdivia and probably Puerto Montt (Los Lagos Region), and from the Pacific Ocean coast to ca. 50 km inland, ca. 34–41.3°S, 72– 73.50°W. It occurs in humid open or cleared locations in deciduous to evergreen humid forest vegetation. I have not had yet the possibility to examine several specimens from the Puerto Montt area (cited below as possible additional collections). However, these collections have been identified as either *C. ciliata* or (effectively; Hershkovitz, 2020a) *C. pilosiuscula*. My thesis here is that the former identification not only is incorrect, but that this misidentification of plants from south-central Chile *correctly* diagnoses plants of *C. jompomae*. Meanwhile identification as (effectively) *C. pilosiuscula* likely was assumed based only on Chilean provenance. Peralta and Ford-Werntz (2008) and Rodriguez et al. (2018) listed *C. pilosiuscula* (as *C. compressa*) as present in Chile's La Araucanía and Los Ríos Regions. It is a weedy species and may well occur there. But I have reviewed several virtual herbaria databases (including GBIF; GBIF Secretariat, 2017), and I cannot locate an image of a specimen of *C. pilosiuscula* from south of 38°S (Bío-Bío Region).

Additional specimens examined. CHILE: Without locality, C. Gay, without date (P! [P05276860 {det. as isotype of C. axilliflora Barnéoud; the inflorescence is immature, the sepals are like C. jompomae and not C. axilliflora; image!}]); Without collector, without date (LE [LE01010326]); {"Chile austr. mant. Octbr. [1?]828;" det. as Calandrinia; image!}]). Bío-Bío Region, Arauco Province, along. Chile national Rte. 160 10 km s of turnoff to community of Curanilahue, 37°30'S 73°30'W [NOTE: 100–200 m], 29 Sept 1991, C. M. Taylor 10596 (MO, ASU [ASU0029919 {flower color "pale purple with dark purple lines," collected from a pine plantation clearing; plant much smaller (stunted) than collections from further south; Calandrinia compressa fide D. I. Ford, 1991; image!}]). Valdivia Province, without locality, O. Buchtien s. n., 1896 (L [L1686641 {locality illegible; Calandrinia compressa fide Buchtien; Calandrinia axilliflora non C. compressa fide S. J. van Ooststroom and Th. J. Reichgelt; image!}], US! [US03613483 {Calandrinia compressa fide Buchtien; image!}]); H. Gunckel 3684, without date (US! [US03613432 {"San Carlos; species not determined; Calandrinia sp. aff. ciliata or compressa fide Hershkovitz, 1992; image]]); P. A. Hollermayer 398, without date (E [E00033160 { Calandrinia compressa fide Skottsberg; Calandrinia *ciliata* fide I. E. Peralta, 1992; image!}]); Panguipulli Municipality, Arique, ca. 39°48'S 72°02'W, W. Lechler 585, Nov – Dec 1852 (P! [P05276729 {"Dec.;" original det. Calandrinia pilosiuscula; C. sp. aff. compressa fide Hershkovitz, 1992; image!}], U [U1523952 {"Nov.;" det. Calandrinia pilosiuscula; image!}]); Valdivia Municipality, "near Valdivia," Bridges 738, without date [late 1832] fide Johnston (1928: 101, 106)] (E [00033159 {original det. as "Calandrinia valdiviana" (nom. nudum.) ?fide W. J. Hooker; C. ciliata fide I. E. Peralta, 1992; image!}]); Without locality, C. Joseph 2420, Oct 1923 (US! [US03612428 {Calandrinia compressa fide C. Joseph; image!}]); Werdermann 1951 (leg. Auth. Hollermayer), Nov 1928, ca. 200 m (U [U1523977, U1523978, U1523979 {det. as Calandrinia; images!}], US [US03613612 {det. as Calandrinia image!}])

Possible additional collections, not examined. CHILE: La Araucanía Region, Malleco Province, Angol Community, Lealtad Station, elev. 140 m, 6 Nov 1958, *G. W. H. Kunkel 1961 (492)* (B [B100538885 {*Calandrinia* sp.}]), *G. W. H. Kunkel 1963 (490)* (B [B100538887 {*Calandrinia* sp.}]); Lumaco Community [ex Traiguén Department], San Gerardo, elev. c. 100 m, 28 Oct 1958, *G. W. H. Kunkel s. n.* (B [B100533321 {*C. compressa*}]). Los Lagos Region, Llanquihue Province, Lake Frutillar [ca. 41°7'S, 73°3'W; elev. ca. 62 m], date illegible, *M. Ohme s. n.* (B [B100557922 {*C. procumbens* Moris}]); Puerto Montt, without date, C. M. Hicken s. n. (SI {*C. ciliata*}).

In addition to the above, I saw several specimens of *C. jompomae* in CONC during a visit in ca. 2004, but I have lost these notes. Some specimens there likely are duplicates of some cited above. I recall that at least one specimen had been collected after 2000 from the coastal town of Lebu, near Concepción.

Etymology. Calandrinia jompomae honors Dr. Jorge M. "Jompoma" Mpodozis of the Laboratory of Neurobiology y Biology of Knowledge of the University of Chile. Mpodozis was a student and disciple of Humberto Maturana and coauthor of Maturana and Mpodozis (2000), "On the origin of species by means of Natural Drift." I met Mpodozis during my 2000–2006 tenure as assistant professor in U. Chile, before I was fired for academic incompetence. Mpodozis, like his mentor, studies the electrophysiology of the pigeon visual system, introducing into the pigeon's visual field a red dot from a laser pointer, and then tracing the path of neural impulses in the pigeon brain in order to divine what the pigeon "sees," and therefore "thinks" and "does." Mpodozis is in Department's charge of the Biology undergraduate course in "evolution," and already in 2000 had invited me to present a lecture on plant taxonomy. My initial thought was, what World could this Third pigeon brain electrophysiologist possibly know about evolution? Indeed, the course, much to the vociferous chagrin of Chile's neo-Darwinian



dogmatists, is eclectic and unstructured, scarcely if at all pontificating on Fisher and Wright and the Price Equation and the "31 Flavors" of Natural Selection. Rather, it departs from the definition of biological organisms as sensorially deterministic beings and the quality of life as the materialization of autopoiesis. Thereafter, much of the course is presented by an odd lot of researchers invited to discuss their empirical research on subjects ranging from molecular biology to physiology to taxonomy to geology, all tied together ultimately by the process supposed to be evolution. No, this knowledge does not materialize from the study of the pigeon brain visual system. But what emerges from the latter is an understanding of how "scientific knowledge" of evolution is conditioned by sensorial experience. It is perhaps better termed "attitude." It demonstrates that what we take for scientific "discovery" often merely is its very expectation or "premise." And, of course, it demonstrates that what we are *taught* about evolution is propaganda. The only possibility to understand nature is to abandon dogma and its methodology and view it naïvely and from as many vantage points as possible. Ultimately, this "natural drift" approach modified my own erstwhile linear - *learned* - conceptualization of evolution and inspired my attempt to extend the concepts of Natural Drift and autopoiesis to biological systematics and phylogenetics, yielding the Principle of Evolutionary Idiosyncraticity (Hershkovitz, 2019a, b).

Discussion. Calandrinia jompomae is a species clearly distinct from all other currently accepted species of Calandrinia. At the same time, it is very similar to C. bonariensis and unidentified calandrinias of the western FI. Indeed, all three of these entities may be considered eventually as the same species, in which case the prioritized name would be C. bonariensis. In this

case, the present paper would name no new species, but otherwise would be no different, because all three of these entities remain distinct from the other species to which they have been referred erroneously, their collective similarities have not been noted previously, and their collective geography has not been articulated. But I maintain that synonymy of *C. jompomae* with *C. bonariensis* is not yet justified, pending additional analysis not immediately forthcoming. Furthermore, additional analysis may in fact corroborate differentiation from *C. bonariensis*. Discussed below are the taxonomy, biogeography, and evolution of C *jompomae*, along with implications for the identity of "Tutuca Feuillée" and knowledge of the Chilean flora generally.

1. Taxonomy of *C. jompomae.* Herbarium specimens of *C. jompomae* (Fig. 1) and *C. bonariensis* (Fig. 5) indeed are very similar. All share the lengthy apical pedicels. The protolog of *C. bonariensis* (described from a herbarium specimen) indicates that the flowers are white and the number of stamens 6–7. The flower color of *C. jompomae* and the western FI plants is pale (see below).and stamen number reported by Barnéoud (1847 ["1846"]: 488) for the holotype of *C. jompomae* (as *C. glauca*) is seven. *Calandrinia bonariensis* has been considered a synonym of *C. ciliata* (see above), but now I consider it to be quite distinct from the latter morphologically and ecologically. *Calandrinia ciliata* is a high montane species distributed in the American cordillera from southern Mexico to northernmost Argentina. Its pedicels are shorter than those of adjacent leaves (Fig. 2).

I recognize *C. jompomae* as distinct from *C. bonariensis* (Fig.5) based mainly on the 1200 km disjunction (albeit at ca. the same latitude) as well as the ecological differences between the two habitats. Barnéoud described the habitat of *C. jompomae* as humid and shady, and the elevation of collections seems to be in the range of 0–150 m. The vegetation is humid forest, with annual precipitation in the range of 1000–2200 mm, falling primarily in winter. The habitat of *C. bonariensis* appears to be restricted to rocky sites near the summits of low peaks, elev. 150–250 m, in the Tandil mountain ranges west of Mar del Plata, Buenos Aires Province, Argentina, ca. 37°S 57.5–59°W (Añon Suarez de Cullen, 1953; Echeverria et al., 2017; reported as *C. ciliata*). The vegetation here has been described as mesophytic shrubby steppe-like (Oyarzabal et al., 2018: 52). Annual precipitation is 800–900 mm and distributed somewhat more evenly throughout the year. Summer temperatures are higher and winter temperatures somewhat lower than in the range of *C. jompomae* (climate data from numerous climate web sites; cf. Echeverria et al., 2017).

The significance of the macroecological distinction between Tandil and central-southern Chile must be qualified. An annual species might be accommodated microecologically in vegetations macroecologically vastly distinct (cf. Hershkovitz, 2020a). Moreover, annual *Calandrinia* species tend to be weedy and apt to enter disturbed sites. It is interesting, in this regard, that the type locality of *C. bonariensis* is Cerro de la Piedra Movediza en Tandil, Argentina. This is an urban-area park and a local tourist attraction. The mountain system itself comprises relatively undisturbed islands in a vast and otherwise heavily modified landscape (Echeverria et al., 2017). And despite the proximity to and accessibility from Buenos Aires, the species was not discovered until 1919. This evidence invokes the possibility, far from corroborated, that the species was introduced anthropogenically to eastern Argentina (see also below).

Calandrinia jompomae also is similar to an unidentified annual calandrinia found on six western Falklands islands (Fig. 6; Hershkovitz, 2006; Falklands Conservation, 2007: 15), evidently growing in humid habitats. The FI plants also bear lengthy pedicels. The specimens I have seen seem rather more delicate than Chilean specimens, but this possibly reflects a combination of environmental variation and plant immaturity. The plants apparently share with *C. jompomae* a similar and distinctive pale purple flower color. This color was noted in a single collection of *C. jompomae* [*C. M. Taylor 10596* (MO, ASU)] and is evident in a photo of an FI plant (Falklands

Conservation, 2007: 15). All other annual calandrinia species have either white or pink to deep rose flowers with occasional white mutants. The western Falkland Islands (ca. 52°S 61°W) are much colder and drier than either south-central Chile or Tandil, although the former compensates for the latter in terms of maintaining high humidity.

It is possible that the FI plants are the same species as the Chilean and/or Argentinean plants and were dispersed to the FI naturally or anthropogenically. Or they might be a distinct entity. But, again, additional research is necessary to verify. Hershkovitz (2006) analyzed DNA sequence data from one locus each from the nuclear and chloroplast genomes of several Calandrinia species, including two samples of the unidentified FI plants. Notwithstanding morphological divergence and geographic separation (Hershkovitz, 2020a), sequences of C. ciliata and C. pilosiuscula (reported as C. compressa) were identical for both markers. This was notable, because these sequences were divergent from samples of C. menziesii, which is morphologically indistinguishable from C. ciliata. Sequences of C. nitida (reported as C. axilliflora) were divergent from all of these. Sequences of the nuclear marker of the unidentified western FI plants differed from C. nitida at only one base position, while the chloroplast sequences differed from C. ciliata/pilosiuscula at only two. For this reason, Hershkovitz (2006) suggested that the FI plants and possibly the similar Chilean forms (viz., C. *jompomae*) had a hybrid origin. However, Hershkovitz (2019a, b) emphasized the difference between gene and species trees, and that hybridization and lineage-sorting during divergence can be difficult to distinguish on the basis of genomic data. In this context, it is notable that sequences from both the nuclear and chloroplast markers of the Falkland Islands plants were unique, i.e., not identical to either supposed "parental" sequence. This means that if the origin indeed owes to hybridization, this event did not occur "recently."

2. Biogeography and evolution of *C. jompomae*. Regardless of whether the FI plants originated via hybridization or lineage sorting or even whether they are genetically identical with *C. jompomae* and/or *C. bonariensis*, the DNA data of Hershkovitz (2006) and also Goolsby (2018a, b) do aid in biogeographic understanding of *Calandrinia*. Hershkovitz (2019a; 2020a) proposed that this genus originated in Patagonia no earlier than the Oligocene, whereas modern species diversified no earlier than the Pliocene, viz. after the final uplift of the Andes and establishment of the modern climates and vegetations on both sides. This scenario rules out a vicariance relationship between *C. bonariensis*, *C. jompomae*, and the FI plants.

The earlier recognition of C. bonariensis as a synonym of C. ciliata implied that the former was disjunct from populations of the latter in the northern provinces of Argentina (Peralta and Ford-Werntz, 2008) and hence the Central Andes. The present interpretation demonstrates a disjunction from south-central Chile. Calandrinia originated and diversified in the Chilean Floristic Region (ChFR; Hershkovitz, 2019a). At least 12 of 19 thus accepted species are endemic to the ChFR, and another four occur in the adjacent high Central Andes, two extending to southern Mexico. Two annual species are disjunct in North America. The species "missing" in this equation was the collective of C. bonariensis, C. jompomae, and the FI plants: interpretation of their biogeographical distribution depends upon their taxonomic interpretation. In fact, Hauman (1925) suggested a biogeographic relation between C. bonariensis and FI and Chilean plants. This suggestion was partially erroneous, because he referred to FI collections of C. menziesii (as C. feltonii Skottsb.), which is a western North American species introduced to the Falkland Islands (Hershkovitz, 2006; Falklands Conservation, 2007: 15). He was unaware of the unidentified FI plants forms with longer pedicels. In the case of Chile, he referred to C. nitida and its elongated and recurved pedicels, which indeed may be homologous. Hauman (1925) did not mention Argentinean C. ciliata, which elsewhere he considered distinct from C. bonariensis (Hauman and Irigoyen, 1923). Evidently, Hauman had access only to specimens in Argentinean and not Chilean or European herbaria, lest he might have discovered also C. jompomae.

Regardless of taxonomic interpretation, the preceding renders clear that *C. bonariensis* and the FI plants dispersed relatively recently from the ChFR. The mode of dispersal, natural or anthropogenic, is not established. The presence of the otherwise weedy *C. menziesii* in the Falkland Islands has been explained as anthropogenic (Hershkovitz, 2006). The possibility of natural dispersal cannot be eliminated (Hershkovitz, 2019a), but this plant was first collected at a maritime settlement and is not otherwise known from undisturbed vegetation. Meanwhile, the unidentified calandrinia has been described as "flourishing" on six historically relatively undisturbed islands and was discovered only following intensive ecological survey. Anthropogenic introduction cannot be ruled out, but the evidence favors natural and presumably bird dispersal.

There are no DNA data for *C. jompomae*, but its morphology and distribution alone yield biogeographic insights. The range of *C. jompomae*, ca. 37–41.3°S, seems to be contained entirely within the range of *C. nitida*, the latter extending northward to the Aconcagua Region, ca. 32–41.3°S (Rodriguez et al., 2018). The overlap in the range between *C. jompomae* and *C. pilosiuscula* is less certain based on data available to me at this moment. The range of the latter extends north at least to the Coquimbo Region (hence north of *C. nitida*), ca. 28°S (Hershkovitz, 2020a). Based on available data, I can verify that *C. jompomae* and *C. pilosiuscula* overlap at least at ca. 37–38°S, but I have no data at hand documenting the latter further south than this. Both Peralta and Ford-Werntz (2008) and Rodriguez et al. (2018) cite the southern limit in the Los Lagos Region (cf. Gotschlich, 1913), thus the same as *C. jompomae*. But, as I have noted, *C. jompomae* historically has been misidentified, sometimes as *C. pilosiuscula*.

There is reason to believe that *C. pilosiuscula* indeed occurs as far south as the Los Lagos Region but, at the same time, reason to believe that it would be separated from *C. jompomae* ecologically, and that the lack of specimens of *C. pilosiuscula* in GBIF and other non-Chilean herbaria is an historical collecting artifact. As to the last point, up until the 20^{th} Century, plant collecting in south-central Chile concentrated around port cities, especially Concepción and Valdivia. The inland routes between these cities were somewhat treacherous and hostile, both physically and politically. The vegetation of Valdivia and the adjacent coastal ranges is temperate evergreen rainforest. This environment might be too cool and wet for the evidently more dry-adapted *C. pilosiuscula*, though suitable for both *C. jompomae* and *C. nitida*. However, the interior valleys in the La Araucanía, Los Ríos, and Los Lagos Regions are considerably drier and in summer much warmer than both the coastal ranges to the west and the High Andes to the east. In many places, the vegetation is similar to the sclerophyll woodland several hundred km to the north and includes many of the same woody species. Here, *C. pilosiuscula* would be expected.

Despite expectations, literature evidence for the presence of *C. pilosiuscula* in warmer/drier habitats of these southern regions is meager. Ramírez et al. (1991; cf. Gotschlich, 1913) listed this species, (as *C. compressa*) as present in these regions, especially in recently burned forest. This is a reported niche of *C. pilosiuscula* at ca. 35°N (Litton and Santelices, 2002). However, Ramírez et al. (1991) did not list specific localities. Notably, the species is not listed in detailed surveys of specific southern region sites otherwise similar to the habitat of *C. pilosiuscula* throughout central Chile (e.g., Ramírez et al., 1984, 1989, 1998, 1999; Schlegel and Martinez, 1987). Quintanilla and Matute (2005) reported *C. pilosiuscula* (as *C. compressa*) in cleared forests on Chiloé Island, ca. 42°S. In view of the present work, the identity of these plants should be verified.

The distribution data suggest that, while the range of *C. jompomae* is wholly sympatric within that of *C. nitida*, it is effectively largely but not completely parapatric with respect to *C. pilosiuscula*. I say "not completely," because one collection of *C. jompomae*, *C. M. Taylor 10596* (see above), indeed was collected in cleared plantation forest at ca. 37°S, in the documented range and habitat of

C. pilosiuscula. Notably, the plants in this collection appear stunted relative to specimens from the Los Ríos Region. It must be appreciated, in any case, that current and historical ranges likely differed along with their respective vegetational zones, e.g., during the Pleistocene.

Hershkovitz (2006) suggested that the FI plants represented a nothospecies. Indeed, these plants have a chloroplast genome similar to *C. nitida* and a nuclear genome similar to *C. pilosiuscula* and *C. ciliata*. While the conclusion is reasonable and possibly true, it might have been biased subliminally by the chronological order in which these taxa were discovered. It also may have been biased by an assumption that the FI plants were singularities. This interpretation is modified by the present conclusion that *C. jompomae*, *C. bonariensis*, and the FI plants at the very least pertain to the same lineage. The form and range of *C. jompomae* suggests that it may be a species no older or younger than *C. pilosiuscula* and *C. nitida*.

Genomic data (Goolsby et al., 2018a, b) corroborates the notion that the form of *C. jompomae*, if not the "species" itself, is as old as any or all species of *Calandrinia*. The data indicate that the annual species, C. sect. *Calandrinia*, are paraphyletic with respect to the perennials, *C.* sect. *Caespitosae* Philippi (cf. Hershkovitz, 2019a), and that *C. nitida* is sister to the latter. Morphologically, *C. nitida* bears traits apparently derived in the genus: the orbicular form of the sepals and capsule, deeply sculptured seeds, and pedicels markedly reflexed in fruit as though to bury seeds in the litter layer (similar to violets; Hauman, 1925: 435). The unique calyx morphology of *C. pilosiuscula* (Hershkovitz, 2020a) also must be a derived trait. Thus, the morphology of *C. jompomae* is somewhat more generalized than either of these species, although the pedicel length trait is shared with *C. nitida* and the perennial species. Indeed it is possible that *C. jompomae* is an ancient hybrid between *C. pilosiuscula* and *C. nitida*, imparting *C. jompomae* with a form suggestive of *C. ciliata*. But it is possible also that *C. jompomae* emerged from this complex independently without subsequent interspecific gene flow.

3. The identity of "*Tutuca* Feuillée." The recognition of *C. jompomae* renders somewhat ambiguous the identity of "Tutuca Feuillée" (nom. inval.; Feuillée, 1725), not to be confused with Tutuca Molina, which is Chusquea Kunth (Hershkovitz, 2020a, b). "Tutuca Feuillée" was listed as a synonym of C. pilosiuscula by Hooker and Arnott (1830 ["1841"]). Feuillée (1725) described this plant from the latitude of Concepción, and the description and illustration (Fig. 7) betray an annual calandrinia. However, it is not clear whether the plant was C. pilosiuscula or C. jompomae. The inflorescence in the illustration appears immature, but the pedicels on the first flowers are elongate. Feuillée (1725) described the sepals as separating after anthesis, and the illustration suggests that they are ovate and free rather than deltoid and substantially fused. This suggests sepals of C. jompomae rather than C. pilosiuscula. Feuillée described the flower color as violet, though he did not indicate intensity. Flowers of C. jompomae are pale violet, those of C. pilosiuscula usually rather deep pinkrose, not violet. Feuillée described the stamen number as 10. The number reported in C. jompomae is seven (Barnéoud, 1847 ["1846"]; as "C. glauca"). Stamen number in C. pilosiuscula and its segregates range from 3–13 (Hershkovitz, 2020a). Given the variation in C. pilosiuscula, I suspect that stamen number varies also in C. jompomae. Of course, the question of the identity of "Tutuca Feuillée" has no taxonomic implications. It is purely a historical question, notable because "Tutuca Feuillée" was not only the first described species of Calandrinia, it was the first described South American Montiaceae.

4. ANOTHER overlooked species in the Chilean flora. The title of the present work alludes to the fact that *C. jompomae* is not a newly discovered or rare or cryptic species. It is easily distinguished from its congeners, has a fairly extensive range and frequency, and it has been collected many times beginning since the earliest botanical explorations in Chile. Moreover, it evidently was

recognized as a distinct species by W. F. Hooker, who never described it, and F. N. Barnéoud, who described but misidentified it. After that, it "disappeared" taxonomically speaking.

This history somewhat parallels other Chilean species recognized recently, i.e., collected, easily distinguished, even recognized as distinct, yet perennially ignored in the Chilean floristic literature. Another example is *Cistanthe philhershkovitziana* Hershk. (Hershkovitz, 2018a, b), a conspicuous and locally abundant species with a range > 400 km (evidently 700 km; unpublished data), first collected by Carlo Bertero in 1829 and several times after that. While locally restricted, *Cistanthe subspeciosa* Hershk. also was collected and illustrated but misidentified long before it was recognized as a distinct species (Hershkovitz, 2019c).

Watson (2019) reported that the bizarre *Cistanthe floresiorum* J. M. Watson was discovered in 2008. In fact, it had been collected several times during the preceding half century and analyzed genetically in Hershkovitz (2006). I had planned to describe it, but my career abruptly ended and my collections and photos eventually destroyed. I had hoped to name it for the late Claudio Marticorena, who not only collected the species, but grew up in Vallenar, very near the type and only known locality.

Other examples are the fairly common central Chilean annuals *Cistanthe trigona* (Colla) Hershk, *Cistanthe chamissoi* (Barnéoud) Carolin ex Hershk., and *Cistanthe vicina* (Phil.) Carolin ex Hershk. These long have been misidentified as *Cistanthe arenaria* (Cham.) Carolin ex Hershk., which, if the original description and type are consulted, proves to be a perennial from coastal Concepción (Hershkovitz, 2019a), south of the range of the confounded annuals. Additional examples can be cited, but the picture becomes clear.

The preceding seems to be a pattern, which, in the interest of advancing biodiversity research, itself merits description and explanation. Indeed, some species relatively recently described in the Chilean flora represent correspondingly recent discoveries, e.g., *Calandrinia ranunculina* J.M.Watson, A.R.Flores & Elvebakk (Elvebakk et al., 2015). But this, perhaps, is an exception that proves the rule, because Elvebakk et al. (2015) also demonstrated clearly the distinctiveness of two other previously described species that long had been lumped with *C. caespitosa* Gillies ex Arn. Again, many additional examples can be cited that suggest that many newly accepted species in the Chilean flora base on rather older collections that were variously misidentified, inadequately studied, or otherwise slipped through the cracks. *Calandrinia pilosiuscula* is an example of the last. The name more or less "disappeared" from Chilean floristic literature. But it was not difficult to trace and typify this name and determine that it has priority over the widely adopted synonym *C. compressa*, nor to determine that the latter is *not* typified (Hershkovitz, 2020a).

To explain this pattern, I offer several critical observations

- 1. The most recent fully articulated flora of Chile, that of Karl Reiche, was published over 100 years ago. Many taxa have been critically revised since, but far from all, including most Chilean Montiaceae.
- 2. Chile's two published floras (those of Claudio Gay and Karl Reiche), almost all critical monographs and revisions, and the overwhelming majority of Chilean species descriptions are works of non-Chilean botanists, though some, notably Rodolfo Philippi, have been foreign-born and foreign-trained researchers that later settled in Chile.
- 3. At the same time, the non-Chilean authors of most of the taxonomy of Chilean plants have had less field experience in Chile, limiting their ability to corroborate taxonomic conclusions based only on herbarium specimens, these sometimes cultivated from seed of uncertain provenance, rather than field collections (e.g., Hershkovitz, 2018d, 2019a). For example, W. J. Hooker (GL

and K) authored more than 1000 names/combinations of Chilean plants; ca. 775 names are attributed to De Candolle (G), and ca. 200 to Barnéoud (P), including especially Chilean Montiaceae. These workers never visited Chile. Numerous other significant contributors to the floristic taxonomy visited only briefly, e.g., I. M. Johnston (GH), who authored ca. 250 names. Yet these species could not have been described *except* in the context of these researchers' knowledge of the *cosmopolitan* flora and collections thereof amassed in European and North American herbaria.

- 4. Chilean biodiversity research has produced mainly local, regional, and national inventory lists of names of species "accepted" according to the works of non-Chilean botanists. The most recent national list (Rodriguez et al., 2018) was the first revision in 33 years. Such lists offer no insight into the actual taxonomy of the species and deceptively appear to be overly-definitive.
- 5. Botanical research in Chile generally has been restricted to plants growing within geopolitical Chile, ignoring distributions of nominally native Chilean species outside of Chile and the taxonomy of non-Chilean congeners of Chilean species. Hershkovitz (2019a) discussed how this anthropocentric/nationalistic perspective constrains/distorts *biological* understanding of the geopolitically Chilean flora.

The preceding is offered not as a criticism (such as it is), but rather as an *explanation* for thus expected and observed oversight of even common, widespread, distinctive, and well-collected species in Chile, as well as overlooked geographic variability and occasional hybridization. I contrast the case of Chile with my experience as a graduate student in California in then1980s. There, a botanical student *never* went to the field, not even for an afternoon, without porting a well-worn copy of Munz and Keck's (1973) "*A California Flora and Supplement*," a 1681-page manual that, however imperfect, rendered clear whether a plant in the field had as much as a single stamen more than that previously reported. In contrast, Chilean botanical students go to the field armed only with a checklist or, at best, one of the popular local/regional and incomplete botanical guides.

The lack of a modern manual of vascular plants in Chile is peculiar. The California flora is 50% more diverse and an order of magnitude more complex taxonomically. Yet, Munz wrote the manual largely by himself in the 1950s–1960s, long before the personal computer age, with only a meager salary and -no – research funding. Thus one emergent explanation for the lack of a Chilean floristic manual is that modern Chilean botanical researchers are too well-paid and well-funded.

The persistently impoverished simplicity of Chilean botanical references likely engenders a false sense of completeness of taxonomic knowledge of the Chilean flora. Indeed, as noted in Hershkovitz (2019a), one distinguished and very well-funded Chilean plant ecologist, Aníbal Pauchard (University of Concepción and Millennium Institute of Ecology and Biodiversity) recently asserted that "we *already* know" what are the species in Chile (Heselaars, 2019; italics mine). Evidently not. *Calandrinia jompomae* grows near Concepción and numerous collections are stored in the herbarium in Pauchard's department (CONC), all misidentified. Pauchard likely has been conditioned by checklists, which evoke the sensorial simplicity of a laser pointer. Which demonstrates, as Jompoma understands, that scientists' brains really are not that different from a pigeon's.

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Fig. **1.** Holotype of *Calandrinia jompomae* [C. Gay 104 (P [P05276741]). http://coldb.mnhn.fr/catalognumber/mnhn/p/p05276741 **Fig. 2.** *Calandrinia ciliata* (Ruiz & Pav.) DC. Note the short length of the pedicels in fruit. ARGENTINA: Tucuman Province, Chicligasta Department, Estancia Las Pavas, elev. 3200 m, 12 Feb 1925, *S. Venturi* 6765 (US [US Cat. 1546261]).

https://ids.si.edu/ids/deliveryService/id/ark:/65665/m302fb0b9efcc440a5af98ea970e9b147c/640



Fig. 3. Holotype of *Calandrinia pilosiuscula* DC. Note the form of the calyx and the short length of the pedicels in fruit. CULTIVATED: *W. J. Hooker s. n.*, without date (K [K000424682]). http://specimens.kew.org/herbarium/K000424682



Fig. 4. *Calandrinia nitida* (Ruiz & Pav.) DC. Note the long, reflexed pedicels and leafy stems. CULTIVATED: without collector, without date, ex St. Petersburg Botanical Garden (US [US Cat. 10634]).

https://ids.si.edu/ids/deliveryService/id/ark:/65665/m31766ae78149f47519cc89ba48b7927eb/640



Fig. 5. Original material of *Calandrinia bonariensis* Hauman. ARGENTINA: Buenos Aires Province, Tandil, Cerro de la Piedra Movediza, 1 Nov. 1919, *L. R. Parodi 1664* (FI [FI005087]). http://parlatore.msn.unifi.it/img72/FI005087.jpg





Fig. 6. *Calandrinia* sp. UNITED KINGDOM: Falkland Islands, Hummock Island, 24 Dec 2001, R. W. Woods, s. n. (FINH).

Fig. 7. "*Tutuca* Feuillée," illustration from Feuillée (1725).

