Phenological and life history/form idiosyncraticity of facultatively annual *Cistanthe philhershkovitziana* Hershk. (*C.* sect. *Cistanthe*; Montiaceae) in Chile's southern Central Littoral Zone, with comments on the incidence of the facultative annual condition among "Portullugo" (Caryophyllales) and other angiosperms

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ABSTRACT

Cistanthe philhershkovitziana Hershk. was described from the north-central Chilean coast in 2018. Based on the apparent absence of plants during drought years, it was described as the only species of *C.* sect. *Cistanthe* with a putatively annual life history (~therophytic life form). The species occurs primarily in coastal habitats, but also in some seasonally moist sites up to perhaps 50 km inland. Its range spans ca. 600 km of latitude, ca. 28–33S. Detailed reinvestigation especially of the southernmost populations in Chile's perennially humid southern Central Littoral Zone (CLZ) demonstrates that this species is a *facultative* annual, viz. a perennial that flowers from seed during its initial seasonal cycle, in this case ca. 10–12 weeks after germination. Here, I suggest that most species of *C.* sect. *Cistanthe* have this facultative capacity. However, unlike the other species, *C. philhershkovitziana* is cryptophytic, which contributes to its appearance as annual. Moreover, the plants are comparatively short-lived. Plants of *C. philhershkovitziana* grow in seasonally dry sites, and seeds germinate in response to precipitation, whether the typical Mediterranean climate winter rains or irregular rains that arrive during other seasons. Phenology thus is mediated primarily by hydration and less so by temperature and light, and phenology varies both interannually and locally. Southern CLZ populations mostly comprise primarily first and second-year individuals, and caudices rarely survive more than three years. High mortality here owes to a variety of site-specific circumstances. In northern Chile, high mortality probably owes the inability of the young caudices to withstand multi-year droughts. The largely unreported incidence of the facultative annual condition among Montiaceae and angiosperms in general is likely to be consequential to interpretation of life history/form and phenological macroevolution and ecology.

Key words: *Cistanthe*, Montiaceae, Portullugo, Chile, life history, life form, annual, perennial, phenology.

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Introduction

Hershkovitz (2018a) described *C. philhershkovitziana* from a coastal dune population in Petorca Province, Valparaiso Region, Chile. Hershkovitz (2018b) later demonstrated that the species had been collected but (not identified or) misidentified multiple times since the early 19th Century, and also (Hershkovitz, 2022a) that its range extended along and near Chile's coast from c. 33.8S to c. 28.5S, or nearly 600 km in latitude. A significant update on the distribution and environmental ecology of *C. philhershkovitziana* will be published separately.

Morphologically, *C. philhershkovitziana* differs from other species of *C.* sect. *Cistanthe*, first and foremost, by its relatively small size. The above-ground stem system probably never exceeds 50 cm in length and usually is 10–30 cm in length. Moreover, it life form is more rosettiform and cryptophytic (see later discussion). Stem systems of other species commonly extend 1 m or more, and the habits are subrosettiform hemicryptophytic to chamaephytic to phanerophytic (see below). Other traits distinguish *C. philhershkovitziana* from "small" plants of other species, e.g., its cylindrical rather than angular inflorescence stems and its leaves that are green rather than purplish abaxially.

More notably, Hershkovitz (2018a) also asserted that *C. philhershkovitziana* is the only species of *C.* sect. *Cistanthe* with an annual[1] life history or, alternatively, a therophytic life form[2] (discussed later). This was inferred on the basis of evidently first-year flowering of plants in Chile's Coquimbo Region, which experiences multiyear droughts. Here I report on the phenology and life history/form variability of plants growing in Chile's southern Central Littoral Zone (southern CLZ; ca. 33.0–33.4S, in between Santo Domingo to the south and Valparaiso to the north[3]), which receives rainfall perennially. This distribution was unknown in 2018. These observations demonstrate that *C. philhershkovitziana* is a *facultative* annual[4] that, nonetheless, in its natural circumstances, often *behaves* as an annual. I conclude that both its phenology and life span are influenced primarily by hydration, but that both are influenced idiosyncratically. I discuss evidence for the facultative annual condition among successive outgroups and in other angiosperms, and the consequences of this unappreciated evidence towards understanding of life history/form and phenological evolution.

Methods

The ecological field data reported here were derived from observations at four localities of *C. philhershkovitziana* in between November 2023 and October 2024, supplemented by data gleaned from the iNaturalist.org internet site during 2022–2024. The four sites are:

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[1] Hershkovitz (2018a) surmised that caudices with senescent shoots can reinitiate vegetative and reproductive growth following drought if substantial rain falls later in the *same* growing season. It was not established whether or not the plants could reinitiate vegetative/reproductive growth in *subsequent* growing seasons. Hershkovitz (2018a) intimated that this was unlikely in arid northern Chile, where drought normally persists for several years. Hershkovitz (2018a) described the species as functionally *winter* annual because the seeds germinate and grow vegetatively following the first significant rainfall, which in central and northern Chile normally occurs (if at all) during latest autumn and winter (May to August). Reproductive growth *normally* occurs in spring (September to November). *Summer* annuals germinate in spring and reproduce in summer.

[2] "Life history" refers plant lifespan, e.g., annual, biennial, or perennial. An alternative distinction bases on flowering phenology: semelparous, which flowers only once, and iteroparous, which flowers repeatedly during its lifetime. "Life form" refers to vegetative morphology, classically (annual = perennial) herbs, and (perennial) shrubs, trees, etc. I apply the Raunkier categories (Niklas, 2008) based on perennation point position: therophyte (~ annual) versus various perennial forms. The terms "growth form" and "habit" have been used in the literature to refer variously to life history and life form.

[3] Up until perhaps the mid-20th Century, CLZ referred only to the current southern CLZ. This was the littoral zone most easily and frequently accessed from Santiago. Today, CLZ refers to the littoral zone extending to the northern coastal limit of the Valparaiso Region at ca. 32.3S.

[4] This refers to an iteroparous perennial that reproduces from seed during its first season and de facto *behaves* as an annual under conditions that prohibit survival to the following season. A "true" or "obligate" annual is semelparous and it dies completely (including roots) following reproduction. Complete senescence is physiologically "programmed" (see Hjertaas et al., 2023).

- **i.** The Gota de Leche subpopulation (Fig. 1), a ca. 2 ha subpopulation in a sandy depression behind the beach foredune at ca. 33.47S, the latitude of the El Tabito sector of the Municipality of El Tabo. This particular subpopulation occurs in a dune area that in 2024 formally was declared as Santuario de la Naturaleza "Dunas de Chépica" or "Gota de Leche." The subpopulation is part of a shoreline distribution of *C. philhershkovitziana* comprising > 100 ha that extends southward from El Tabito almost 4 km to Punta Lacho in Las Cruces.[5] But the Gota de Leche subpopulation is denser than other localities within this distribution.
- **ii.** The Cartagena population[6] (Fig. 2), ca. 33.53S, relatively few plants on the north slope of a dune along the Estuario de Cartagena, ca. 300–500 m from the shoreline.
- **iii.** The Playa Hanga Roa population[7] (Fig. 3), ca. 33.24S, on ca. 0.25 ha of compacted and heavily foot-trafficked sand among low rocks on a heavily modified/urbanized beach in central El Quisco.
- **iv.** The Punta de Tralca populations (Fig. 4), ca. 33.25S, one population that extends from a sandy beach along an estuary northwards to a rocky beach,[8] and a separate population on a ± rocky beach to the south.[9]

Geographic data were supplemented and/or analyzed using Google Maps[10] and/or Google Earth.[11] Distances and areas were estimated using Google Earth. Plants of coastal populations of *C. philhershkovitziana* are "altitudinally" restricted in their localities at a very fine scale. They occur above the level of estuaries but below that of the low dune peaks. This is a scale far to fine to measure using Google Earth elevation estimates and possibly even a GPS device, which I do not have in any case.

In order to facilitate phenological interpretation, precipitation and temperature (T°) data for Chile's southern CLZ were derived from Dirección Meteorológica de Chile.[12]

This work references, in both footnotes and bibliography, information from numerous internet sites. To avoid excess text following each link citation, I state here that the information is current and/or was accessed on the dates indicated in the text.

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[5] https://www.inaturalist.org/observations/101839827; https://www.inaturalist.org/observations/131652712; https://inaturalist.mma.gob.cl/observations/131652712; https://inaturalist.mma.gob.cl/observations/143951841; https://inaturalist.mma.gob.cl/observations/185665495; https://inaturalist.mma.gob.cl/observations/122867285; https://www.inaturalist.org/observations/169363991; https://inaturalist.mma.gob.cl/observations/122867122; https://inaturalist.mma.gob.cl/observations/137363244; https://inaturalist.mma.gob.cl/observations/137303869; https://inaturalist.mma.gob.cl/observations/137363167; https://inaturalist.mma.gob.cl/observations/238846012

[6] https://www.inaturalist.org/observations/42613439; https://inaturalist.mma.gob.cl/observations/68742666; https://www.inaturalist.org/observations/136217959; https://www.inaturalist.org/observations/177571309; https://www.inaturalist.org/observations/185353241; https://www.inaturalist.org/observations/185335935; https://www.inaturalist.org/observations/244580334

[7] https://www.inaturalist.org/observations/119102624

[8] https://inaturalist.mma.gob.cl/observations/96634941

[9] https://www.inaturalist.org/observations/228908198

[10] https://www.google.com/maps/

[11] Version 10.41.0.6

[12] https://www.meteochile.gob.cl/PortalDMC-web/index.xhtml

Results

1. Climate data

Lowland[13] Central Chile (ca. 32–38S), including the southern CLZ, is characterized by a Mediterranean climate, experiencing cool and wet winters contrasting warm/hot and dry summers. Low-elevation interior valleys of near-northern Chile[14] are characterized by milder winter T°. Precipitation normally arrives during winters, but the region experiences multi-year droughts. Southern Chile experiences cooler T° and a longer and perennially wet season. At all latitudes, coastal climates are more equable (viz. lower high and higher low T°) than interior valley climates. In northern Chile (and southern Peru), coastal fog at many localities mitigates nearly year-round drought, and also moderates both diurnal and seasonal T° fluctuation.

Climate in Chile is modulated by the effects of the El Niño - Southern Oscillation (ENSO) phenomenon in the Pacific Ocean. In El Niño years, winter precipitation is much greater in central Chile, and it extends at least to near-northern (ca. 26–32S) Chile, whereas during La Niña years, winter precipitation is much less in central Chile, and practically no rain falls in northern Chile. One consequence of ENSO is that there are few years of nominally "normal" precipitation in central and northern Chile, because "normal" averages alternating ENSO extremes over some multi-year interval. However, the trend over the past century or so has been towards aridification (see, e.g., Squeo, 1999: Fig. 3).

I hasten to add that the above description is generally accurate, but simplistic. While the climate in central and most of northern Chile is influenced mainly by the Pacific Ocean, the Atlantic Ocean adds complexity. The altiplano of northeastern Chile normally experiences cool, wet (austral) summers known as the "invierno boliviano," consequent to cooled moisture generated by Atlantic Ocean tropical cyclones. While the Andes generally shields central Chile from austral summer "monsoons" on the eastern slope, it does not always.[15] Moreover, upper atmosphere effects from the east (and north and south) evidently can influence weather system tracts on the western slope. These and other effects, in turn, influence precipitation in central Chile at a local scale.

Precipitation distribution and chronology in Chile during 2022–2024 differed from the pattern of recent decades. 2022 marked the end of an extended La Niña period and 2023 the beginning of an El Niño. 2024 was supposed to bring a new La Niña, but this did not materialize as expected.[16] The distribution of precipitation in Chile during these periods was somewhat different than during such periods in the past. In

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[13] This work is concerned with plants growing at elevations < 1000 m above sea level and mostly much less than that. I ignore here more complex high elevation climates and consequent hydrological conditions except to note that some low elevation areas receive considerable water runoff from high elevations, and that this runoff can greatly alter hydrological conditions locally for a period well beyond the lowland rainy season (Squeo et al., 2006).

[14] I refer here to the area known locally as the "Norte Chico," which includes the Coquimbo Region and most of the Atacama Region This is the region southeast of South America's "Arid Diagonal" whose climate is "desert Mediterranean." But its climate *patterns*, physiognomy, and phytogeographic characteristics extend further north along the coast to southern Peru (Rundel et al., 1991). Hershkovitz (2019) included the coastal regions of southern Peru as part of a phytogeographically natural "Chilean Floristic Region" (cf. Luebert, 2011).

[15] Inland valleys of central and near-northern Chile received 5–10 mm of precipitation on 7–8 October 2024; higher amounts fell in the cordillera. But the CLZ received ca. 1 mm or less. This humidity was trans-Andean in origin, though its westward passage across the Andes was facilitated by a weak low pressure system off the central Chilean coast. Additional small amounts of precipitation of trans-Andean origin fell in central Chile 20–22 October.

[16] https://www.emol.com/noticias/Nacional/2024/09/05/1141896/balance-meteorologia-invierno-2024.html

the 2022 La Niña winter, Chile's normally xeric Coquimbo and Atacama Regions (ca. 26–32S) did not receive especially high total annual precipitation, yet, owing to a single anomalous event in July, it received enough to spawn a "flowering desert" event similar to that of an El Niño year. Indeed, *C. philhershkovitziana* was reported from several localities (Hershkovitz, 2022a). But central and southern Chile received less than "normal" precipitation and was still considered to be under drought.

In contrast, 2023 saw (very little to) no precipitation in the Coquimbo and Atacama Regions and near- to above-normal in central Chile, with the largest surplus occurring in the Maule Region (35–36S). But the precipitation pattern was unusual in two ways. First, the precipitation arrived relatively late in the year, mostly after mid-August and extending to mid-November. Usually, precipitation concentrates May–August (viz. winter), and precipitation in mid-November is rare. Second, the Pacific low pressure systems traversed Chile from decidedly more south to north rather than west to east, stalling over transversal mountain ranges in northern central Chile, and not extending north of c. 32S. The result was higher rainfall in inland valleys relative to the coast. Still, coastal precipitation in central Chile was more than adequate to effect herbaceous plant growth and reproduction.

The austral summer of 2023–2024 was dry, as usual, but continued the trend of past years of increasing T°. However, significant 2024 autumn/winter precipitation arrived to central Chile much earlier than in 2023, and even somewhat earlier than "normal."[14] The littoral zone at ca. 33S received up to 5 mm of rain on 21 April, followed by up to 15 mm on 29/30 April. The coast and interior zones received 25–30 mm on 7 May, followed by additional significant rains in between late May and late June, totaling to > 300 mm for the year. Unlike 2023, the Coquimbo Region also received 100–200 mm from these systems, and significant rains extended to the Atacama Region. The result was exceptionally early winter emergence and even flowering of herbaceous species that "normally" flower in late August and September.

But *no* rain fell in central and northern Chile during a six week period between late June and the end of July 2024. This "normally" is the wettest period here. Then a frontal system during the first days of August brought 50–100 mm of additional rain to central Chile and, once more, physiologically significant rain extended to the Atacama Region. A smaller system on 5 August added 10–20 mm to central Chile and the southern Coquimbo Region. A system on 20–21 August added ca. 12 mm to the southern CLZ, and a system on 18–19 September added 8–18 mm. These amounts were significant in terms of plant responses, but July–September 2024 southern CLZ totals were < 60 mm, which is "extreme drought" for this period.

I did not record daily T° data for the southern CLZ. But diurnal T° ranges were on the order of 10–20C in late spring 2023 and 12–24C in midsummer 2024. During the rainy months of May and June 2024, the range commonly was 8–14C. July 2024 was dry and relatively cold, the range often 4–10C, increasing slightly beginning in August, but August–October highs in the CLZ mostly were ca. 3–5C lower than "normal" (see footnote 14 above).

In summary, in fall and winter, 2024, lowland central and near-northern Chile received relatively ample precipitation, although not as much as in El Niño years. But ca. 75% of the precipitation arrived in late autumn rather than the more usual winter months. Consequently, the drought period of the CLZ was relatively short, since 2023 rains arrived in this zone relatively late. Although significant rain fell in the winter months, the amounts were comparable to those in drought years. At the same time, winter T° in central Chile were cooler than average. Consequently, while the early rains evidently effected seed germination and emergence of perennial species, the plants were growing under winter rather than spring conditions, viz., shorter days (hence less photosynthesis) and colder T° (hence presumably lower metabolic rates).

2. Phenological and life form/history data

i. The Gota de Leche subpopulation

This subpopulation occurs on a sandy depression ca. 200 m broad and extending ca. 400 m immediately behind beach foredunes that rise ca. 3–4 m above the level of the depression (Fig. 1A–B). The vegetation is herbaceous to suffrutescent and sparse, and the most common co-occurring species are *Alstroemeria recumbens* Herb. (Alstroemeriaceae)[17] and the ubiquitous exotic *Ambrosia chamissonis* (Less.) Greene. Other species common in the depression are *Astragalus trifoliatus* Phil. (endemic to this reserve), *Carpobrotus chilense* (Molina) N.E.Br.,[18] *Oeonotherum picensis* Phil., *Quinchamalium chilense* Molina, and *Sisyrinchium arenarium* Poepp. subsp. *arenarium*.

Especially because of its orthogonal shape and borders planted with exotic Monterrey cypress trees (*Cupressus macrocarpa* Hartw. ex Gord.), it is not clear to me the degree to which this sandy depression had been modified for purposes of tidal mitigation. The sand in the depression is notably more reddish-brown than the beach and dune sand. And it is littered with fragments of broken/degraded clam shells whose species I have not identified. I do not know if the shells are fossils from earlier marine incursions or "litter" left behind by shore birds.

I first visited the Gota de Leche subpopulation on 14 November 2023. The plants were in late stages of flowering/fruiting (Fig. 1B–C). The leaves were green. My next visit was midsummer, 23 January 2024. At this point, the above-ground organs of *most* plants were senescent and skeletal (Fig. 1D). However, the below-ground caudices were very much alive, and some caudices still had live hair roots. Some caudices were fairly long (10–15 cm) and ramified. But I also located a very few small plants with green leaves and flowers (Fig. 1E–F). Their caudices were slender, shorter (5–7 cm), and hardly or not ramified. I collected some of the larger plants and stored the bare caudices in black plastic bags.[19] As of late August 2024, the caudices were shriveled, but most appeared to be viable and all sprouted etiolated shoots from near the apex.[20] But by November, 2024, all had succumbed.

I suspect that the smaller plants described had germinated more recently than most of the plants. There had been two atypical rainfalls in this zone in late spring, one on 28–29 October (ca. 20 mm) and the other on 9–10 November (ca. 15 mm). These amounts are more than adequate to effect at least germination of herbaceous plants, especially in this particular depression, which probably receives some runoff from adjacent slightly elevated substrate. Seedling establishment would depend on the ability of the root to reach

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[17] Often classified as a subspecies of *A. hookeri* Lodd.

[18] It is not clear that this species is "native" to Chile (Novoa et al., 2023). But this species challenges the very notion of native versus introduced. Clearly the species is not an *autochthonous* element of the Chilean or otherwise American flora. Presumably it arrived to Chile relatively recently, presumably from either California or Africa, and presumably its morphological (hence taxonomic) distinction owes to a founder effect. Clearly it is "naturalized" (and invasive) and not "native" in many of the often highly disturbed sites where it occurs in Chile, and it is considered "invasive" on other continents. At the same time, it is not clear the degree to which the equally ubiquitous naturalized invasive exotic *C. edulis* (L.) N.E.Br. has introgressed into *C. chilensis*.

[19] During each of my visits, I collected a few caudices for subsequent study and photographing. These I stored in loosely closed "grocery store size" black plastic bags. This was not intended as an "experiment." I just never threw them away. The bags probably preserve relative humidity better than in dry, hot sand. But the caudices were stripped of finer roots that may have had access to moisture at greater depths…at least for a *while*. Following prolonged droughts common in northern Chile, it seems most likely that even deeper moisture would dissipate.

[20] However, it is quite common for the shoots of nonviable *Cistanthe* specimens to sprout new shoots and even flower after many weeks and perhaps months in a plant press.

moisture some distance below the surface. This could be a limiting factor on well-drained sand given the high evaporative potential in late spring.

My next visit was late summer, 9 March. By this time, the above-ground portions of the plants were almost completely absent. Digging in the sand, I was able to locate some caudices, still very much alive. But I discovered something completely unexpected. Throughout the population site, hundreds of *uprooted* caudices were lying prone, in various stages of desiccation, on the *surface* of the sand (Fig. 1G). I swear to God, *I* didn´t do it. But who did?

There were at the site, as usual, several species of shorebirds, most notably and abundantly *Haematopus palliatus* Hemmink, the American oystercatcher, known as *pilpilen* in Chile. Although I did not observe it, I suppose that the subterranean naked caudices were uprooted by foraging birds and, being inedible, were left behind. I do not know how the birds located the caudices or why they uprooted them in the first place.

Noteworthy, however, is that this site is littered with broken clam shells. Birds generally have keen eyesight. Notably, I saw no uprooted caudices when above-ground portions of this and other herbaceous species were present, alive or dead. But in late summer, with the herbaceous cover largely gone, the site is mainly bare sand with broken clam shells, rather like the beach, where shore birds normally forage. So I suppose that the birds were fooled into believing that the site was indeed a good foraging ground. But when they probed what they believed to be a dimple in the sand betraying a clam, all they found was a fleshy plant caudex.

The cause of the uprooting of caudices in late summer is not so important here. What is important is that a large number of caudices, perhaps the majority, were uprooted and therefore doomed to die. But the plants already had flowered and fruited. So even if the plants were potentially perennial, this mortality rendered them de facto annual.

My next visit to this site was in mid-autumn, on 13 May. But, as I noted above, significant rain arrived two weeks earlier, so conditions already were winter-like. Numerous rosettes and seedlings were present at the site (Fig. 1H–J). The rosettes were of two types: plants with rosettes 3–4 cm broad and often branched caudices > 10 cm long that evidently flowered/fruited during the spring or summer (Fig. 1J), and seedlings with rosettes 1–3 cm broad and caudices < 3 cm long (Fig. 1I). The two forms superficially appeared to be in equal proportion considering the largest rosettes of each form, but close inspection revealed that the seedlings, the smallest of which were difficult to detect, were far more abundant. In addition, there were smaller individuals that evidently germinated more recently than the individuals above (Fig. 1H).

The above observations are nuanced, though I do not believe these nuances affect my conclusions. One is that the second-season caudices that I collected in May 2024 all were relatively small and possibly represented germlings consequent to the “anomalous” late October and November 2023 precipitation events. This may represent luck of the draw. Rosettes of recurring caudices were fairly uniform in size, hence may not have reflected caudex size. Possibly there were caudices that germinated in spring of 2023 or earlier. But I did not want to dig up a large number of caudices to confirm this. It also is possible that most of the larger caudices were uprooted by shorebirds.

I visited this population again on 31 August 2024. Rosettes ranged in size from ca. 2–8 cm, the size range apparently representing waves of germination following numerous rains after 13 May. Thus, even the largest plants were no larger than the “average” plants I observed here in November 2023, and most were much smaller. Some plants bore developing inflorescence stems no longer than ca. 7 cm. Although I observed no more than three (somewhat) open flowers in the population, the larger inflorescences generally bore a flower that was post-anthesis. Some plants with developing inflorescences clearly were first-year plants similar to those in Fig. 1E–F.

ii. The Cartagena population

Here, the plants of *C. philhershkovitziana* all occurred towards the base of a large anthropogenically modified dune, well above the water table, on the south bank of the Estuario de Cartagena (Fig. 2A–B). This north- to east-facing dune currently includes ca. 15 ha and is fairly steep, rising ca. 25 m above the estuary. On the top is a housing subdivision. The dune itself is densely populated with the invasive exotic shrub *Lupinus arboreus* Sims. (Fabaceae). Presumably, the peak is a "hard" geological feature, and the dune is sand that accumulated on its north and east faces.

The plants of *C. philhershkovitziana* recorded at this locality were notably larger than plants at other localities in the southern CLZ and are as large as the largest plants I have seen north of Valparaiso. I attribute this to the artificially high fertility of the soil consequent to the *Lupinus* shrubs, since, like all legumes, this plant harbors nitrogen-fixing bacteria. This also would explain the relatively high "elevation" of these plants above the water table. In particular, following winter precipitation, germlings would grow faster and larger than plants in less fertile substrates, hence develop a longer taproot that can access a deeper water table.

I visited this locality on 7 December 2023. I found here only a single large caudex underneath the canopy of a *Lupinus* shrub. The plant had been grazed to near the branch apices (Fig. 2C). It had numerous actively growing caudical branches emerging just above the soil line. But ca. 12 active rosettes were secondary, viz. had emerged from the axils of leaves of the primary rosettes. I had not encountered previously such a high number of actively growing rosette branches. As described in Hershkovitz (2018a), I had encountered caudices with a few branch scars, but these individuals all had a single *active* rosette. I describe below plants from other southern CLZ localities with 2–3 active rosettes, but the ca. 12 rosettes of the Cartagena plant appears to be exceptional. The caudical root extended ca. 60 cm. I do not know the age of the plant at the time of collection, but the thickness of the caudical stems and hierarchical succession of branch scars suggest that it was at least two years old. However, these characteristics may owe as much or more to high substrate fertility than they do to age. But it is difficult to escape an interpretation that the plants growing at *this* location *behave* as perfectly good perennials.

I extracted and cultivated the caudex in sandy loam in the base of a transparent 2 l soda bottle. I put only the caudical root below the soil, with the thick caudical branches above. The container was placed out of doors in a sunny location ca. 1 km inland in Isla Negra and later El Quisco and watered periodically.

Following watering, new fine roots were visible on the side of the bottle within three days. After perhaps two weeks, the sides of the bottle were densely covered with new fine roots. When I first planted the caudex, a small developing inflorescence was evident in the rosette of each of the thick branches. These all aborted, as did several of the rosettes themselves. But new rosettes emerged from the axillary buds, and numbering *at least 30*, and the plant had the aspect of a dwarf individual of *C. crassifolia* (Phil.) Carolin ex Hershk. (Fig. 2D; see below). However, the leaves in cultivation were rather smaller and narrower than in the in situ plants recorded from this locality.

Inflorescence primordia were evident within some of the rosettes by early September, but some plants in other CLZ populations already had flowered by this date. Almost half of the rosettes aborted at this point, and their subtending stems died back to the subtending branch. The plant first flowered by the end of

September, but the first flowers were "abnormal:" the largest sepals were near normal in size, but they did not open; the petals, stamens, and gynoecium were mature but extremely small (Fig. 2E).

At this point, the plant was moved to a less sunny site indoors for further study. Most (17/19) of the remaining rosettes produced inflorescence primordia. For 13 of these primordia, the inflorescences eventually elongated to 10–20 cm and produced flowers. The remaining four inflorescence primordia remained unelongated as of 20 October. Subsequent flowers were about half the size of those documented from the iNaturalist.org site from the Cartagena locality. Some of the flowers eventually opened only partially or not at all before senescing. Opened flowers evidently self-pollinated (see later discussion). Unopened flowers senesced, hence did not manifest cleistogamy.

In early November, the termini of the active inflorescences suddenly simultaneously senesced, wilting and turning dark. By late November, numerous new shoots emerged from the axils of the caudical branches and the basal nodes of the senescent inflorescences. Shoots of the caudical branches and some basal inflorescence nodes were leafy secondary rosettes. More apical shoots of the inflorescence nodes were not leafy. Rather, they developed directly as new inflorescence primordia. But these aborted within a week. A further observation is that senescent rosette leaves of the plant turned yellow and abscised. Inflorescence bracts dehydrated and became scarious, but they did remain firmly attached to the culm. Finally, I note that the plant in cultivation was treated multiple times with insecticide. While all of the observations above were observed in a manipulated plant in vitro rather than in situ, they still undeniably reflect the natural developmental potential.

iii. The Playa Hanga Roa population

The Playa Hanga Roa population extends throughout a rocky area of perhaps 0.25 ha in between the beach proper to the north and the adjacent Playa Las Conchitas area to the immediate south (Fig. 3A–B). The combined beach areas extend ca. 500 m, bordered by rocky outcrops to the north and south. Although the geology of Playa Hanga Roa and Playa Las Conchitas is very similar, *C. philhershkovitziana* is restricted to the former. The landform suggests that this beach area at one time comprised two natural drainages adjacent to gentle slopes. But now the two drainages are heavily modified with sewers, presumably to stabilize the slopes, now completely urbanized, and they are separated by concrete retaining wall.

This population occurs in pale grayish to whitish sands in between weathered granitic boulders on the coastline and a completely paved urban esplanade. Moreover, many of the plants occur in compacted sands that form trails that are heavily trafficked by beachgoers and littered with cigarette butts[21] and beer bottle shards. Rosettes of plants in this habitat tend to be extremely prostrate (Fig. 3C) compared to plants on less trafficked or protected substrates. Interior rosette leaves of the latter ascend above the soil line.[22]

The seaward portion of the site includes, besides exotics, native herbs and subshrubs typical of CLZ coastal scrub, including *Alstroemeria recumbens*, *Astragalus amatus* Clos, *Cristaria glaucophylla* Cav., *Leucheria* (nee *Polyachyrus*) *poeppigii* (Kunze ex Less.) Hershk. ssp. *poeppigii*., *Nolana paradoxa* Lindl., *Nolana crassifolia* Poepp., *Oxalis megalorrhiza* Jacq., *Tristigma porrifolium* (Poepp.) Traub, and *Verbena sulphurea* D.Don. Towards the esplanade, the ground is carpeted with the "native invasive" *Carpobrotus chilensis*.

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[21] Not mine, of course. Dr. Carolina Villagrán's maybe, but I did not see her in this area during the past year.

[22] This phenomenon is common among weedy herbaceous species, viz. more prostrate in trafficked areas and more ascending-erect otherwise.

I visited Playa Hanga Roa on 2 and 8 July 2024, about 2–3 weeks following the rainy period of May–June, which yielded > 300 mm of precipitation. Here I found plants in the same condition as those in Gota de Leche: small first-year well-established germlings that probably germinated following the first rains in late May and probably second-year plants that had flowered the previous year (Fig. 3D–E). I also found abundant younger germlings growing alongside older plants, some with the early stages of swollen root development, others lacking this (Fig. 3F). These plantlets presumably germinated following the rains in later June. But I also found plants with considerably larger rosettes and caudices (Fig. 3G). The largest caudices bore multiple rosettes (Fig. 3H) and may be more than one year old. These plants were growing next to boulders,[23] which evidently offered them protection from stumbling drunk beachgoers. And, ¿who knows? maybe the drunk beachgoers pee and/or vomit on the boulders, fertilizing the substrate.

On 30 July, I found that plants now were nearly absent in the most highly trafficked areas. Presumably they were crushed. Plants in adjacent open less trafficked areas were damaged, and the oldest leaves were senescent. Meanwhile, the plants protected by rocks were growing vigorously. *Some* prostrate plants in open areas showed inflorescence and floral primordia (Fig. 3I) in a stage more advanced than I found on 22 July at Punta de Tralca (see below). Others lacked primordia. A more protected individual bore a young inflorescence elongated ca. 6 cm with a well-developed terminal floral bud (Fig. 3J).

On 11 August, I found that a very few of the more protected plants had flowered for the first time that very morning (Fig. 3K). Meanwhile, inflorescence primordia on many of the most exposed prostrate rosettes had not advanced, and many still lacked primordia. It seems possible that these plants could perennate without reproducing, since vegetative growth favors caudex growth while reproduction is metabolically costly.

On 17 September, individuals exhibited a range of developmental stages, ranging from nonreproductive rosette to early flowering to mid-flowering to latest flowering and rosette senescence (Fig. 3L–P). Individuals also varied in size and aspect (viz. prostrate to erect). Larger individuals bore secondary rosettes emergent from axils of leaves of the primary rosette. The size variability presumably relates to the growth conditions of the individual, but, as noted, individuals germinated at different times following precipitation events in between late April and late June and then again during August. Because I did not tag individuals during earlier visits, I was unable to establish the age of plants in September.

iv. The Punta de Tralca populations

The Punta de Tralca locality is a crescent-shaped 1500 m long beach area defined ± by the Punta de Tralca peninsula (known as “Piedra del Trueno”) to the south and Punta Taulanque to the north (Fig. 4A). A narrow and rockier beach, “Playa de Jaibas Ermitañas, Las Conchitas,” is situated just to the north of Punta Taulanque. This narrow beach terminates at a rocky outcrop at its northern extreme. Another beach is situated on the south side of the Punta de Tralca peninsula. Its expanse is sandy, but large boulders line the tidal zone. This beach does not appear to have a government-sanctioned name, but it is at the base of a slope known unofficially as “Refugio Natural Challa Malal,” so I will call it “Challa Malal” beach.[24]

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[23] The plants only grew on the north side of the boulders, viz. in full sun. Individuals of all of the other native species could be found on all sides of boulder, viz. also in partial shade. *Cistanthe philhershkovitziana* is not necessarily shade-intolerant; possibly the seeds require light for germination.

[24] https://www.algarrobodigital.cl/2022/08/punta-de-tralca-vecinos-impiden-intento.html. Both Google Maps and Google Earth show this and other ecological features at this locality, none of which are recognized officially, hence represent “user” annotations. Challa Malal and other such features are what are known in Chile as “tomas,” formally illegal

The Punta de Tralca beach area is bisected by the Estero de Totoral and associated coastal marsh. North of the Estero, the beach area is well-defined by a cliff ca. 10 m high. The cliff base is somewhat muddy owing to seepage. South of the Estero, the slope to the coastal terrace is less steep and the substrate is drier.

Two discontiguous populations of *C. philhershkovitziana* occur here. One extends from just south of the Estero ca. 800 m northward to Playa Jaibas Ermitañas. Here, individuals or clusters thereof are somewhat dispersed throughout a ca. 4 ha perimeter. The other is disjunct ca. 600 m to the south of the Estero and extends linearly ca. 150 m along Challa Malal beach. Here, the plants are distributed somewhat more densely throughout ca. 0.8 ha.

The substrates of the northern population plants range from the pure sands of low dunes towards the Estero to the rockier substrates of Punta Taulanque and Playa de Jaibas Ermitañas. Plants of *C. philhershkovitziana* also occur on some more disturbed, compacted, and otherwise “weedy” substrates. The substrates of the Challa Malal beach plants are sands ranging from more brownish granitic to whitish and calcareous because of decomposing mollusk shells. Foot traffic at these localities is modest during winter and spring, especially Playa de Jaibas Ermitañas. Foot traffic is much greater at the Challa Malal beach because it is adjacent to the main Punta de Tralca parking and commercial zone. But because it is well separated from urbanized areas, it is trafficked not nearly as heavily as Playa Hanga Roa.

Plants of the northern population are themselves somewhat separated, almost as subpopulations. They are concentrated towards the northern Playa de Jaibas Ermitañas area and southern Estero area, (as “subpopulations”), but the range is essentially continuous. Vegetation in the dune substrate is mainly herbaceous, but dominated by the exotic *Ambrosia chamissonis*. Towards the cliff, *Carpobrotus chilensis* dominates. Native shrubbier species [e.g., *Haplopappus foliosus* (Hook. & Arn.) Hook. & Arn. and *Leucheria poeppigii* ssp. *poeppigii*] occur on the rockier substrates of Punta Taulanque and Playa de Jaibas Ermitañas. The Challa Malal beach vegetation is intermediate, mostly herbaceous, but some suffrutescent plants also occur.

I first visited a dune portion of the Punta de Tralca northern population on 26 October 2023. I found relatively small plants in advanced flowering stages and with rosette diameters mostly < 6 cm. I visited again on 29 January 2024 and found only a very few skeletalized shoots. Because the vegetated area is small and “fragile,” and also because *C. philhershkovitziana* is not especially common here, I did not excavate the sand to look for caudices.

I returned to this population on 9 July 2024 (following April–July rains), at this time also visiting the Playa de Jaibas Ermitañas population. I found plants in conditions similar to those described above at Gota de Leche, viz. abundant small plants, both evidently second-year plants and first-year plants with well-developed caudices that probably germinated following the rains of late May and early June (Fig. 4B). As at Playa Hanga Roa, I also found seedlings that germinated following later rains, both with and without caudical development.

However, I also found a few relatively large plants on less disturbed dunes near the Estero, though these were less than half the size of the Cartagena plants. Based on the pattern of abscised growing points, I judge that these plants are > 2 years old (Fig. 4C). The original caudex apices were buried > 5 cm in the

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expropriations of private property by small bands of citizens, often who profess ideological rejection of the concept of “private” property (excepting their *own*, of course). Sometimes these informal expropriations are ratified legally by like-minded judges.

sand. The caudices showed no morphological evidence of contractile behavior, though it is possible that late season shrinkage of the deeper fine roots pull the caudex deeper into the sand (see below). Otherwise, caudex depth owes to natural sand accumulation on the dune (see below). My interpretation is that survival of these plants owes to the consequent protection of the caudex against both aridity and physical damage. This results in a larger/longer caudical root, hence, greater access to groundwater at greater depth. I found no such large plants in the northern portion of sandy Punta de Tralca beach or the rockier Playa de Jaibas Ermitañas habitat. To the contrary, I estimate that at least half of the rosettes in these areas were first-year plants.

On 22 July 2024, I first visited also the Challa Malal beach population. As in the other localities, plants were mainly first- and second-year. I found a single individual that I believe to be > 2 years old. During this visit, I also noted that several plants from the Estero sector bore a single flower bud, perhaps 3 mm long, in the center of the rosette. The rosette age is unknown, but based on rosettes observed at Gota de Leche on 13 May, I estimate the age to be ca. 12 weeks.

On 18 September 2024, I surveyed the entire Punta de Tralca beach area, including Challa Malal beach. Throughout the locality, I found numerous plants in mid-flowering stage, viz. with the oldest flowers post-anthesis and developing fruits, while floral primordia continued to develop. Larger plants bore more secondary rosettes emergent from the axils of leaves of the primary rosettes. I located a few individuals that were still in the rosette stage and lacked inflorescence primordia, perhaps consequent to later germination, but none were in the senescent stage as found at Punta de Tralca. More notably, I located seedlings that probably germinated following rains in late August (Fig. 4D). As noted, additional rain fell here that evening and following morning. This may provoke additional germination. But in the case of no further rain in 2024, I cannot speculate on the fate of these seedlings. Finally, in one area, I found that numerous relatively young plants indeed had become partially to completely buried (Fig. 4E) by drifting sand. This phenomenon also is evident in some photos in iNaturalist.org.

Additional information

I have not visited the coastal population of *C. philhershkovitziana* in the vast dune area along Estero Casablanca in the Santuario de la Naturaleza Humedal de Tunquén (ca. 33.28S), documented by numerous iNaturalist.org observations.[25] This area is more isolated from the more urbanized localities above, hence much less trafficked, especially in non-summer months. The corresponding photos show plants rather larger than those at all but the Cartagena locality. The observation from late May 2024 includes a photo of a rather large caudex, which obviously is not that of a first-year plant.

I also have not visited the population at the southern extreme of the species distribution, on the beach of the El Yali National Reserve just south of Santo Domingo (ca. 33.8S). This area likewise is geographically well-buffered from the urbanized zone and less trafficked. But plants from here are not especially large.[26]

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[25] https://www.inaturalist.org/observations/189701159; https://www.inaturalist.org/observations/189701302; https://www.inaturalist.org/observations/189703311; https://inaturalist.mma.gob.cl/observations/189700904; https://www.inaturalist.org/observations/190129626; https://www.inaturalist.org/observations/218253245; https://www.inaturalist.org/observations/218248397

[26] https://www.inaturalist.org/observations/135392268; https://www.inaturalist.org/observations/100016168; https://www.inaturalist.org/observations/66773715; https://www.inaturalist.org/observations/94387767

iNaturalist.org also documents the virtual absence of 2023 observations of *C. philhershkovitziana* north of Los Vilos (Choapa Province, Coquimbo Region). This is not surprising, since this region received very little rainfall during 2023. It may, however, also reflect the lack of botanical exploration during a drought year. The only 2023 iNaturalist.org observation of *C. philhershkovitziana* in this zone was at the mouth of Quebrada San Pedro, also known as Quebrada del Teniente.[27] I cannot determine from the photo the age of the plant. As I will discuss elsewhere, there may have been a "moisture anomaly" at this particular locality that permitted growth of this species. Nonetheless, the otherwise absence of 2023 reports from north of Los Vilos compared with numerous 2022 reports (Hershkovitz, 2022a) is consistent with the notion that the species does not emerge during drought years, whether from seed or from caudices.

Discussion

My initial characterization of *C. philhershkovitziana* as an annual herb was abductive, based on my observations of plants growing in Chile's Coquimbo Region. There, it seemed to me that the caudices could not withstand the frequent incidence of multiyear drought. Given that the plants could flower from seed in a single season following rains, there was no *need* to invoke perenniality to explain the thick caudices, hence no need to hypothesize it in the absence of empirical evidence. The branch scars on the caudex thus were interpreted as same-year growth.

But the present empirical observations of plants growing in southern Valparaiso Region, where rains arrive every year, demonstrates that caudices of *C. philhershkovitziana* indeed characteristically survive the dry summer and produce new shoots following subsequent rains. This means that the plants are *perennial*. Nonetheless, plants also evidently characteristically reproduce within 10–12 weeks following germination (but see below), and this renders them *facultative annuals*, regardless of their potential longevity.

The first-year plants evidently experience considerable mortality, and, in the studied localities, very few show evidence of three or more years duration. But the reason for mortality…*and* longevity…may be site-specific, viz. idiosyncratic. First-year mortality may be consequent to massive pseudopredation by shore birds, i.e., at Gota de Leche, anthropogenic mechanical damage at other localities, and extended drought in northern Chile. Longevity beyond two years seems also to depend on site-specific caudex protection, such as in rock crevices (e.g. at Playa Hanga Roa), caudex burial in open dunes, or high substrate fertility (e.g., at Cartagena). Quite likely, especially in the arid and drought-prone northern portion of the range, caudices survive more than one year but die before flowering a second time. From a *survival* standpoint, such plants might be described as de facto perennial. But from a reproductive standpoint, their behavior is de facto annual.

While the present observations demonstrate that *C. philhershkovitziana* can survive perennially, many ecological and evolutionary biological (EEB) questions remain: **(1)** questions pertaining to the life history/form and phenology of *C. philhershkovitziana* itself, since the observations offered here are scant given the latitudinal range of the species; **(2)** questions pertaining to the life history/form and phenological similarity/difference between *C. philhershkovitziana* and other species of *C.* sect. *Cistanthe* and clades more inclusive, and hence **(3)** questions pertaining to life history/form and phenological *evolution* of *C. philhershkovitziana*.

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[27] https://es.wikipedia.org/wiki/Quebrada_del_Teniente

1. Life history/form and phenology of *C. philhershkovitziana*

Seeds of *C. philhershkovitziana* germinate following “adequate” hydration, whether this is direct substrate hydration via precipitation or indirect via runoff or a combination. The exact amount of hydration necessary is not known. Some seeds evidently germinated following light rains in late spring 2023, while multiple heavier rains in late autumn 2024 spurred not only massive germination, but additional waves of germination following each rain event. Germination otherwise does not seem to depend on “season,” viz. annual T° variation or photoperiod. It is not clear whether the seeds have any sort of dormancy requirement, whether seedlings observed in this study are offspring of the most recent generation, or how long seeds remain viable.

At some point after germination and the development of perhaps 4–6 rosette leaves, the caudex develops at the level of the (subterranean) embryonic node, yielding the caudical taproot and the “caudical rhizome” (Hershkovitz, 2018a), the latter so-called because, evidently under natural conditions, this portion of the stem remains completely subterranean and, moreover, it may form subterranean branches. It is not clear whether caudex initiation is developmentally constitutive or influenced by environmental factors.

Similar to seeds, dormant caudices reactivate following adequate hydration and generate new rosettes. The effect of multiple hydration events within a season is not clear, viz. whether caudices generate *additional* vegetative/reproductive rosettes. Possibly this depends upon the developmental stage of the existing rosettes. Possibly precipitation events might spur development of secondary rosettes in the axils of leaves of the primary rosette. In Gota de Leche, no new rosettes were observed in late-stage flowering caudices following additional precipitation. In the Cartagena plant extracted and cultivated following grazing, initially subterranean caudex branches resituated above the soil line generated new rosettes.

Under natural conditions, only the leaves of an active rosette emerge above the soil, while the perennating buds of the caudex remain below ground or possibly marginally above it. As noted, during the dormant season, the caudices are not evident on the substrate surface. This would *approximate* the condition of the *geophyte* form of *cryptophyte* in the life form terminology of Raunkier [Niklas (2008); but cf. World Checklist of Vascular (2021; hereafter WCVP), as referenced in Plants of the World Online (2023; hereafter POWO)[28]]. The Raunkier classification emphasizes the position of perennating buds relative to the soil level (see later discussion). In this case, it is a *passive* form, because this condition does not seem to be maintained by an active mechanism, e.g., contractile roots. But it is possible that root shrinkage owing to dehydration can pull the caudex deeper into the substrate.

As noted, in cultivation, healthy caudex stem branches can be maintained above the soil, and these can form abundant additional branches at the aerial nodes. This would qualify as a *subrosettiform chamaephyte* in the Raunkier classification. But in nature, the caudex remains subterranean.

The secondary rosettes that commonly but not always form in rosette leaf axils also render the plant architecture as subrosettiform. Secondary rosettes are common even in annual species of *Cistanthe* sect. *Rosulatae* (Hershkovitz, 2022b). But these do not render the plant a subrosettiform *chamaephyte*, because their meristems do not *perennate*. The entire rosette shoot system is ephemeral, just as in annual plants. In any case, even a potentially perennial plant that dies after first-year reproduction de facto *behaves* as an annual or *therophyte*. In this case, since the caudex does not de facto perennate, the position of its perennating bud is undefined, regardless of other aspects of plant architecture.

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[28] https://powo.science.kew.org/about-wcvp

Under both natural and cultivated conditions, the caudical (viz. vegetative) branches are mostly "short shoots," viz. lack elongated internodes, or shoots with elongated but very short internodes. For example, the internodes of stems subtending secondary rosettes emerging from the axils of primary rosettes may be several millimeters long (Fig. 5). Subterranean caudex internodes likewise may elongate to a few mm. Otherwise, the stem portions with more elongated internodes are those of the inflorescence, and these have a few elongated internodes along the culm, and more condensed flowering nodes towards the apex. The culm nodes are bracteate, but the basalmost nodes may bear a leaf and/or leaf-bract intermediate.

Plants may have one to several actively growing rosettes, a few primary (caudical) and more secondary. The number of active rosettes does not seem to be fixed to the size of the caudex. This is demonstrated by photos of relatively large caudices with single active rosettes in Hershkovitz (2018a) compared with a few smaller caudices with two rosettes found in the present study (Fig. 3B).

The time to flowering of *C. philhershkovitziana* following germination is not established, nor is it established how it is influenced by moisture, T°, photoperiod, or "other." I noted at Gota de Leche very small flowering individuals in early summer, ca. 10 weeks following significant precipitation. I believe that these individuals were much younger than most individuals at this site, but I cannot establish whether they were, in fact, only ten weeks post-germination. Meanwhile, I estimate that inflorescence/floral *primordia* at Punta de Tralca and Playa Hanga Roa localities did not develop until after ca. 12 weeks of rosette development (whether via germination or caudex reemergence). But I suggested that this long "gestation" owed to short days and perhaps also cold T°. These early winter plants emerged consequent to unusually early precipitation in latest autumn.

The category of "other" emerges in the Playa Hanga Roa population. Here, plants growing in protected sites initiated flowering, while inflorescence primordia were poorly or not developed in plants growing a few meters away on compacted substrate in trafficked areas. The reason might be mechanical or hydrological or both. This underscores the importance of *demographic* as opposed to individual variation in life history/form and phenology (see below).

Flowering in *C. philhershkovitziana* is *determinate*: inflorescences form ± simultaneously during a short period and then not again within the *same* growing season after those inflorescences flower (cf. Friedman, 2020). Plants are iteroparous (polycarpic), but they can be de facto semelparous (monocarpic) if they die before reproducing a second time (cf. Friedman, 2020).

The inflorescence appears as a raceme, but larger inflorescences may have one or two basal branches. In any case, it is cymose, viz., each flower is terminal and each successive flower emerges from one axil of the pedicel node in a helicoid fashion. However, the cyme is indeterminate. The basal 5–10 nodes develop "normal" flowers, while the last formed nodes develop reduced flowers and eventually just floral primordia.

The flowers in *C. philhershkovitziana* are smaller than flowers of other species of *C.* sect. *Cistanthe*, the floral organs ca. 10–20% shorter than most species. In *natural* populations, flowers of *C. philhershkovitziana* appear to last one day. The aestivation is quincuncial, a spiral phyllotaxis with two abaxial petals (P1 and P2), two adaxial petals (P4 and P5), and one petal (P3) with one margin adaxial to P1 and the other abaxial to P5. Still, the petals appear to "untwist" as they open (in nature) at about midday when in full sun. They "unopen" close by late afternoon (or sooner): they twist about the sporophylls as they deliquesce, and they dry into a sort of pointed cap that adheres to the developing capsule and breaks away during capsule dehiscence. During floral aestivation, the sepals spread apart abaxially to ca.90° with respect to each other. The ca. 50 stamens spread ca. 30–75° abaxially relative to the style. I did not record the presence/absence of nectar. Next year.

On colder, cloudy days or cultivated indoors, flowers may not open fully, possibly even at all. *Cistanthe philhershkovitziana* seems to be generally self-compatible and I recall that plants collected similarly over the past 20 years were highly fecund without deliberate cross pollination. In the present effort, I confirmed self-compatibility in the cultivated individual extracted from Cartagena. There is no specialized mechanism for cross-pollination (e.g., herkogamy). Self-pollination of individual flowers results from a passive mechanism. The stamens and stigmas normally mature at the same height. In flowers that never open, the stamens are in close contact with the stigma, but my observations of a cultivated individual suggests that there is no cleistogamy. But in unpollinated opened flowers, the closing of the flower in the afternoon brings the dehisced anthers in contact with the stigma. These flowers produce fruits/seeds. The flowers then close completely, and the capsule begins to develop.

After flowering, the closed sepals enlarge somewhat and firmly enclose the floral remnants and developing capsules. It is not clear whether this enlargement involves new cell division. At this stage, they remain foliaceous and seem to be somewhat firmer and more succulent than before flowering. They become drier and more membranous towards dehiscence, but they are never deciduous, viz. they do not abscise from the receptacle/pedicel (cf. Hershkovitz, 2021a). During capsule development, each successive pedicel elongates and reorients towards the soil surface, viz. it evidently is hyponastic. Again, it is not clear whether this process involves additional cell division.

I erroneously reported in Hershkovitz (2022b) that, unlike in certain species of *C.* sect. *Rosulatae*, the downwardly oriented post-anthesis pedicels in *C. philhershkovitziana* and other *C.* sect. *Cistanthe* species *do not* then reorient *upwards* (epinasty) just before capsular dehiscence. In fact, the pedicels do reorient upwards, as I have observed in vivo in a cultivated plant and in the field. This reorientation is especially evident in one particular iNaturalist.org image[29] and somewhat less so in Fig. 1B. It is evident also in iNaturalist.org images of other species of *C.* sect. *Cistanthe* (not shown). After dehiscence, the desiccating pedicel may reorient passively any which way before abscising.

As the final flowers senesce, the entire rosette system senesces, viz. the inflorescence stem and its subtending rosette leaves. These together constitute a *metamer*. The senescence timeline seems to be mediated mainly developmentally, viz. by termination of flowering and initiation of fruit development. Hydration/drought may be a secondary factor. Thus, plants in a population vary in their developmental state, viz., some are green with (or without) developing inflorescences while others are post-anthesis and senescent. A population in this state might occur in the southern CLZ in late winter (viz. cooler and lower light conditions) or late spring to early summer, depending on precipitation history. *Eventually*, all of the rosettes will succumb to drought regardless of developmental stage.

I have not established the timeline from anthesis to fruit dehiscence or from initial anthesis to final fruit dehiscence and inflorescence senescence. But this clearly can vary among individuals within a population. At Playa Hanga Roa, observed senescent plants were not among the first to flower. In the cultivated Cartagena plant, following transplantation, rosettes terminating several branches, a few with small inflorescence buds, senesced and aborted in entirety.

Metamer senescence may proceed to include a subtending node on the caudical branch, or the entire caudical branch might senesce back its origin on the caudex axis. In the large Cartagena plant later cultivated, first, second, and even third order caudex branches persist. But under natural conditions, it seems more common for caudex branches to senesce to the main caudex axis.

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[29] https://www.inaturalist.org/observations/139835849

Following senescence and disintegration of the rosette(s), the caudices remains alive for what can be inferred to be at least eight months without additional precipitation. At least for some weeks in this phase, it appears that fine roots also remain alive, possibly continuing to hydrate the caudex from the water table. However, it is clear that actively growing caudices contain considerable water, and that they emaciate considerably in desiccating conditions. In other words, the dormant caudex does not form a hardened/resistant perennating structure. I do not have anatomical data, but it does not appear that the caudex tissue becomes significantly lignified. How long the caudices remain viable under these drought conditions is not established, nor the degree to which it depends on substrate T° and humidity.

Under its idealized seasonal natural conditions, viz. winter rain followed by summer drought, *C. philhershkovitziana* plants presumably undergo a single cycle of vegetative development, flowering, and senescence. Noting that the caudices of some flowering individuals at the type locality in southern Choapa Province (Coquimbo Region) bore scars of abscised metamers, Hershkovitz (2018a) suggested that late season rains might cause caudices to reactivate and flower again within a single season. I now consider possible, if not likely, that these scars represented prior years' growth. I also had reported a failure to find caudices in a known habitat in the northern Coquimbo Region during a drought year. I now consider possible that live caudices may have been present deeper in the soil profile. But confirmation requires empirical observation of caudex reemergence following winter rain.

In the southern CLZ, no subsequent within-season reemergence/flowering of caudices was detected in post-flowering caudices following late spring 2023 precipitation. Rather, at Gota de Leche, it appears that this precipitation spawned germination of a new generation of individuals that flowered in mid-summer 2023. Numerous new rosettes emerged from the large Cartagena caudex following transplantation to a container. But this individual had been severely cut back by grazing. This may have stimulated regrowth. No inflorescence development was observed until the following September, when natural populations had begun to reproduce.

The descriptions above are somewhat reductionist and typological. Although variability is addressed, they *attempt* to idealize a "normal" life history/form and phenology of *C. philhershkovitziana* as though the species is an individual (viz. a "type") and in terms of that which is most commonly observed under the most commonly observed conditions. While not quantified here, this is effectively a statistical approach, viz. averages and variances. This is useful for summary descriptive purposes, but not for purposes of phenomenological *analysis*. As will be elaborated later, however constrained by their biological history, individuals are not constrained by *averages*. Variation might be *measured* statistically, but it is a *biological* and not statistical phenomenon. It reflects the moment-to-moment improvisational realization of the ontogenetic phenotype (Maturana & Mpodozis, 2000; Mpodozis 2022). This realization is *idiosyncratic*.

Phenology and life history/form vary at the demographic scale. Demographically, populations of *C. philhershkovitziana* vary in size/density. Based on population area, population size at most localities is relatively small. Nonetheless, given adequate precipitation, in some localities of *both* the southern CLZ and the Coquimbo Region, populations of *C. philhershkovitziana* can become relatively "dense," I would guess on the order of 1–5 reproductive individuals/m^2 extending > 100 m^2. Some seedling densities observed during 2024 were much higher than this, but I did not formally count/measure them.

Superimposed over this demographic variability is phenological variability. Most notably, *C. philhershkovitziana* flowering populations probably appear perennially in the southern CLZ, whereas flowering populations in the Coquimbo and Atacama Regions appear only in years with adequate precipitation. These years may be interrupted by multiyear droughts. Examples of marked demographic phenological variability within populations include the second "generation" of flowering individuals found at the Gota de Leche locality and the marked delay in reproductive development among protected and exposed plants at the Playa Hanga Roa locality. Demographic variability in phenological behavior with respect to biotic and abiotic ecological interactions manifests in the uprooting of caudices at the Gota de Leche locality and the effects of variable foot traffic at the Playa Hanga Roa locality.

Chronological/developmental age structure also varies demographically. I estimate that the overwhelming majority (perhaps 90%) of individuals at examined southern CLZ localities are no more than two years old. However, the age structure of recurring individuals is conditioned by many factors, including events of prior years, e.g., the southern CLZ received well below "normal" rainfall in 2020 and 2021. This might have increased caudex mortality. At the same time, the relatively short six month span between "abnormal" late spring 2023 and "abnormal" late autumn 2024 rainfall might have decreased caudex mortality of 2023 germlings. Furthermore, the abnormal late spring 2023 precipitation evidently induced a wave of seed germination and added an additional "generation" of caudices to the 2024 population.

Populations of flowering individuals in northern Chile following a multiyear drought may be primarily or completely first-year plants. However, plant phenological demographics in northern Chile must be established by empirical study of rosettes emerging after adequate precipitation. It is possible that that caudices survive long droughts in locations where there is perennial runoff, i.e., alongside major Andean drainages and/or in coastal fog deserts. I reported my failure to find caudices during a drought year at a site in northern Coquimbo Region (Hershkovitz, 2018a). But the age structure of plants at this site needs to be verified by examination of caudices emergent following precipitation.

Part of the phenological and life history/form variability at the demographic scale owes to the seed bank, since the fate of seeds and seedlings undoubtedly varies interannually and geographically. Hershkovitz (2018a) estimated that the largest plants growing at a site in Choapa Province (Coquimbo Region) could produce on the order of 4000 seeds. Plants are smaller at most southern CLZ sites, and these have correspondingly fewer flowers and smaller fruits. Still, fecundity at these sites should be on the order of 1000 seeds per plant. Other than fecundity, practically nothing is known about this seed bank or seedling ecology, e.g., germination requirements, seed longevity, seed dispersal, or other causes of seed and seedling mortality. But evidently, successive precipitation periods may result in successive waves of seed germination. This complicates demographic analysis, because the succession of precipitation events also varies interannually and geographically.

2. Life history/form and phenology of other *Cistanthe* sect. *Cistanthe* species

I preface this section with remarks about the taxonomy of *C.* sect. *Cistanthe* in Chile. I estimated in Hershkovitz (2019a) that this section includes ca. 12 species, ten in Chile; I revise these figures downward here by one species.[30] I commented on historical difficulties with the taxonomy there and in Hershkovitz (2018a, 2019b, c; see also below). The most recent taxonomic treatment of the Chilean species is that of Reiche (1898a, b), who, evidently based mainly on relatively few herbarium specimens and literature descriptions, lumped all of them under *Calandrinia grandiflora* Lindl. [≡ *Cistanthe grandiflora* (Lindl.) Schltdl.]. Likewise based on study of few herbarium specimens, Hershkovitz (1991a, b, c) followed Reiche. More recent and current references, e.g., Rodriguez et al. (2018), GBIF (GBIF Secretariat, 2017), WCVP, POWO, World Flora Online (2024), Flora Cono Sur (without year), and iNaturalist.org, accept multiple Chilean species, but no two of the taxonomies are identical and none agree completely with my current notions.

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[30] Hershkovitz (2019b) described *C. subspeciosa* Hershk. Based on additional information, and pending further study, I concede that it is better to classify this as *C. cabrerae* (Añon) I.E.Peralta.

Hershkovitz (2019a) did not provide a conspectus or even a list of the species that I accept, much less a taxonomic revision. I do not provide this here, either. The species names, identifications, and characterizations provided here correspond to taxonomic species (*synspecies* sensu Hershkovitz, 2019a, 2021b, 2022b) that I accept per the classical typological criterion. This means that I conceive of these as taxonomic species that comprise individuals that pertain to the same taxonomic species as the Type of that name, and that I regard that Type as an *apospecies*, viz. as *not* pertaining to the same taxonomic species any *other* Type that I *also* recognize as an apospecies.[31]

Thus, the species names used here represent taxa among those I currently accept. I identify accordingly specimen images that I cite that are identified differently by their source. As I pointed out in Hershkovitz (2018a), specimens identified in Hershkovitz (2006) as *Cistanthe discolor* (Schrad.) Spach are *C. grandiflora*, as *C. grandiflora* are *C. philhershkovitziana*, and as *C. speciosa* Lilja ex Heyn. is *C. cabrerae* (Añon) I.E.Peralta (incl. *C. subspeciosa* Hershk.; see above).

Although I have studied most species of *C.* sect. *Cistanthe* in the wild, I confess remarkable ignorance about their phenology and both geographic and interannual phenological variation. Like many systematists, I had been concerned mainly with their morphological distinctions and distributions, which manifest in concert at the stage of full flowering and fruit/seed development. The study and documentation of phenology and phenological variation – under both natural and cultivated conditions –represents an expensive and multiyear proposition. It requires annual year-round study of populations distributed from south central Chile to northern Peru and varying in elevation from sea level to perhaps 2500 m. Nonetheless, my ignorance is mitigated slightly by adding to my own observations a fair number of live and preserved specimen images available from GBIF and iNaturalist.org, and also information gleaned from some horticultural literature and websites.

Cistanthe philhershkovitziana is distinguished easily morphologically from other *Cistanthe* sect. *Cistanthe* species, but this per se does not mean that its life history/form and phenological characteristics are distinct absolutely. Critical traits for comparison include: **(i)** life form morphology; **(ii)** whether the plants can reproduce during their first season following germination; **(iii)** whether the plants flower during a short period or continuously throughout the idealized "normal" season; **(iv)** the degree to which the rosette and rosette stem senesce following flowering; **(v)** the longevity of the caudex; and **(vi)** demographic variability.

i. Life form morphology. Most species of *C.* sect. *Cistanthe* behave as subrosettiform hemicryptophytes, viz. their perennating buds occur near the soil level and they emerge as rosettes, but their inflorescence stems may have leafy nodes separated by elongate internodes, especially towards the base. This morphology can occur in *C. cabrerae* (incl. *C. subspeciosa*), *C. discolor*, *C. grandiflora*, *C. mucronulata* (Meyen) Hershk., *C. paniculata* (Ruiz & Pav.) DC, and *C. tovarii*. There are nuances, however. In general, the first-year caudex of the subrosettiform species (including *C. philhershkovitziana*) produces a single basal rosette, and then caudex branches may produce additional basal rosettes in the second and later years. In some subrosettiform species and under some conditions, the elongated portion of the inflorescence may lack leafy nodes. And in some subrosettiform species and under some conditions, the perennating buds may be located on above-ground succulent short-shoot branches several cm long (as in the cultivated *C. philhershkovitziana* specimen). This represents a developmental transition to the

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[31] Thus excluding Types that I do *not* accept as apospecies because I consider them to be synspecific (viz. taxonomic synonyms) with Types whose apospecificity I accept.

chamaephytic condition. The chamaephytic life form occurs in nature in older plants of *C. paniculata* under some conditions (see also below),[32] coastal plants of *C. mucronulata*,[33] and *C. grandiflora*.[34]

Meanwhile, larger/older pachycaulescent plants of the closely related species *C. aegitalis* (Phil.) Carolin ex Hershk.[35] and *C. crassifolia*[36] qualify as phanerophytic. But even these qualifications are nuanced. The plants evidently emerge as rosettiform and, in this state, can be considered as hemicryptophytic. Later, they become subrosettiform, then chamaephytic, and, finally, most definitely phanerophytic. Large individuals resemble pachycaul phanerophytes that have evolved in numerous divergent angiosperm clades, viz. bearing thickened branches that terminate in foliar rosettes. *Cistanthe laxiflora* (Phil.) Peralta & D.I.Ford is another species that could qualify as phanerophytic. Its short-shoot stems may grow to 2 m. In seasonally drier habitats, these die back towards the caudex. In perennially more humid habitats, such as in the southern CLZ, they may persist.[37] In any case, in all of these species, the perennating stems are short-shoots, whereas perennating stems in many other angiosperm taxa classified as chamaephytes and phanerophytes have elongated internodes.

In summary, species of *C.* sect. *Cistanthe* vary in their life form morphology under natural conditions, ranging from cryptophytic in *C. philhershkovitziana* to hemicryptophytic to chamaephytic to phanerophytic in *C. crassifolia*. But species themselves vary according to both natural and artificial ecological conditions and developmental age. This blurs the distinctions among life forms, hence among species in this respect. *Cistanthe philhershkovitziana* is the only species that can be qualified as cryptophytic in its natural circumstances, but its chamaephytic behavior in cultivation demonstrates that it can span most of the life form spectrum in the section. Likewise, *C. crassifolia* spans the spectrum from rosette hemicryptophytic to phanerophytic according to developmental age.

ii. First-year flowering. I have observed and noted elsewhere first-year flowering in *C. grandiflora*. This capacity renders this species potentially facultatively annual. But I have no data on mortality of post-reproductive first-year ´plants in nature, though entropy dictates that it must happen sometimes. Plants of *C. grandiflora* can become quite large (perhaps up to 2 m high and broad), and I have seen ample evidence of reemergence of branches from the caudex during subsequent seasons. Lindley (1839; cf. Hooker, 1834) renders evident that *C. discolor* flowers during its first season. Jacques (1832) and Loudon (1840) also remarked that this species can be cultivated as an annual.

Another species I now diagnose as facultatively annual is the weedy and polymorphic *C. paniculata*, endemic to the coastal lomas from north-central to southern Peru at elevations 0–2500(– 2750?) m (Brako & Zarruchi, 1993; cf. Macbride, 1937). Macbride (1937) described it as perennial. Brako & Zarruchi (1993) described it as an herb or subshrub. But Hershkovitz (2018a, 2019a) overlooked three references that described it as a therophyte or annual: Schwarzer et al. (2010), Lleelish et al. (2015) and De la Cruz (2016).

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[32] https://www.gbif.org/es/occurrence/1228585591

[33] https://inaturalist.mma.gob.cl/observations/154367367; https://inaturalist.mma.gob.cl/observations/111603230; https://inaturalist.mma.gob.cl/observations/199157475; https://inaturalist.mma.gob.cl/observations/199157469. These images document an essentially evergreen life history (late summer through the winter) in coastal populations of *C. mucronulata*, as well as their chamaephytic to nearly phanerophytic life form. Note the persistent thick, succulent stems in the winter (August) photos.

[34] https://www.inaturalist.org/observations/216405333. Late autumn images of a *C. grandiflora* individual in the southern CLZ. The leaves emerged following autumn rains. Note the thick, succulent stems of prior years' growth.

[35] https://www.inaturalist.org/observations/146717456

[36] https://www.inaturalist.org/observations/196993219; note that one of the images shows a young rosettiform individual.

[37] https://www.inaturalist.org/observations/229617041

[38] GBIF includes images of specimens that show both chamaephytic older plants with large caudices (see above) and probable first-year plants with more slender roots.**[39]** One specimen shows caudical roots rather similar to those of *C. philhershkovitziana*.**[40]** I also reported in Hershkovitz (2018a) my *suspicion* that *C. tovarii*, a diminutive species described from Peru, may exhibit annual behavior.

Other than the above species, I cannot *verify* whether first-year flowering does or does not occur in any other species of *C.* sect. *Cistanthe*. Information from some horticultural websites seem to suggest that *C. laxiflora*[41] can be grown as an annual, which means that it flowers in its first year. But the technical details are lacking and/or it is not clear whether the information pertains to the illustrated/described species or to "calandrinias" in general. *Cistanthe laxiflora* is much larger than most other species, with perennating branches that may exceed 2 m in length (see also below). It might seem odd that the subarborescent pachycaul *C. crassifolia* would flower in its first year, but this possibility cannot be ruled out. An internet image[42] clearly shows flowering in the rosettiform hemicryptophyte stage, but the age of this individual is unknown.

In summary, it appears that most, and possibly even all, species of *C.* sect. *Cistanthe* are at least capable of flowering from seed during their first year. Thus, the *entire* section, *possibly* with one or two exceptions, can be characterized as facultatively annual rather than strictly perennial. This, in turn, renders insignificant the distinction emphasized in the original description of *C. philhershkovitziana* (Hershkovitz, 2018a), as well as erroneous the sectional description in Hershkovitz (2019a) and other works where this distinction or characterization was mentioned. The distinction is valid only to the degree that, unlike other species of the section, *C. philhershkovitziana* might behave *primarily* as an annual in northerly habitats were multiyear droughts normally occur. Otherwise it is distinguished by its much smaller maximum size and normally cryptophytic life form.

iii. Flowering phenology. Flowering in *C. philhershkovitziana* in "nature" can be described as "vernal," viz. a *single* spring flowering event following adequate winter hydration and vegetative development, followed by senescence of the above-ground organs in later spring, and then dormancy. Whereas this phenology appears to be constitutive, it does not seem to depend strictly on time of year. As noted, plants germinating following late spring rains at Gota de Leche were flowering in summer when the above-ground organs of the rest of the population were completely dead.

I had been under the impression that this flowering phenology was shared by several, though not all, *Cistanthe* sect. *Cistanthe* species. But my focus had been on "season" (viz. T° and photoperiod) and not on the evidently more influential moisture parameter. Several species manifest continuous extended flowering under more humid, including cultivated conditions.

Among species I *had* considered to be *strictly* vernal are *C. grandiflora*, *C. discolor*, and *C. mucronulata* (Meyen) Carolin ex Hershk. These are among the species that can be described as

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[38] Strangely, Brako & Zarruchi (1993) and Macbride's (1937) classical Flora of Peru were not cited in these three works.

[39] https://www.inaturalist.org/observations/104282782

[40] https://www.gbif.org/es/occurrence/4038825436

[41] Variously under the "vernacular" scientific names (viz. Latin binomials without authority) *Calandrinia grandiflora*, *C. speciosa*, *C. spectabilis*, or *Cistanthe grandiflora* (see Hershkovitz, 2019b, c). The identity as *Cistanthe laxiflora* can be deduced from images and/or descriptions.

[42] https://www.cactuspro.com/forum/read.php?1,402982,403055. Two images on this page show rosettiform stage. Other images show the phanerophytic stage.

"subrosettiform," at least under some of their naturally occurring conditions. Their caudices often bear two or more above-ground fleshy "short shoot" branches near the base, and each branch terminates in a flush of leaves, followed by an inflorescence stem with elongated internodes. The inflorescence stem of *C. grandiflora* may bear leaves at more basal inflorescence nodes, while basal foliar organs in the other two species usually are very small and more bract-like. However, I also have seen individuals of *C. grandiflora* that are highly branched and ca. 2 m in height and breadth, and their branches are leafier. This occurs in localities of high humidity (e.g., in the fog desert near Taltal, Antofagasta Region) or vernal drainage (e.g., along sloped roadcuts).

Cistanthe grandiflora [including *C. cachinalensis* (Phil.) Peralta & D.I.Ford] occurs in both coastal and inland habitats between ca. 23–33S. I have observed that in the more humid conditions of the southern CLZ and also in cultivation, *C. grandiflora* continues to grow vegetatively and flower throughout the summer. This does not seem to relate per se to plant size. Plants growing large in vernally moist sites that later become much drier senesce with the onset of summer drought.

Cistanthe discolor is distributed mainly in the precordillera and coastal ranges above 500 m altitude from ca. 29–34S, but also occurs at low elevation coastal sites at ca. 28S.[43] In the field, the species undergo a single flowering event in early spring, followed by rapid desiccation and senescence with the onset of late spring and summer drought in these habitats. But Lindley (1839) reported that in cultivation, the species blooms all summer until the onset of frost.

Cistanthe mucronulata is distributed mainly in the precordillera and coastal ranges of Chile's Maule Region, but it also occurs in coastal habitats from southern General O'Higgins to Biobío Regions. The inland plants behave as subrosettiform vernal plants. They flower in spring and then die back to the caudex with the onset of drought. But the southernmost populations on the Hualpén and Tumbes peninsulas near Concepción evidently have a longer flowering period. iNaturalist.org documents their continuous flowering as early as September[44] and as late as January.[45]

In its natural habitat on coastal cliffs, and under natural conditions, the shrubby to scandent *C. laxiflora* seems to begin to flower perhaps a month later than the more compact rosettiform vernal species. Similar to the coastal populations of *C. mucronulata*, the vegetative stem internodes are not elongated, and they remain leafy for an extended period. However, unlike *C. mucronulata*, there is no inland vernal subrosettiform hemicryptophyte form of *C. laxiflora*. This species characteristically flowers throughout the summer in its natural habitat. I had considered that flowering began with the onset of longer/warmer days and terminated with the onset of shorter days and/or colder weather. But in cultivation in California (Huffman, without year) and in Chile (pers. obs.), this species flowers nearly year round. I have observed

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[43] https://www.inaturalist.org/observations/227319064; https://www.inaturalist.org/observations/235752555. The life form and coastal locality would suggest *C. philhershkovitziana*, but plant clearly corresponds to *C. discolor*: the adaxial leaf surface is deep green with "embossed" major veins, and the abaxial surface is purplish. However, the petals are red at the base, characteristic of *C. grandiflora* and *C. philhershkovitziana* in this zone, rather than white as in *C. discolor* elsewhere. Note also the mid-winter observation dates.

[44] https://inaturalist.mma.gob.cl/observations/133963176. September is rather "early" for such a southerly locality. In the Coquimbo and even Atacama Region, with sufficient winter precipitation, herbaceous perennials commonly flower in September, and then not until October/November in inland Maule to Biobío Regions. Likewise, flowering in the above localities usually has terminated by January.

[45] https://inaturalist.mma.gob.cl/observations/196396516. Flowering of coastal *C. mucronulata* near Concepción probably extends beyond January, since iNaturalist observers, having already photographed the plants at peak flowering, probably shift their focus to other plants and localities

(irrigated) cultivated plants in gardens in Choapa Province (Coquimbo Region) flowering in mid-September when natural coastal populations at that latitude were just beginning to leaf out.

In summary, strictly vernal flowering observed in at least some *C.* sect. *Cistanthe* species may be an artifact of the precipitation pattern in Mediterranean-type climates. Flowering may occur repeatedly when hydration is maintained, as in cultivation. But there is not yet evidence that repeated flowering occurs naturally in *C. philhershkovitziana* within a single growing season. Hershkovitz (2018a) hypothesized that caudical stem scars on flowering plants observed in mid-spring 2018 in Choapa Province (Coquimbo Region) were remnants of flowering stems that developed and later aborted consequent to an early but modest winter rain. The late spring flowers were interpreted as consequent to secondary caudex reactivation, in turn consequent to more substantial later precipitation. Hershkovitz (2018a) noted that the size and inflorescence development of plants having and lacking such stem scars were the same.

The present investigation suggests that the stem scars may have indeed represented prior years' growth. But this population requires reexamination. Perhaps more significant are the midsummer observations at Gota de Leche. As noted, some small flowering individuals most likely germinated following late spring precipitation. More importantly, this late rain did not appear to have provoked new metamer development by the live caudices of plants with senescent metamers.

However, in the Cartagena plant, secondary inflorescence primordia indeed were present in plants that had been grazed. But these metamers all aborted following transplantation to a container. New rosettes emerged from axils of subtending nodes. These did not develop inflorescence primordia until latest winter. Since hydration was maintained, these observations indicate that inflorescence development per se is not mediated by hydration.

iv. Floral aestivation, morphology, and breeding system. To my knowledge, the only published experimental breeding data available for *C.* sect. *Cistanthe* indicated high but not absolute self-compatibility for *C. discolor* at a single locality (Arroyo & Uslar, 1993[46]). During the present study, I was able to conduct a simple test of self-compatibility in two cultivated individuals of *C. grandiflora* of likely CLZ provenance.[47] Both self- and cross-pollinated flowers developed capsules. Fertility of both seemed about equal, though I did not quantify this, nor intend to at this point.

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[46] The authors reported ca. 70% fertility of self- versus cross-pollinated individuals in *Calandrinia grandiflora* Lindl. [≡ *Cistanthe grandiflora* (Lindl.) Schltdl.]. But at that time, all Chilean species of *C.* sect. *Cistanthe* were lumped in *C. grandiflora* (see below). *Cistanthe discolor* is common in the study area; I doubt that *C. grandiflora* s. str. occurs there.

[47] For the test, I collected two flowering metamer branches from each of two individuals cultivated out of doors in containers in El Quisco. The branches were transferred indoors and placed in water in separate containers. The containers were placed in separate rooms to avoid cross-pollination. Studied flowers in this species opened in the morning and remained open all day. Nectar was conspicuous when the flowers opened, but it is resorbed within a few hours. I self-pollinated newly opened flowers on several successive days. I also cross-pollinated the individuals, on *different* days, using branches collected from other individuals. In contrast to *C. philhershkovitziana*, the pollinated flowers closed only slightly if at all during the evening, but were fully open the following day. The anthers still were spread mid-morning on the second day. But by afternoon, the petals began to senesce and the stamens began to close about the stigma. Petal senescence in this species differs from that in *C. philhershkovitziana*: rather than "de-opening," they begin to deliquesce from the apex basipetally, rolling inwards. By the evening of the second day, all of the stamens were agglomerated around the style, and the petals had deliquesced/inrolled to just above sporophyll level. Rather than a twisted cap, the petals and stamens form a sort of dense plug above the ovary. By the third morning, the sepals were closed, but unlike *C. philhershkovitziana*, only loosely. Also unlike *C. philhershkovitziana*, the sepals of pollinated flowers withered and shrunk somewhat. But capsules developed in both self- and cross-pollinated flowers.

The style and stigma heights are ± equal in *C. discolor*, *C. grandiflora*, and *C. paniculata*. They are equal in most photos I have seen of *C. mucronulata*, but notably exserted in one. The style height is exserted ca. 2X the stamen height in *C. cabrerae* (incl. *C. subspeciosa*) and *C. laxiflora*. Style exsertion seems to be variable in *C. crassifolia*. The floral organs of *C. grandiflora* are perhaps 20% longer than in *C. philhershkovitziana*, but their length proportions are ± the same. Thus, the petals are ca. 2.5X as long as the stamens and gynoecium. They have ca. the same number of stamens, and the sepals and stamens orient similarly in open flowers.

Although there are no experimental data, self-compatibility seems to be common among *C.* sections *Rosulatae* and *Thyrsoideae*, and possibly the rule in the annual species. Both sections include species with very small flowers, ca. 5 mm broad. Some annual species of *C.* sect. *Rosulatae* have exserted styles: *C. arenaria* (Cham.) Carolin ex Hershk. *C. fenzlii* (Barnéoud) Carolin ex Hershk., *C. litoralis* (Phil.) Carolin ex Hershk., *C. longiscapa* (Barnéoud) Carolin ex Hershk., and *C. trigona* (Colla ex Bertero) Carolin ex Hershk. In *C. litoralis*, as the day progresses, the style bends markedly and makes contact with the stamens. Styles are not exserted in the alpine perennial species. Styles are not exserted in the annual species of *C.* sect. *Thyrsoideae*, but they are exserted 3–4X the stamen height in the insular pachycaulescent *C. guadalupensis* (Dudley) Carolin ex Hershk.

v. Phenology of senescence of above-ground organs. As noted, in *C. philhershkovitziana*, after flowering, the metamer senesces, viz. the inflorescence senesces, followed by senescence of the subtending rosette. Under natural conditions, this often is accompanied or followed by senescence of the subtending succulent stem back to its origin on the main caudex. Obviously not always, or caudex branches would not exist. But, as noted, in the large cultivated Cartagena specimen, these branches persisted and generated new rosettes at several nodes.

I have not studied "comparative senescence" empirically in detail in other species. And little can be gleaned from the descriptive literature, iNaturalist or specimen images. This is not surprising: both professional and lay observers focus on the "living," not the "dying." But a very few observations lead me to conclude tentatively that senescence in other species of *C.* sect. *Cistanthe* is *essentially* the same as in *C. philhershkovitziana*.

In my experience, in drier localities, the above-ground organs of subrosettiform hemicryptophytic forms of *C. grandiflora*, *C. discolor*, and *C. mucronulata* "disappear" from inland landscape with the onset of summer drought. The caudices may be visible above the soil, but they tend to be covered over by other vegetation. This means that the leaves and inflorescences in the species also behave as metamers and senesce as a unit to the level of the caudex, much as in *C. philhershkovitziana*. But, in contrast to *C. philhershkovitziana*, in more humid localities, basal branches may perennate.

In the more chamaephytic to phanerophytic *C. laxiflora*, senescence of the lengthy stems following flowering seems to be sensitive to humidity. *Cistanthe laxiflora* ranges more or less continuously at coastal sites in between Algarrobo[48] (ca. 33.3S; Valparaiso Region) and Limarí Province[49] (ca. 31.1S; Coquimbo Region). I have observed that in winter in drought years in the Coquimbo Region, the long stems are gone and only the crown of the caudex and perhaps the bases of the largest branches remain. Meanwhile,

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[48] According to Eric Rojas Abarca (El Quisco, Chile), this is the southern limit of the natural range (written comm.., 1 Nov. 2023).

[49] The northernmost record I can confirm in this continuous range is documented at https://inaturalist.mma.gob.cl/observations/142283359.

iNaturalist documents overwintering of the long stems in Algarrobo.[50] In cultivation, the plants may be essentially "evergreen:" senescing metamers are replaced by new metamers, such that the plant always bears green leaves.

For coastal chamaephytic *C. mucronulata* near Concepción, the only photo of autumn plants available shows large stems scars near the caudex crown.[51] Interestingly, however, despite the autumn date, leaves of some rosettes with dead and disintegrated inflorescence culms remain green, and some new rosettes appear to be developing. This form is thus more "evergreen," and possibly it can be maintained as such in cultivation. A single available image of "dormant" *C. crassifolia* (Fig. 6) shows that the metamers senesced to the persistent "trunk" branches. Evidence from other species suggests the possibility that this dormancy is conditional.

In summary, the senescence of above-ground organs is similar in species of *C.* sect. *Cistanthe* in that metamers comprising rosette leaves and the inflorescence die back to at least the subtending node, and that this process is constitutive and not conditional. At the level of the whole plants, differences among species are incidental to their life form morphology and also ecological circumstances. Thus, the degree of senescence of caudical branches varies both among and within species. The result is that, under natural conditions, caudical branches in some species might live longer and attain greater girth and/or length, such that the life form among species ranges from cryptophytic to (sub)rosettiform hemicryptophytic to chamaephytic to phanerophytic. But species manifest different life forms over the course of their developmental history and under different natural and, even more so, artificial ecological circumstances. Likewise, while senescence tends to precede seasonal dormancy under (at least some of their) natural conditions, dormancy itself may be obviated under other natural or artificial conditions.

vi. Caudex longevity. As noted, nonstatistical examination of caudices of *C. philhershkovitziana* growing in most southern and perennially humid CLZ populations in the 2023–2024 suggests that most of them germinated either in the current or prior year. Based on bud scars, few appeared to be older than two years. Average caudex age in populations growing in inland localities in northern Chile probably is less, but this requires empirical verification. In populations of other species of *Cistanthe*, the caudices are on average probably decidedly older. This must be the case for the pachycaul *C. crassifolia*. But caudex age estimation requires more precise techniques.

Caudex age demographics among the species not unexpectedly seem to be related with the size of above ground organs. In most populations of *C. philhershkovitziana* in the southern CLZ, the largest leaves are on the order of 5 cm x 1 cm (5 cm^2). Leaves of other species are much larger, e.g., 10–20 cm x 5–10 cm (50–200 cm2), and the number of leaves per plant often is much greater. The result is 1–2 orders of magnitude greater photosynthetic capacity. This allows for a much larger caudex and roots that penetrate much deeper in the soil, hence plants that survive many more years, even in hyperarid conditions.

A notable exception to the "rule" of small *C. philhershkovitziana* plant size in the southern CLZ is the exceptionally large plant size at the Cartagena locality. Here, I supposed that the size owes to high soil fertility consequent to the local dominance of an invasive shrubby lupine. The overall conditions allow plant size here to "phenocopy" the normal larger size of other species, although they still are much smaller. Nonetheless, the plants here appear to survive much longer than in populations a few km distant.

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[50] https://www.inaturalist.org/observations/229617041

[51] https://inaturalist.mma.gob.cl/observations/199157475

Meanwhile, plants in some populations of the Coquimbo and Atacama Regions appear to be on average twice the size of those in the southern CLZ.

vii. Demographic variability. The demographic variability of other *C.* sect. *Cistanthe* species shares some similarities with that for *C. philhershkovitziana* when scaled for "size" and its consequences. The most notable similarity is that the species emerge and flower mainly in response to hydration, and the phenology varies geographically accordingly. But there are differences also. However, comparison of demographic variability is constrained by range differences. The only two species with significant and extensive range overlap are *C. grandiflora* and *C. laxiflora*. I ignore here *C. aegitalis*, because its range is very small and, furthermore, unlike *C. grandiflora* and *C. laxiflora*, it does not seem to occur in "intimate" physical proximity to *C. philhershkovitziana*.

The range of *C. grandiflora* includes that of *C. philhershkovitziana*, and individuals of the former often occur within 1–100 m of the latter. The southern limit of both species is similar, but, as noted, *C. grandiflora* extends to ca. 23S and inland to the precordillera. And even within the shared range perimeter, *C. grandiflora* is more "common" (occurs, e.g., in far more 100 ha quadrats), and it occurs more frequently on anthropogenically disturbed sites. And although the plants can flower during their first year, I suspect that on average, flowering plants in the wild are > 2 years old. This seems to be consequent to the much larger size of *C. grandiflora*. But as with *C. philhershkovitziana*, emergence of *C. grandiflora* is consequent to hydration, and caudices may remain dormant in drought conditions. The generally longer flowering period of *C. grandiflora* also is consequent to size, viz. the deeper roots of the larger caudex extend the hydration period.

Because of its larger size and generally longer flowering period, individuals of *C. grandiflora* produce more flowers, hence presumably more seeds per season than individuals of *C. philhershkovitziana*. At the same time, the larger size presumably restricts the density of individuals. Still, the seed bank per unit area may be much larger. But I have no data regarding seed bank ecology of this species. Although *C. grandiflora* presumably germinates in response to hydration, I have no data regarding successive waves of germination during a single season.

The range of *C. laxiflora* is included within that of *C. philhershkovitziana*, and individuals may occur within a few meters (see, e.g., Hershkovitz, 2018a). In contrast to *C. grandiflora*, it is strictly coastal and does not even extend as far inland as *C. philhershkovitziana*. It can dominate coastal cliffs conspicuously over hundreds of meters. But the density of *individuals* in these populations is not clear. As noted, individual branches on these cliffs may extend 2 m, and, under natural conditions, the flowering period extends throughout the summer. This, along with the larger flowers and fruits of this species, means that the seed bank can be greater in this species than in *C. philhershkovitziana*. But I have no hard data or any other information on phenological variability in this species at the demographic scale.

viii. Summary. Hershkovitz (2018a, 2019a) described *C. philhershkovitziana* as annual and the remaining species of *C.* sect. *Cistanthe* as perennial or, in one case (*C. grandiflora*), facultatively annual. The revised view here is that species of *C.* sect. *Cistanthe* are mostly if not all facultatively annual, but species and populations thereof vary with respect to the degree to which they manifest annual behavior. Otherwise they vary in their perennial longevity, their size, and their life form, ranging from cryptophytes to phanerophytes. Yet, the characteristics and behavior typical of any species under natural conditions can be to one or another degree phenocopied in other species under artificial conditions. The life history under natural conditions seems to correlate with plant size. The smaller *C. philhershkovitziana* is shorter-lived in nature, and individuals often behave as annuals, even producing locally dense populations with brief flowering periods. The larger species behave more as "typical" perennials.

While life history differs among the species, a commonality is that phenology is influenced more by hydration than by T° or light. This was evident especially because of the phenological consequences of precipitation events in late spring 2023 and late autumn 2024. These provided exceptions to the reductionist characterization of central and northern Chilean climate as "winter rain, summer drought." The latter pattern, however "normal," correlates with T° and light minima/maxima, rendering difficult the dissection of the independent effects of each. But these precipitation anomalies caused *C. philhershkovitziana* in the southern CLZ to manifest "spring" growth behavior in early summer and early winter. And it seemed to alter the senescence and reemergence behavior of other *C.* sect. *Cistanthe* species.

However, climate anomalies aside, the phenological and life history sensitivity of *C.* sect. *Cistanthe* species to hydration manifests in other ways, such as in the natural variability of *C. mucronulata*. In arid inland localities, the species behaves as a vernal subrosettiform hemicryptophyte whose leafy and flowering phases are brief. In humid costal sites, the species behaves as a chamaephyte whose leafy and flowering phases extend throughout the summer under natural conditions, much like *C. laxiflora*. In cultivation (viz. with irrigation), the leafy phase extended throughout the summer in the induced chamaephytic form of the normally cryptophytic *C. philhershkovitziana*. But the flowering period the following spring was determinate, and the metamers simultaneously senesced, even with adequate irrigation. Indeterminate flowering can be can be induced other subrosettiform hemicryptophyte species. *Cistanthe laxiflora* in cultivation behaves more or less as an evergreen, producing flowers nearly year round. Other species can be induced at least to be "evergreen" in cultivation.

3. Phylogenesis of life history/form of *C. philhershkovitziana* viewed from a broader phylogenetic context

***i. Phylogenesis of life history/form variation in* Cistanthe.** To review, this work described the empirical behavior of a short-lived facultatively annual species, *Cistanthe philhershkovitziana*. These plants can and generally do flower determinately (see below) within 2–3 months following seed germination, but often do not survive to repeat the reproductive cycle during a second year, and evidently only rarely survive more than three years. The species pertains to a clade of ca. 11 spp., *C.* sect. *Cistanthe*, whose plants otherwise are larger and generally longer-lived but, nevertheless, also flower during their first year. This clade pertains to a broader clade, *Cistanthe*, that otherwise includes a clade of ca. 28 spp. of obligate annuals[52] and perennials in which perenniality evolved 2–3 times.

Looking more broadly, *Cistanthe* pertains to a clade of ca. 300 spp., Montiaceae, which otherwise also includes both obligate and facultative annuals and perennials, and in which transitions between these occurred in both directions. Moreover, the phylogeny evidences 3–5 instances of shoot- rather than root-derived perennation (rhizomes, etc.). Thus, *C. philhershkovitziana* pertains to a diversification characterized by, among other things, relatively high frequency of life history transitions (Ogburn & Edwards, 2015; cf. Hershkovitz, 2018c, 2019a). The species itself is characterized not by a *categorical* life history transition, but nonetheless evidently a shorter life span than its closest relatives, along with smaller size and higher frequency of first-year mortality.

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[52] The few species I have cultivated all die following reproduction, whether hydration was maintained or the plants were rehydrated following shoot senescence. This does not mean that there are no "exotic" means by which the plants might be reanimated.

Phylogenetic evidence for the evolution of the life history/form of *C.* sect. *Cistanthe* is tantalizing but not definitively informative (see discussion in Hershkovitz, 2019a). The question, specifically, is which of the forms, ranging from small, short-lived, and cryptophytic to large, long-lived, and phanerophytic, is ancestral. The taxonomically most common and geographically and ecologically most widespread form is the subrosettiform hemicryptophyte form. But one cannot presume that "common is primitive." Existing ribosomal and chloroplast DNA "species barcode" data are of no help. They manifest essentially no phylogenetic structure or even species-specificity (Hershkovitz, 2006).[53]

Outgroup comparison is somewhat confounding, because it is not clear whether the ancestor of *Cistanthe* Spach or even its tribe, Cistantheae (Hershkovitz, 2019a), was annual or perennial.[54] *Cistanthe* sect. *Cistanthe* is sister to a clade comprising the clades *C.* sect. *Thyrsoideae* and *C.* sect. *Rosulatae* (Hershkovitz, 2019a). Both include nominally perennial and obligate annual species. But the DNA markers also failed to resolve species phylogeny within these sections. Based on morphology and geography, the ancestral state in the former section seems to be annual.[55] Also based on morphology, Hershkovitz (2022b) concluded that it is annual also in the latter section, but this is less certain.[56]

However, regardless of the ancestral life history/form of *Cistanthe*, a subrosettiform hemicryptophyte ancestry of *C.* sect. *Cistanthe* might be inferred by deduction. The only other decidedly chamaephytic/phanerophytic species among Montiaceae is the pachycaul *Cistanthe guadalupensis* (Dudley) Carolin ex Hershk., endemic to Guadalupe Is., Mexico. This form is derived within *C.* sect. *Thyrsoideae* (Hershkovitz, 2019a). The chamaephytic/phanerophytic species (*C. aegitalis* and *C. crassifolia*) or forms (e.g., of *C. mucronulata* and *C. paniculata*) of *C.* sect. *Cistanthe* seem to be biogeographically derived. With one exception that I suspect is a hybrid, the first two occur in fog desert habitats, whereas the ancestral habitat of Montiaceae generally and *Cistanthe* in particular most likely was more arid, warm, and inland (Hershkovitz, 2019a). *Cistanthe paniculata* and *C. mucronulata* occur not only in cooler and more humid habitats, but also in, respectively, the northern and southern extremes of the geographic distribution of the genus.

Other cryptophytic forms occur among Montiaceae, but most are phylogenetically remote from *Cistanthe* and/or otherwise likewise derived. Possible exceptions include at least the littoral zone forms of *Cistanthe arenaria* (Cham.) Carolin ex Hershk. and *C. fenzlii* (Barnéoud) Carolin ex Hershk. (*C.* sect. *Rosulatae*) of southern central Chile. These superficially bear life history/form resemblance to *C. philhershkovitziana*: thicker taproots and possible perenniality. But the phylogenetic and phylogeographic evidence suggests that these forms are derived. These two species occur in cool/humid habitats at the southern limit of the generic distribution, whereas other *C.* sect. *Rosulatae*, along with the remainder of the genus, concentrate in arid north central Chile (Hershkovitz, 2022b). Here, the annual species have thinner taproots.

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[53] The misidentification of several samples here is irrelevant – the corrected identifications do not change this conclusion.

[54] See also Ogburn & Edwards (2015), who derived almost diametrically contrary reconstructions of Montiaceae life history determined using two different evolutionary models over their particular phylogenetic tree. Their parsimony reconstruction indicated a perennial ancestor for *Cistanthe* and all polymorphic genera, but their phylogenetic sampling was incomplete and their Montiaceae tree now is superseded by Hancock et al. (2018).

[55] The only perennial species

[56] Hershkovitz (2022b) cited the annual species with foliaceous (and succulent) sepals and hairy seeds, both traits shared with *C.* sect. *Cistanthe* and *C.* sect. *Thyrsoideae* species. But Hershkovitz (2022b) overlooked hairy seeds in some of the alpine perennial species formerly classified in *Calandrinia* sect. *Andinae* Reiche (Kelley, 1973). However, the alpine habitat itself seems to represent a derived condition in *Cistanthe*. To be safe, I leave as unresolved the ancestral life form of *C.* sect. *Rosulatae*.

In summary, it is most parsimonious at this point to consider the relatively small size, relatively short life span, cryptophytic life form, and littoral habitat of *C. philhershkovitziana* as derived (ultimately) from a larger and longer-lived subrosettiform hemicryptophyte form of *C.* sect. *Cistanthe* that extended further inland. And it is most parsimonious to consider likewise derived the relatively large size and longer life span of the chamaephytic/phanerophytic species/forms. Thus, these contrary forms seem to represent contrary evolutionary trajectories from a common ancestor. Yet, these contrary forms share coincident littoral habitat.

ii. Phylogenesis of life history/form variation in Montiaceae. Expanding the view to include other Cistantheae and Montiaceae helps explain the ambiguity of life history/form phylogenesis in *Cistanthe*, but also provides clues as to the explanation for these transitions. Notably, this expanded phylogenetic view does not clarify the ancestral form of *Cistanthe*. Cistantheae also includes Calyptridinae, which includes *Lenzia* Phil. and its sister, a clade comprising *Calyptridium* Nutt., *Philippiamra* Phil. and *Thingia* Hershk. The latter clade is ancestrally annual. The only two nominally perennial species are derived within *Calyptridium* (Hershkovitz, 2019a), and these reportedly are facultatively annual (Hinton, 1975). *Lenzia* is an acaulescent rosettiform perennial, but it lacks a well-developed caudex. I have interpreted its perenniality to be consequent to rhizomes viz. consequent to clonal and not, as in the case of perennial *Cistanthe* species, caudex longevity. This suggests that *Lenzia* is derived from an annual, rendering the ancestral condition of Calyptridinae as annual.

Cistantheae also includes *Montiopsis*, but the relation of this genus to *Cistanthe* and Calyptridinae is unresolved (Hershkovitz, 2019a). The genus includes caudicose hemicryptophytic to chamaephytic perennials and an annual clade, which is derived. At least one nominally perennial species, *Montiopsis umbellata* (Ruiz & Pav.) D.I.Ford, is a facultative annual.[57] I have no information on the condition of the other perennial species.

In the Montiaceae phylogeny of Hancock et al. (2018), Cistantheae is flanked by Phemerantheae, which defines the basal split of the family, and then, moving successively up the ladder, *Parakeelya* Hershk., *Calandrinia* Kunth, and Hectorelleae plus the North American clade, which includes *Lewisiopsis* Govaerts, *Lewisia* Pursh, *Claytonia* L., and *Montia* L.. Since *Lewisiopsis* was not included in the analyses of the relations of Hectorelleae (Applequist et al., 2006; Wagstaff & Hennion, 2007; cf. Hancock et al., 2018), the precise position of the latter remains unresolved, though this is not important for the present purposes.

Phemerantheae includes *Phemeranthus* Raf. and, provisionally, *Schreiteria* Carolin (Hershkovitz, 2019a). Species of the former are caudicose hemicryptophytic to chamaephytic perennials. At least one species is reportedly facultatively annual (Price, 2012). I have no information on the condition of the others. *Schreiteria*, possibly extinct, is a caudicose perennial. Likewise, its capacity for first-year flowering is unknown.

Parakeelya is ancestrally annual, and its caudicose perennial species are derived (Hancock et al., 2018). *Calandrinia* includes annuals and both caudicose and rhizomatous perennials, but its ancestral

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[57] This species has a long history of cultivation in temperate northern hemisphere gardens. Numerous commercial horticultural websites (not shown here; often under the generic name *Calandrinia*) indicate that it can be grown as an annual.

condition is not established (Hershkovitz, 2019a). The caudicose *Calandrinia acaulis* Kunth reportedly can be grown as an annual.[58]

The clade comprising Hectorelleae plus the North American clade appears to be ancestrally perennial and caudicose. This characterizes Hectorelleae, *Lewisiopsis*, and *Lewisia*, and these are the outgroups of the sister genera *Claytonia* and *Montia.* Hectorellaceae reportedly are very slow growing, so I presume that they cannot flower during their first year. An informal document reports flowering 2–3 years post-germination in *Lewisiopsis*.[59] First flowering of *Lewisia rediviva* Pursh reportedly is two or more years post-germination (DeSanto, 1993). In cultivation, first flowering of *L. cotyledon* (S.Wats.) B.L.Rob. and *L. pygmaea* (A.Gray) B.L.Rob. is reported as, respectively 14 and 12 months (Cristescu et al., 2010). For practical purposes, this could not be "first-year" in their natural circumstances. These data are significant, because they suggest that three successively diverging lineages of Montiaceae are not only perennial, they are *not* facultatively annual. Meanwhile, all of the earlier-diverging lineages and the succeeding lineage include both annual and perennial species, and many of the perennials are facultative annuals.

Claytonia includes annuals and both clonal and caudicose perennials. Phylogenetic context suggests that the last condition is ancestral. I have no information on whether these species can flower during their first year. The relations of the annual, perennial, and clonal lineages are unresolved (O'Quinn et al., 2005). It is clear, thus, that the annual and clonal lineages are not phylogenetically nested *within* the caudicose lineage. *Montia* includes annuals, two of which produced adventitious roots at their nodes, and clonal perennials, but no caudicose perennials (see Les, 2017). The phylogeny of *Montia* (O'Quinn et al., 2005) renders somewhat ambiguous the ancestral state. It favors slightly a clonal perennial ancestor. But that is problematic, because, even if so, the ancestor of that clonal perennial ancestor itself may have been an annual.

iii. Phylogenesis of life history/form variation in Portulacineae. Ambiguity of ancestral life history/form extends to the clade comprising the other Portulacineae lineages. These include Basellaceae (somewhat herbaceous phanerophytes), Didiereaceae (woody phanerophytes), Halophytaceae (monotypic, annual herb), and the ACPT clade, comprising Anacampserotaceae, Cactaceae, Portulacaceae, and Talinaceae.[60] The last is sister to an unresolved clade comprising the first three (Hershkovitz, 2021c). Talinaceae includes chamaephytic to weakly phanerophytic herbs and woody phanerophytes. At least two species of the chamaephyte/phanerophytic herbs are facultative annuals.[61] I have no information on the others. Anacampserotaceae are succulent cryptophytic to hemicryptophytic to chamaephytic herbs, except for the shrubby phanerophytic *Grahamia bracteata* Gillies ex Hook & Arn. I find no reference to flowering time post-germination. I presume that *G. bracteata* does not flower during the first-year post-germination.

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[58] https://propagate.one/how-to-propagate-calandrinia-acaulis/

[59] https://www.google.com/url?sa=t&source=web&rct=j&opi=89978449&url=https://courses.washington.edu/esrm412/protocols/2018/CITW2.pdf&ved=2ahUKEwitmqPO4P2JAxVKGbkGHWiZLxo4FBAWegQIEhAB&usg=AOvVaw33snl8IjX9aPycF7PlyEQR; the original institutional link is broken.

[60] Another genus, *Amphipetalum* Bacigalupo, is Portulacineae incertae sedis. No molecular data is available. Carolin (1993) considers it most closely related to *Talinum*, and I am inclined to agree. The monotype is a perennial herb similar to *Talinum* spp., hence provides no exception to my summary here. Whether it can flower during its first year is not reported.

[61] *Talinum paniculatum* (Jacq.) Gaertn. and *T. fruticosum* (L.) Juss. are low subshrubs. The former is cultivated ornamentally as "Jewels of Opar," and commercial horticultural sites indicate that it can be grown as an annual. POWO erroneously lists *T. fruticosum* as an annual. It is a pantropical perennial weed, but indeed it flowers rapidly from seed.

Cultivation information for the herbaceous species leads me to believe that they also do not, but some species are advertised as growing faster than others. "Basal" Cactaceae are phanerophytic shrubs and trees. I presume that flowering occurs > 1 year post-germination. But Portulacaceae includes both annual and perennial herbs. Ocampo & Mair-Sánchez (2018 and earlier works) did not reconstruct life form transitions on their Portulacaceae phylogeny. But, based on WCVP and POWO life form information, their tree suggests an ancestor that is annual or perhaps facultatively annual. The first tree split defines a small clade of species that POWO classified variously as annual, suffrutescent, or, interestingly…annual *or* suffrutescent. The last, if accurate, is equivalent to facultatively annual.

iv. Phylogenesis of life history/form variation in "Portullugo." Portulacineae is sister to Molluginaceae; these together have been termed "Portullugo" (Edwards & Ogburn, 2012).[62] Molluginaceae appear to be even more labile for life history than Portulacineae. Thulin et al. (2016) recognized 11 smallish monophyletic genera that, together, sum to ca. 90 species. Two of the genera include only annual species, another two only perennial species, and the remaining seven *both* annual and perennial species. Thulin et al. (2016) did not comment on the first-year flowering capacity of the perennial species. I did not attempt to reconstruct the life history transitions along their published phylogeny. But just eyeballing the tree, I would expect that the number of transitions to be no less than ten…in a clade of just 90 extant species.

. ***v. Summary.*** This work is concerned with the evolution of life form/history of *Cistanthe philhershkovitziana*. But the above discussion demonstrates that this presumably very recently evolved species**[63]** is successively nested in clades that are "hypervariable" for life form/history. The deepest node of this diversification has been dated to ca. 85 mybp (Yao et al., 2019; cf. Hershkovitz, 2024). Thus, as an "underlying trait," the variability in more recently diverged clades seems to have been itself conserved throughout this history, possibly lost in less variable lineages, e.g., among Cactaceae.

But another important observation is that many nominally herbaceous to suffrutescent perennial Portulacineae taxa can and perhaps normally do flower in their first season following germination. In other words, they are facultative annuals. But in many cases among Portulacineae and in general among Molluginaceae, this capacity is neither reported nor refuted. I suspect that it is more common than appreciated, and that it is highly significant towards understanding of life history/form evolution, as elaborated below.

4. General conclusions

This study demonstrated three principal phenomena:

(a) that *C. philhershkovitziana* is not annual, but facultatively annual, and that most or all other nominally perennial species of *C.* sect. *Cistanthe* also are facultatively annual. Thus, on the basis of life history alone, the taxonomic distinction of *C. philhershkovitziana* is blurred, if not obliterated.

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[62] Hershkovitz (2024) commented briefly on the morphological synapomorphy that distinguished Portulacineae.

[63] Yao et al. (2019) effectively dated Cistantheae divergence at ca. 50 mybp. This estimate is nearly twice as old as previous estimates (Hershkovitz, 2019a; see also Hershkovitz, 2024). But Hershkovitz (2006; note corrections in Hershkovitz, 2018a and described above) demonstrated that "species barcode" genetic divergence among *Cistanthe* sect. *Cistanthe* species is very low, and that genotypes of *C. philhershkovitziana* are identical to those of other species. The fossil-calibrated age estimate would be so low as to be "undefined."

(b) that the facultatively annual condition is common among nominally perennial herbaceous species of the successive outgroups: *Cistanthe*, Cistantheae, Montiaceae, Portulacineae, and probably "Portullugo." This demonstrates the *ontological inadequacy* of the categorical annual/perennial distinction for descriptive and, more so, analytical purposes.

(c) that the individual life history behavior of *C. philhershkovitziana* varies within and among populations and interannually, and that this behavior is *idiosyncratic* and not consequent to any single environmental parameter.

(d) that the ontological inadequacy of life history categories extends also to life form and phenological categories. Life form behavior of nominally perennial herbaceous plants varies constitutively with development and among individuals, and, again *idiosyncratically*. Likewise flowering phenology and parity vary.

The observations above are not novel in the sense that similar and even more "extreme" observations have not been reported in studies of other species (e.g., Gremer et al., 2019 ["2020"]).[64] Among other Chilean Floristic Region lineages, Dillon (2023) described 11 of 92 species of *Nolana* L. (Solanaceae) as, effectively, facultatively annual.[65] These species were interspersed phylogenetically throughout the genus. Somewhat taxonomically independently, an even larger proportion of species were described effectively as polymorphic for life form, e.g., herbs or subshrubs. In the course of the present study, I had numerous encounters with *N. paradoxa* Lindl., which sometimes grows alongside *C. philhershkovitziana*, although, being a halophyte, it prefers smellier waste places. I would describe the life history of *N. paradoxa* as "deeply disturbed." This is partially because flowering in this species is indeterminate. Within a population, one can find individuals ranging from seedlings to plants 1 m in diameter, in each condition variously proliferating or senescing and variously vegetative or reproductive. In this and other *Nolana* species, life history/form may be mitigated by edaphic salinity, which varies at a small temporal scale.

Friedman (2020), among others, emphasized that, classification categories notwithstanding, life history and phenological variation is not discrete. The significance of the present observations is how they contribute to empirical and experimental evidence that life history/form and phenological traits: **(a)** are more developmental (behavioral) than physical; **(b)** manifest de facto indeterminately and *relative* to independent *events*, viz. reproductive events relative to plant germination and death; and **(c)** are *epiphenomenological*, viz. consequent to multiple and interacting independent constitutive and environmental processes (Hjertaas, 2023; Rehman et al., 2023).

The present observations underscore this evidence by demonstrating that the facultative annual condition is more common than evidently appreciated (see below), probably not only among "Portullugo," but among nominally herbaceous perennials throughout angiosperms. At the same time, the present observations demonstrate that facultative annuals are distinct from both obligate annuals and perennials that are not facultative annuals, and that facultatively annual species phylogenetically intersperse among species that are obligate annuals or perennials. The same appears to be true in other lineages, e.g., *Nolana* (Dillon, 2023; see above).

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[64] Gremer et al. (2019) reported that *Streptanthus tortuosus* Kellogg (Brassicaceae) behaves variously as a vernal annual, winter annual, biennial, or (effectively, facultatively annual) perennial. WCVP and POWO classifies it only as biennial or perennial, viz. not annual or even facultatively annual.

[65] Dillon sometimes used the term "facultative(ly) perennial."

Despite repeated descriptions of nominally perennial species as, effectively, facultatively annual, especially in the horticultural realm for > 200 years (viz. “can be *cultivated* as an annual”), the distinctness and phylogenetic ubiquity of the condition has not been appreciated. This possibly reflects a conceptual bias to emphasize the perennial state (or “essence”) even in species where first-year flowering is directly *observed*. But more broadly in taxonomic investigation, the failure to recognize the condition is consequent to *lack* of observation. Species taxonomy is based primarily on the morphology of plants that are collected in their natural state and not cultivated. They are “snapshots.” And, in the case of herbaceous species, there may well be a bias, conscious or subconscious, to collect individuals that manifest their perenniality. The result is that taxonomic references and databases *systematically* exclude diagnosis of the facultative annual condition. The life history generally is recorded simply as perennial. Exceptions, if recorded at all, thus appear as anomalies rather than indicative of an ontologically distinct condition.

Thus, the present observations bear on phenomenological interpretation of life history/form and phenology in the biological and environmental sciences. This is an active area of current and multidisciplinary research (e.g., Friedman, 2020; Hjertaas et al., 2023; Rehman et al., 2023). In the macroevolutionary ecological realm, a currently popular mainstream approach contrasts the geographic distribution of species classified as *either* annual *or* perennial (the discrete, independent variable) with associated climate variables estimated globally at some km^2 scale (the continuous, dependent variable; e.g., Ogburn & Edwards, 2015 for Montiaceae; Boyko et al., 2023 and Poppenwimer et al., 2023 for angiosperms generally).**[66]** The contrasts are used to define the “climate niche” of species, lineages, or the phenotypes themselves. With “phylogenetic correction,” the approach aims to understand the causes of life history evolutionary transitions and/or distributions as a function of variables that supposedly “drive” those transitions. The approach often involves “data mining,” viz. third-party database data, and many analyses apply the parameters and criteria of outsourced software. Often one or more of data classes derives from disciplines outside of the researchers’ area of critical expertise.**[67]** In this case, the analyses outsource the species taxonomy and the life history classification data. Commonly also the phylogenetic trees are outsourced (e.g., Boyko et al., 2023; Poppenwimer et al., 2023).

Presumably, macroevolutionary and ecological interpretation of life history/form and phenological phenomenology is contingent upon diagnosis of the conditions as accurately as the ontology permits. The present observations demonstrate the inadequacy/inaccuracy of diagnoses as *either* annual *or* perennial, especially because the facultative annual condition is not only “intermediate,” but because this intermediacy tends naturally to be distributed near or at the phylogenetic nodes where the dependent variable transitions are inferred. Adding the facultatively annual condition to the reductionist classification partially mitigates misinterpretation, but it does not solve the underlying problem of state heterogeneity and plasticity. The present observations demonstrate that most species of *C.* sect. *Cistanthe* are facultatively annual. They might be classified accordingly. But clearly they manifest *different* life histories, ranging from more annual-like to more perennial-like, with associated (but also plastic) differences in life form, and aside from this, phenological plasticity. *Nolana* presents the same or possibly even more extreme problem.

Both Boyko et al. (2023) and Poppenwimer et al. (2023) outsourced species and life history data to WCVP. Ogburn & Edwards (2015) used taxonomic references for Montiaceae, but the result is essentially

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[66] Similar studies evaluate a life form trait rather than life history, viz. herbaceous versus woody, e.g., Zanne et al. (2013 [“2014”]) and Beaulieu et al. (2013).

[67] The approach can be described as an *ensemble reductionistic* approach to macroevolutionary ecology, because reduced data sets from many phenomenological dimensions, each stripped of its “variance” or error, are reduced further into a unified model. It also has been called “big data” research. This can be contrasted with *simple* reductionism, involving as few as two more or less objectively defined variables whose values and variances are determined directly by the researcher.

the same, especially given both the taxonomic ambiguities (Hershkovitz, 2019a, 2022b) and the unappreciated incidence of facultative annuals. In any case, and never mind the taxonomic accuracy/reliability, database evidence for the facultative annual condition is not only scarce, but this scarce evidence itself was systematically excluded by these researchers.**[68]**

I can only speculate on the consequences of distinction of the facultative annual condition in ensemble reductionist analyses of angiosperm life history/form and phenological evolution. In the case of Ogburn & Edwards (2015), the authors indeed concluded that life history among Montiaceae is evolutionarily labile. The present observations and discussion would *support* this conclusion. But this conclusion is obvious simply by reviewing the phylogenetically-based taxonomy. The present observations demonstrate that Ogburn & Edwards (2025) calculations severely *underestimate* the *true* lability. This is because no degree of statistical sophistication and precision can correct for inadequate/inaccurate data (cf. Hershkovitz, 1977: 64).[69]

But since empirical life history data availability is insufficient, there is not much point in speculating on the downstream analytic effects of upstream data inadequacy in above-cited ensemble reductionist studies. This is because the *principal* inadequacy is not operational, but *epistemological*. In particular, these analyses represent an extension of the neo-Darwinian statistical population genetics "natural selection" (NS) paradigm to macroevolution. I reject this paradigm in favor of the Natural Drift (ND) paradigm (Maturana & Mpodozis, 2000; Mpodozis, 2022), which derives logically from the notion of autopoiesis (Maturana & Varela, 1972), incorporates a broader sense of the notion of epigenesis (Vargas et al., 2020), and which I have extended further to deduce the Principle of Evolutionary Idiosyncraticity (PEI; Hershkovitz, 2018c, 2019a, d, 2020, 2021b).

The observations presented in this work are examples of Natural Drift that cannot be accommodated easily or at all according to NS dogma. Per ND, population averages emphasized in NS analysis have descriptive and heuristic value but no biological *significance*. Regardless of any of its trait parameter values, *every* living organism ("autopoieton") is as "adapted" as any other, its ontology is simultaneously material and processual**[70]** (the "ontogenetic phenotype"), its evolution *embodies* epigenesis (sensu Vargas et al., 2020), its evolutionary transitions are temporally infinitesimal ("moment-to-moment"), its reproduction is systemic, and its lineage persists as long as its adaptability (structural coupling with its evolving ontogenetic niche) is conserved. In this conceptualization, the genotype "determines" neither the phenotype nor the "fitness" of the individual or lineage. The genome is simply an "initial condition" that specifies nothing more or less than its own systemic reproduction and behavior and what "gene products" the organism may

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[68] Ogburn & Edwards remarked that "*assigning life history strategy is less subjective than assigning plants to typological growth form categories*," and that nearly all analyzed Montiaceae could be "*assigned unambiguously as either annuals or perennials*." They classified the few exceptions according to their most "widespread" condition. The criterion for evaluating most "widespreadness" was not specified. Boyko et al. (2023) and Poppenwimer et al. (2023) excluded from their analysis taxa whose WCVP classification was ambiguous or variable. This, of course, would include taxa described *effectively* as facultatively annual. They also classified biennial taxa as perennial, which is simply *wrong*. The biennial condition refers to *semelparous* plants with a vernalization requirement that delays their reproduction to their *second* warm season. Then, unlike *iteroparous perennials*, they *die*. They differ from "winter annuals" only in (apparently) having two vernalization requirements, one for germination, and another for flowering. Biennials can be induced to behave as annuals (but also iteroparous perennials) both artificially and naturally (e.g., Gremer et al., 2019 ["2020"]).

[69] "*....the more extensive the mathematical interventions, the more complicated become the statistical analyses and the more sterile, futile, and unrealistic their results.*" It seems nothing less than kismet the relevance here of this aphorism authored by the very person for whom *Cistanthe philhershkovitziana* was named.

[70] Not unlike the mass/energy identity.

or may not eventually produce. The environment, meanwhile, is a "limiting condition." The organism itself *mediates* apparent associations between genome and environment.

The present work demonstrated, first and foremost, that the life history of *C. philhershkovitziana* is dynamic and transcends the "either/or" categories that mainstream life history theory idealizes. Individuals of *C. philhershkovitziana* persist in a range of climatic and edaphic conditions, and those conditions themselves evolve independently at a very small spatiotemporal scale. For example, climatic conditions reported as "averages" actually vary significantly year-to-year, and their parameters themselves can decouple. The *realized* (not the "average") "climatic niche," along with the realized edaphic environment, may seem to affect individual germination, growth, and reproduction. But neither the genome nor the environment determine, e.g., whether or not birds uproot caudices. Ultimately, it is the organism that determines its fate. It may adapt under conditions that NS says it should not, or it may not adapt under conditions that NS says it should.[71] This is ND.

PEI, meanwhile, emerges from the observation that, because the organism's history represents a continuous and *uninterrupted* historical biological process (since the origin of life), its evolution cannot be modeled *stochastically* (viz. as a first-order Markov process), as the NS paradigm *requires*. Its history and hence behavior per se are *determinate* (an asymptotically infinite-order Markov process, or a *~chaotic* process).[72] Yet, the ontogenetic phenotype and niche indeed exist in a milieu that formally is defined as stochastic. But it is the very *product* of this relation that makes life itself possible, such that the continuity of life – *evolution* – *cannot* be a stochastic process. Hershkovitz (2018c, 2019d, 2021b) thus described idiosyncraticity not as a descriptive quality, but a *mathematical* relation that describes the behavior and evolution of organisms. Just as important, it demonstrates that NS is untrue.

Aside from being powerful concepts in themselves (Mpodozis, 2022), autopoiesis and ND have tremendous implications for plant life history/form and phenological evolutionary theory. But it is important to appreciate that ND and NS derive from incompatible assumptions about organisms, hence are mutually incompatible models. Thus, there cannot be *some* instances where ND operates and others where NS operates (as supposedly is the case for NS and *genetic* drift). In fact, evidence for ND is ubiquitous, as it should be. But it is hidden in massive literature that converts data into averages and variances and forces them into an NS framework.[73] Often careful decomposition of the original data is necessary to discover the discrepancies. But not always. Latron et al. (2023) framed their analysis of life history evolution in NS terms. But they reported…*idiosyncraticity!* There are many such examples in the recent literature. But a thorough articulation and comparative analysis of empirical evidence in *both* NS and ND frameworks is beyond the scope of the present work. This will have to wait for a subsequent work. Also beyond the scope of this work is a likely provable *mathematical* conjecture that is compatible with ND and falsifies NS. This

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[71] This is not an exaggeration. "*...it is not clear why more annuals do not perennate under favorable conditions.*" (Friedman, 2020: 476).

[72] Current mainstream macroevolutionary analyses "fit" data parameters using stochastic (Brownian motion) models. In general, a stochastic and chaotic process cannot be distinguished statistically. The question is whether they can be distinguished at least heuristically in "special cases."

[73] Some current macroevolutionary analyses appeal explicitly to NS. Others do not, but it is "built in" to the epistemological and/or methodological assumptions. For example, while invoking the teleological notion of "strategy," mainstream life history theory at its core appeals to the notion that life history evolution is driven by mean population/species "fitness" maxima. Phylogenetic comparative methods were *invented* by neo-Darwinist population biologists. Ornestein-Uhlenbeck models currently applied are not inherently selectionist, but are applied operationally to infer, e.g., presumed stabilizing or directional selection. These paradigms could be recast in ND terms, e.g., with life history modalities and convergent evolution interpreted as chaotic function attractors.

is not a trivial finding, as much of current mainstream evolutionary ecology is focused on prediction of organismal responses to climate change. False models cannot be relied upon to make true predictions.

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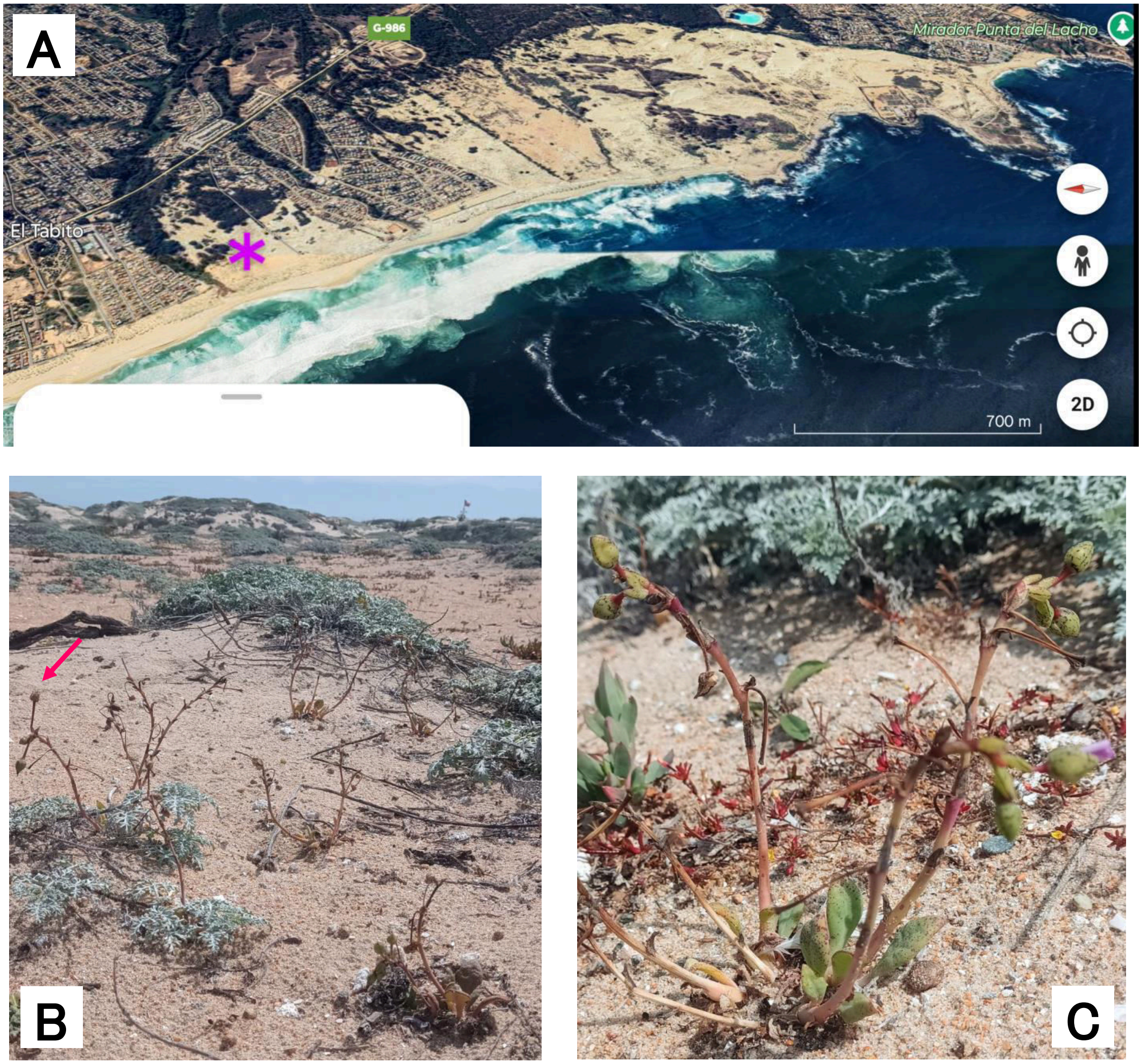
Figures 1 – 6. *Cistanthe philhershkovitziana*. The millimeter ruler appearing in some photos for scale is 10% too short. The cigarette appearing in other photos for scale is ca. 10 cm long and the lines on the paper are spaced ca. 1 mm apart, with ca. 99% accuracy.

Fig. 1. The Gota de Leche subpopulation (asterisk) of *C. philhershkovitziana*. **A.** Google Earth 3D satellite image from ca. west of the Santuario de la Naturaleza Gota de Leche dune area in between El Tabito (left side) and Las Cruces (delimited ± by Mirador Punta de Lacho on the right side). The species occurs ± throughout the Santuario, which comprises the nonurbanized portion of the crescent-shaped dune area. **B.** View from the subpopulation towards the foredunes on 14 November 2023, with the Pacific Ocean in the background. The mature ascending inflorescences are ca. 20 cm long. Note the upward orientation of pedicel bearing a dehiscent capsule (arrow). **C.** A single individual. **D.** An individual extracted on 23 January 2024 showing senescent leaves and stems on the live caudex bearing long live finer roots. After six months of storage in a black plastic bag, the plant had the same appearance, but the caudex was slightly shriveled and bore etiolated short shoots ca. 3 cm long. **E.** A small flowering individual observed on 23 January 2024. **F.** The same individual unearthed demonstrating that it is a germling much younger than the larger individuals illustrated above. **G.** Uprooted caudex lying prostrate on the surface of the sand, as found on 9 March 2024. The site was “littered” with such caudices. **H–I.** Individuals extracted on 13 May 2024. **H.** Young seedlings showing early stages of caudex development. **I.** First-year plants with larger caudices. **K.** Reemergent second-year individuals. The individual on the right bears a mummified inflorescence.



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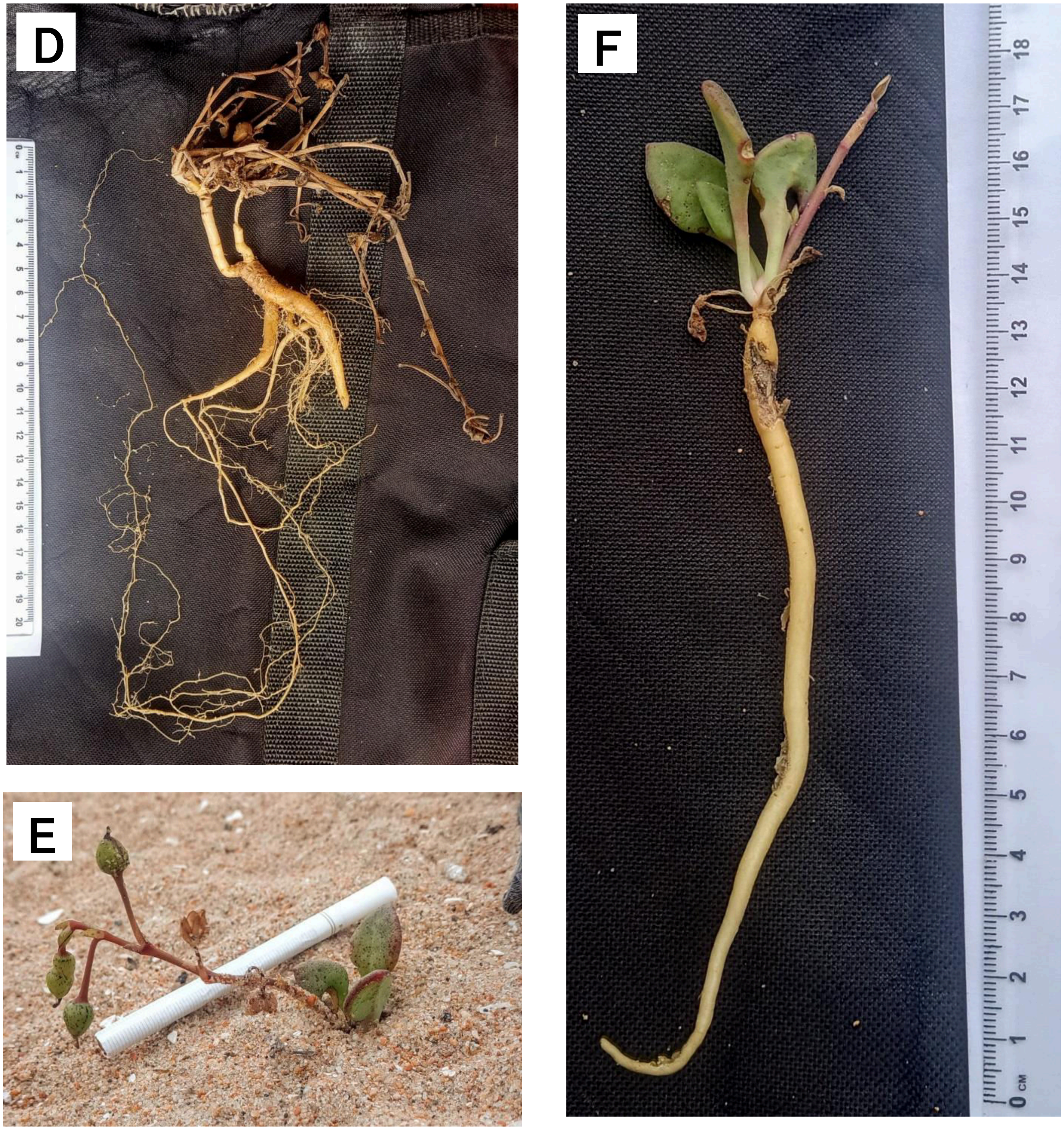

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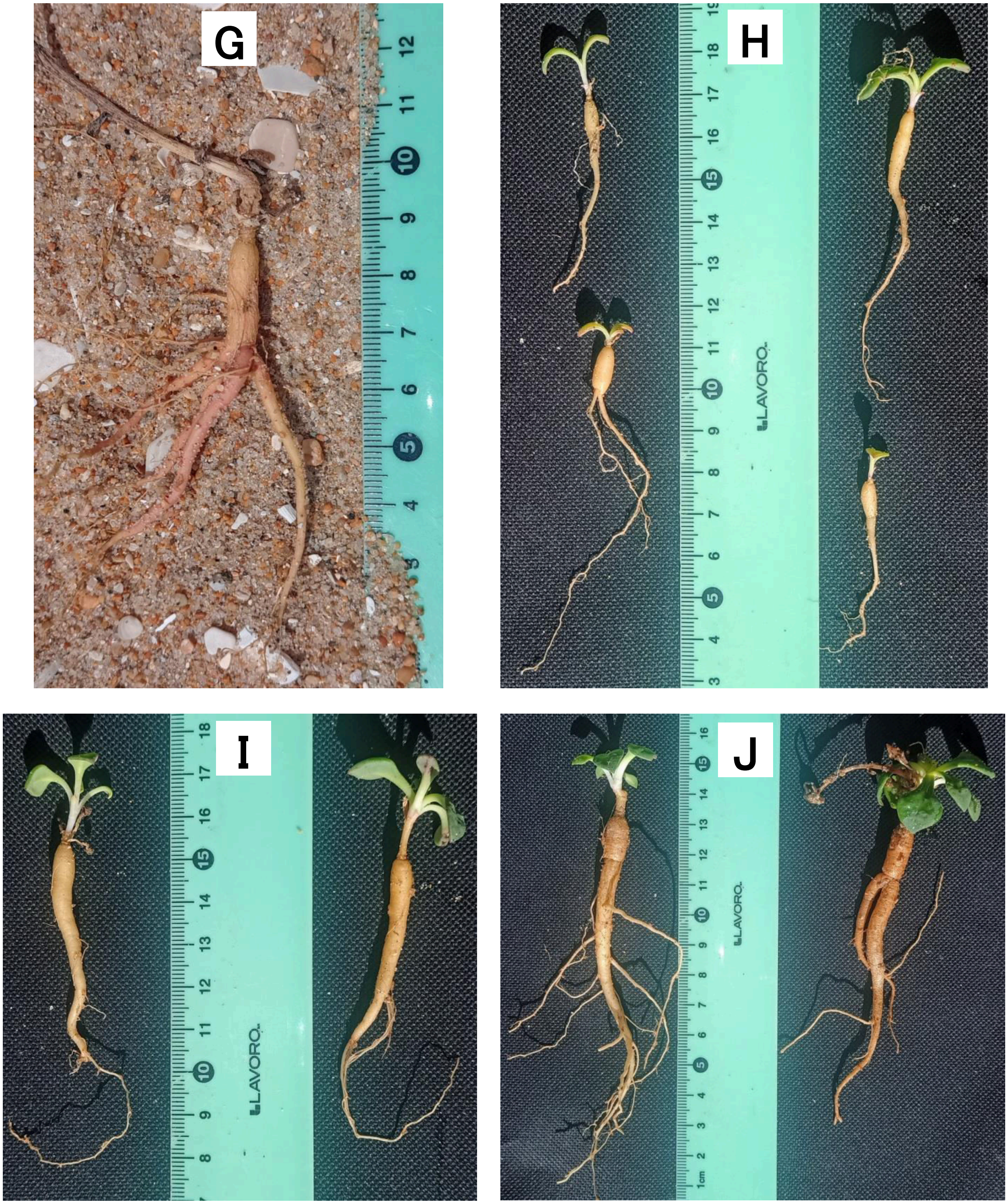
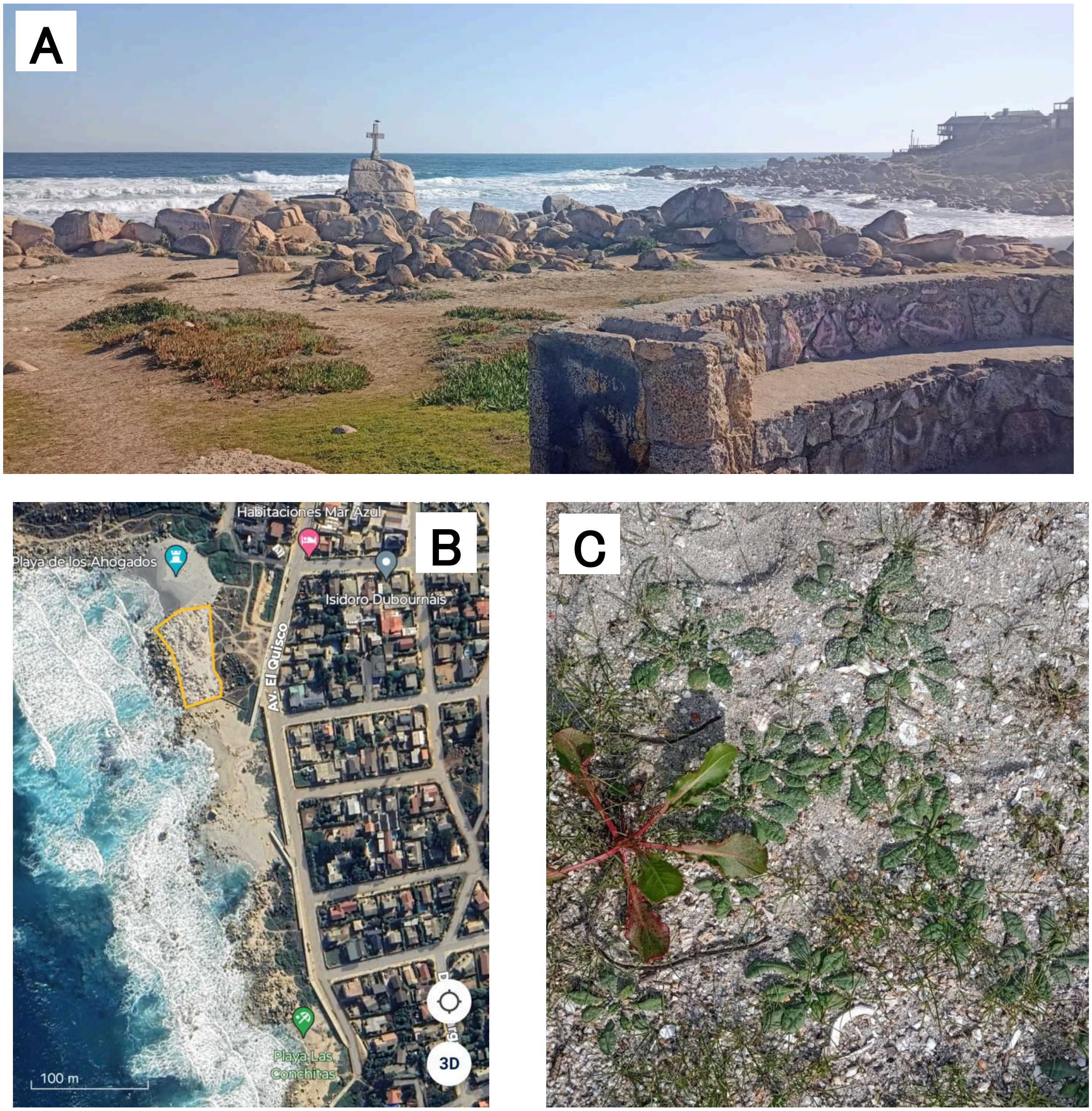


Fig. 2. The Cartagena dune population of *C. philhershkovitziana*. **A.** Google Maps Street View of the dune looking south from the north side of the Estuario de Cartagena. The population occurs toward the right side. **B.** Google Maps 2D north-normal satellite image. The arrow indicates the location and direction of the Street View above. An asterisk marks the approximate location of the population. **C.** Individual photographed a few days after its extraction on 7 December 2023. This individual had been grazed to the level of the caudex. **D.** The same individual photographed on 8 September 2024 after nearly ten months of cultivation in this container. Inflorescence primordia are scarcely visible (arrows). **E.** Nearly "mature" flower dissected on 29 September. The petals are tinged pink, the stigma deep fuchsia and papillate, and the pollen in the well-developed anthers yellow.

Fig. 2, continued.

Fig. 3. The Playa Hanga Roa population of *C. philhershkovitziana*. **A.** View of the populated area. **B.** Google Earth 2D north-normal satellite image of Playa Hanga Roa (syn. Playa de los Ahogados) and Playa Las Conchitas (bottom) areas. The yellow line demarcates the limits of the population. **C.** Prostrate rosettes in compacted sand of a trafficked footpath on 2 July 2024. **D.** Extracted first-year caudex. **E.** Extracted second-year caudex. **F.** Seedlings without (left) and with (right) caudical development. **G.** Larger individuals growing next to a granite boulder. **H.** Close-up of the caudex apex of a large individual showing multiple rosettes. **I.** Small individuals on exposed (unprotected) compacted sand on 30 July 2024. Small inflorescence primordia are evident. **J.** Larger and more protected individual on 30 July 2024, showing substantial inflorescence development. **K.** Individual from G above in flower on 11 August 2024. **L–P.** 17 September 2024 observations. **L.** Small individuals lacking inflorescence primordia on trafficked, compacted sand. **M.** Prostrate flowering individuals on trafficked, compacted sand. **N.** Small erect flowering individual in protected site. **O.** Mid-flowering stage individual in protected site. **P.** Senescent individual on exposed site.



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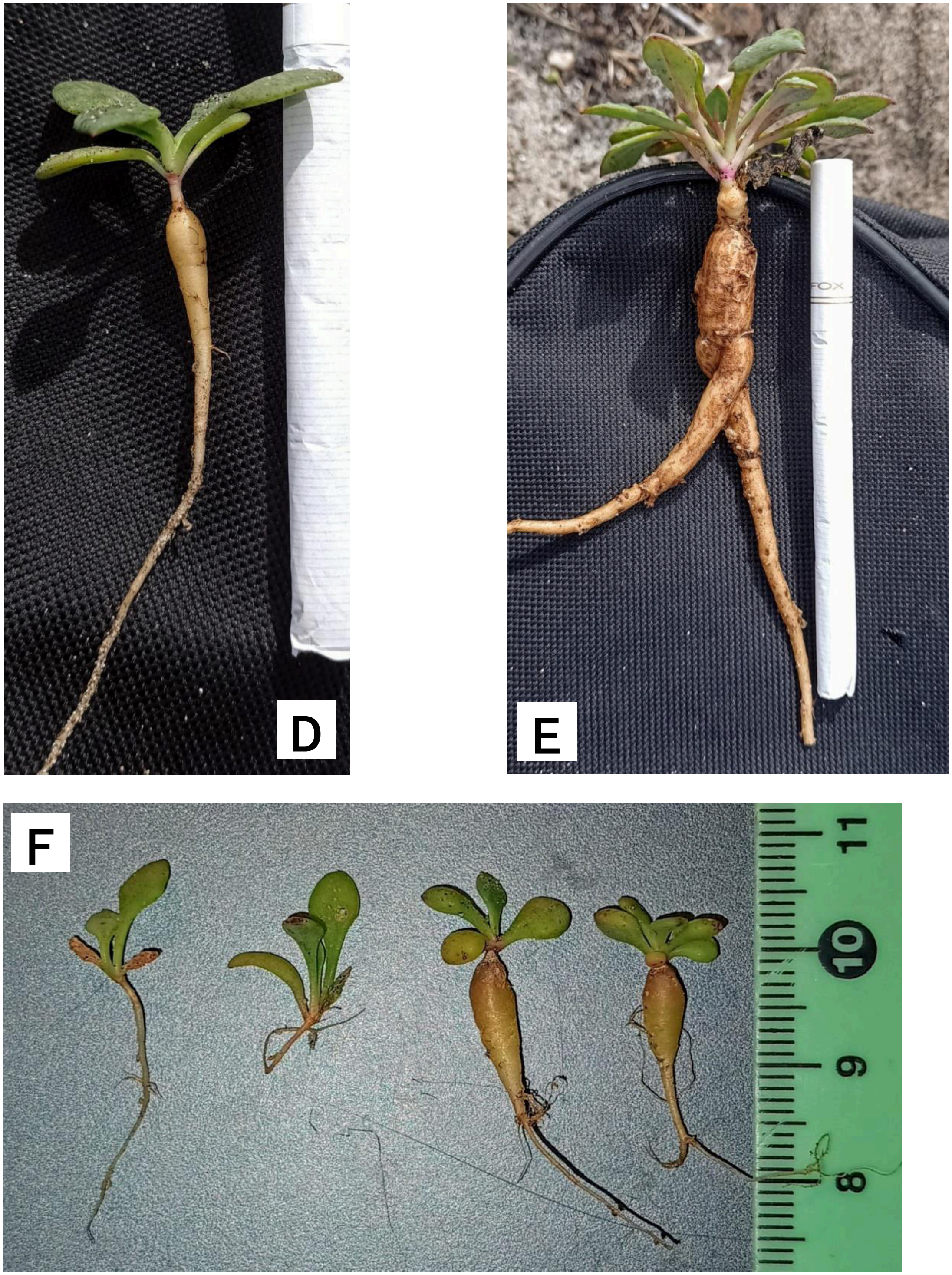

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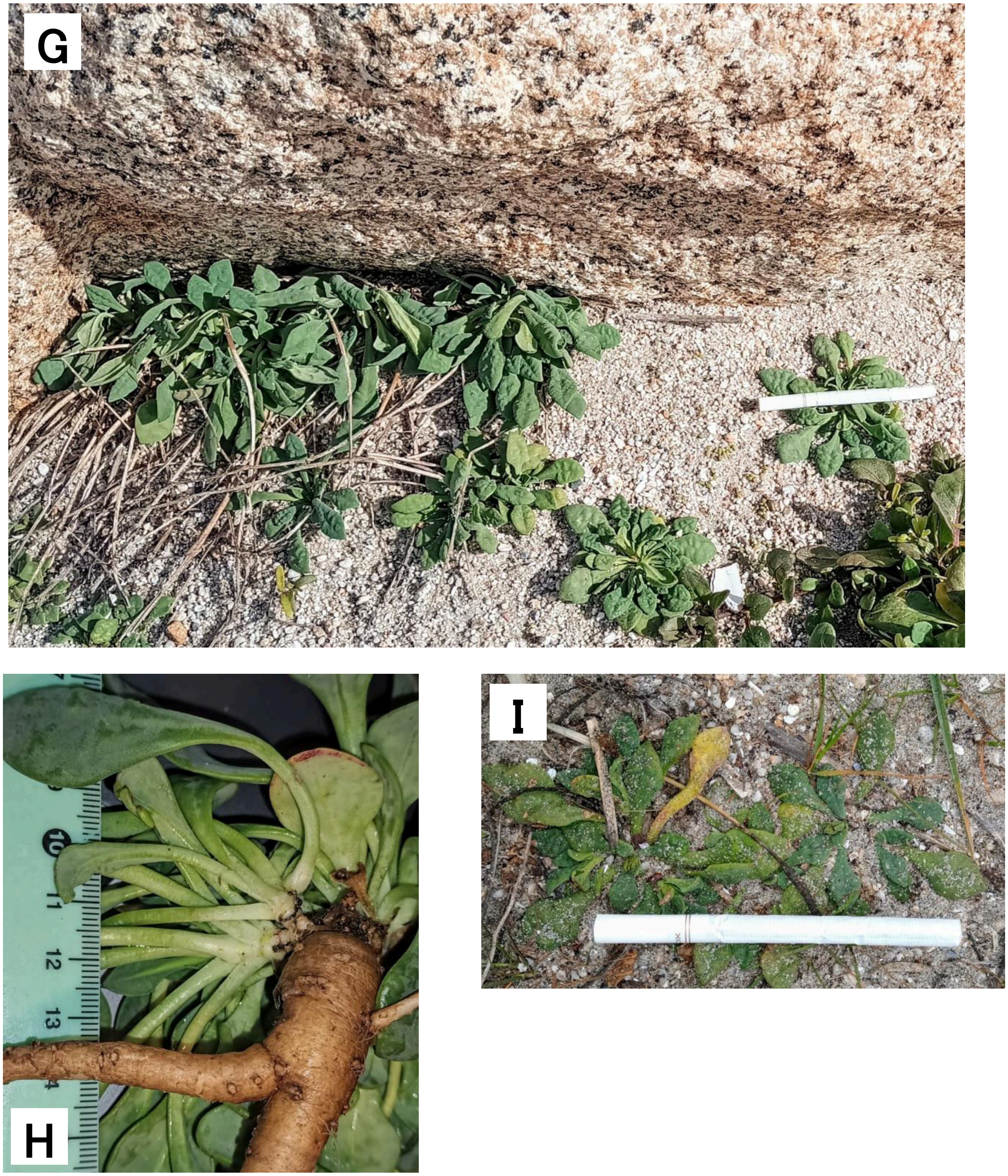

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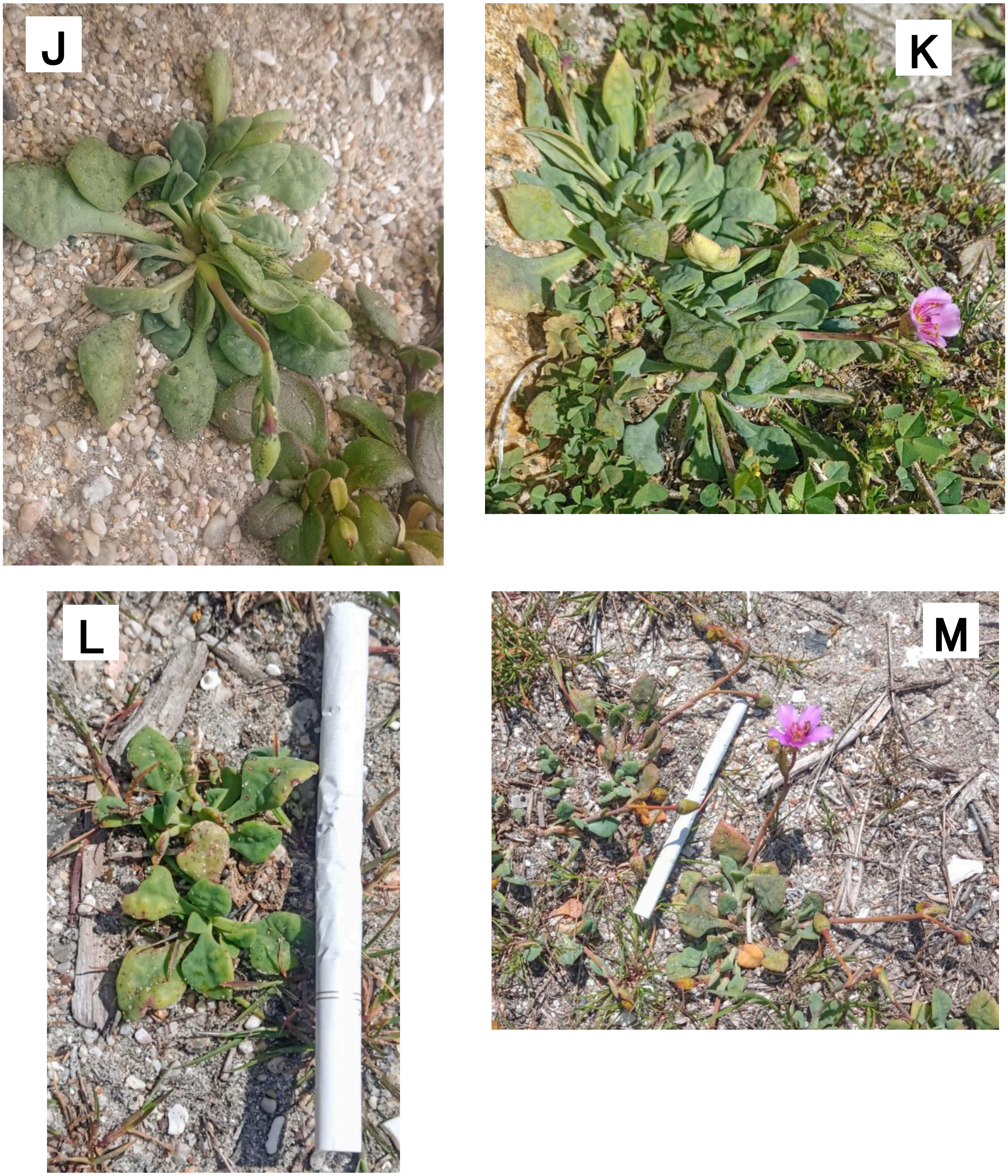

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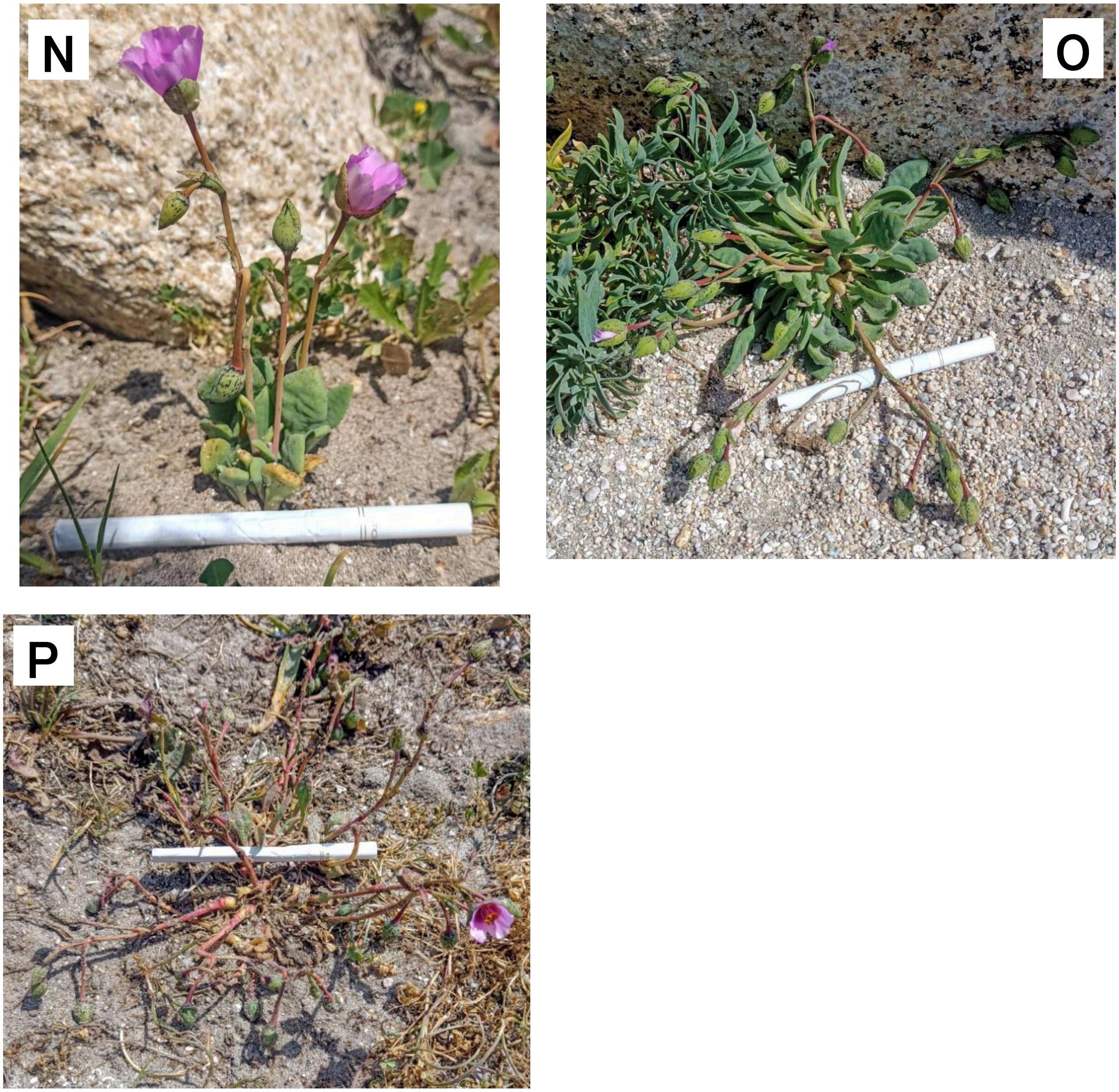
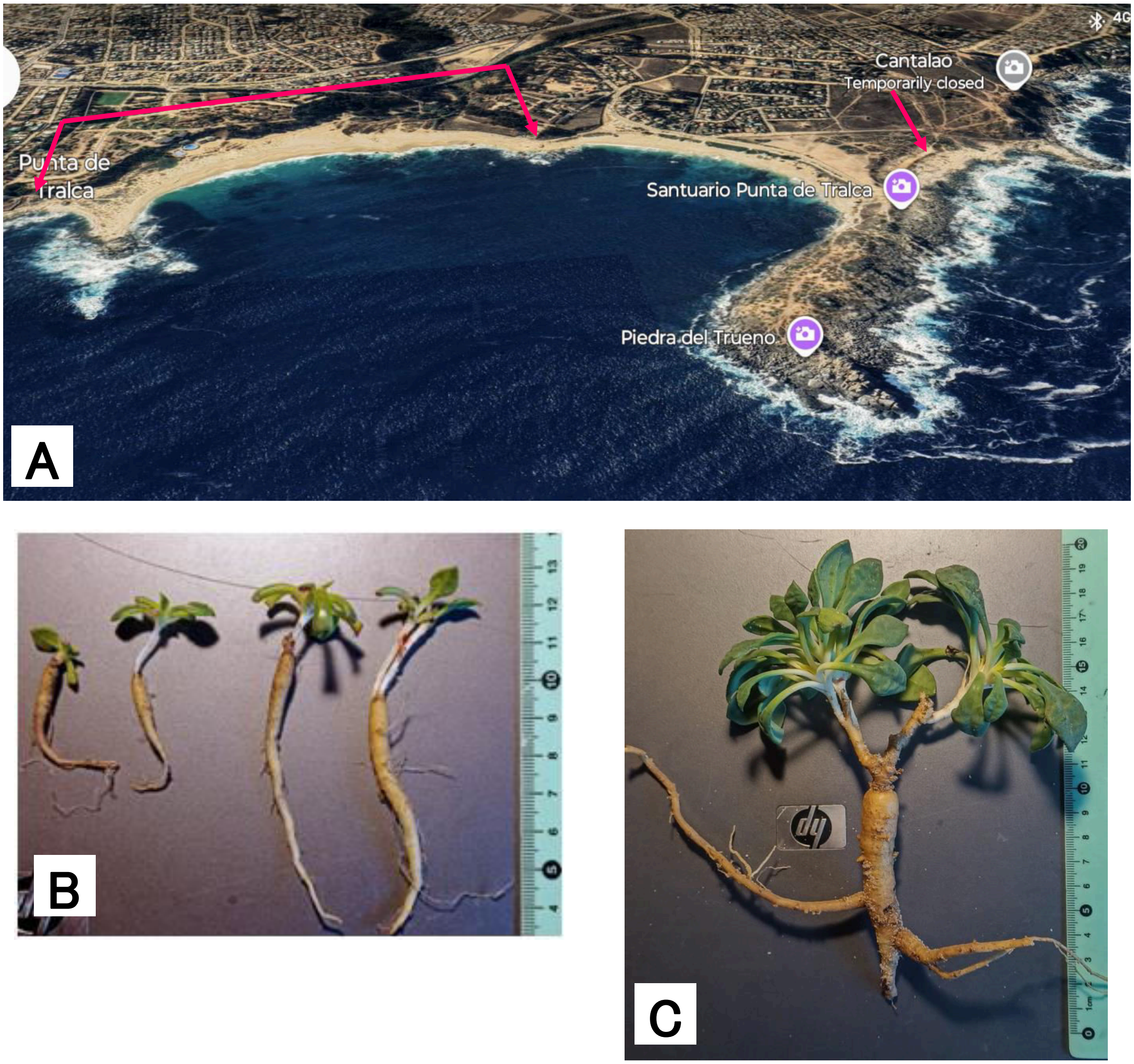


Fig. 4. The Punta de Tralca populations of *C. philhershkovitziana*. **A.** Google Earth 3D satellite image from ca. west of the Punta de Tralca area. The small peninsula on the left labeled Punta de Tralca is Punta Taulanque. The Punta de Tralca peninsula is to the right. The serpentine dark patch top center left defines the Estero de Totoral. The plants are distributed on the beach between the arrows on the left and discontiguously on the beach at the far right arrow. **B.** Small individuals as observed commonly on 9 July 2024. **C.** A rare large individual observed on 9 July 2024. **D.** Seedlings collected on 18 September 2024. **E.** Flowering individual naturally buried in the sand, observed on 18 September 2024.



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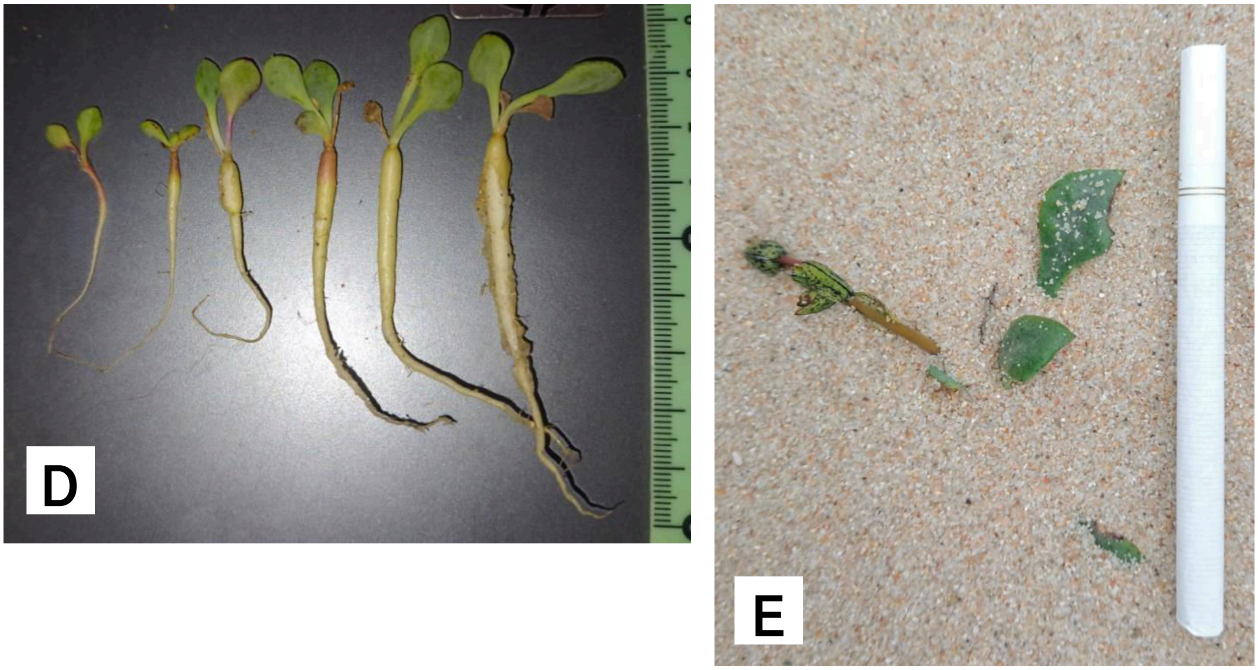

Figure 5. Stems of secondary rosettes of *C. philhershkovitziana*. Note the length of the secondary rosette(arrows) emerging from the primary rosette leaf axils. **A.** Adaxial view. **B.** Abaxial view.

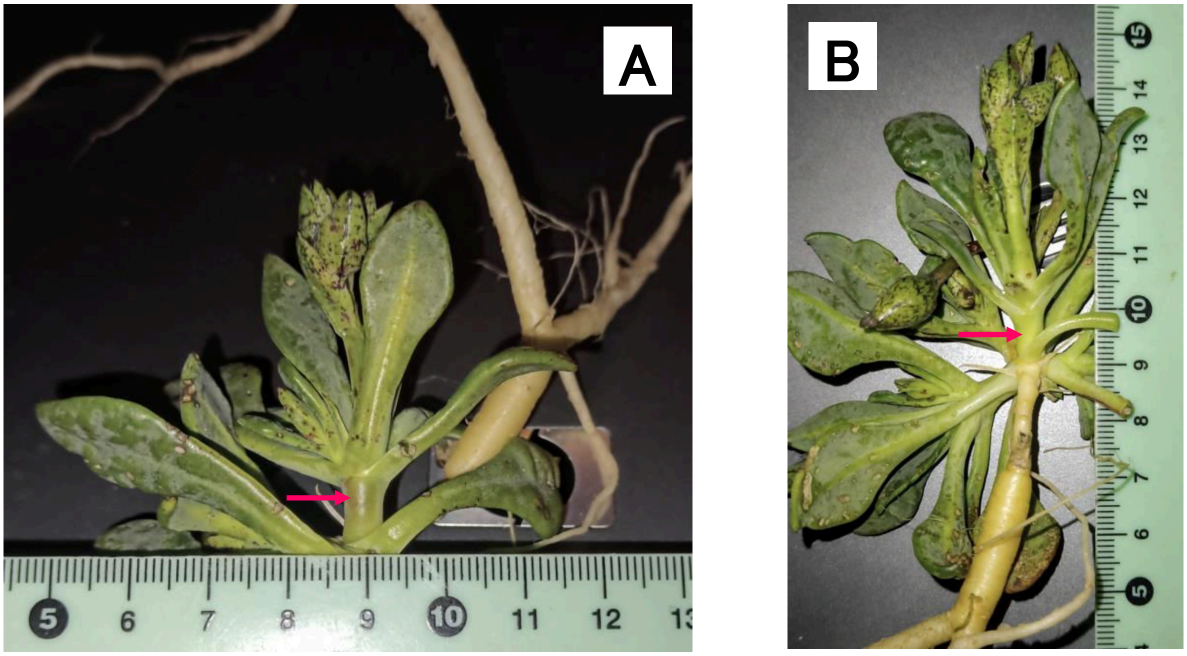

Figure 6. Dormant individual of *C. crassifolia*. This image was downloaded from the internet, but I can no longer locate the source page. The color and quality of the original image has been enhanced.