COMPOSITAE OF CENTRAL AMERICA–IX. *TALAMANCASTER* (ASTEREAE), A NEW GRANGEOID GENUS FROM GUATEMALA, COSTA RICA, PANAMA, AND VENEZUELA

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ABSTRACT

The new grangeoid genus Talamancaster Pruski, gen. nov. (Compositae: Astereae), is described and includes six páramo-centered species. *Talamancaster* is known only from Guatemala, Costa Rica, Panama, and Venezuela, but should be looked for in Mexico and Colombia. Talamancaster is distinguished by its short, pinkish rays in few series, bisexual 5-merous disk florets with glabrous corollas and apiculate anthers, and epappose, compressed cypselae. The six component species are small herbs, either subscapose or with few-leaved stems, and were described in Lagenophora, then transferred to Myriactis (both Lagenophorinae). Talamancaster differs from circumaustral scapose Lagenophora by bisexual (vs. functionally staminate) disk florets with campanulate (vs. funnelform), glabrous (vs. papillose-glandular) corollas, and from leafy stemmed Myriactis by 5-merous (vs. 4-merous) disk florets with glabrous (vs. papillose-glandular) corollas. Phylogenetic study by Noves and Rieseberg and Nakamura et al. (coupled Nesom's with subtribal classification) are neither complete nor fully resolved, but nevertheless recovered Lagenophora (Talamancaster) panamensis as sister to Laennecia Cass. (Podocominae) rather than to Myriactis (Lagenophorinae). Talamancaster, however, matches no genera of either subtribe (or of tribe Astereae) and is described as a new genus, albeit unplaced subtribally. Six new combinations are proposed: Talamancaster andinus (V.M. Badillo) Pruski, comb. nov., T. cuchumatanicus (Beaman & De Jong) Pruski, comb. nov., T. minusculus (Cuatr.) Pruski, comb. nov., T. panamensis (S.F. Blake) Pruski, comb. nov., T. sakiranus (Cuatr.) Pruski, comb. nov., and T. westonii Cuatr.) Pruski, comb. nov. SEM micrographs of cypselae in Laestadia, Lagenophora, Myriactis, Podocoma, and Talamancaster are provided, as are figures that illustrate key differences in habit and flowers.

The new genus *Talamancaster* Pruski (Compositae: Astereae) is described and includes six neotropical species. The species are short-radiate, small, subscapose herbs with pauciseriate pistillate florets usually with pinkish corollas, bisexual 5-merous disk florets with glabrous corollas and apiculate anthers, and cypselae that are epappose, compressed, glandular-subrostrate, and prominently costate marginally (viz Figs. 1, 11–14). Each of the six species of *Talamancaster*, by their epappose glandular-subrostrate flat-cypselae, was described in Patagonian and New Zealand-centered *Lagenophora* Cass. (conserved in spelling over the orthographic variant *Lagenifera*). The earliest described species, *L. panamensis* (now *T. panamensis*), was noted by Blake (1939) to resemble *L. maviensis* H. Mann, treated by Nesom (2001) as *Keysseria maviensis* (H. Mann) Cabrera within *Keysseria* sect. *Sandwicactis* Nesom. Indeed, *K. maviensis* is similar in its glabrous disk corollas, but *Keysseria* differs from *Talamancaster* by being a thick-leaved, moderately stout perennial with deltate anther appendages composed of bullous cells, and by having 4-merous disk corollas.

Cabrera (1966) revised *Lagenophora*, recognizing 15 species and placing 12 of them in scapose *Lagenophora* sect. *Lagenophora*, which contained the type element from Patagonia as well as the Old World species. In a review of *Lagenophora* in New Zealand, Drury (1974) noted that Cabrera (1966) "following the lead of Beaman & De Jong (1965)" placed the three then-described neotropical species (*L. andina* V.M. Badillo 1947, *L. cuchumatanica* Beaman & De Jong 1965, and *L.*

panamensis S.F. Blake 1939) in the newly described subscapose *Lagenophora* sect. *Pseudomyriactis* Cabrera (1966). Drury also noted that the glabrous disk corollas of sect. *Pseudomyriactis* Cabrera serve to set it apart from section *Lagenophora*. Subsequently, Cuatrecasas (1982) described three further species in *Lagenophora* sect. *Pseudomyriactis*: *L. minuscula* Cuatr., *L. sakirana* Cuatr., and *L. westonii* Cuatr., each endemic to the Talamanca Mountains in southeastern Costa Rica and western Panama. Vélez (1981) and Cuatrecasas (1986) transferred all six species of *Lagenophora* sect. *Pseudomyriactis* to Asia- and Malaysia-centered leafy-stemmed *Myriactis*. Placement of these species in either *Lagenophora* or *Myriactis* is supported by roughly similarly compressed cypselae.

Morphologically, however, notwithstanding the moderately flattened cypselae, Talamancaster does not match either Lagenophora or Myriactis. The three genera share the characters of grangeoid genera, a group mostly characterized by herbaceous habit, 2+-seriate pistillate florets (viz Figs. 2, 7, 27), moderately herbaceous phyllaries, and obviously compressed cypselae (Fayed 1979; Nesom 1994a, 2000; Nesom & Robinson 2007; Pruski 2011). Lagenophora is a rosette plant with obviously rostrate cypselae and functionally staminate 5-merous disk florets with papillose-glandular, funnelform corollas (Fig. 2). Myriactis is a tall leafy stemmed plant, has 4merous, bisexual disk florets with papillose-glandular, campanulate-salverform corollas, and mostly erostrate cypselae (Figs. 3-4). In herbarium material of Myriactis the 4-merous disk florets and their 4-lobed corollas are often discernible at a glance by their overlapping corolla lobes, two spreading to the right and two to the left.

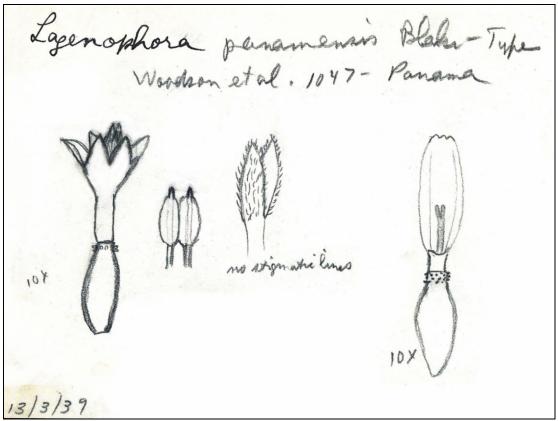


Figure 1. *Talamancaster panamensis* floral sketch by Sidney Fay Blake, clipped to holotype of *Lagenophora panamensis*. The essential generic characters drawn include apiculate anthers, the flattened glandular-necked cypselae of a ray floret and a bisexual disk floret, and the glabrous campanulate disk corolla. Cabrera (1966: 305) mistakenly characterized the disk florets of *Talamancaster panamensis* as "apparently mostly sterile," but instead the disks on the holotype set fruit. (From *Woodson et al. 1047*, US).

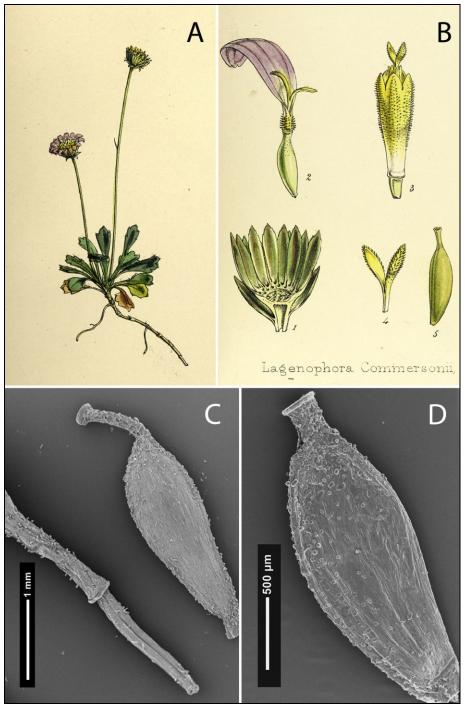


Figure 2. Diagnostic characters of *Lagenophora* (subtribe Lagenophorinae). A. Habit of *Lagenophora nudicaulis* (Lam.) Dusén. B. *Lagenophora nudicaulis* floral details, including a functionally staminate 5merous disk floret with a funnelform, papillose-glandular corolla. C. SEM micrograph of sterile disk floret (lower left) showing papillose-glandular corolla tube and cylindrical ovary, and mature flat rostrate ray cypsela (upper right) of *Lagenophora stipitata* (Labill.) Druce. D. SEM micrograph of mature flat ray cypsela of *Lagenophora hariotii* Franch. (A–B from J.D. Hooker, Bot. Antarctic Voy., vol. 1, part 2 (i.e., Fl. Antarct.) tab. 108 left, 1846, as *Lagenophora commersonii* Wedd., which along with the generitype of *Lagenophora, Calendula magellanica* Willd., were given by Cabrera 1966, 1971 as synonyms of *Lagenophora nudicaulis*; C Papua New Guinea, *Croft et al. 65116*, MO; D Tierra del Fuego, *Roivainen 1643*, MO).

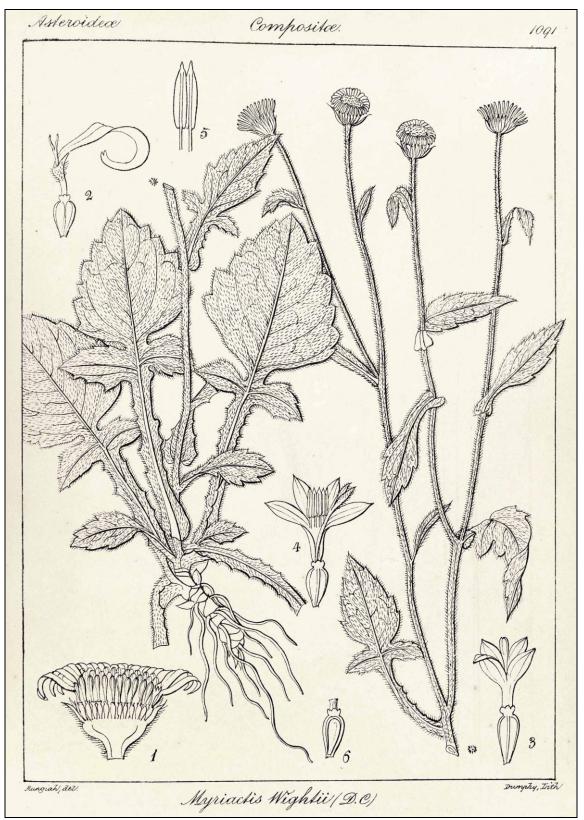


Figure 3. *Myriactis wightii* DC. (subtribe Lagenophorinae), showing leafy stem and the 4-merous, campanulate-salverform disk corollas. (From R. Wight, Icones plantarum Indiae Orientalis 3: tab. 1091. 1846).

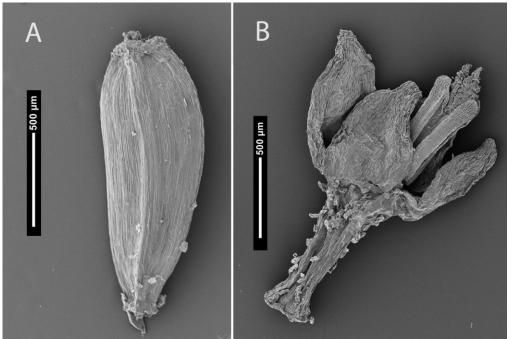


Figure 4. SEM micrographs of *Myriactis nepalensis* Less., the generitype of *Myriactis* (subtribe Lagenophorinae). A. Moderately compressed disk cypsela showing truncate apex and lateral face with a weak medial nerve. The abaxial (outer) margin of the asymmetrically curved cypsela is on the right. B. Campanulate-salverform, 4-merous disk corolla showing papillose-glandular trichomes of the tube. Some species of *Myriactis* have short-rostrate cypselae. (China, *Heng et al. 20639*, MO).

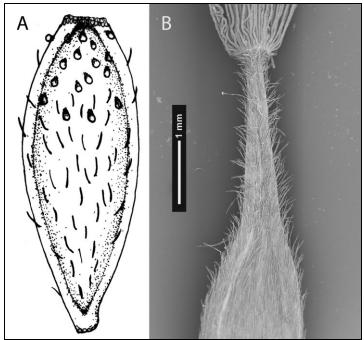


Figure 5. Thick-margined compressed cypselae of representative pappose genera of subtribe Podocominae. A. Erostrate, distally glandular cypsela of *Laennecia araneosa* (Urb.) G. Sancho & Pruski, pappus bristles removed. B. SEM micrograph of rostrate, pappose cypsela of *Podocoma hieraciifolia* (Poir.) Cass. (A Dominican Republic, *Ekman 13566*, US, reproduced from Sancho & Pruski 2004; B Paraguay, *Zardini & Vera 48287*, MO).

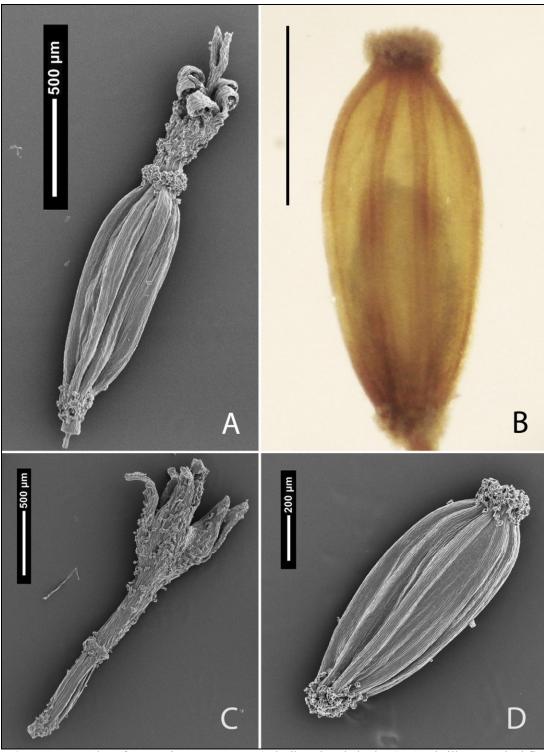


Figure 6. Terete cypselae of *Laestadia costaricensis* (subtribe Hinterhuberinae). A. Pistillate marginal floret with narrowly campanulate corolla and maturing fruit. B. Five-ribbed ovary of marginal floret showing erect basal ovule. C. Functionally staminate disk floret with cylindrical sterile ovary and broadly campanulate corolla. D. Mature pluricostate cypsela of marginal floret. The voucher for this figure is from Cerro Chirripó (Suessenguth 1942 noted the species there), where three of the six *Talamancaster* species occur. (Costa Rica, *Pruski et al. 3948*, MO). [A, C–D are SEM micrographs; scale bar in B 0.8 mm].



Figure 7. Capitulum of *Talamancaster andinus*, showing the many pauciseriate pink rays and fewer disk florets. (*Pruski et al. 3935*).



Figure 8. Unusually robust individual of *Talamancaster andinus*, showing stems few-branched distally. (*Pruski et al. 3935*).

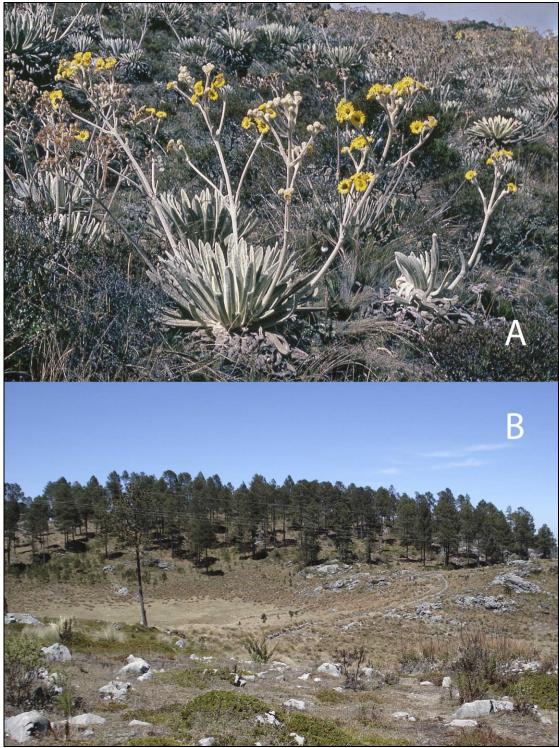


Figure 9. Two extra-Talamancan habitats of species of *Talamancaster*. A. The type locality of *Talamancaster andinus* in páramo near Laguna de Mucubají, Venezuela, showing yellow-rayed caulirosulate *Espeletia schultzii* Wedd. (*Pruski et al. 1346*). B. Type locality of *Talamancaster cuchumatanicus* near *Pinus* grove in the Sierra de los Cuchumatanes, Guatemala. This locality is near Todos Santos Cuchumatán, which sits in the glacier-carved U-shaped Río Limón valley. *Talamancaster cuchumatanicus* is found also in pine forests on the Tecúm Uman Ridge. Neither *Pinus* nor *Espeletia* is native to Costa Rica or Panama.

LAGENOPHORA	TALAMANCASTER	MYRIACTIS
Basically circumaustral, slightly extending into Malaysia and SE Asia.	Guatemala, Costa Rica, Panama, and Venezuela.	Asia- and Malaysia-centered.
Scapose.	Subscapose or leafy stemmed.	Leafy stemmed.
Disk florets functionally staminate.	Disk florets bisexual.	Disk florets bisexual.
Disk corollas 5-lobed, funnelform, papillose-glandular. Cypselae rostrate.	Disk corollas 5-lobed, campanulate, glabrous. Ray cypselae and usually disk cypselae collared (disk cypselae of <i>T. minusculus</i> and <i>T. sakiranus</i> without collar).	Disk corollas 4-lobed, campanulate-salverform, papillose-glandular. Cypselae erostrate and flat on top (generitype) to other species short-rostrate or collared.
Disk ovaries terete, never forming fruit, obviously much shorter than ray cypselae.	Disk cypselae compressed, sometimes midnerve visible, thick-margined, similar to rays, when not pollinated ovary nearly as long as ray cypselae.	Disk cypselae compressed, sometimes weakly 4-ribbed, sometimes slightly dissimilar to those of rays.

Table 1. Select characters of Lagenophora, Talamancaster, and Myriactis.

Talamancaster, on the other hand, is distinguished from both by being a small leafy- or bracteate-stemmed herb, by having bisexual, 5-merous disk-florets with glabrous, campanulate corollas, and by ray (and often disk) cypselae with a densely viscid-glandular collar. Table I summarizes the differences between *Lagenophora*, *Myriactis*, and *Talamancaster* and updates Hind (2004), where a larger table distinguishing the core genera (viz Nesom 2001) of the *Lagenophora* group was given. As mentioned by Drury (1974), *Talamancaster* as a distinct lineage was first noted by Beaman and De Jong (1965), who said "the Central and northern South American species seem to have more characters in common among themselves than with the other members of *Lagenophora*."

While *Talamancaster* is distinct from *Lagenophora* and *Myriactis*, by morphology *Talamancaster* nevertheless seems similar to them, as well as to the remaining core genera of the *Lagenophora* group. *Talamancaster* is also moderately similar to terete-fruited *Laestadia* (subtribe Hinterhuberinae; viz Fig. 6). Phylogenetic studies by Noyes and Rieseberg (1999) and Nakamura et al. (2012), although neither complete nor fully resolved, coupled with Nesom's subtribal classification (Nesom 1994a; Nesom & Robinson 2007) recover *Lagenophora* (*Talamancaster*) panamensis as sister to *Laennecia* Cass. (Podocominae) rather than to *Myriactis* (Lagenophorinae) or *Laestadia* (Hinterhuberinae). Noyes and Rieseberg (1999) said *Lagenophora* (*Talamancaster*) panamensis is close "to the base of the North American clade, supporting a possible South American origin for North American Astereae." Nakamura et al. (2012) found *Lagenophora* to be monophyletic. Jafari et al. (2015) noted *Myriactis* is monophyletic, based on *Myriactis wallichii* Less. (their sequence data) recovered as sister to *Myriactis humilis* Merr. (as sampled by Noyes & Rieseberg 1999). *Myriactis* as

circumscribed here is excluded from the Americas and no longer should be used as an example of an amphitropically distributed genus.

The phylogenies suggest that *Talamancaster* should not be positioned in Lagenophorinae, but morphologically *Talamancaster* matches neither Hinterhuberinae nor Podocominae. All Hinterhuberinae are terete-fruited and all Podocominae are pappose (viz Nesom 1994a, 1994b; Nesom & Robinson 2007; Sancho & Karaman-Castro 2008; Karaman-Castro & Urbatsch 2009; Sancho et al. 2010), thus flat-fruited epappose *Talamancaster* is at odds with both. In any event, *Talamancaster* matches no genus of tribe Astereae, and although unplaced subtribally, it is described here as a new genus. *Talamancaster* is named in advance of its appearance in *Flora Mesoamerica*, where its type is intentionally not stated, albeit given as heterotypic from *Lagenophora* sect. *Pseudomyriactis*.

TALAMANCASTER Pruski, **gen. nov. TYPE:** *Lagenophora westonii* Cuatr. [≡ *Talamancaster westonii* Cuatr.) Pruski].

Lagenophora sect. Pseudomyriactis Cabrera, Blumea 16: 303. 1966. **Type:** Lagenophora panamensis S.F. Blake $[\equiv Talamancaster panamensis (S.F. Blake) Pruski].$

Herbae perennes humiles rhizomatosae, foliis radicalibus vel caulinis et alternis; caulibus 1-10+ decumbentibus vel erectus simplicibus vel superne divaricatus; folia remota alterna simplicia vel bipinnatisecta sessilia vel longipetiolata, lamina oblanceolata vel orbicularis chartacea margine subintegra vel crenato-dentata; capitulescentia terminalis monocephala vel oligocephala cymosa; capitula radiata flosculis numerosis, involucrum campanulatum vel hemisphaericum, phyllaria herbacea paullum inaequalia pauciseriata, clinanthium epaleaceum convexum glabrum; flosculi radiati pistillati 1-4-seriati, corolla brevis rosea; flosculi disci hermaphroditi, corolla campanulata glabra quinquelobata, anthera palida apiculata; cypselae complanatae epapposae subrostratae obovatae, margines incrassatis, collum vicidum.

Small perennial herbs (rarely collected in first year and appearing as annuals), commonly with rhizomes, subscapose, remotely bracteate-leaved, or leafy to near capitula, never truly scapose; stems single or more commonly few-branched from base, often brownish red, leaves commonly basal and cauline, present at flowering, proximal ones spreading laterally, cauline leaves increasingly appressed distally toward capitula; roots fibrous; herbage with mostly patent simple non-colored trichomes. Leaves usually simple to infrequently bipinnatisect, alternate, often slightly rugulose adaxially, surfaces eglandular, glabrous or densely hirsute-pilose, margins crenate, toothed, to rarely deeply divided to near midrib; basal leaves few-several, typically present when flowering, usually long-petiolate; cauline leaves few-several, longer than internodes or often bracteate and remote, usually sessile. Capitulescence monocephalous to 1-few(-several)-capitulate in open cymes, main axis flexuous-ascending to sometimes stiffly erect, lateral branches not over-topping central axis, capitula pedunculate. Capitula radiate, small; involucre campanulate to hemispheric; phyllaries nearly subequal, 2–3-seriate, usually oblong, herbaceous, flat, green with thin brownish-red margins, midvein somewhat conspicuous, glabrous or sparsely pubescent, sometimes appearing pustular distally, margins ciliate and hyaline, apex usually subobtuse; clinanthium slightly convex, epaleate. Ray florets several-many, 1-4-seriate, pistillate, the outer ray florets with longer corollas than the inner series; corolla with limb mostly pinkish or pinkish-white to rarely ochroleucous (never yellow), fading to brownish red, weakly papillose-glandular (mostly on tube, trichomes biseriate, ca. 5-tiered) or glabrous, tube typically very short, usually only about as long as developed collar on cypselae, infrequently tube about twice as long as collar, limb directed outward, narrow, lanceolate or oblong, entire to weakly 2–3-denticulate, not lobed; style purplish. Disk florets relatively few and typically fewer in number than rays, bisexual, fertile and usually forming fruits; corolla campanulate, glabrous, tube, throat, and lobes more or less subequal, characteristically 5-lobed (very rarely an occasional capitulum with a single 4-lobed corolla, never consistently 4-merous), pink fading to brownish red distally, often green proximally, lobes spreading to sometimes reflexed; anthers thecae often yellowish, rounded basally, appendages flat, apiculate, distinctly narrower than anther thecae, laterally thin-celled, endothecial tissue polarized; style 2-veined, one vein each continuing to about middle of branches (i.e., near end of stigmatic surfaces), base simple, never nodular, glabrous, immersed within small annular nectary, branches triangular-lanceolate, pinkish-red, stigmatic lines proximal, marginal but not very distinct, about as long as sterile appendage, appendage acute at apex, papillose abaxially, papillae sometimes present abaxially also on fertile portion, papillae oblong, often moderately spreading. Cypselae epappose, obovate (or sometimes disk cypselae subcylindrical), compressed (radially), exalate, both faces brown, rarely with midnerve visible or developed, raphide crystals not seen in pericarp, with pale-colored thickened lateral margins, rays and usually disks with narrowed apical collared (short-rostrate), collar densely glandular and sticky, collar of disk florets often smaller or in two species consistently vestigial, margins glabrous or infrequently pubescent with duplex trichomes and/or biseriate papillose glands, plants sometimes collected immature with nonfully developed cypselae in disk florets narrower than the more mature peripheral rays, infrequently disk florets not pollinated and then the sterile subcylindrical ovary nearly as long as ray cypselae.

Typology. Lagenophora westonii is designated as the generitype — it has all critical generic features, i.e., it is moderately leafy stemmed, has glabrous 5-merous disk corollas, and has bisexual disk florets forming fruit. The type of Lagenophora sect. Pseudomyriactis is L. panamensis, the earliest named species. But Cabrera (1966) characterized (erroneously I believe) L. panamensis as having disk flowers "apparently mostly sterile," and it is thus not chosen as the generitype of Talamancaster. As such, Talamancaster and Lagenophora sect. Pseudomyriactis are heterotypic and not nomenclatural synonyms.

Etymology. Although the genus ranges from the Venezuelan Andes (Fig. 9A) to the Sierra de los Cuchumatanes, Guatemala (Fig. 9B), the masculine generic name *Talamancaster* is coined to draw attention to the geographic epicenter (the Talamanca Mountains; Fig. 10) of the genus as well as its placement in tribe Astereae.

The "core genera" (Nesom 2001) of the *Lagenophora* group of Grangeoids are mostly small herbs characterized by their 2+-seriate pistillate florets and flat viscid-collared cypselae with no pappus. Cabrera (1966) and Sancho et al. (2015) suggested such fruits could be bird-dispersed. The species are very similar to one another and are restricted to geologically relatively recent Alpine mountain tops (viz Graham 2006; Van der Hammen & Cleef 1986). For example, Gregory-Wodzicki (2000) gave the final northern Andean uplift at about 2.7 mya, and Rauscher (2002) noted suggestions that páramos developed soon thereafter. Five of six species treated here in *Talamancaster* are found in the páramo ecosystem, although they are also found sporadically in wet forest and grassy or marshy areas below páramos. Islebe and Kappelle (1994) stated that the Pleistocene glaciation carved the U-shaped valleys on Chirripó in the Talamancas (Fig. 10A) and in the Cuchumatanes. Other important studies of Costa Rican páramos include those of Weber (1958) and Kappelle and Horn (2005, 2016).

The *Lagenophora* group contains a few genera with functionally staminate disk florets, and on occasion disk florets in *Talamancaster* may not (or have been said to not) set fruit. For example, see Cabrera's (1966: 305) characterization of disk florets in *T. panamensis* as "apparently mostly sterile" as compared to the Sidney Fay Blake holotype sketch of the species that is reproduced here in Figure 1. The Blake sketch instead shows an obviously fertile bisexual disk floret with a developing cypsela. Also, in the minute capitula of *T. minusculus* non-fruit forming disks may be found, but neither this nor Cabrera's statement are taken by me as more taxonomically significant than the

glabrous disk corolla character that serves to unite the species of *Talamancaster*. The genera *Rumfordia* DC. (tribe Millerieae; Sanders 1977), *Zyzyura* H. Rob. & Pruski (tribe Eupatorieae; Robinson & Pruski 2013), and *Electranthera* Mesfin, Crawford, & Pruski (Tribe Coreopsideae; Pruski et al. 2015) are 'typical' Compositae characterized by their fertile bisexual disk florets, but on occasion inner disks of these latter three genera were similarly noted not always to reach anthesis or form fruits.

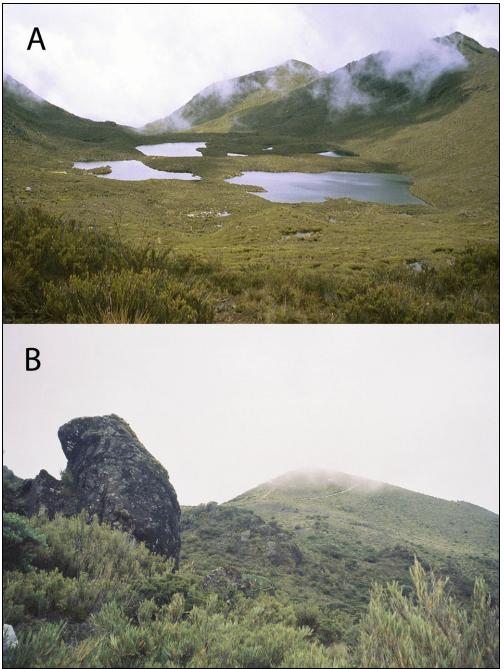


Figure 10. Grassy páramo habitats of *Talamancaster* in the Cordillera de Talamanca, Costa Rica. A. Lakes of glacier-carved U-shaped (viz Islebe & Kappelle 1994) Valle de las Morrenas, Cerro Chirripó, locality of *Pruski et al. 3945*. B. Summit (background) of Cerro de la Muerte (Cerro Buenavista), locality of *Pruski et al. 3857*. *Chusquea* spp. are dominant bamboos in each páramo.

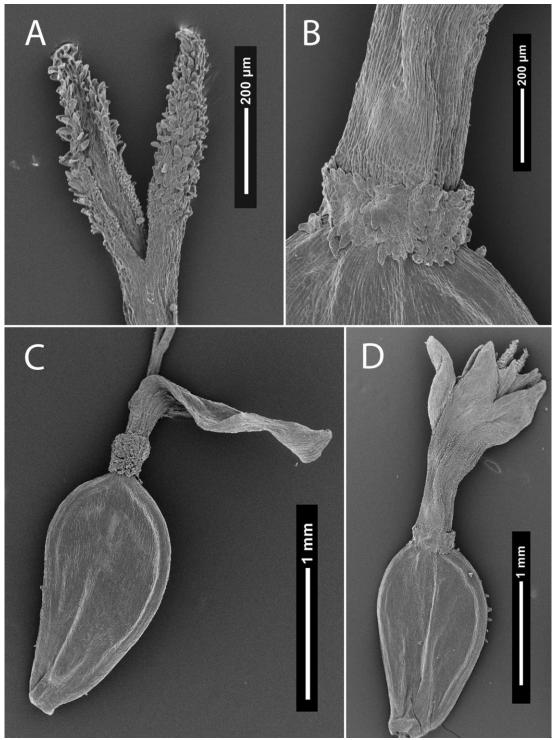


Figure 11. SEM micrographs of *Talamancaster andinus*, showing diagnostic generic characters. A. Disk floret style branches, adaxial (inner) face of one branch (on left) showing proximal ventromarginal stigmatic lines, and abaxial (outer) face of second branch (on right) showing collecting papillae concentrated on sterile apical appendage. B. Close-up of glandular collar of disk floret. C. Ray floret showing compressed cypsela with viscid-glandular collar. D. Bisexual disk floret showing the glabrous, 5-lobed, campanulate corolla and maturing fruit with collar. The abaxial marginal rib (on right) of the cypsela is pubescent with duplex trichomes and biseriate papillose-glands. (*Pruski et al. 3935*, MO).

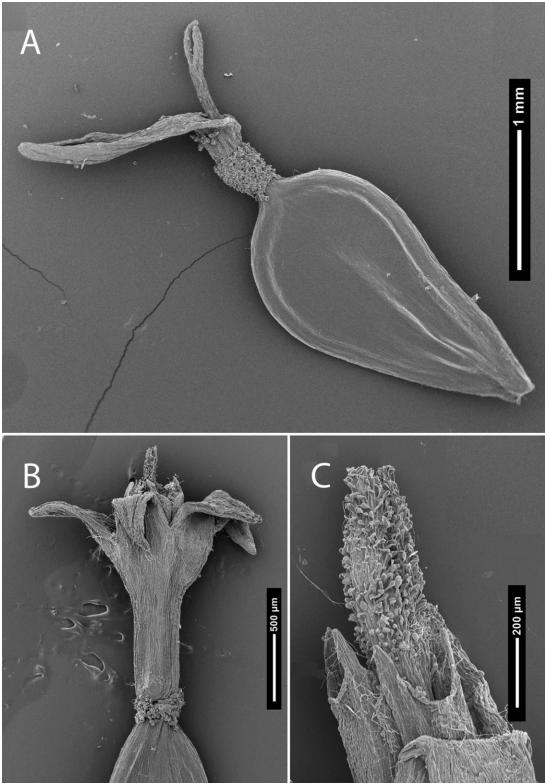


Figure 12. SEM micrographs of *Talamancaster westonii*, the generitype, showing diagnostic generic characters. A. Ray floret with maturing compressed cypsela showing viscid glandular collar. B. Disk floret showing glabrous, campanulate, 5-merous corolla and collar of immature fruit. C. Apiculate anther appendages (left center) and style showing distal abaxial papillae. (*Weston 5867*, MO, an isotype).

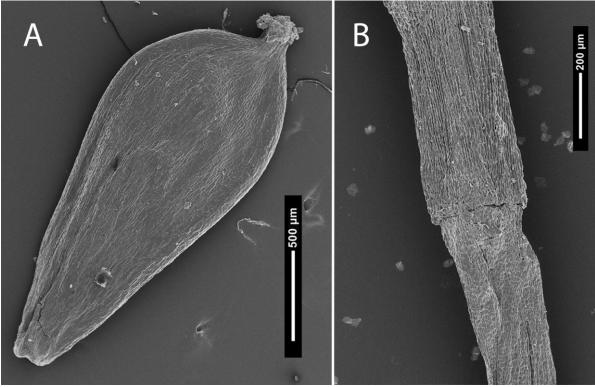


Figure 13. SEM micrographs of *Talamancaster minusculus*. A. Immature ray cypsela showing the short (much shorter than usual) glandular collar. B. Non-pollinated disk floret showing corolla tube and the cylindrical ovary without a collar; the disk ovary is about as long as ray cypsela. (*Davidse & Herrera 29400*, MO).

The leafy-stemmed vs. subscapose nature of the plants may vary but is nevertheless used as a key character below in lead 2. For example, both leafy-stemmed *Talamancaster andinus* and *T. cuchumatanicus* in late flower may have the central capitulum long-pedunculate and ebracteate, but these forms still key as leafy-stemmed because the proximal portions of the stems are leafy with leaves longer than internodes.

Among Mesoamerican Astereae, in its flat, epappose cypselae and non-yellow radiate capitula, *Talamancaster* is similar to *Astranthium* Nutt., *Bellis* L., and *Egletes* Cass. Both *Lagenophora* and *Myriactis* have been treated traditionally (e.g., Bentham & Hooker 1873; Hoffmann 1890-1894) in subtribe Bellidinae. On occasion *Talamancaster* has been identified as *Bellis*, which along with *Astranthium*, differs by cypselae neither rostrate nor apically collared. *Egletes* differs from other Central American genera by its stipitate-glandular herbage. *Lagenophora* and *Myriactis* were subsequently placed (Beaman & De Jong 1965) in Grangeinae and more recently into Lagenophorinae (Nesom 1994a; Nesom & Robinson 2007), although the phylogeny of Noyes and Rieseberg (1999) would preclude placing *Talamancaster* in Lagenophorinae.

Smith and Turner (1975) listed *Talamancaster andinus* as possibly having the Kranz syndrome. Beaman and De Jong (1965) suggested *T. cuchumatanicus* could be autogamous because of its low population density.

Talamancaster is known only from Guatemala, Costa Rica, Panama, and Venezuela (Appendix 1), but should be looked for in Mexico and Colombia. It was not reported in Colombia by Cuatrecasas (1969). A single species of *Talamancaster* is known from Guatemala and a single from Venezuela; three species are reported in Panama (one endemic); and four species are found in Costa

Rica (one endemic). Three of the six species of *Talamancaster* are single-country endemics: *T. cuchumatanicus*, *T. panamensis*, and *T. sakiranus* (Fig. 21). Two species occur in both Costa Rica and Panama: *T. minusculus* and *T. westonii*; and only *T. andinus* occurs in Costa Rica and Venezuela. Only *T. andinus* occurs in *Espeletia* páramos (Fig. 9A) and only *T. cuchumatanicus* occurs in extra-páramo alpine meadows and alpine pine forests (Fig. 9B). Five species are known from páramo and/or subpáramo vegetation (viz Figs. 9A, 10). *Talamancaster andinus* and *T. panamensis* are the only species known to occur on volcanos. The most broadly distributed species is *T. andinus*.

Many Costa Rican localities cited below are along the continental divide or on Chirripó and mostly on the borders between one of more of the following: Cartago, Limon, Puntarenas, and San Jose. The collections cited here are sometimes simply listed in alphabetic order by collector without mention of provinces.

Key to species of Talamancaster

- 2. Plants subscapose, cauline leaves proximal, remote and bracteate; disk cypselae without collars.
 - Basal leaf blades glabrous, narrowly obovate to spatulate, base long-attenuate; southern Talamancas.
 Basal leaf blades hirsute-pilose, ovate, bases short-attenuate; Cerro de la Muerte and Cerro
- 2. Plants leafy-stemmed; disk cypselae with collars.

 - 4. Leaf blades abaxial surface hirsutulous to pilose or villous, adaxial surfaces sometimes subglabrous (*T. cuchumatanicus*) or hirsutulous to pilose or villous; Guatemala, Costa Rica, and /or Venezuela.
- TALAMANCASTER ANDINUS (V.M. Badillo) Pruski, comb. nov. Lagenophora andina V.M. Badillo, Darwiniana 7: 331. 1947. Myriactis andina (V.M. Badillo) M.C. Vélez, Mitt. Bot. München 17: 38. 1981. TYPE: VENEZUELA. Mérida. Laguna Mucubají, 3600 m, 21 Jul 1944, Steyermark 57501 (holotype: VEN; isotypes: F, MO, NY, US). Figs. 7–8, 11, 14–17.

Perennial leafy-stemmed (at least proximally) herbs 7.5–18 cm tall, not subscapose; stems ascending, 1-6 from base, leaves in basal rosettes but stems leafy with leaves only slightly smaller to near capitula, villous. **Basal leaves** long-petiolate, blade $2.5-5 \times 1.3-2.5$ cm, ovate to elliptic, surfaces villous, base short-attenuate, margins 7–8-toothed, apex subobtuse, petiole 3–5 cm; cauline leaves $1.5-3 \times ca$. 0.4-0.8 mm, sessile, surfaces hirsutulous to pilose-villous, base clasping, vaginate, margins 1–3-toothed, apex subobtuse to obtuse. **Capitulescence** in cymes, 1–4-capitulate, ultimate capitulum sometimes held above distal most cauline leaves, at least capitula on lateral branches

mostly held within stem leaves as pressed and seen on herbarium sheets; peduncles 3–30 mm long, sparsely villous. **Capitula** (40-)50–72-flowered; involucre 4–6 × 5–7 mm, hemispheric, sometimes moderately closely subtended by very small bracteate leaf partly overlapping phyllaries but more acute than phyllaries; phyllaries subequal or the outermost shorter, 2–3-seriate, $3.5-6 \times 0.8-1$ mm, relatively narrowly acute to nearly obtuse. **Ray florets** (25–)35–55, 2-seriate; corolla 1.5–2.2(–2.6) mm long, glabrous or sometimes weakly papillose abaxially at tube-limb juncture, tube 0.3–0.4(–0.8) mm long, white to brownish-purple, glabrous or glandular, limb ca. 1.5-1.8 mm long, apex bidentate. **Disk florets** 15-17; corolla (4–)5(–6)-lobed, 1.8-2.1 mm long, yellow-green, lobes 0.6–0.9 mm long; anthers small, 0.4-0.5 mm long. **Cypselae** 1.5–2 mm long, cypselae of rays and disks more or less similar, body glabrous or very rarely papillae 50 µm long or twin trichomes ca. 70 µm long, collar in rays 0.3-0.4 mm long, collar in disks to ca. 0.2 mm long.



Figure 14. Line drawing of *Talamancaster andinus*, showing collars on both ray and disk cypselae. (Reproduced from Aristeguieta 1964: 258, t 30 as *Lagenophora andina*).



Figure 15. Habit photograph on Cerro de la Muerte (Cerro Buenavista) of *Talamancaster andinus*, showing the leafy, erect or prostrate stems. (*Pruski et al. 3857*).

Distribution and ecology. *Talamancaster andinus* is the most widespread species of *Talamancaster*. It is the only species to occur in *Espeletia* páramos (Mérida, Venezuela) and the only Costa Rican member found on volcanos. The species flowers mostly from July–September at about 2900–4000+ meters elevation.

Representative collections examined. COSTA RICA. Cerro de la Muerte, 3400–3500 m, 25 Jul 1945, *Holm & Iltis 597* (MO); Floor of the crater of Turrialba Volcano, 3200 m, 26 Jul 1965, *Lent 674* (MO); Cordillera de Talamanca, Cerro de la Muerte (Cerro Buenavista), 3400 m, 9 Sep 2004, *Pruski et al. 3857* (INB, LP, MO); between Cerro Jaboncillo and Cerro Estaquero, 2960 m, 9 Sep 2004 (late fr), *Pruski et al. 3873* (INB, LP, MEXU, MO); Cerro Chirripó, Valle de los Conejos, 3500 m, 15 Sep 2004, *Pruski et al. 3915* (INB, MO); Cerro Chirripó, Crestones, 3460 m, 15 Sep 2004, *Pruski et al. 3926* (INB, LP, MO); Cerro Chirripó, Slightly north of Cerro Pirámide, 3640–3660 m, 16 Sep 2004, *Pruski et al. 3935* (INB, LP, MO, NY, USM, VEN); Cerro Chirripó, Valle de las Morrenas, 3475 m, 16 Sep 2004, *Pruski et al. 3945* (INB, LP, MO, NY, USM, VEN); Cerro Chirripó, Crestones, 3460 m, 17 Sep 2004, *Pruski et al. 3949* (INB, MO). **VENEZUELA. Mérida.** Laguna Negra, 1952, *Aristeguieta 978* (VEN; cited by Aristeguieta 1964); Pico de Mucunuque, 4000+ m, 26 Nov 1959, *Barclay & Juajibioy 9917* (MO, US); Laguna Negra, 3500 m, 12 Sep 1971, *López-Figueiras & Huber 8766* (MERF, US); Páramo de Muchuchies, 3630 m, 17–30 Sep 1952, *Humbert 26310* (P, US); Cordillera de los Andes, 1968–1969, *Oberwinkler 13915* (M). **Trujillo.** Tuñame–Guirigay, 3200 m, Aug 1958, *Aristeguieta 3522* (US, VEN; cited by Smith & Turner 1975).



Figure 16. Representative specimen of *Talamancaster andinus* showing fibrous roots, spreading proximal leaves, ascending distal leaves, and a few-branched flowering stem. (*Pruski et al. 3935*, unmounted duplicate).



Figure 17. Capitula of *Talamancaster andinus*, the terminal capitulum showing biseriate pinkish ray corollas and nearly subequal, moderately herbaceous phyllaries, lateral capitulum on right is immature. (*Pruski et al. 3935*, unmounted duplicate). [A metric scale is towards the left].

Here I follow determinations of Jose Cuatrecasas (in sched.), who referred Costa Rican material to this singular Andean species, typified by Venezuelan material. In Costa Rica plants where the terminal capitulum is sometimes exserted, *T. andinus* often resembles *T. sakiranus* but *T. andinus* may generally be distinguished by the more densely pubescent stem leaves, disk cypselae with collar, and on average the slightly shorter ray corollas. In Venezuela, *López-Figueiras & Huber 8766* is an exceptionally robust specimen, whereas *Barclay & Juajibioy 9917* has larger than average capitula, but these are fewer-flowered than usual. The variation is not seen as taxonomically significant.

The protologue illustration of *Talamancaster andina* in Badillo (1947) shows a very narrow disk cypsela collar, but the more typical well-developed disk collar of the species is illustrated in Figure 14 (reproduced from Flora of Venezuela, Aristeguieta 1964) and Cabrera (1966: Fig. 10H). The fruits of *Oberwinkler 13915* (M) were illustrated by Vélez (1981).

 TALAMANCASTER CUCHUMATANICUS (Beaman & De Jong) Pruski, comb. nov. Lagenophora cuchumatanica Beaman & De Jong, Rhodora 67: 36, pl. 1309. 1965. Myriactis cuchumatanica (Beaman & De Jong) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. TYPE: GUATEMALA. Huehuetenango. Sierra de los Cuchumatanes, between Tojiah [Tojuia] and Chemal at Km 320 on Ruta Nacional 9 N, ca. 3365 m, 29 Jul 1960, Beaman 3756 (holotype: MSC; isotypes: DUKE, F, GH, K, LP, TEX, UC, US-2). Figs. 18–19.

Low perennial leafy-stemmed herbs 8–21 cm tall from small rhizome-caudex to ca. 0.5 cm diam., usually with 3–7 basal leaves and 1–4 flowering stems from very base; roots several, to 10+

cm long, fibrous; stems decumbent or sometimes ascending, simple, pilose, trichomes mostly 0.5–0.8 mm long, often leafy to near apex with 7-12 gradually reduced cauline leaves slightly longer than internodes, less commonly leafless peduncles elongating in fruit to ca. 7 cm long. Basal leaves few, long-petiolate, blade $1-1.7 \times 0.8-1.3$ cm, elliptic-ovate to orbicular, subglabrous adaxially, abaxial surface pilose or sometimes only midrib pilose, trichomes to ca. 0.5 mm long, base rounded to narrowly cuneate, margins 3–5 crenate-dentate, apex obtuse, petiole 0.7–2.5(–3) cm long, villous, sheathing basally; cauline leaves narrowly winged-petiolar base or sessile, blade $0.9-1.8 \times 0.4-0.8$ cm, spatulate or obovate to oblanceolate, subglabrous adaxially, abaxial surface pilose or sometimes only midrib pilose, base subclasping or clasping, margins 1–3-toothed or distal most subentire, apex usually obtuse. Capitulescence monocephalous, stem leafy to near apex or sometimes greatly elongating in fruit; peduncle 0.5-3.5(-7) cm long, villous. Capitula 18-34-flowered; involucre 4-5 \times 5–7 mm, broadly campanulate; phyllaries nearly subequal, ca. 3-seriate, subimbricate and weakly overlapping distally especially once pressed, $3.5-5 \times 0.8-0.9$ mm, linear-lanceolate, greenish to near thinly scarious margins, sometimes purplish apically, midrib distinct, the few secondary veins basically obscure, glabrous or outer ones sparsely pilose proximally, distal margins often weakly fimbrillate-ciliolate, apex acute to narrowly obtuse. Ray florets 10-20, 1-seriate; corolla 2.1-2.4 mm long, tube 0.1–0.2 mm long, obviously glandular-pubescent, limb $2-2.2 \times 0.5-0.7$ mm, ochroleucous or becoming purplish and reflexed with age, glabrous, apex 2–3-denticulate. Disk florets 8–14, bisexual; corolla 1.8–2.4 mm long, yellow-green, lobes 0.7–0.8 mm long; style branches ca. 0.6 mm long, stigmatic surface and sterile appendage subequal. Cypselae 2.8-3.7 mm long, rays and disks similar but ray rostrum ca. 0.4 mm long and disk rostrum ca. 0.2 mm long.

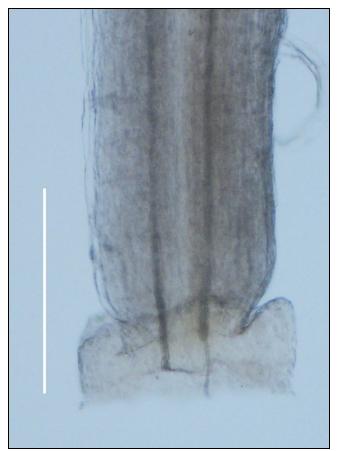


Figure 18. Low, annular nectary and immersed style base of *Talamancaster cuchumatanicus* showing two vascular bundles. (*De Jong 694*, NY). [Scale bar 0.1 mm].

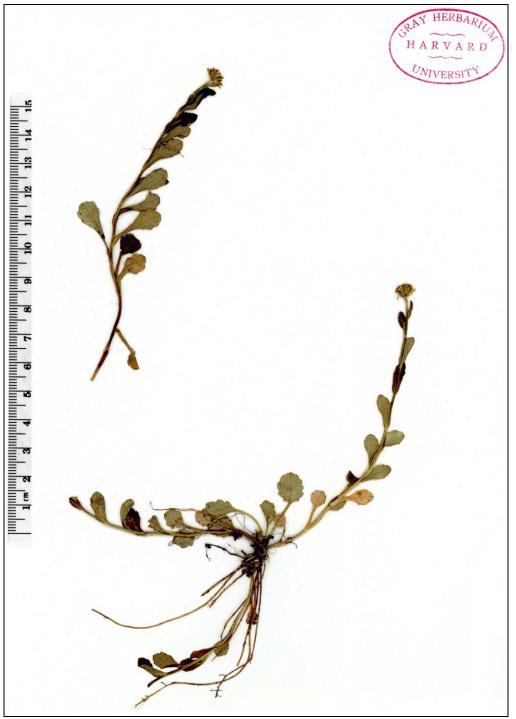


Figure 19. Isotype of Lagenophora cuchumatanica [\equiv Talamancaster cuchumatanicus] showing stems leafy to capitula. (Beaman 3756, GH).

Distribution and ecology. *Talamancaster cuchumatanicus* is endemic to alpine meadows and alpine pine forests in the Sierra de los Cuchumatanes and on the Tecúm Uman Ridge in southwestern Guatemala, where it has been collected from 3200–3365 meters elevation, flowering in July and August. The species was not found flowering by Rosa Ortiz and the author in March 2007 (off-season) when we searched for it at the type locality.

Additional collections. GUATEMALA. Huehuetenango. Sierra de los Cuchumatanes, between Chemal and Tojiah at km 319.5 on Ruta Nacional 9 N, 3365 m, 30 Jul 1960, *De Jong 694* (LP, MSC, NY, TEX); Sierra de los Cuchumatanes, 26 Aug 1961, *De Jong 1145* (MSC); Sierra de los Cuchumatanes, km 322–323, 3200 m, 27 Aug 1961, *De Jong 1147* (MSC). Totonicapán. On the Tecúm Uman Ridge at km 154 on Ruta Nacional No. 1, ca. 20 km E of Totonicapán, ca. 3340 m, 14 Aug 1960, *Beaman 4170* (MSC).

Talamancaster cuchumatanicus is the northernmost species of *Talamancaster* and is the sole species of the genus found well northwest of páramo ecosystems. Graham (2006) noted that uplift in the Cuchumatanes was in the Pliocene and subsequent development there of alpine habitats, however, roughly coincided with northern Andean uplift and associated development of páramo ecosystem that developed in the last 2.5 my. The species occurs in the Sierra de los Cuchumatanes and on the Tecúm Uman Ridge, which are each older geologically "than neighboring Quaternary volcanic cones" (Beaman & De Jong 1965). The species has not been found on nearby volcanos. *Talamancaster cuchumatanicus* is occasional at the type locality, but Beaman and De Jong (1965) noted that only a single plant was found on Tecúm Uman Ridge east of Totonicapán, some 100 kms SSE of the type locality.

Although most Compositae are outcrossers, Beaman and De Jong (1965) suggested, on the basis of being few-flowered with low population densities, that *T. cuchumatanicus* might be autogamous. The ray florets in species of *Talamancaster* are characteristically 2+-seriate, but in *T. cuchumatanicus* the ray florets are uniseriate. The uniseriate rays in *T. cuchumatanicus* appear to be basically a by-product of the capitula being few-flowered, and this condition is not interpreted here as generically significant. Elsewhere in *Talamancaster*, small-capitulate *T. minusculus* and *T. sakiranus* may also have uniseriate rays. Photographs of the cypselae of *T. cuchumatanicus* are found in the protologue, and fine line drawings appear in Cabrera (1966) and Nash (1976).

 TALAMANCASTER MINUSCULUS (Cuatr.) Pruski, comb. nov. Lagenophora minuscula Cuatr. (as "Lagenifera"), Phytologia 52: 172. 1982. Myriactis minuscula (Cuatr.) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. TYPE: PANAMA. Bocas del Toro (as Chiriquí on label and in protologue). Cerro Fábrega and vicinity (between Cerro Bine and north end of Cerro Fábrega ridge), near the Costa Rican frontier, 3150–3335 m, 7–8 Apr 1976, Weston 10154 (holotype: MO). Figs. 13, 20–21.

Perennial rhizomatous subscapose herbs 3-30 cm tall; the small caudex long-fibrous rooted; roots several, to 11 cm long, in small plants sometimes longer than the aerial portion of plant; stems spreading thence quickly ascending, 1–3 from base, sparsely hirsutulous to moderately pilose distally, glabrate proximally, cauline leaves remote and bracteate. Basal leaves long-petiolate, blade $1-2 \times 0.3-1$ cm, narrowly obovate to spatulate, surfaces glabrous, base long-attenuate, margins 2-4crenate-dentate, teeth forward-directed, apex obtuse, petiole 1-8 cm long, long-ciliate to sometimes glabrate, flattened proximally, vaginate at the base; cauline leaves 1–8, in the proximal half of stem, quickly reduced with the distal ones becoming remote, bracteate, sessile, $0.6-0.9 \times 0.1-0.2$ cm, oblong, often much shorter than internodes, surfaces subglabrous, base clasping, margins 1–3-toothed distally, apex broadly acute to nearly rounded. Capitulescence monocephalous. Capitula 27-41flowered; involucre $3-4 \times 4-6$ mm, broadly campanulate; phyllaries subequal or the outermost shorter, ca. 3-seriate, $2.5-3.5 \times 0.8-0.9$ mm, glabrous, sometimes purplish distally, apex broadly acute. Ray florets 17-23, 1-2-seriate; corolla 2.8-3.5 mm long, white or pinkish-tinged to reddishpurple with age, glabrous or infrequently tube sparsely glandular, tube 0.4–0.5 mm long, limb 2.4–3 x 0.5–0.6 mm, submarginally 2-nerved, apex 2(-3)-denticulate. Disk florets 10–18, sometimes abortive; corolla 2–2.4 mm long, (4–)5-lobed, white to greenish-yellow, tube ca. 0.7 mm long, lobes 0.5–0.7 mm long; style branches 0.7–0.8 mm long, stigmatic surface usually slightly shorter than the

narrowly pointed sterile appendage. **Cypselae** 1.8–2 mm long, collar of ray florets to ca. 0.1 mm long, irregularly sparse-glandular viscid towards corolla base, cypselae of disks florets without collar.

Distribution and ecology. *Talamancaster minusculus* is endemic to marshy páramos and scrub páramos in the Cordillera de Talamanca on Cerro Kasir in southeastern Costa Rica and near or on Cerro Itamut and Cerro Fábrega in western Panama (near the Costa Rican border). *Talamancaster minusculus* has been collected from 2950–3335 meters elevation, flowering in March–April and September.

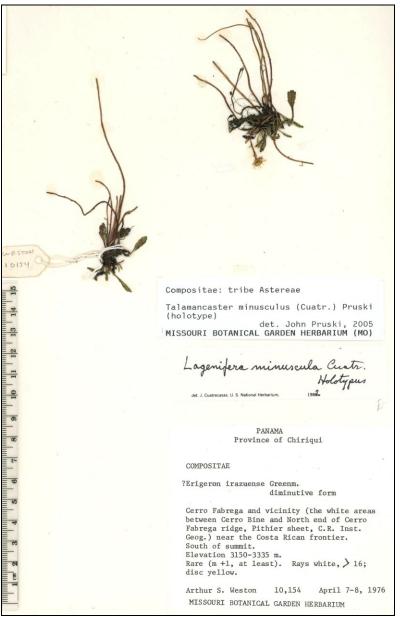


Figure 20. Holotype of *Lagenophora minuscula* [\equiv *Talamancaster minusculus*] showing the diminutive habit and short, leafless scapes. The plants are mounted upside-down with the several fibrous roots extending upwards towards the top of image. These diminutive plants have equally diminutive capitula and lessened physical space for florets; the ray florets are only 1-2-seriate, and the disk florets are sometimes abortive. (*Weston 10154*, MO).

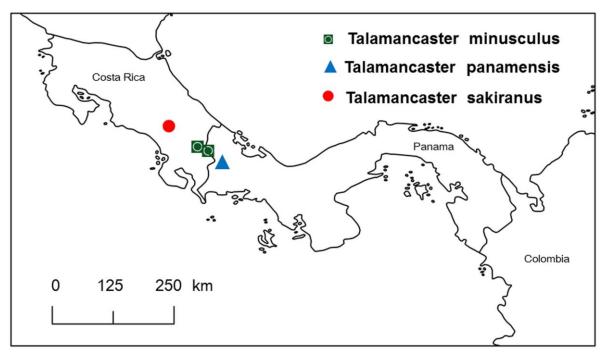


Figure 21. Distributions of regional endemics *Talamancaster minusculus*, *Talamancaster panamensis*, and *Talamancaster sakiranus* in southeastern Costa Rica and western Panama, the distributional epicenter of the genus. *Talamancaster westonii* occurs throughout much of the range of species plotted here.

Additional collections examined. COSTA RICA. Limon-Puntarenas border. Cordillera de Talamanca, Cerro Kasir, 2950 m, 22 Mar 1984, *Davidse et al. 25873* (MO); Cordillera de Talamanca, Cerro Kasir, 2950 m, 20 Sep 1984, *Davidse & Herrera 29400* (MO, US). PANAMA. Bocas del Toro. Between Itamut and Bine peaks, Fábrega massif, 3200 m, 5–9 Mar 1984, *Gómez et al. 22446* (CR, MO); 1–2 km SWW of Cerro Itamut camp, [Cerro Fábrega], 3175 m, 6–7 Mar 1984, *Gómez et al. 22593* (CR, MO), *Gómez et al. 22605* (CR, MO); Parque Nacional La Amistad, Cerro Fábrega, 3250 m, 18 Mar 2003, *Klitgaard et al. 843* (BM, MO, PMA).

Talamancaster minusculus has disk cypselae without apical collars but nevertheless is included in *Talamancaster* by its bisexual disk florets with glabrous, campanulate, 5-merous corollas. *Talamancaster minusculus* is distinct from similarly collarless *T. sakiranus*, although it is on average only smaller in stature, glabrous-leaved, and further to the southwest in distribution.

4. TALAMANCASTER PANAMENSIS (S.F. Blake) Pruski, comb. nov. Lagenophora panamensis S.F. Blake, Ann. Missouri Bot. Gard. 26: 314. 1939. Myriactis panamensis (S.F. Blake) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. TYPE: PANAMA. Chiriquí. Volcán de Chiriquí, 2500–3380 m [presumably 2900+ m], 4–6 Jul 1938, Woodson, Allen & Seibert 1047 (holotype: US; isotypes: GH, MO, NY, US ex NA). Figs. 1, 22–23.

Perennial rhizomatous leafy-stemmed herbs 7–26 cm tall, not subscapose; stems 1–5 from base, ascending, subglabrous to distal portions strigillose or hirsute, cauline leaves gradually reduced and overlapping in pressed specimens, slightly longer than the internodes. **Basal leaves** narrowly winged-petiolate to base, $2.5-5.5 \times 0.7-1.4$ cm, oblanceolate or narrowly obovate, surfaces glabrous or sometimes blade margin or petiole margin sparsely long-ciliate, base vaginate, long-attenuate with the narrow winged portion often longer than moderately expanded blade, margins 5–8-dentate, sometimes ciliate, teeth 1–2 mm deep, forward-directed, rarely petiole with a single lobe-tooth ca. 3.5 mm long, apex broadly acute to obtuse; cauline leaves often overlapping and longer than internodes,

 $1.5-2.5 \times 0.4-0.6$ cm, oblanceolate to oblong, surfaces glabrous, base clasping, margins 1–4-toothed, apex obtuse. **Capitulescence** cymose, leafy with capitula characteristically not held above leaves; peduncles 4–15 mm long, usually strigillose or hirsute. **Capitula** 1–5, ca. 85-flowered; involuce 4– $4.2 \times 6-8.5$ mm, hemispheric; phyllaries subequal or the outermost shorter, $3-4.2 \times ca$. 0.8 mm, ca. 3-seriate, glabrous or subglabrous, sometimes purplish distally. **Ray florets** ca. 57, 2-seriate; corolla 2.2–2.7 mm long, glabrous tube 0.2–0.3 mm long, limb 2–2.4 mm long, glabrous. **Disk florets** ca. 28; corolla 1.6–2.2 mm long, lobes 0.6–0.8 mm long. **Cypselae** 1.8–2 mm long, glabrous, ray and disk cypselae more or less similar but the disks sometimes narrower and disk collar 0.1 mm tall, the ray cypselae with collar ca. 0.3 mm long.



Figure 22. Holotype of *Lagenophora panamensis* [\equiv *Talamancaster panamensis*] showing the stems leafy to near apex; a photograph of this specimen unmounted appears in the protologue. (*Woodson et al. 1047*, US).

Distribution and ecology. *Talamancaster panamensis* is the sole species endemic to Volcán Chiriquí (Volcán Barú) and is distinguished by its simple leaves from *T. westonii*, the other congener found (in part) on Chiriquí. The species flowers mostly in July and August seemingly from about 2900–3200 meters elevation.

Additional collections examined. PANAMA. Chiriquí. Volcán de Chiriquí, Potrero Muleto, 10400 ft. [= 3170 m], 18 Jul 1938, *Davidson 1037* p.p. (GH); Volcán Barú, bottom of 2nd crater, 3000 m, 16 Aug 1983, *Schmalzel et al. 1731 p.p.* (MO; voucher cited by Noyes & Rieseberg 1999). Both collections are mixed with *Erigeron maxonii* S.F. Blake (viz Nesom & Pruski 2011).

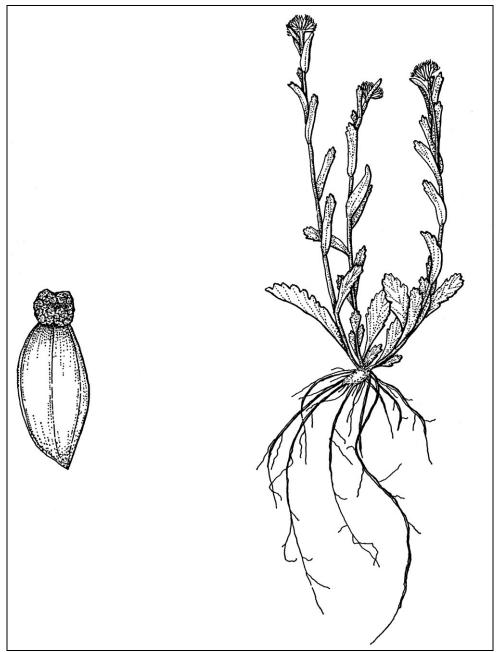


Figure 23. Line drawing of *Talamancaster panamensis* from the Flora of Panama, showing a ray cypsela with viscid-glandular collar. (Reproduced from D'Arcy 1975: 1030, t. 39 as *Lagenophora panamensis*).

Talamancaster panamensis has simple basal leaves, and although an occasional lanceolate petiole lobe has been seen it is never consistently and obvious deep-lobed as in *T. westonii*. The two species are recognized as distinct, but they are obviously similar to each other. The report by Weston (1981) of *T. panamensis* is taken here as erroneous, and presumably is in reference to material of either *T. andinus* or *T. westonii*, the two species that are known to occur on Chirripó. I have seen Weston material from Chirripó of only *T. westonii*, although it seems equally likely that the Weston report may be based on the much more common *T. andinus*. An illustration of *T. panamensis* from the Flora of Panama (D'Arcy 1975) is reproduced here as Figure 23, and another was given by Cabrera (1966).

 TALAMANCASTER SAKIRANUS (Cuatr.) Pruski, comb. nov. Lagenophora sakirana Cuatr. (as "Lagenifera"), Phytologia 52: 170. 1982. Myriactis sakirana (Cuatr.) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. TYPE: COSTA RICA. Cerro Sakira, 3300 m, 14 Aug 1969, Weston 5834 (holotype: US). Figs. 21, 24.

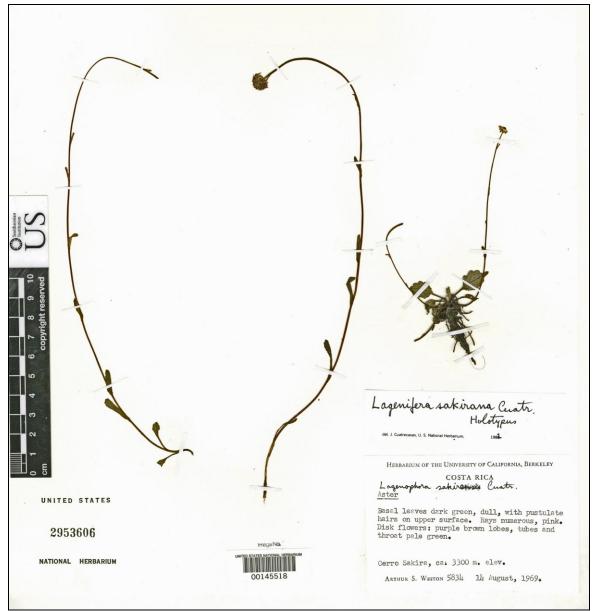


Figure 24. Holotype of *Lagenophora sakirana* [\equiv *Talamancaster sakiranus*] showing the weakly leafy stems. (*Weston.* 5834, US).

Perennial rhizomatous subscapose herbs 8-25(-40) cm tall; stems ascending, 1-2 from base, sparsely pilose, cauline leaves remote and bracteate. **Basal leaves** present or absent at flowering, long-petiolate, blade $1.5-2.5 \times 1-1.4$ cm, ovate, surfaces hirsute-pilose, base short-attenuate, margins shortly 4–7-crenate, apex obtuse, petiole 1-3.5 cm long, pilose, vaginate basally, purplish; cauline leaves bracteate, 2-6, sessile, $0.5-2 \times 0.1-0.3$ cm, oblong, surfaces subglabrous, margins very sparsely ciliate, base subclasping, margins 1-2-toothed distally, apex obtuse to acute. **Capitulescence** monocephalous to much less commonly cymose with 1-2 lateral capitula, on leafless

peduncles held well above rosette leaves. **Capitula** 40–48-flowered; involucre $3.5-4.2 \times 4-5$ mm, broadly campanulate; phyllaries 2–3-seriate, glabrous, $3-4.2 \times 0.7-1.1$ mm, apex sometimes fimbriate. **Ray florets** 25–30, 1-seriate; corolla 2.1–3.1 mm long, tube ca. 0.3 mm long, glabrous or with a few glandular trichomes, limb 1.8–2.8 mm long, glabrous. **Disk florets** 15–18; corolla 2–3 mm long. **Cypselae** 2–2.2 mm long, glabrous, ray cypselae with collar 0.2–0.3 mm long, cypselae of central florets reduced, narrow, collar absent (sometimes very thinly annular), eglandular.

Distribution and ecology. *Talamancaster sakiranus* is a rare endemic in the Cordillera de Talamanca, where it has been found on Cerro de la Muerte and Cerro Sakira. It has been collected at about 3300–3400 meters elevation flowering in August and September.

Additional collections examined. COSTA RICA. Cordillera de Talamanca, Cerro Sakira, 3400 m, 10 Sep 2004, *Pruski et al. 3873* (INB, unicate, only one small plant found, topotype); Cerro de la Muerte, s. elev., 27 Aug 1967, *Raven 22062* (F).

6. TALAMANCASTER WESTONII (Cuatr.) Pruski, comb. nov. Lagenophora westonii Cuatr. (as "Lagenifera"), Phytologia 52: 169. 1982. Myriactis westonii (Cuatr.) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. TYPE: COSTA RICA. Cerro Jaboncillo, 3200 m, 14 Aug 1969, Weston 5867 (holotype: US; isotype: MO). Figs. 12, 25–27.

Perennial leafy-stemmed herbs 17–32 cm tall, not subscapose; stems ascending, bracteateleafy, pilose-villous, usually few-branched in the capitulescence, cauline leaves gradually reduced. **Basal leaves** long-petiolate, blade $6-7 \times 2.5-3$ cm, pinnatilobed to bipinnatisect, lobes oblong and subobtuse, surfaces pilose-villous to very sparsely so, margins ciliate, petiole 3–4.5 cm long, pilosevillous, vaginate at the base; cauline leaves bracteate, sessile, blade $2.5-3 \times 0.4-1$ cm, base clasping, the proximal cauline leaves mostly pinnatifid, the distal cauline leaves mostly 2–3-lobed, lobes oblong. **Capitulescence** in racemes or cymose or sometimes monocephalous; peduncles 5–18 mm long, pilose-villous to densely so immediately below capitulum. **Capitula** (1–)2–5, ca. 54-flowered; involucre $3.3-5 \times 5.5-8$ mm, campanulate to hemispheric; phyllaries 2–3-seriate, $3-5 \times 0.8-0.9$ mm, glabrous, apex often purplish, acute to obtuse, often slightly fimbriate or very narrowly hyalinemargined. **Ray florets** ca. 40, 2-seriate; corolla 2.2–2.8 mm long, white to purplish, tube ca. 0.3 mm long, glandular-papillose, limb 1.9–2.5 mm long. **Disk florets** ca. 14; corolla 2.2–3 mm long, yellow-green, lobes 0.6–1 mm long. **Cypselae** 1.5–3 mm long, ray and disk cypselae similar with collar well-developed, or sometimes disk collar minute and represented only by a narrow ring of viscid glands.

Distribution and ecology. *Talamancaster westonii* is the type of the genus, and among species endemic to Costa Rica and/or Panama it has the broadest distribution. The species was described from the northwestern Cerro Jaboncillo but occurs southeast to Volcán Chiriquí (Barú) and flowers sporadically year-round, at 3000–3500 meters elevation.

Additional collections examined. COSTA RICA. P.N. Chirripó, Sabana Los Leones, 3300 m, 30 Jan 2002, *Alfaro 3858* (INB, MO); Sabanas del Cerro Echandi, 3000–3150 m, 13 Aug 1997, *Quesada et al. 1999* (INB, MO); Valle de los Lagos, Chirripó massif, 3500 m, 7 Sep 1969, *Weston 6064* (US). PANAMA. Bocas del Toro. 1-2 km SWW of Itamut camp, 3175 m, 6-7 Mar 1984, *Gómez et al. 22601* (CR, MO); 2 km SW of Itamut camp, Fábrega, 3100-3200 m, 8 Mar 1984, *Gómez et al. 22645* (CR, MO). Chiriquí. S of Paso Respingo, N of Volcán summit, 10000–10800 ft. [= 3048–3292 m], 4 Apr 1979, *Hammel et al. 6717* (MO); E side of Volcán Barú, ca. 3000 m, 24 Jul 1975, *Mori & Bolten 7436* (MO).

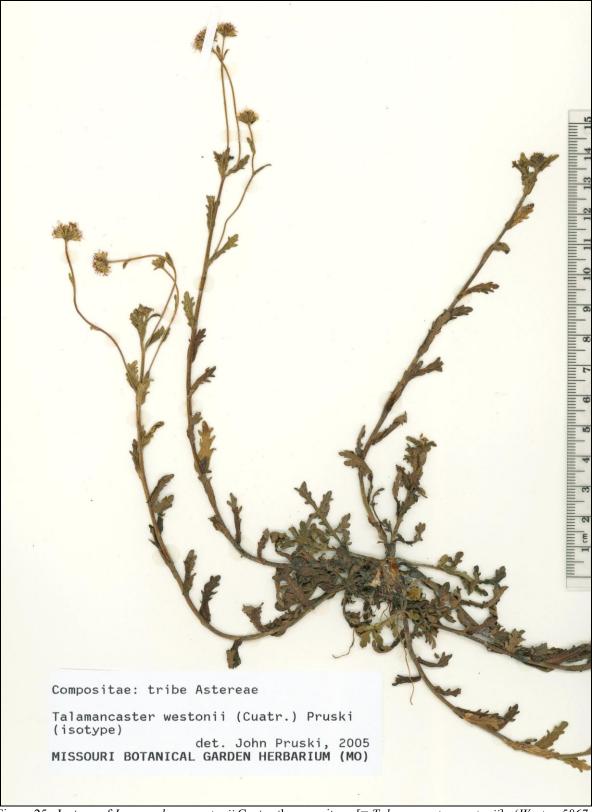


Figure 25. Isotype of *Lagenophora westonii* Cuatr., the generitype [\equiv *Talamancaster westonii*]. (*Weston 5867*, MO).



Figure 26. Representative specimen of *Talamancaster westonii* showing pinnatifid basal leaves. (*Quesada et al. 1999*, unmounted duplicate).

Talamancaster westonii is the generitype of *Talamancaster* and is diagnosed by its pinnatisect leaves and often cymose capitulescence. The disk cypselae collar size may be variable, sometimes being hard to discern and seen only as a low ring of viscid glands. Typical *T. westonii* has deeply lobed leaves with surfaces moderately hirsute. Two collections seen from the highest reaches of Volcán Chiriquí, however, have leaves weakly pinnatilobed with subglabrous surfaces, and recall the very narrowly endemic *T. minusculus*. The low ring of disk collar glands and biseriate rays of the two odd-leaved Volcán Chiriquí collections are used to refer this material to *T. westonii*, albeit these placed there with some hesitancy.



Figure 27. Capitula of *Talamancaster westonii*, showing biseriate ray florets and nearly subequal, moderately herbaceous phyllaries. (*Quesada et al. 1999*, unmounted duplicate). [A metric scale is towards the left].

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Guatemala:		
Cuchumatanes, Tecúm Uman Ridge	Talamancaster cuchumatanicus (endemic to Guatemala)	
(Pine forests)		
Costa Rica:		
Volcán Turrialba	Talamancaster andinus	
Costa Rica:		
Cerro Jaboncillo, Cerro Sakira	Talamancaster andinus	
	Talamancaster sakiranus (endemic to Costa Rica)	
	Talamancaster westonii	
Costa Rica:		
Cerro de la Muerte (Cerro	Talamancaster andinus	
Buenavista)	Talamancaster sakiranus (endemic to Costa Rica)	
Costa Rica:		
Cerro Chirripó	Talamancaster andinus	
	Talamancaster westonii	
Costa Rica:		
Cerro Kasir	Talamancaster minusculus	
Costa Rica:		
Cerro Echandi	Talamancaster westonii	
Panama:		
Cerro Fábrega, Cerro Bine, and	Talamancaster minusculus	
Cerro Itamut (these peaks are only a	Talamancaster westonii	
few kms from Costa Rican Cerro		
Echandi)		
Panama:		
Volcán de Chiriquí (Volcán Barú)	Talamancaster panamensis (single locality endemic)	
	Talamancaster westonii	
Venezuela:		
Mérida, Trujillo (<i>Espeletia</i> páramos)	Talamancaster andinus	

APPENDIX 1. Localities (from NW to SE) and reported *Talamancaster* species.