

Hecastocleis shockleyi (Hecastocleideae), the desert enigma: close encounters with one of Compositae's most solitary lineages

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DOI: <http://dx.doi.org/10.53875/capitulum.04.1.03>

ABSTRACT

The desert subshrub *Hecastocleis shockleyi* is the sole member of tribe Hecastocleideae and sub-family Hecastocleidoideae, a species that raises questions about the biogeographic history of the Compositae. It features a unique floral morphology, with single-flowered capitula aggregated together in a terminal inflorescence that is subtended by spiny, papery bracts. Additionally, its corolla and style branches resemble those of basal members of the family. Molecular phylogenetic data support *H. shockleyi* as an early diverging lineage sister to all other members of the large radiation of subfamilies Carduoideae and Asteroideae, yet it is found only in the southwest U.S., far from other early diverging lineages found in South America. In spite of this mysterious biogeography, which links the family's early radiations to its eventual global spread, little is known about the ecology and genetic diversity of the species. This report briefly summarizes three field trips in 2023, 2024, and 2025 that aimed to address this gap in our understanding of this charismatic and important Compositae.

Keywords: Asteraceae, biogeography, dispersal, Great Basin, Mojave, natural history, phenology, pollination.

INTRODUCTION

Few Compositae stand out to synantherologists as much as the desert subshrub *Hecastocleis shockleyi* A. Gray (Hecastocleideae), lone member of sub-family Hecastocleidoideae. Described in the late 1800s (Gray, 1881), *Hecastocleis* bears a name aptly derived from the Greek *hekastos* ("each") and *kleis* ("shut up"), pointing to the plant's unique floral structure (Williams, 1977). Each capitulum of *H. shockleyi* features just a single floret subtended by a multiseriate involucre, but 3–5 of these capitula are aggregated together at the end of stems and enveloped by 4–5 ovate to orbiculate bracts with spiny margins that turn from light green to white

during flowering. The specific epithet commemorates a prolific, early collector of Nevada's flora, William H. Shockley (1855–1925).

The morphology of *H. shockleyi* is even more striking in relation to its biogeography. It shares many characteristics with other early-divergent lineages of the family. For example, its actinomorphic corolla features five, deeply dissected lobes that reflex at ninety degrees, and its style features reduced branches with a continuous stigmatic surface, both common characters of the Barnadesieae. Yet, unlike those early-divergent lineages it is restricted to western North America, far from the family's South American origins. In the dated phylogeny of Mandel

Refuge on the ridge

Hecastocleis shockleyi establishes on exposed limestone ridges and gravel slopes of the Mojave Desert. The reason why *H. shockleyi* is only found on these xeric, nutrient poor substrates remains unknown.

Spring Mountains, Nevada
Photo by Colin Hoag

et al. (2019), *Hecastocleis* diverges from the rest of the family in the Eocene, approximately 50MYA, and occupies a position between the South American lineages and the remaining members of the family. In this way, *Hecastocleis* represents a crucial link between the family's early radiations and its eventual global spread. As Funk and Hind (2009) point out, this suggests one of three possibilities: 1) after arriving in North America, it left by long-distance dispersal to Africa, perhaps via Europe or Asia; 2) it was part of a larger radiation, of which it is the sole remaining member; or 3) the genetic evidence is incorrect. The latter seems unlikely, as molecular phylogenetic analyses to date consistently support the placement of *Hecastocleis* with high confidence (Mandel et al., 2019).

This story has captured the synantherological imagination for generations. Gray (1881) considered its discovery "a remarkable addition to the few known North American [Mutisieae], to stand near *Ainsliea*, but altogether *sui generis* and of peculiar habit." More recently, Funk and Hind (2009) also explain: "Very little is known about the biology of *Hecastocleis*; no pollinators were seen during visits to the Red Pass/Titus Canyon populations [in Death Valley National Park]. Since the florets and bracts are whitish, perhaps they attract night visitors. Likewise, there is no information on the ecology or ethnobotany." Indeed, 15 years since their writing, my literature search turned up only scattered mentions about its habitat preferences, ecology, and distribution (Williams, 1977; Ackerman, 2003; Funk and Hind, 2009; Ward & Bittman, 2024). I learned that it prefers rocky, gravelly soils on steep slopes between 1280-2,200masl, typically on a limestone or shale substrate. From digitized herbarium specimens, I learned that it occupies the Mojave and Great Basin Deserts in scrub and chaparral plant communities. Although long considered a species of conservation concern, recent field research has revealed that *H. shockleyi* is far more widespread than previously assumed (Ward & Bittman, 2024). Some of these populations feature thousands of individuals, and because it prefers such inaccessible habitats we can be confident that additional populations are yet to be found.

As an ecologist captivated by this historical biogeographic story sketched by researchers like Funk and Hind—and *magno amore in familiam*

Synantherearum captus—I needed to investigate further. What explains its patchy distribution? How is it pollinated and dispersed? How is it structured on the landscape? How are its populations, which occur often in discrete, disjunct, and difficult to access sites, related to one another? Where is its genetic diversity concentrated? And how might answers to those questions inform our interpretation of its longer-term geographical movements?

With the generous guidance of Mauricio Bonifacio and Jennifer Mandel, I set out in the late spring of 2023 to examine its genetic diversity, and collect leaf material from populations across the plant's range in Nevada and California. In the early summers of 2024 and 2025, I returned to focus entirely on one site in the Spring Mountains of Nevada, making natural history observations and mapping the structure of a single population. The following briefly describes my encounters with this famously enigmatic comp.

MAY 2023: A TOUR OF ITS RANGE

Hecastocleis shockleyi is often associated with Death Valley, but this is misleading. It occurs in Death Valley, and the association certainly gives a sense of its extreme habitat preferences, but in fact the plant lives quite widely across the Great Basin and Mojave Deserts. Thanks to digitized herbarium specimens deposited by researchers over decades, I was able to locate nine populations across its range in California and Nevada.

The first was just outside Las Vegas in the stunning Spring Mountains National Recreation Area, part of the Humboldt-Toiyabe National Forest. My visit was a rude awakening about the difficulties of *Hecastocleis* research—and one answer to my question about why so little is known about its ecology. The site was located seven miles off Highway 160, a full hour's drive down a gravelly 4x4 double-track that traversed Mojave Desert washes full of large rocks and flanked by sprawling creosote bushes (*Larrea tridentata* (DC.) Cov., Zygophyllaceae) and Joshua trees (*Yucca brevifolia* Engelm., Agavaceae).

From the pull-out where I parked my rented truck, the population was a short but arduous hike up



In Search of *Hecastocleis*

Across the Mojave and Great Basin, purple dots mark studied populations of one of *Compositae*'s most solitary lineages. These locations traced the narrow range of *Hecastocleis shockleyi* — from sun-baked bajadas to wind-cut ridges, a journey through extraordinary desert landscapes.

Where the land and the plants are one

Water is fundamental for plant life, yet on these steep, layered slopes of calcareous rocks where soil depth and moisture retention are minimal - a plant community as austere and singular as the landscape itself is able to thrive.



Spring Mountains, Nevada
Photo by Colin Hoag



Figure 1. *Hecastodeis shockleyi* in bloom, its bracts turning milky white as the florets open, set against the dramatic mountain landscape of the Mojave Desert.

a steep, rocky slope past cacti (e.g., *Ferocactus cylindraceus* (Englem.) Orcutt, Cactaceae), buckwheats (e.g., *Eriogonum inflatum* Torr. & Frém., Polygonaceae), herbaceous Compositae (e.g., *Baileya multiradiata* Harv. & A. Gray, Helenieae), and subshrubs (e.g., *Ephedra viridis* Cov., Ephedraceae; *Coleogyne ramosissima* (Ridl.) M.W.Chase & Schuit., Rosaceae; *Ericameria* spp., Astereae). Clambering over rock ledges and periodically losing my footing on the gravelly slopes, I followed my handheld GPS to the point—all the while worried about the wisdom of embarking on this difficult project in the late-May heat.

Then I found one! And another! As so often happens in field botany, once I saw one, I saw them everywhere. When they first leaf out in spring, the

bracts surrounding the flower heads are light green in color and easy to recognize from afar. As spring turns to summer, they become white and even more conspicuous (Figure 1). Sadly, none had yet flowered, but it was clear that they were on the verge of doing so.

Without permits to collect leaf material in Death Valley National Park, I drove through to the Owens Valley. Whereas the Spring Mountains near Las Vegas represent the southern edge of the plant's distribution, populations in the Owens Valley on the western slopes of the Inyo Mountains appear to occupy its western edge. Surrounded by the most fantastical geological formations I have ever seen, including the snowcapped Sierra Nevada Mountains

An extravaganza of unique traits

Cluster of single flowered capitula of *Hecastocleis shockleyi*, enclosed by spiny, papery bracts. The florets are exposed, with styles extending beyond the syngenesious anther tube. The style is stout and glabrous, with slight thickenings below the apex and short style branches, features characteristic of early-divergent lineages within the Compositae.



Spring Mountains, Nevada
Photo by Colin Hoag



Figure 2. **A.** After flush, flowerheads emerge with bracts light green. **B.** Just before flowering, the bracts become whiter. **C.** In flower. **D.** After flowering, bracts become brittle and somewhat translucent before heads fall.

Desert opportunities

A bee visits the solitary floret of a *Hecastocleis shockleyi* capitulum. Each capitulum bears a single tubular flower subtended by papery, spine-tipped bracts — an unusual condition within Compositae. The floret's pale corolla and exposed anthers facilitate access for small insect visitors.

Spring Mountains, Nevada
Photo by Colin Hoag



Figure 3. **A.** Medium-sized individual growing among *Coleogyne ramosissima* on a rocky slope; note the conspicuous inflorescence bracts that turn milky white at flowering. **B.** A shoot from this year (right) alongside one from last year (bottom). New shoots produce spiny, sparsely toothed leaves that broaden at the base. In the subsequent year, these turn brown along with the stem, while soft, linear leaves emerge in brachyblasts from the axils of those spiny leaves. **C.** A rhizome. **D.** A close-up of brachyblasts in the axils of already senescent leaves.

looming to the west, I scrambled up rocky slopes in search of these small, prickly shrubs.

My next stop was near the plant's possible northern limit at Walker Lake, 170 km south of Reno. This area is decidedly not Mojave Desert, lying firmly in the Great Basin, which receives somewhat more annual rainfall and is dominated by sagebrush (*Artemisia tridentata* Nutt., Anthemideae) rather than creosote and Joshua trees. The two populations I found inhabited parallel valleys of the Wassuk Range running east-to-west. Unlike previous

populations that I'd found, which were on north- or west-facing slopes, these faced south, though the sites still featured steep, gravelly slopes and some plant species common to other sites, such as *Stanleya pinnata* (Pursh) Britton (Brassicaceae), *Xylorhiza tortifolia* var. *tortifolia* (Torr. & A. Gray) E. Greene (Asteraceae), and *Sphaeralcea ambigua* A. Gray (Malvaceae).

On my way back toward Las Vegas, I located two additional populations of *Hecastocleis*. The first was located in the geographic center of its range along

Holding ground

Hecastocleis shockleyi is capable of growing on loose gravel slopes where many botanists would lose their footing. Its shallow roots bind the coarse soil together and keep it from eroding away with the shifting landscape.

Wassuk Range, Mineral County, Nevada
Photo by Colin Hoag

the road near Coaldale in the Great Basin. It was the easiest population to access of them all—near to the highway and on a very moderate slope—but the individuals did not appear to be thriving. They were relatively small, with fewer flowerheads, and often displaying insect damage and signs of water stress including brittle, yellowing leaves. Their flowers seemed furthest from bloom compared to other populations.

The second population was near the possible eastern edge of *Hecastocleis shockleyi*'s range: back in the Mojave Desert near Alamo, Nevada. This population was much healthier, but mystifyingly it was situated on an east-facing slope! This variation in aspect would be unremarkable if it weren't so often the case that each population was narrowly circumscribed on the landscape by aspect. Populations may be abundant on one slope yet absent on the next, as though confined by subtle, unseen boundaries in the terrain.

JUNE 2024: ECOLOGY & NATURAL HISTORY I

Because of my ambitious goals during my first trip, I had little time for observation and site description. In the first week of June 2024, I decided to focus more narrowly on a single population in the Spring Mountains National Recreation Area near Las Vegas. This time I would arrive a week later to ensure that I could see the plant in flower. My goals were to make natural history observations about the site, to try to observe and collect pollinators, and to map the structure of the population on the landscape with a high-precision Global Navigation Satellite System device.

When I first arrived, the plants were not yet in flower, and I feared the worst. But within two days, it was as though someone had flipped a switch: dozens and then hundreds of plants were blooming. The flowers are quite small and somewhat inconspicuous from a few feet away, but the bracts by this time had turned a deep, milky-white color, making the plant even more conspicuous on the landscape than before ([Figure 2](#)). A single plant can feature many hundreds of florets.

My interest in mapping individuals across the landscape stemmed from my first impressions of the spatial structure of desert flora as someone unfamiliar with these arid landscapes. For example, during my first trip I was struck by just how rare it was to encounter juvenile plants, desert recruitment being extremely difficult. And, more so than in other landscapes I'd visited, plants seem to clump together, given that the micro-characteristics of a site (particularly soil moisture) act as a strong filter on plant presence or absence.

I was struck by just how expansive some individual plants can be, too. When *Hecastocleis* flushes in spring, new shoots emerge from buds in old stems, as well as from the base of the plant. These basal shoots push the circumference of the plant even wider, but some are apparently rhizomatous. I dug at the base between neighboring plants and encountered dead rootstock that had clearly once connected the two. From the gnarled, woody base of another plant, I found new shoots extending outward underground that were soft, white, and clearly not intended as aerial shoots ([Figure 3](#)).

Funk and Hind (2009) suggested sensibly that the white flower might attract night-time visitors such as moths. My camera trap and light trap failed to capture anything overnight, I did record a variety of insects visiting the plant ([Figure 4](#)). Notably, this included two species of bees that were active on pollen-covered florets. I managed to photograph and capture one of them, which appears to be *Lasioglossum* in the *Dialictus* group (Sam Droege, 2024, *pers. comm.*). Scanning electron microscope (SEM) images of the bee showed the distinctive *Hecastocleis* pollen described by Funk & Hind (2009).

I am still unclear about how *Hecastocleis* disperses. It is rare to find an individual with heads and bracts from the previous year, as they are completely shed during the brutally hot and dry summer, or during the rains and winds of winter. The pappus is a crown of scales (Panero & Funk, 2002), limiting its ability to disperse by wind or fur. The achene is glabrous and unlikely to stick to animals, though the entire inflorescence could do so, given the spines on the bracts (or even perhaps entire branches, given the spiny leaves on new flower-bearing shoots). Water dispersal from torrential rains is almost certainly a

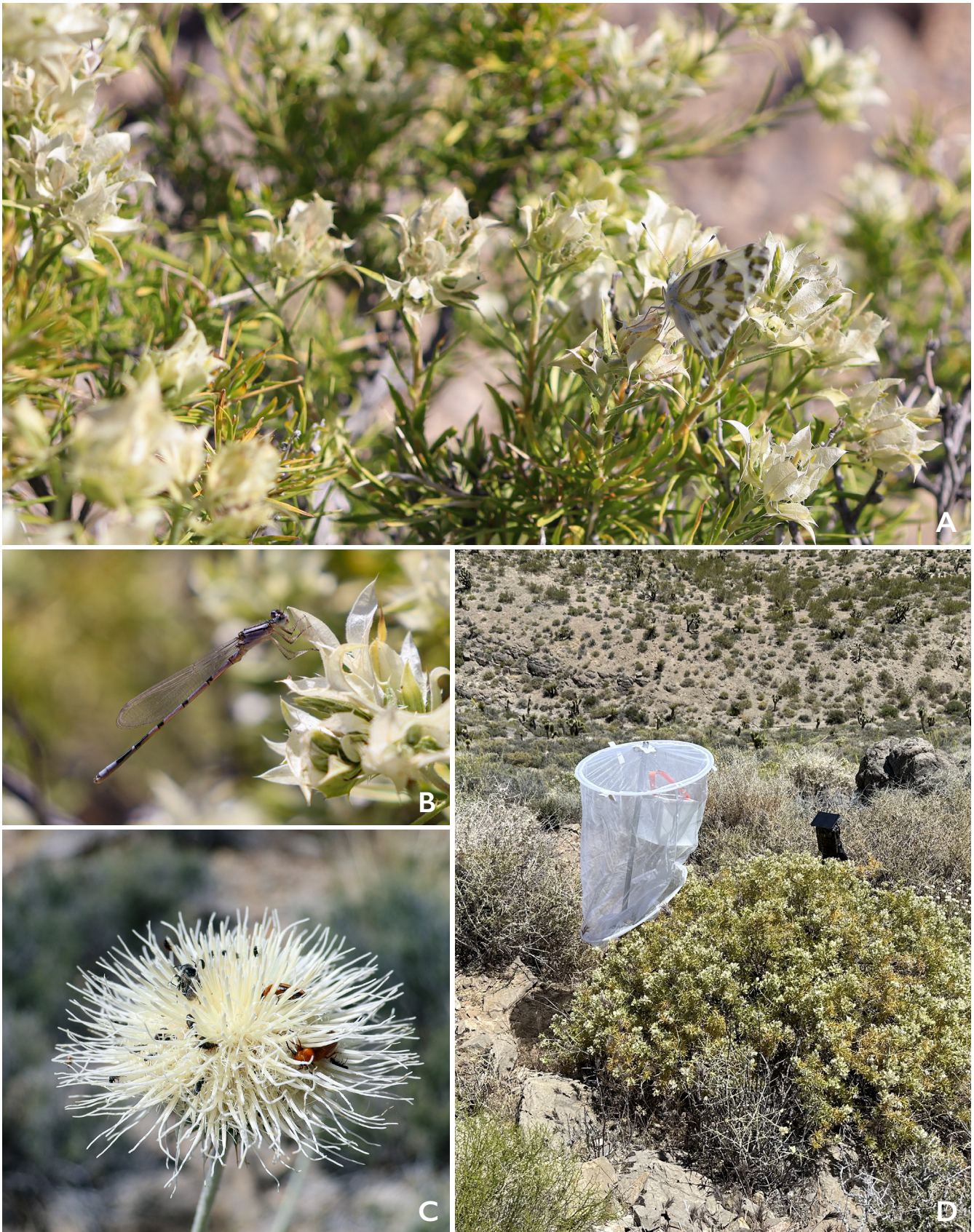


Figure 4. Observations and trapping efforts were conducted to document potential pollinators of *Hecastodeis* and associated desert Compositae. **A–B.** Lone rangers of the desert flora visiting *Hecastodeis*. **C.** *Cirsium neomexicanum* A. Gray (Cardueae) offers abundant florets that attract multiple visitors to a single head. **D.** Unsuccessful overnight moth trap.

The perennial ephemeral

Observed on the central Mojave margin, *Hecastocleis shockleyi* entering senescence as temperatures rise. Leaves, previously glaucous-green, now turn yellow and desiccate within as little as a week from anthesis. The species exhibits a brief vegetative and reproductive phase following seasonal moisture, retreating rapidly to dormancy under increasing aridity — a survival strategy finely tuned to desert pulse dynamics.

Spring Mountains, Nevada
Photo by Colin Hoag



Figure 5. Some other Compositae from Mojave desert. **A.** *Psathyrodes ramosissima* A. Gray (Helenieae). **B-C.** *Psilostrophe cooperi* (A. Gray) Greene (Helenieae). **D.** *Erigeron concinnus* Torr. & A. Gray (Astereae). **E.** *Ericameria linearifolia* (DC.) Urbatsch & Wussow (Astereae).

In transit

SEM of *Hecastocleis shockleyi* pollen grains adhering to the body of a bee. The grains are spheroidal to suboblate and tricolpate, with finely microechinate ornamentation characteristic of early-divergent Compositae.

Pollen grains found on body of bee depicted on page 21.
Photo by Eva Bruce

Extreme diversity

The Mojave is vast. Compositae are regular components of the bajadas stretching between distant ridges, as seen here, but finding them safely takes preparation. Even with these sweeping views, it's easy to lose sight of your truck among the arroyos, creosote, and Joshua trees.



Spring Mountains, Nevada
Photo by Colin Hoag

factor, but this only works downslope. Perhaps birds consume and disperse them.

Seeing desert Compositae just a week later than on my previous visit offered valuable insight into the ecological dynamics of the Mojave (Figure 5). I fell short of my goal to sample every plant in the valley because I ran out of time, but I did manage to sample an entire hillslope, including a total of over 3,000 points. Using a digital elevation model and my natural history site descriptions, I will analyze these data for clues about the structuring of the population on the landscape. With the leaf material I collected from those 9 populations in 2023, I hope to investigate their genetic diversity in relation to one another.

JUNE 2025: ECOLOGY & NATURAL HISTORY II

The following summer, I returned to this site—this time in the second week of June rather than the first. I came to capture additional points for my mapping project, which now includes 5,000 individual plants and counting. Additionally, I hoped to make observations of the plant further along in its annual life cycle. The temperatures were markedly hotter, and my workday therefore shorter. The plant community at large had begun to head toward dormancy, and *Hecastocleis* was no different. In place of the dark-green leaves with bright, white flowerheads, I found *Hecastocleis* almost entirely yellow. Most plants were no longer in flower, and many lacked flowerheads. Last year's brown stems had now turned grey, and this year's green stems had turned brown. The leaves were so brittle they fell off when touched. I noticed no visiting insects, though many capitula had been bored through by an insect seeking its fruit.

This visit taught me two important things. First, it appears that the plant's active period is quite narrow, in flower for just over a week, pointing to the opportunism required to survive and reproduce in the narrow window of a desert rainy season. Second, I learned that the plant likely disperses locally via the tumbleweed action of the aggregated capitula surrounded by the spiny bracts. As I brushed up against a plant, these structures would

often spring off the plant, rolling and blowing away on the ground. This might help explain why these plants sometimes aggregate at the base of other plants and, more broadly, why they have such a patchy dispersion across the landscape. How they manage to travel beyond that landscape is still an open question.

CONCLUSIONS

The geography of *Hecastocleis shockleyi* is mysterious, not only in its phylogeographic history but also in its current distribution. My three field research trips took me through some striking environmental changes, from the arid Mojave to the Owens Valley at the edge of the Sierra Nevada Mountains, to the sagebrush steppe of the Great Basin. Seeing a diversity of sites where *Hecastocleis* occurs only reinforced my sense for just how peculiar the spatial patterns of this plant are: narrowly restricted yet abundant within a given site, and occurring across a large geographic range on slopes facing every cardinal direction in two distinct desert environments.

What could be the driver of this strange pattern? Did the plant previously occur more widely before becoming restricted to higher elevation zones by climatic changes? After all, we know this process from elsewhere in the world (Sandel et al., 2011), and the Mojave and Great Basin were both cooler and wetter even just 10,000 years ago (Walker & Landau, 2018). Or, is this a story of stochastic dispersal events? What prevents *Hecastocleis* from colonizing new spaces that otherwise appear to suit them? My research will not answer these questions definitively, but hopefully it can shine some light on their edges.

I contacted Jerry Tiehm, the herbarium curator at University of Nevada, Reno—a long-time field botanist and an authority on the flora of Nevada—to ask him why *Hecastocleis* occurs where it does. He confirmed how difficult it was to characterize its preferences, explaining: “you don't so much go looking for the plant as you do stumble upon it.”

Dear reader, when you do stumble upon this incredible plant—and someday I hope you do—be careful. The slopes are steep, the desert is hot, and the plant is quite spiny.

ACKNOWLEDGEMENTS

Thanks to those who have helped me with this work, including Mariana Abarca, Kara Barron, Mauricio Bonifacino, Eva Bruce, Centre National de la Recherche Scientifique, Olivia Curtis, Kala'i Ellis, Naomi Fraga, Jimmy Grogan, Corinne Hoag, Maria Jesus, Christina Lund, Jennifer R. Mandel, Riccardo Racicot, Meredith Root-Bernstein, Smith College, Jerry Tiehm, Julie Wallis, and Judith Wopereis.

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