Hecastocleideae (Hecastocleidoideae)

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HISTORICAL OVERVIEW AND MORPHOLOGY

Hecastocleis shockleyi A. Gray was described in 1882 and its unusual morphology and restricted distribution has made it sought after for herbarium specimens. This shrub is easily identified because of its single flowered heads that are re-aggregated on a receptacle in groups of one to five heads; each group of heads is subtended by a relatively large spiny whitish or greenish bract (Fig. 16.1). Gray (1882) commented that is was "a remarkable addition to the few known North American Mutisieae, to stand near Ainsliaea DC. but altogether sui generis and of peculiar habit." According to Williams (1977) the generic name Hecastocleis, "... comes from the Greek roots, ekastos meaning 'each' and kleio meaning 'to shut up'", referring to each flower having its own involucre. The species was named after William H. Shockley one of the first botanical collectors from Nevada (Barneby 1977). Bremer (1994) placed the genus in the tribe Mutisieae subtribe Mutisiinae, and Hind (2007) placed it in Mutisieae in a group by itself.

PHYLOGENY

Hecastocleis has always been placed in Mutisieae (Cabrera 1977). The first molecular evidence concerning the relationship of the genus was presented by Panero and Funk (2002, 2008); they reported that the genus did not belong in any existing tribe or subfamily and placed it in its own tribe, Hecastocleideae, and subfamily, Hecastocleidoideae. The monotypic genus occupies the node just below the

Carduoideae—'rest of the family' split (see Chapters 12 and 44) and this placement has 100% bootstrap support. Its current position is supported by its distinct morphology and strong support from molecular data. Its nearest downstream neighbor, however, is somewhat tenuous, because the position of the branch just below it (Gochnatieae) has only 65% bootstrap support (Panero and Funk 2008) and might collapse into a polytomy with Mutisieae s.str. If one does the phylogenetic analysis without *Hecastocleis*, there is no change in the phylogeny of the family.

TAXONOMY

The genus is monotypic and has always been recognized as such since its original description by Gray (1882).

Subfamily Hecastocleidoideae

Tribe Hecastocleideae Panero & V.A. Funk in Proc. Biol. Soc. Wash. 115: 909–922. 2002 – Type: Hecastocleis shockleyi A. Gray in Bot. Gaz. 7: 100–101. 1882.

Subshrubs or shrubs to 40–80(–150) cm. Leaves alternate, cauline, sessile, blades linear to narrowly ovate with three main veins, stiff, margins entire, apex acute usually with a spine, base attenuate, margins with a few spines, surfaces glabrous or minutely tomentose. Heads single-flowered, clustered in second-order heads, each cluster with 1–5 heads and subtended by ovate to orbiculate bracts with spiny margins. Involucres (each enclosing one floret) cylindric to fusiform, 10 mm. Receptacle flat, naked. Florets 1, bisexual, fertile; corollas reddish purple

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Fig. 16.1. Hecastocleis shockleyi A. Gray. **A** Red Pass, high point on the road to Titus Canyon, Death Valley, California, USA, Hecastocleis in the foreground; **B** habit; **C** close up of florets, involucre tightly appressed to single-flowered heads and bracts (greenish); **D** close up of several single-flowered heads, corollas deeply lobed, pink turning white, bracts whitish. [Photographs, V.A. Funk of Funk et al. 12487–12488.]

to greenish white, actinomorphic, deeply 5-lobed; stamens 5, anther basal appendages slightly fimbriate, apical appendages lanceolate to acute; style branches short (0.1–0.5 mm), apices rounded. Achene terete, not beaked, obscurely 4–5-nerved, glabrescent; pappus of six unequal, lanceolate or multi-toothed scales sometimes fused to form lacerate crowns. — Information for this description was taken from several sources (Keil 1993; Panero and Funk 2002; Simpson 2006; Hind 2007, and pers. obs.).

Hecastocleis is obviously a well-defined genus without close relatives and confined to high elevations (ca. 5000 ft) in southern Nevada and adjacent California (Fig. 16.1A). It is easily recognizable from a distance by its relatively large whitish to greenish bracts that subtend the clusters of single flowered heads (Fig. 16.1A–D).

POLLEN

The pollen of *Hecastocleis* is psilate and tricolpate (Fig. 16.2). The presence of colpate pollen is believed to be unusual

in the family (it has never been surveyed for this character), and its presence in this genus was first pointed out by Tellería and Katinas (2005); Fig. 16.2 confirms this finding and shows the colpi to contain "pebbly" or "scabrate" particles. Figures 16.2B–D do not indicate a pore in the colpi, but the good pollen preservation may actually be covering it up. Figure 16.2E is important because if a pore were present, it would show in this "inside" view of the colpus, and it does not. The exine of the pollen of *H. shockleyi* is scabrate-microechinate with small puncta; the exine is regularly thickened over the complete grain (Tellería and Katinas 2005).

Wodehouse (1929), based on his examination of the pollen and the literature, stated that "Hecastocleis is a monotypic genus with no close connections in the tribe, but is regarded as closest to Ainsliaea; its pollen grains are rather dissimilar to any in the tribe, but show greatest similarity to those of Ainsliaea". Tellería and Katinas (2005) stated that the tricolpate pollen supported the previous hypothesis that Hecastocleis and Ainsliaea were related but noted that the psilate, regularly thickened exine, did not support

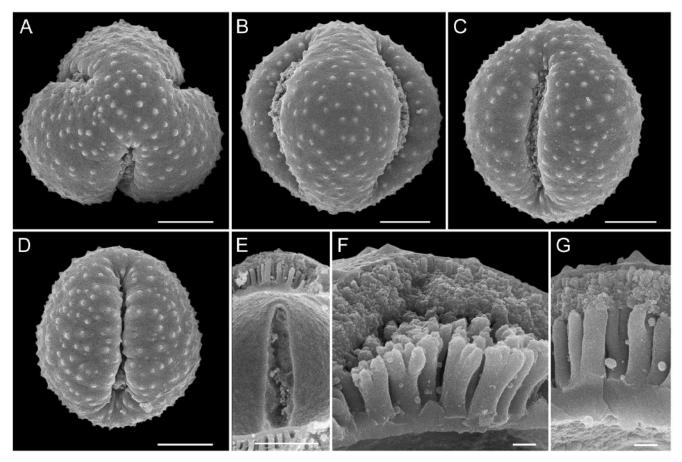


Fig. 16.2. Scanning electron micrographs of pollen of *Hecastocleis shockleyi* A. Gray. A polar view; **B** lateral view; **C**, **D** apertural views; **E** internal apertural view of fractured grain; **F**, **G** fractured grains. Scale bars: $A-E = 10 \mu m$; F, $G = 1 \mu m$. [SEM photographs by J. Skvarla of *Funk et al. 12487*, US.]

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this relationship but is similar to more basal lineages in the family (e.g., Mutisieae, Gochnatieae).

The most recent phylogeny of the family, based on cpDNA (Panero and Funk 2002, 2008), indicates that *Hecastocleis* is separated from *Ainsliaea* by intervening Carduoideae. In fact, *Hecastocleis* is bracketed by African Mutisieae (Dicomeae, *Oldenburgia* Less., Tarchonantheae) plus Cardueae on one side and Gochnatieae on the other. Over all, the pollen seems to resemble that of the basal grade, especially Gochnatieae, which has somewhat variable pollen.

CHROMOSOME NUMBER

The basic chromosome number is estimated to be x = 8, based on one count of 2n = 16 (Powell et al. 1974).

CHEMISTRY

No information is available on the chemistry.

BIOGEOGRAPHY

The distribution of *Hecastocleis* is confined to the southwestern USA. It has been collected from the mountains surrounding Death Valley and on many of the isolated mountains in southern Nevada. In fact, just about every local flora that is published from the southern Nevada/Death Valley area lists this species as occurring in its range, i.e., Charleston Mountains (Clokey 1951), Nevada Test Site (Beatley 1976), Grapevine Mountains (Kurzius 1981), and the flora of the Desert National Wildlife Range (Ackerman 2003). In general, it seems to be widespread in the southern Nevada and adjacent California area but growing in small isolated populations. The easiest place to see it is on the way to Death Valley, at Red Pass, the highest point on the dirt road from Beatty, Nevada to Leadfield and Titus Canyon, California (Fig. 16.1A).

Hecastocleis is an anomaly in the area cladogram for Compositae (see metatree, Chapter 44). Below the node where one finds this genus, the branches are estimated to have a southern South American distribution. Above Hecastocleis the more highly nested clades have radiations in Africa and Asia but most resolve to Africa, especially southern Africa. What happened in the past, therefore, that has left this pattern where a plant from southern Nevada is on the main stem of the cladogram between the basal South American grade and the African and Asian explosions? There are several possible explanations, two of which are equally likely based on the area cladogram: (1) there was a dispersal event from South America to North America and then one from North America to Africa, or (2) there was a dispersal event from South America to North America followed by radiation across North America and Europe and down into Africa and over to Asia followed by extinction of all northern taxa except the ancestor of Hecastocleis. Dispersal from South America to North America has happened in several of the groups in this part of the tree, for instance, Gochnatia hypoleuca (DC.) A. Gray is a member of the Gochnatieae tribe which is found at the node below Hecastocleis. There is, of course, a third possibility, that the placement of Hecastocleis is incorrect. It is a rather long branch and there might be some 'long branch attraction' affecting the phylogeny. However, bootstrap support for the separation of Hecastocleis from Gochnatieae is strong (100%).

BIOLOGY, ECOLOGY, ETHNOBOTANY

Very little is known about the biology of *Hecastocleis*; no pollinators were seen during visits to the Red Pass/Titus Canyon populations. Since the florets and bracts are whitish, perhaps they attract night visitors. Likewise, there is no information on the ecology or ethnobotany. It does not appear to be invasive nor does it have any commercial uses. The common name is prickeleaf.

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