

**TOIYABEA (ASTERACEAE: ASTEREAE)  
ENLARGED TO INCLUDE FOUR SPECIES**

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**ABSTRACT**

The genus *Toiyabea* is enlarged from a single species to include four: *Toiyabea alpina* (Anderson & Goodrich) Roberts et al., **Toiyabea eximia** (H.M. Hall) Nesom, **comb. nov.**, **Toiyabea peirsonii** (Keck) Nesom, and **Toiyabea granitica** (Tiehm & Shultz) Nesom, **comb. nov.** Three first three species are tightly coherent in geography and in morphology but in 2006 FNA treatments were placed in three separate genera, *Toiyabea*, *Tonestus*, and *Lorandersonia*, weighting interpretations of molecular data. The fourth, while morphologically divergent, is part of the geographic group and shares features indicative of a close relationship. A taxonomy hypothesized here to best reflect the evolutionary history recognizes all four as congeneric. The morphological and geographic evidence suggests that DNA data need to be supplemented and interpretations reexamined.

The genus *Toiyabea* was established by Roberts et al. (2005) to include the single species *Haplopappus alpinus* = *Tonestus alpinus* (nomenclatural details below). The present discussion points out that species originally named as *Haplopappus eximius* and *H. eximius* subsp. *peirsonii* are closely similar to each other and apparently inextricably related to *H. alpinus*. These taxa are referred to below as "**eximius**," "**peirsonii**," "**alpinus**," and the "**eximius trio**."

A fourth species, *Haplopappus graniticus* = *Tonestus graniticus*, also appears to be part of this group. It shares herbaceous perennial, taprooted habit, coarsely toothed leaves, herbaceous phyllary apices, and vestiture of long, erect, multicellular hairs, some of which are stipitate-glandular, and it is endemic to southwestern Nevada in close proximity to the **eximius trio**. In leaf and head arrangement and involucre morphology, however, it is distinct from the **eximius trio**. It might be given separate taxonomic standing at generic rank, or it might be considered as congeneric with the other three, alternatives considered here.

**Three species**

Hall (1915) noted that the affinities of his new species *Haplopappus eximius* are with *H. lyallii* A. Gray and *H. pygmaeus* (Torr. & Gray) A. Gray, differing in its deeply toothed leaves and more foliaceous involucre bracts. He also noted similarities of **eximius** to *Haplopappus aberrans* A. Nels. The second taxon, **peirsonii**, was originally described by Keck (1940) as a "very distinct geographic subspecies" of *Haplopappus eximius*, emphasizing the larger leaves, involucre, and florets of **peirsonii**. In raising its rank to species, Howell (1950, p. 87) noted that between the two taxa there were "a few small qualitative differences but in all parts there are marked quantitative differences, [*Haplopappus*] *peirsonii* being larger and coarser than [*Haplopappus*] *eximius*. These differences ..., taken together with the geographic separation of the two plants, would seem to indicate that we are concerned with two distinct but closely related species."

Anderson (1980) thought the new species *Haplopappus alpinus* to be most closely related to **eximius**, to *Haplopappus aberrans*, and less closely so to **peirsonii** — weighting the eradiate heads of *H. aberrans* as an indication of relationship to **alpinus**. In placing the **eximius trio** in the genus *Tonestus*, Nesom and Morgan (1990) noted that the three species comprise a distinct morphological subgroup characterized by stipitate-glandular vestiture, toothed leaves, and phyllaries in 3-4 nearly equal series.

*Haplopappus aberrans* is endemic to a small area in Idaho and adjacent Montana. Although it has stipitate-glandular vestiture and toothed leaves, the leaf margins are spinulose-serrate, involucre are nearly cylindrical, phyllaries are narrowly lanceolate and strongly imbricate, and the pappus is 2-seriate, among other differences from the **eximius trio**. Nesom and Morgan (1990) placed *H. aberrans* in *Tonestus* but in a different subgroup from the **eximius trio**. Molecular data indicate that *H. aberrans* is sister to subtribe Machaerantherinae (or justifiably included within the subtribe), distantly related to the **eximius trio** (subtribe Solidagininae), and it has been segregated as the monotypic genus *Triniteurybia* (Brouillet et al. 2004).

As a group, the three species considered here are characterized as perennial, taprooted herbs often with caudex branches, densely villous-glandular stems, leaves, and bracts, distinctively shaped and coarsely toothed leaves subclasping at base, one or few heads, campanulate involucre, foliaceous-herbaceous phyllaries in 3–4 series of subequal length, yellow rays (rays absent in **alpinus**), terete achenes, and terete, apically attenuate pappus bristles in a single series. The chromosome number of each is based on  $x = 9$  (**alpinus**,  $2n = 18$ ; **eximius**,  $2n = 18$ ; **peirsonii**,  $2n = 90$ ) (Howell 1950; Anderson 1980). Each occurs in rocky alpine to subalpine habitats and each is narrowly distributed in the same general region of the western USA (Fig. 2) — central Nevada (**alpinus**) and the sierra of east-central California (**eximius** and **peirsonii**).

### Three species asunder

Taxonomic treatments in the Flora of North America North of Mexico have placed each of these three species in a different genus: *Toiyabea alpina* (Urbatsch et al. 2006a), *Tonestus eximius* (Morse 2006), and *Lorandersonia peirsonii* (Urbatsch et al. 2006b). Their taxonomic dispersal is underlain primarily by molecular data and its interpretations (Roberts 2002; Roberts et al. 2004; Roberts et al. 2005; Urbatsch et al. 2005).

Morse (2006) treated **eximius** within *Tonestus* but deferred to DNA interpretation regarding **peirsonii**, noting that "... while morphologic evidence indicates that *Tonestus eximius* and *Tonestus peirsonii* are closely related, the work of Roberts and Urbatsch placed the decaploid *T. peirsonii* in a clade with members of *Lorandersonia*, wherein it is treated here" (p. 182).

In treating **peirsonii** as a species of *Lorandersonia*, Urbatsch et al. (2005, p. 1623) noted that it is "a morphologically divergent species in an otherwise relatively uniform genus. ... Even more puzzling than *Lorandersonia peirsonii*'s overall dissimilarity to other *Lorandersonia* is its great similarity to *Tonestus eximius*." They obtained DNA sequences for **peirsonii** "from different specimens at different times with different stock reagents" but results still were essentially identical.

Molecular analyses by Roberts and Urbatsch (2004) and Roberts et al. (2005) show **alpinus** to be within a clade also including *Petradoria pumila* and the sister species *Stenotus acaulis* and *Stenotus armerioides*, although "the position and relationships among the four taxa in that lineage were not congruent across analytical methods or data sets" (Roberts et al. 2005, p. 1648). Bayesian analysis of combined ETS and ITS data sets (their Fig. 1) show an unresolved trichotomy (pumila, alpinus, acaulis/armerioides). Roberts et al. concluded that "The two species of *Stenotus* are morphologically distinctive from *Petradoria* and merit continued recognition at generic rank. We propose *Toiyabea* to accommodate *Tonestus alpinus* because of its [morphological] distinctiveness from *Petradoria* and *Stenotus* and its failure to aggregate with any specific taxon in the sequence-based analyses."

*Toiyabea alpina* emerges as isolated in the morphological key by Roberts et al. (2005, p. 1654), but that is because neither **eximius** nor **peirsonii** was included among the taxa to be identified. Similarly, **eximius** and **alpinus** were not included in the morphological key that distinguishes *Lorandersonia peirsonii* (Urbatsch et al. 2005; the terminal taxon in the key [p. 1628] was mistakenly identified as "*Lorandersonia eximius*" instead of *Lorandersonia peirsonii*).

In the 2006 Flora of North America key to genera, *Toiyabea* is separated from **eximius** and **peirsonii** on the basis of its discoid heads. The key identifies **eximius** within *Tonestus*, as expected by morphology, but **peirsonii** must be assessed as a shrub or subshrub in order to key out as a member of *Lorandersonia*. In the species descriptions, each *Lorandersonia* species is characterized as a "shrub" or "subshrub" except for *L. peirsonii*, which is correctly characterized (Urbatsch et al. 2006b, p. 179) as a "perennial" (vs. shrub or subshrub).

### Three species reunited

Urbatsch (2012), without comment, returned both **eximius** and **peirsonii** to the genus *Tonestus*, implicitly acknowledging that a weighted reliance on molecular evidence led to untenable conclusions. Based on morphology and geography, a close relationship between these two species seems beyond dispute. **Alpinus** essentially differs only in its lack of ray flowers. Within *Tonestus* (*Tonestus lyallii*, the type), however, these three are morphologically and geographically disparate, and joining them within the genus *Toiyabea* (*T. alpina*, the type) provides an effective way of recognizing their coherence. A review of *Tonestus* sensu stricto is underway (Nesom, in prep. — a treatment including several previously undescribed species).

It is plausible that the decaploid genome of **peirsonii** includes a chromosome set from some other species — molecular data associate it with species of *Lorandersonia* but none of those species are sympatric with **peirsonii** and there is nothing about it to suggest genetic influence of a morphologically disparate species. Molecular data indicate that the diploid **alpinus** is related to *Petradoria* and *Stenotus* while morphology and geography place it as closely similar to **eximius** and **peirsonii**. Molecular data indicate that **eximius** is unresolved in relationship or else related to *Amphipappus* and *Chrysothamnus*, and the molecular placement of *H. graniticus* (below) is similar. Positions of these species in molecular analyses used as guides for taxonomic decisions (Roberts 2002; Roberts et al. 2004; Roberts et al. 2005; Urbatsch et al. 2005) make little sense in light of morphological patterns. In the perspective here, the only thing that can be confidently concluded from molecular data regarding these species and others of *Tonestus* (sensu Nesom & Morgan 1990) is that they are members of subtribe Solidagininae of the western USA and are essentially unresolved in placement.

### Where does *Haplopappus graniticus* belong?

*Haplopappus graniticus* (= *Tonestus graniticus*) has been maintained within *Tonestus* by Morse (2006), although he noted (p. 182) that it was included in the genus "mostly as a matter of convenience" because of its divergent morphology. Its leaf morphology and vestiture, however, and its close geographic proximity to the **eximius trio**, indicate that its ancestry lies with those species.

Similarities exist between *Haplopappus graniticus* and **alpina** — both are endemic to isolated mountains of Nevada (vs. the Sierra Nevada distribution of **eximia** and **peirsonii**), both have a tendency to produce numerous heads per stem (compared to the usual single-headed stems of **eximia** and **peirsonii**), and heads of both lack ray flowers (heads of **eximia** and **peirsonii** are radiate). While these features of *H. graniticus* and **alpinus** might be convergent, the parsimonious choice is to regard them as indicative of a sister relationship — the reduced cauline leaves, smaller heads with fewer disc flowers, graduated, less herbaceous phyllaries, and divergent vestiture of *H. graniticus* to be interpreted as autapomorphies.

If the phylogenetic hypothesis here (Fig. 1) is correct, or even if *Haplopappus graniticus* might prove to be sister to the other three, treating all four as congeneric appears to be the more informative taxonomic option. *Haplopappus graniticus* as a monotypic genus might be more pragmatic (a 3-species *Toiyabea* would be more coherent morphologically), but a 4-species *Toiyabea* recognizes their immediate common ancestry and alludes to the apparent saltational changes in *H. graniticus*.

**TOIYABEA** Roberts, Urbatsch, & Neubig, Sida 21: 1653. 2005. **TYPE:** *Toiyabea alpina* (Anderson & Goodrich) Roberts, Urbatsch, & Neubig

1. *Toiyabea alpina* (Anderson & Goodrich) Roberts, Urbatsch, & Neubig, Sida 21: 1653. 2005. *Haplopappus alpinus* Anderson & Goodrich, Great Basin Naturalist 40: 73. 1980. *Tonestus alpinus* (Anderson & Goodrich) Nesom & Morgan, Phytologia 68: 177. 1990. **TYPE: Nevada.** Nye Co.: Slopes of 11,077 ft peak of Toiyabe Crest between Washington Creek and Aiken Creek near county line, 24 air mi SSW of Austin, among white granitic rocks, 10,600 ft, locally established with *H. macronema*, *Chrysothamnus viscidiflorus*, *Erigeron compositus*, and *Eriogonum umbellatum*, 21 Jul 1979, L.C. Anderson 4885 (holotype: BRY; isotypes: GH, MO, NY, RSA). Figures 5-7.

2. **Toiyabea granitica** (Tiehm & Shultz) Nesom, **comb. nov.** *Haplopappus graniticus* Tiehm & Shultz, Brittonia 37: 165. 1985. *Tonestus graniticus* (Tiehm & Shultz) Nesom & Morgan, Phytologia 68: 178. 1990. **TYPE: Nevada.** Esmeralda Co.: Lone Mountain, Springdale Canyon on the NE side of the range, ca 14 mi W of Tonopah, T2N, R40E, in steep, granite rock outcrops, 7800 ft, 12 Sep 1983, A.J. Tiehm 8346 (holotype: NY; isotypes: BRY, CAS, COLO, CS, FSU, G, GH, MO, NSMC, ORE, OSC, RENO, RM, RSA, TEX, US, UTC, WTU). Figures 8-13.

**Additional collections. Nevada.** Esmeralda Co.: Lone Mt. area, ca. 14 mi W of Tonopah, Springdale Canyon on the E side, steep granite rock outcrops, 7800 ft, forming clumps to 3 dm across, 30 Jul 1983, Tiehm 8252 (ASU, KANU, NY, RM); Lone Mtn area, Springdale Canyon on the NE side of the range, ca 14 mi W of Tonopah, steep granitic rock walls, 7800 ft, 21 Jul 1984, Tiehm 9072 (NY); Lone Mtn, Springdale Canyon on the NE side, T2N R40E S16, 38° 01' 38.9" N 117° 29' 00.3" W, steep volcanic rock outcrops, 7100 ft, forming clumps, 9 Sep 2006, Tiehm 15338 (NY, RENO, UNLV).

3. **Toiyabea eximia** (H.M. Hall) Nesom, **comb. nov.** *Haplopappus eximius* H.M. Hall, Univ. Calif. Publ. Bot. 6: 170, f. 2, pl. 20. 1915. *Tonestus eximius* (H.M. Hall) Nelson & Macbr., Bot. Gaz. 65: 70. 1918. **TYPE: California.** El Dorado Co.: 1/2 mi SSW of Angora Peak, crevices of granitic rock on N side of summit of 8800 ft, 8800 ft, Jul 1910, G.R. Hall s.n. (holotype: UC; isotypes: GH, NY, US). Figures 14-16.

4. **Toiyabea peirsonii** (Keck) Nesom, **comb. nov.** *Haplopappus eximius* subsp. *peirsonii* Keck, Madroño 5: 169. 1940. *Haplopappus peirsonii* (Keck) J.T. Howell, Leaflet. W. Bot. 6: 86. 1950. *Tonestus peirsonii* (Keck) Nesom & Morgan, Phytologia 68: 178. 1990. *Lorandersonia peirsonii* (Keck) Urbatsch, Roberts, & Neubig, Sida 21: 1623. 2005. **TYPE: California.** Inyo Co.: Transverse Ridge, Rock Creek Lake Basin, rock crevices, abundant at this location, 11,100 ft, 5 Aug 1933, F.W. Peirson s.n. (holotype: UC; isotype: DS, as cited by Keck). Figures 17-22.

### Key to the species of *Toiyabea*

1. Heads discoid, (1-)2-11 per stem; isolated ranges in south-central Nevada.
  2. Heads (1-)2-4(-5) per stem; vestiture of multicellular, stipitate-glandular hairs; cauline leaves about the same size as the basal; involucre 10-12 mm wide (pressed); disc flowers 30-55; phyllaries mostly herbaceous, in 3-4 series of equal or subequal length ..... **Toiyabea alpina**
  2. Heads (1-)2-11 per stem; vestiture of multicellular hairs sharp-pointed and eglandular at apex, mixed with stipitate-glandular hairs; cauline leaves greatly reduced in size from the basal; involucre narrowly campanulate to narrowly turbinate, 4.5-7 mm wide (pressed); disc flowers 13-23; phyllaries with proximal 2/3 whitish-indurate and apical region green, in (3-)4-5 series strongly graduate in length ..... **Toiyabea granitica**
1. Heads radiate, 1(-2, rarely -4) per stem; Sierra Nevada of California and adjacent Nevada.
  3. Basal leaves 2-4 cm long, 12-15 mm wide; involucre 9-16(-20) mm wide (pressed); rays 10-13;  $2n = 18$  ..... **Toiyabea eximia**
  3. Basal leaves 3-8 cm long, 12-25 mm wide; involucre (15-)20-28 mm wide (pressed); rays 16-20;  $2n = 90$  ..... **Toiyabea peirsonii**

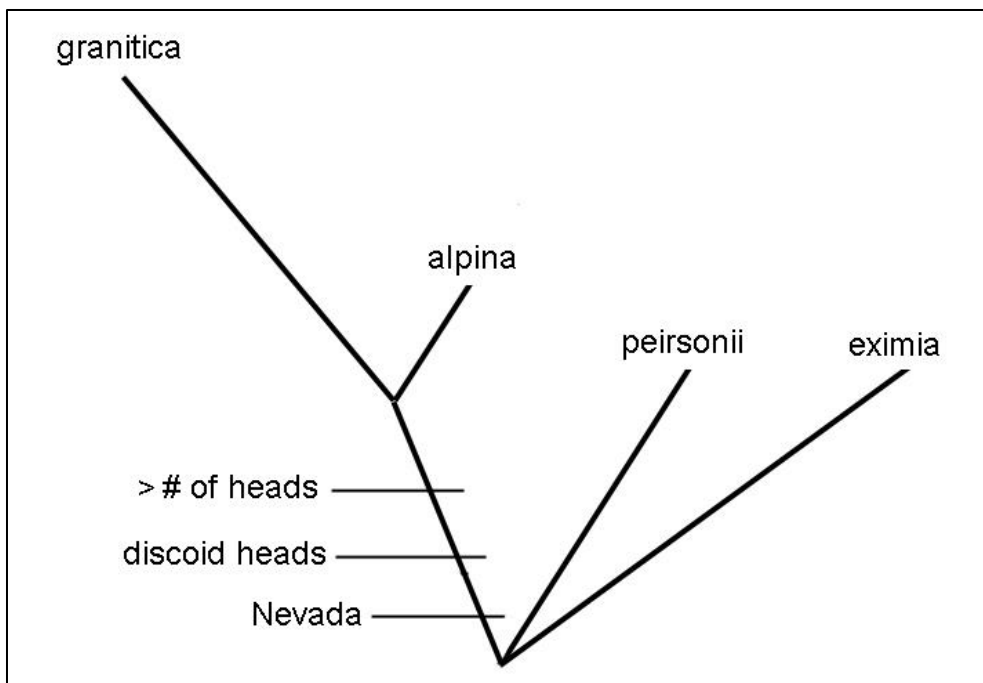


Figure 1. Intuitive phylogeny of *Toiyabea* species. Although *T. granitica* is divergent in morphology (see text and images) from the other three species, it is hypothesized here to share an immediate ancestor with *T. alpina*. Both species have discooid heads, a greater number of heads per stem, and are endemic to isolated mountains in Nevada. If these features were shown to be convergent, then *Toiyabea granitica* might reasonably be treated as a separate genus, perhaps as sister to the others, although a 4-species *Toiyabea* still would be the preferred choice here (see text).

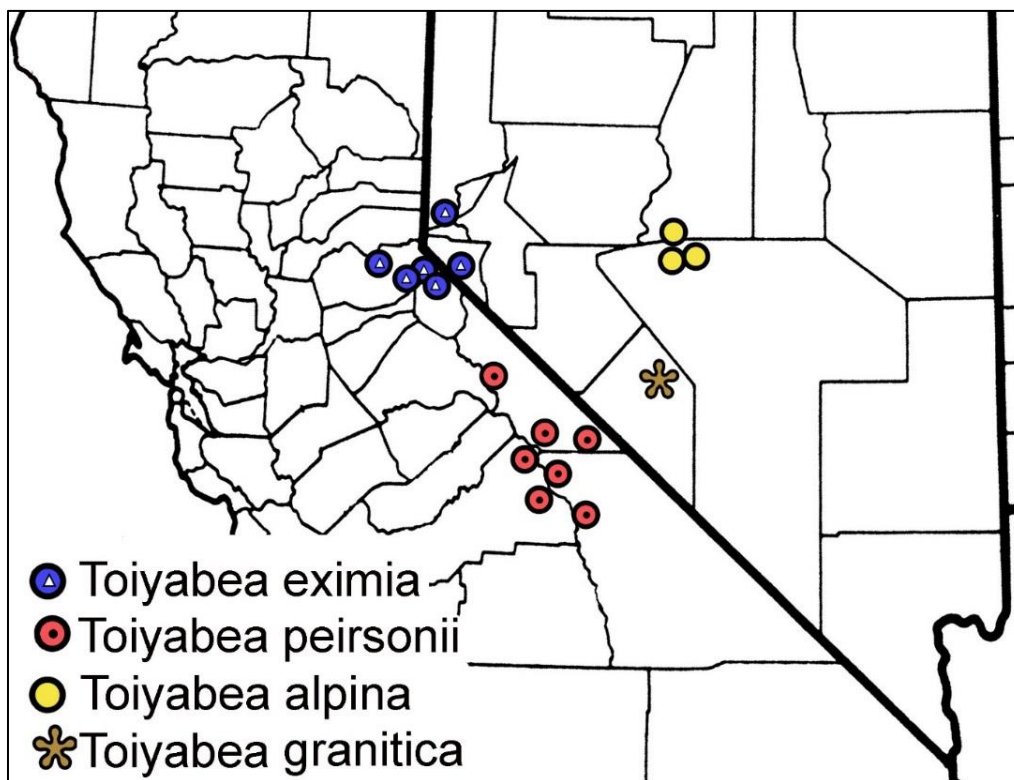


Figure 2. Distribution of *Toiyabea* species.





Figure 3. Vestiture. Top: *Toiyabea granitica*. Bottom: *Toiyabea alpina*.



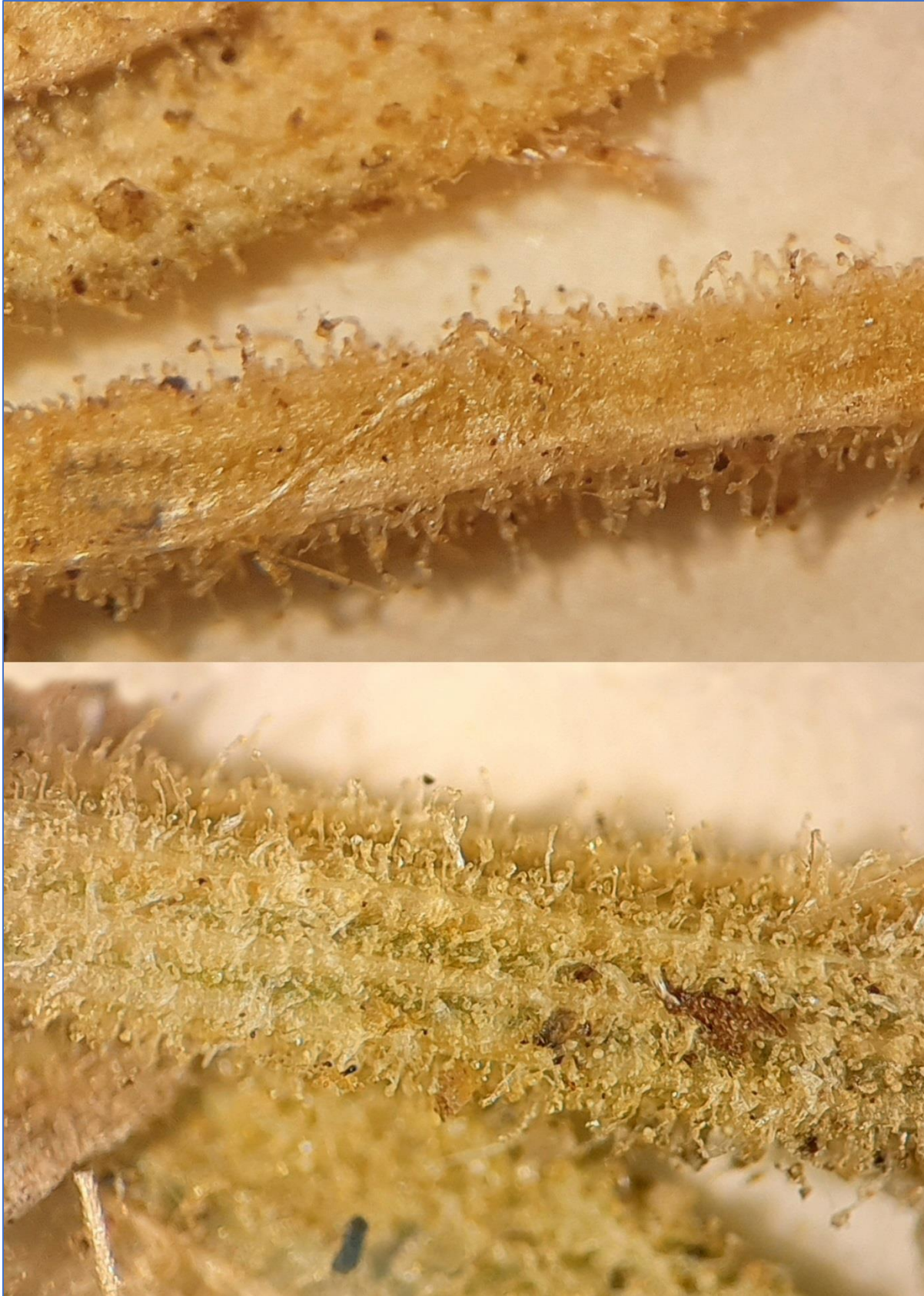


Figure 4. Vestiture. Top: *Toiyabea eximia*. Bottom: *Toiyabea peirsonii*.



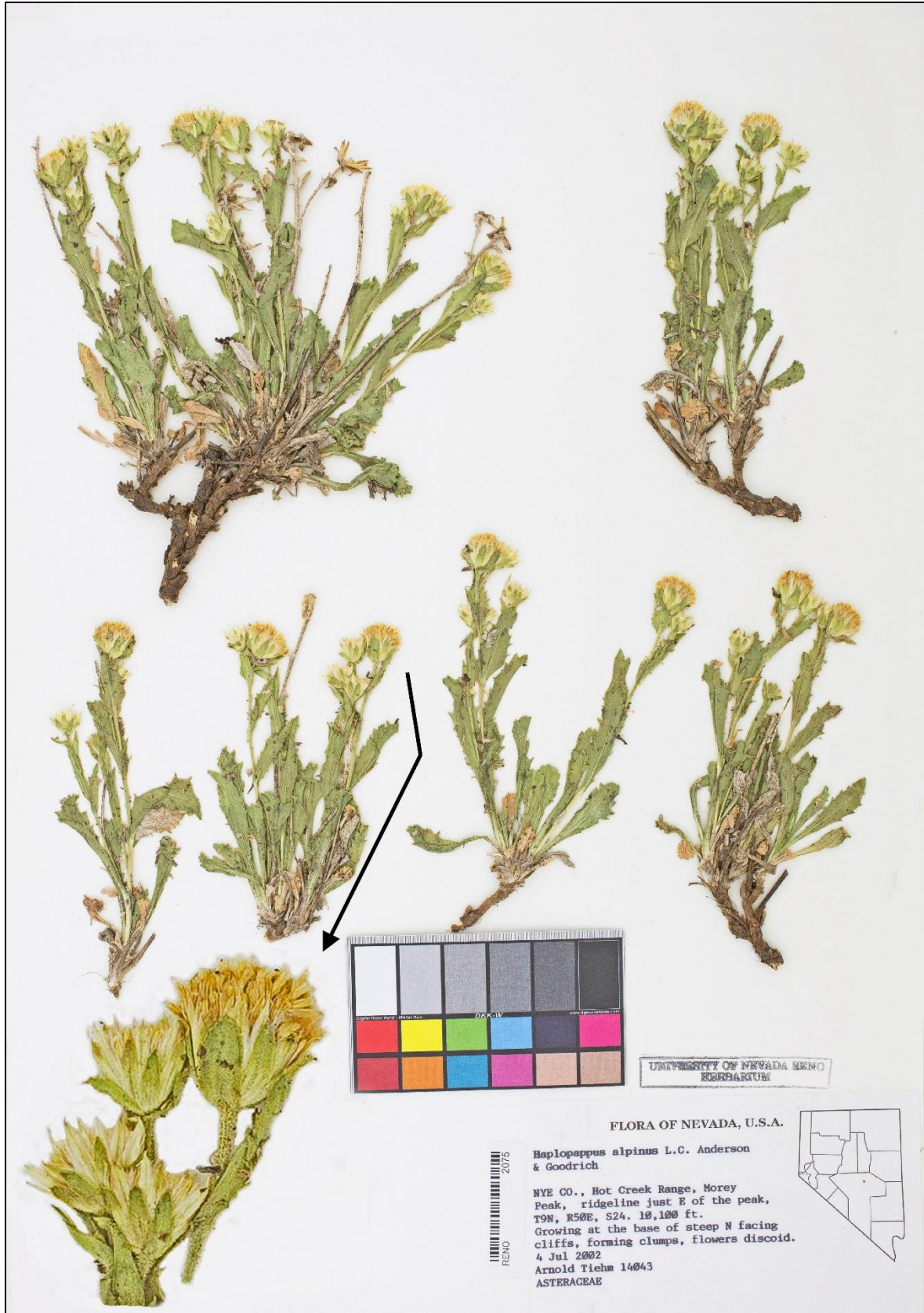


Figure 5. *Toiyabea alpina*, Nye Co., Nevada. Tielm 14043 (RENO).





Figure 6. *Toiyabea alpina*, Nye Co., Nevada. From MO isotype.





Figure 7. *Toiyabea alpina*, Nye Co., Nevada. Photos by Michael P. Spellenberg, 3 August 2013.



Figure 8. *Toiyabea granitica*, Esmeralda Co., Nevada. Holotype NY, Tiehm 8346.





Figure 9. *Toiyabea granitica*, from the TEX isotype.



Figure 10. *Toiyabea granitica*, isotype WTU.



Figure 11. *Toiyabea granitica*, paratype, Tiehm 15338 (NY).





Figure 12. *Toiyabea granitica*, from GH isotype.



Figure 13. *Toiyabea granitica*, leaf variation, from the holotype and isotypes.





Figure 14. *Toiyabea eximia*, Washoe Co., Nevada. Tiehm 2553 (NY).





Figure 15. *Toiyabea eximia*, El Dorado Co., California. From GH isotype.



Figure 16. *Toiyabea eximia*. Top: Alpine Co., California. Photo by Steven Sperry, 30 July 2010.  
Bottom: Washoe Co. Nevada. Photo by Steve Matson, 23 July 2003.



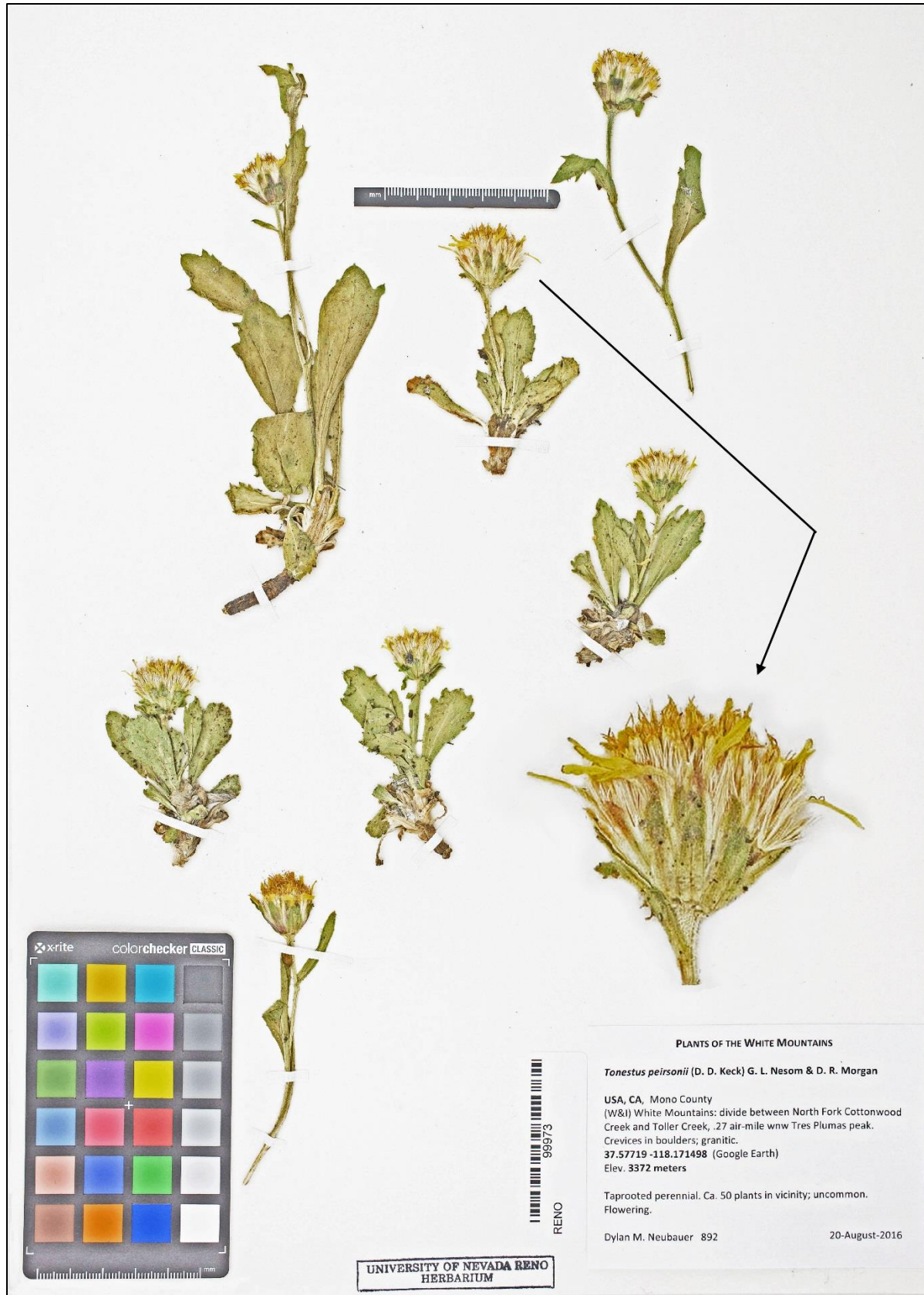


Figure 17. *Toiyabea peirsonii*, Mono Co., California. Neubauer 892 (RENO).



Figure 18. *Toiyabea peirsonii*, Inyo Co., California. From the holotype.





Figure 19. *Toiyabea peirsonii*, Inyo Co., California. Photo by Morgan Stickrod, 21 August 2018.





Figure 20. *Toiyabea peirsonii*, Inyo Co., California. Photo by Jane S. Richardson, 3 August 2013.





Figure 21. *Toiyabea peirsonii*, Inyo Co., California. Photo by Jane S. Richardson, 3 August 2013.



Figure 22. *Toiyabea peirsonii*, Inyo Co., California. Top: Photo by Steven Sharnoff, no date given. Bottom: Photo by Jane S. Richardson, 3 August 2013.



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