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NEW SPECIES OF MONKEYFLOWER (*ERYTHRANTHE*: PHRYMACEAE) FROM THE CALIFORNIA SIERRA

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ABSTRACT

Two new species of *Erythranthe* are recognized, both apparently narrowly endemic to Inyo County in the Sierra Nevada of central California and both members of sect. *Simiolus*. Both are annuals with autogamous flowers and hypothesized to be closely related to *E. nasuta*. **Erythranthe bergeri** Nesom, **sp. nov.**, has distal leaves that are connate-perfoliate with upturned margins. **Erythranthe angulosa** M. Berger, **sp. nov.**, produces swollen axillary organs at bases of stem and peduncles — these organs attract ants and perhaps are extrafloral nectaries. In situ photos document both species.

Field exploration by Berger in northern Inyo County, California, has discovered two highly distinctive species of *Erythranthe*. Both are previously undescribed members of sect. *Simiolus*.

ERYTHRANTHE BERGERI Nesom, **sp. nov. TYPE**: **California**. Inyo Co.: 3.2 air mi NW of center of Big Pine, WSW of Warren Lake, just S of County Road, 37.190678 -118.342133, cracks and fissures in granite outcrop near mouth of large, seasonally wet wash, 4060 ft, 10 May 2020, *M. Berger s.n.* (holotype: RSA; isotype: UC).

Similar to *Erythranthe nasuta* in its annual duration, 4-angled stems, slightly elongate upper calyx lobe, and plesiogamous (and presumably autogamous) flowers but different in its evenly and densely hirtellous vestiture (stems, leaves, calyx), connate-perfoliate distal leaves, the distalmost pairs forming cuplike structures with upturned margins, leaf margins shallowly and irregularly dentate-serrate, and its calyces with raised-thickened ridges and membranous inter-ridge areas.

Annual, taprooted. **Stems** erect to ascending-erect or decumbent, ca. 25–50 cm, 4-angled, simple or branched from proximal nodes, evenly and densely hirtellous, eglandular. **Leaves** basal and cauline, proximal to medial petiolate, distal medial to distal abruptly becoming epetiolate and connate-perfoliate, petioles 4–10 cm long, blades (proximal to medial) broadly ovate to elliptic-ovate or suborbicular, 3–6.5 cm long, palmately 5–7-nerved, proximal largest, apices acute to obtuse or rounded, bases (proximal and lower cauline) cuneate to truncate or subcordate, margins shallowly and irregularly dentate to dentate-serrate or nearly lacerate-dentate, commonly doubly toothed, green on both surfaces or sometimes purplish abaxially, densely and evenly hirtellous on both surfaces with dull, terete, sharp-pointed, nonglandular hairs, eglandular. **Flowers** usually from distal nodes but sometimes from medial to distal, 2 per node; flowering branches from proximal to medial nodes. **Fruiting pedicels** 10–20 mm, densely hirtellous, eglandular. **Fruiting calyces** densely and evenly hirtellous, eglandular, 11–15 mm long, green and without red or purple markings, ridges raised and thickened, inter-ridge areas membranous and transparent, lobes closing, upper lobe often slightly elongate. **Corollas** yellow, sometimes with a sparsely red-spotted tube-throat base, without red marking on the lower lip, tube-throat cylindric, 6–10 mm, exserted 2–4 mm beyond calyx margin, limb weakly bilabiate, expanded ca. 2–3 mm (pressed). **Plesiogamous**; anther pairs and stigma at the same level. Figures 1-7.

Known only from the type collection.

The only other species of *Erythranthe* with connate-perfoliate leaves is *E. glaucescens* (Fig. 10), which is restricted to Butte and Tehama counties (California) and is characterized by broadly bilabiate, herkogamous-allogamous flowers and glabrous-glaucous vestiture (Fig. 8). Given the otherwise wide morphological disparity between *E. bergeri* and *E. glaucescens*, the unique foliar feature probably developed in parallel. *Erythranthe glaucescens* is hypothesized to be closely related to *E. nudata*, *E. percaulis*, and *E. filicifolia* (Nesom 2019).

Erythranthe bergeri has more in common with *E. nasuta* (Figs. 11-14), *E. laciniata*, and *E. pardalis* (subgroup E of the "Guttata group" in Nesom 2019). These plants are annual in duration with flowers often produced at all nodes (proximal to distal). Flowers of *E. nasuta* often are reduced in size and autogamous, like those of *E. bergeri*. *Erythranthe nasuta* is variable and broadly distributed through the western USA; *E. laciniata* and *E. pardalis* are California endemics with relatively narrow ranges. Subgroup E is expanded here to include the two new species described in this manuscript as well as the widely distributed *E. microphylla*, which also has 4-angled stems.

Among the species of subgroup E, the closest evolutionary relative of *Erythranthe bergeri* is hypothesized here to be *E. nasuta*, emphasizing their 4-angled stems and overlap in vestiture. *Erythranthe nasuta* does not produce the pervasively hirtellous vestiture characteristic of *E. bergeri* but the adaxial leaf surfaces usually are hirtellous and stems and calyces are variably so (between populations). Hirtellous vestiture also is produced by *E. microphylla* and especially variants of *E. guttata* sensu stricto.

Figure 1. Locality of *Erythranthe bergeri*. Cracks and fissures of granite outcrop near mouth of large, seasonally wet wash, northwest of Big Pine, Inyo County. Google Earth and Google Maps.

Figure 2. *Erythranthe bergeri*. Habitat on faces of broad granite fissure at the type locality. Photo by Matt Berger, 10 May 2020.

Figure 3. *Erythranthe bergeri*. Cluster of plants from narrow crevice in granite, showing the distinction/transition from proximal, petiolate leaves to distal, perfoliate ones. Photo by Matt Berger.

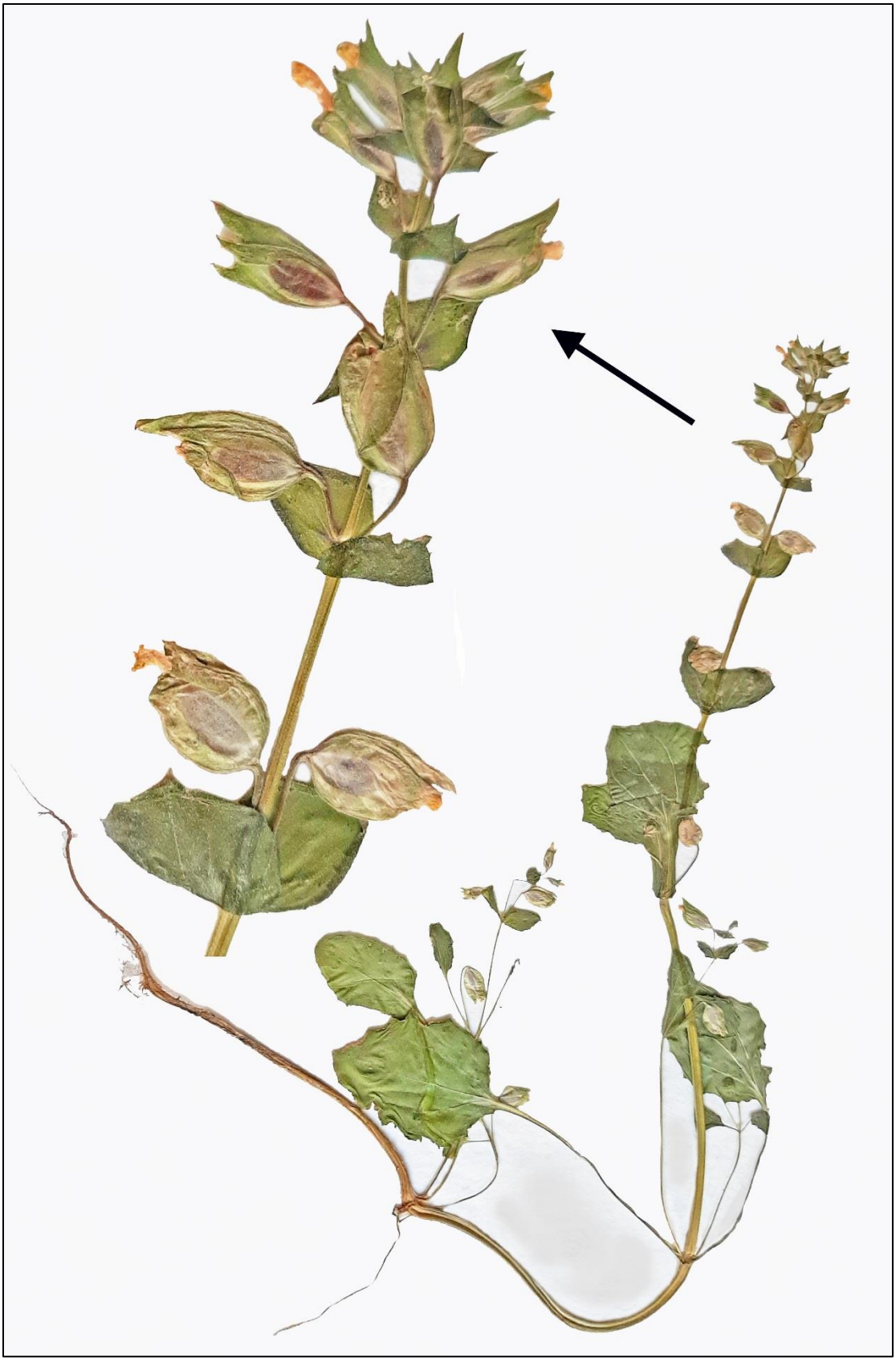

Figure 4. *Erythranthe bergeri*. Isotype (UC).

Figure 5. *Erythranthe bergeri*. Inflorescences and upper cauline leaves, showing the cuplike structures formed by distal connate-perfoliate leaves. Details from Figure 3.

Figure 6. *Erythranthe bergeri*. Top: Upper midcauline leaves. Bottom: lower midcauline leaves, with depauperate branches and flowers from axils, connate-perfoliate by petiole-like base. Photos by Matt Berger.

Figure 7. *Erythranthe bergeri*. Inflorescence of mostly post-anthesis flowers, showing calyces with raised-thickened angles and membranous-transparent inter-ridge areas. Detail from Figure 3.

Figure 8. *Erythranthe bergeri*. Calyx and corolla. Photo by Matt Berger. Photos in Figs. 6 and 9 show corollas with a broader tube-throat and faint red markings on its base.

Figure 9. *Erythranthe bergeri*. Corolla and mature calyx. Photos by Matt Berger.

Figure 10. *Erythranthe glaucescens*, Butte County, California, May 2018. Photo by Evan D. MacKinnon, from CalPhotos. The connate-perfoliate leaves probably developed independently of those of *E. bergeri*.

Figure 11. *Erythranthe nasuta*, Wheeler Co., Oregon. *Stiles 00-02* (WTU).

Figure 12. *Erythranthe nasuta*, El Dorado Co., California, May 2019. Photo by Mark Egger, Flickr, by permission.

Figure 13. *Erythranthe nasuta*, Fresno Co., California, June 2017. Photo by Mark Egger, Flickr, by permission. Distal leaves are epetiolate with bases contiguous but not connate.

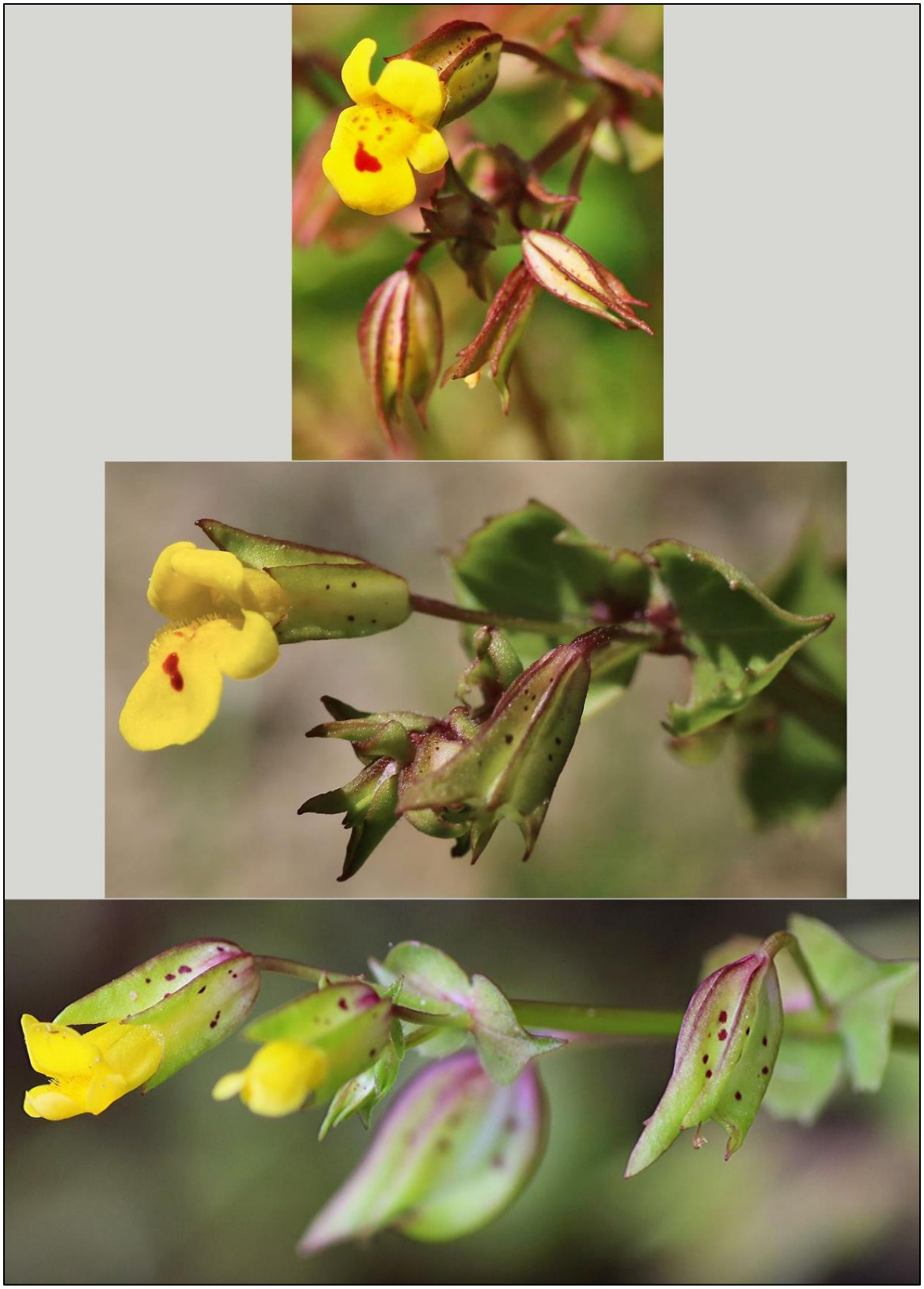

Figure 14. *Erythranthe nasuta*. Top and middle: Monterey Co., California, April 2019. Bottom: El Dorado Co., California, May 2019. Photos by Mark Egger, Flickr, by permission. Variation in flower morphology.

ERYTHRANTHE ANGULOSA M. Berger, **sp. nov. TYPE**: **California**. Inyo Co.: SW of Lone Pine, Horseshoe Meadows Road, 2.5 road mi ENE of Last Chance Meadow Research Natural Area and area of campgrounds and trailheads, 36.467044 -118.134064, granite cliffs and rock faces on N side of road, 9580 ft, 17 Jul 2020, *M. Berger s.n.* (holotype: RSA).

Similar to *Erythranthe nasuta* in its annual duration, 4-angled stems, tendency for stems and leaves to become purplish, and very small, plesiogamous (and presumably autogamous) flowers produced at all nodes (proximal to distal) — but distinct in its habit appressed against cliff faces, swollen axillary organs (at bases of stem and peduncles) that perhaps are extrafloral nectaries, completely glabrous stems, pedicels, and calyces, smaller calyces without a protruding upper lobe, and calyx lobes rolled nearly into cylinders..

Annual (probably), roots not seen. **Stems** decumbent, appressed against rock faces, ca 5–20 cm, sharply 4-angled, simple or branched from proximal nodes, glabrous, eglandular. **Leaves** basal and cauline or basal absent at flowering, sparsely hirtellous on both surfaces with dull, terete, sharp-pointed, eglandular hairs, more or less purplish on the lower surface or both surfaces, proximal to medial largest and persistent, petiolate, petioles 15–35 mm (absent distally), blades (of petiolate leaves) broadly ovate to subreniform, 20–45 mm wide, palmately 5-nerved, margins shallowly crenate to dentate, base truncate to subcordate, apex obtuse to acute, distal epetiolate with deltate blades with long-acute apices. **Swollen organs** produced at base of pedicels and stems at axils, appearing thin-walled and inflated, apparently exuding liquid drops. **Flowers** from basal to distal nodes, 2 per node; fruiting pedicels 10–25 mm, decreasing in length distally, glabrous, eglandular. **Fruiting calyces** mostly 7–9 mm long, nodding, glabrous, eglandular, often purple-spotted, lobes rolled nearly into cylinders with rounded apices, lower lobes curving upward and closing the mouth at maturity, upper lobe not prominently elongate. **Corollas** yellow, red-dotted along the palate ridges and with a red splotch at the base of the lower lip, tube-throats narrowly funnelform, exserted ca. 4–6 mm beyond calyx margin, limb bilabiate, expanded ca. 6 mm (pressed). Herkogamous; anther pairs and stigma at slightly separated levels.

Known only from the type collection.

The axillary organs of *Erythranthe angulosa* are unique in Phrymaceae. As they appear to be exuding liquid droplets (Fig. 23) and ants were observed on leaves and around the axillary organs (Figs. 23, 24), it is possible that they are extrafloral nectaries supporting a mutualistic interaction. On drying, these organs shrink to obscure but still perceptible swellings.

If these organs are extrafloral nectaries, the nature of possible benefit to plants of *E. angulosa* is obscure. Involvement of ants in floral biology is unlikely because the flowers show markings and morphology for bee pollination. *Erythanthe* seeds are minute and probably dispersed by wind and water rather than by insect mediation. Leaf herbivory in monkeyflowers occurs only rarely, but Figure 22 shows calyces and fruits eaten away and ants perhaps are involved with defense from predation. In situ observations are needed.

The species closest in morphology and those presumably most closely related to *Erythranthe angulosa* are *E. nasuta* (Figs. 11-14), *E. laciniata*, *E. pardalis*, and *E. microphylla* — subgroup E of the "Guttata group" (see comments above following *E. bergeri*; Nesom 2019). The present manuscript adds *E. bergeri* and E. *angulosa* to this subgroup and it is hypothesized here that these two with *E. nasuta* and *E. microphylla* form a clade characterized by 4-angled stems (probably an apomorphic feature) and hirtellous vestiture (probably plesiomorphic). Among the "subgroup E" species, even those with herkogamous flowers have small corollas with a slight degree of separation between anthers and stigma, and autogamy is common (Bodbyl Roels & Kelly 2011). *Erythranthe angulosa* differs from *E. nasuta* most conspicuously in its axillary organs and smaller calyces with subcylindric lobes.

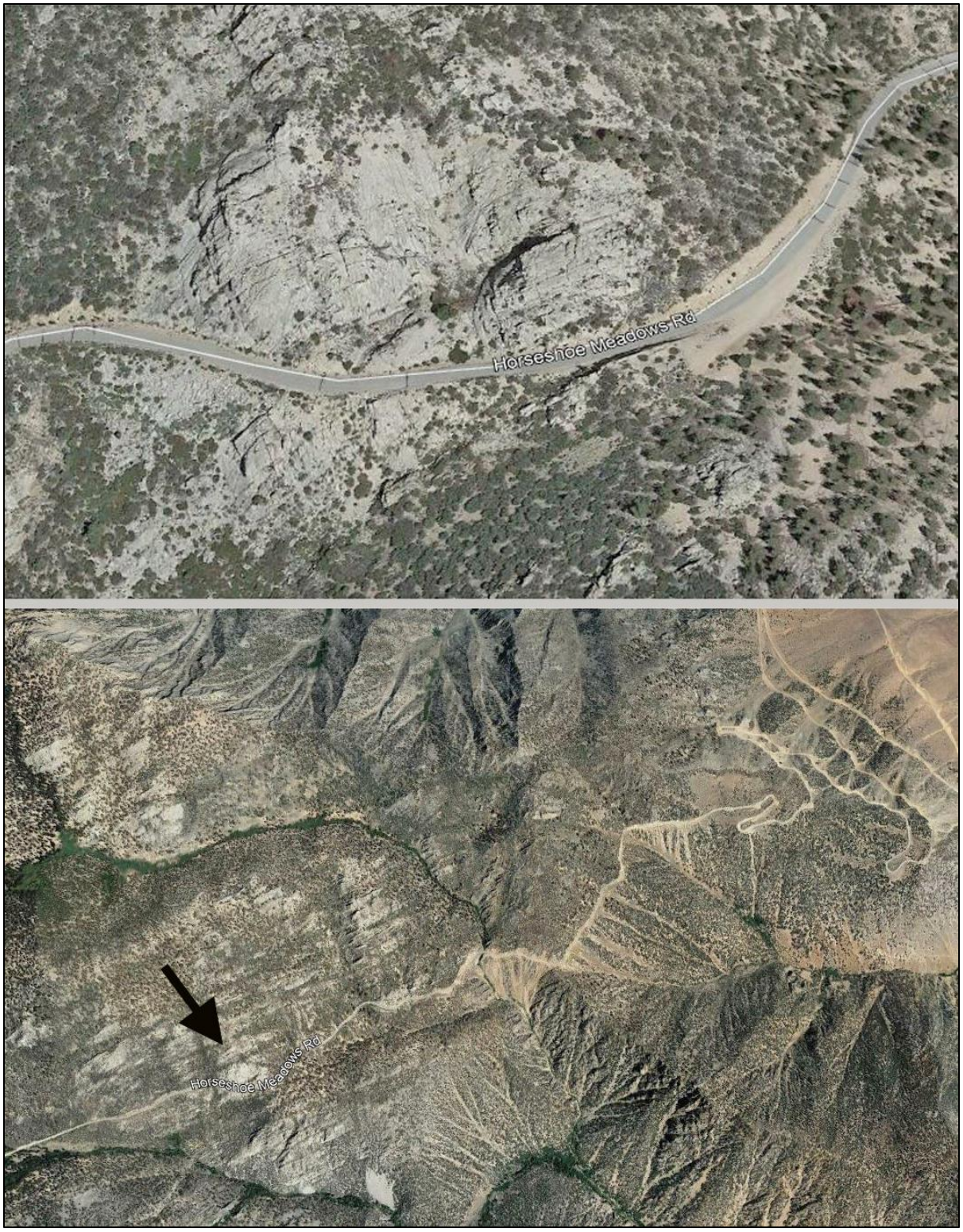

Figure 15. Locality of *Erythranthe angulosa*. Top: Granite cliffs and faces at the type locality along Horseshoe Meadows Road. Bottom: Arrow points to the area of bare, exposed granite pictured in the upper photo. Google Earth.

Figure 16. *Erythranthe angulosa*. Habitat on granite cliff face at the type locality. Photo by Matt Berger, 17 Jul 2020.

Figure 17. *Erythranthe angulosa*. Corolla. Photo by Matt Berger.

Figure 18. *Erythranthe angulosa*. Stems and leaves more or less appressed against the rock face. Photo by Matt Berger.

Figure 19. *Erythranthe angulosa*. Inflorescence from same plant as in Figure 17. Photo by Matt Berger.

Figure 20. *Erythranthe angulosa*. Calyces after corollas shed. Photos by Matt Berger.

Figure 21. *Erythranthe angulosa*. Ant on green adaxial leaf surface. This branch comprises the holotype: Photo by Matt Berger.

Figure 22. *Erythranthe angulosa*. Fruit predation — calyces also partially eaten away.

Figure 23. *Erythranthe angulosa*. Swollen axillary organs at stem and peduncle bases. Arrows point to a small droplet apparently exuded from swollen organ. Photos by Matt Berger.

Figure 24. *Erythranthe angulosa*. Swollen axillary organs at stem and peduncle bases. Photo by Matt Berger.

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