

**AYENIA COMPACTA AND AYENIA FILIFORMIS (MALVACEAE)
IN THE WHITE TANK MOUNTAINS OF THE ARIZONA SONORAN DESERT**

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ABSTRACT

Two species of *Ayenia*, *A. compacta* and *A. filiformis*, are represented in the White Tank Mountains (WTM) of Arizona. However, the confused taxonomic history of Sonoran Desert *Ayenia* and the absence of easily identifiable traits in the literature makes the distinction between them uncertain. This paper details traits that can be used to distinguish them in the field and concludes that they are separate species growing sympatrically in the WTM.

Two species of the genus *Ayenia* appear to be present in the White Tank Mountains (WTM) in the Sonoran Desert west of Phoenix, Arizona. Identification of which species are present, however, is complicated by the confusing and inconsistent taxonomic history of *Ayenia* in the area.

Ayenia is a New World genus consisting of about 80 species distributed from Argentina north through the tropics to the southern USA, with representatives also in some Caribbean islands. Four *Ayenia* species are recognized in Arizona (Dorr 2015): *A. compacta*, *A. filiformis*, *A. jaliscana*, and *A. microphylla*. *Ayenia jaliscana* and *A. microphylla* are found in Arizona to the south and east of the WTM but have not as yet been identified in the WTM. These two species have readily recognizable distinguishing traits (Dorr 2015) and will not be addressed in this paper.

Cristóbal's revision of *Ayenia* (1960) followed a scheme whereby three sections of *Ayenia* species were defined primarily according to differences in the plant petals. In this scheme, *A. compacta* and *A. filiformis* were grouped in one section and *A. jaliscana* and *A. microphylla* were assigned individually to two other sections.

Among the defining differences between Cristóbal's three sections are features of the petal laminae: *Ayenia compacta* and *A. filiformis* laminae have elongated clefts beginning medially on their distal edges and cutting centrally for about one-third to one-half the length of the lamina; *A. jaliscana* and *A. microphylla* do not have these clefts. Second, on the petal lamina outer surfaces, at the proximal ends of the clefts, *A. compacta* and *A. filiformis* have worm-like structures called appendages, whereas *A. jaliscana* and *A. microphylla* do not. Finally, Cristóbal (1960, pp. 158–159) noted that the petal lamina shapes differ between species, with other character differences consistently accompanying specific shapes. In the two WTM *Ayenias*, clefts and appendages are present on the laminae and differences in lamina shapes are accompanied by other specific differences. So it would seem they are *A. compacta* and *A. filiformis* (Figs. 5–7, 10–15), but uncertainty persists in distinguishing one from the other.

The taxonomic history of *Ayenia compacta* and *A. filiformis* has been and continues to be complicated. Since Watson's description of the type specimen of *A. filiformis* in 1889 and Rose's 1905 description of *A. compacta*, the two entities have variously been called *A. filiformis* (Watson 1889), *A. microphylla* (Palmer 1890; see Rose 1905), *A. compacta* (Rose 1905), *A. wrightii* (Standley 1920), *A. pusilla* (Standley 1920), and *A. californica* (Jepson 1925). Cristóbal's revision put *A. compacta*, *A. filiformis*, and *A. microphylla* in Arizona and relegated *A. pusilla* (which had become something of a generic basket for North American species) to northern South America. *Ayenia pusilla* nevertheless

continued to appear in North American flora for several more years (Shreve & Williams 1964; Keil 1973). Cristóbal restricted *A. wrightii* to central Mexico.

More recently, *Ayenia insulicola*, a species Cristóbal (1960) and Dorr (pers. comm., 2019) restrict to the Caribbean, has appeared in herbaria identifications (e.g. Arizona State University, Phoenix Desert Botanical Gardens, University of Arizona, Utah State University) as one of the species names used to replace *pusilla* (Ayers pers. comm., 2019) but how it was determined that *A. insulicola* is a southwestern species is not clear and the reasoning apparently has not been published. It seems unlikely that a genus which demonstrates a considerable ability to evolve and includes a species (*A. insulicola*) which is at home at sea-level in the humid Caribbean environment, would also have the same species existing at an altitude of 1000-3000 feet in the Sonoran Desert, a few thousand miles away.

One last complication has been presented by Felger (2000, 2015), who questioned whether *Ayenia compacta* and *A. filiformis* are really separate species. This question is addressed by the information presented below.

For clarity, I will use the names *A. compacta* and *A. filiformis* throughout the paper, applying them as seems appropriate to the final conclusion.

Material and methods

The 25 WTM plants discussed in this paper were found entirely in washes that are eroding into bajadas on the east side of the mountains. Previous researchers have found other plants on slopes outside of washes and somewhat higher in the mountains (e.g., Keil 1973) but the searches performed for this paper were restricted to washes to prevent soil damage from repeated visits as much as possible. The west side of the mountains have not been searched. All of the plants found were growing in washes at the base of and closely approximated to or from under small to mid-sized (ca. 50x50 cm) rocks; most grew on the downstream sides of their rocks. Healthy plants grew as tall as 40 cm, but many were heavily browsed. Seasonal and weather variations significantly affected the growth and health of the plants over the 3 years they were observed, with a few not surviving the summer heat. Flash floods washed away some plants but also presumably distributed seeds.

Four plants with deep red or purple flowers (*Ayenia filiformis*) were found in three different washes separated by several miles, while 19 plants with yellow/orange flowers and/or distinctive fruit (*A. compacta*) were all found scattered over about 0.5 mile in a single wash, with one of the purple-flowered plants growing among them. Two plants in the same wash, lacking flowers and fruit, were not identified beyond genus.

The following descriptions contrast *Ayenia compacta* and *A. filiformis* in WTM and combine my visual observations with information gleaned from my photographs of the 0.1–4 mm structures on the plants.

Results and conclusions

Overall descriptions of the plants are available in other publications (e.g., Lawrence 1929; Cristóbal 1960; Dorr 2015) so my comments are restricted primarily to diagnostic differences in flowers and fruit, except to note that (a) *Ayenia compacta* branches may be decumbent or erect while *A. filiformis* has an erect branching pattern (Cristóbal 1960) (Figs. 1, 2); (b) *A. compacta* basal leaves are ovate, about 1 cm long, with minimal or no pubescence, while *A. filiformis* basal leaves are ovate and may be small but also may be 2–3 cm long and may or may not retain pubescence; and (c) terminal leaves in both species are 1–3 cm long and either ovate-lanceolate or linear, with those of *A. filiformis* in general being noticeably more pubescent than *A. compacta* (Figs. 3, 4). These branch and leaf traits

may be suggestive but are so variable between plants that their appearance in an individual plant should probably be considered as supportive rather than definitive diagnostic evidence.

Flowers of both species are beautiful and extraordinarily complex, with the most notable features including androgynophores, five stamens alternating with five staminodes, petals composed of filamentous claws and diagnostically-shaped laminae that curve medially to attach to the staminodes (thereby “hiding” the anthers inside the flower), and the appendages (Figs. 5–7, 10–14).

The mature fruit (schizocarp) of *Ayenia* in the WTM is nearly spherical and 4–5 mm in diameter at maturity, with 5 well-defined mericarps, each containing a single seed. It bears evenly spaced spines (variously called *aculeolos*, glands, papillae, prickles, processes, spines) that are 0.3–1.3 mm long and may or may not be pubescent (Figs. 8, 9, 16).

The following traits are found together as a unit in the plants of each presumed species in the WTM.

Flowers:

1. Color: The flower color of *A. compacta* does not seem to have been previously described but may be the best distinguishing trait between the two species. *Ayenia compacta* flowers are pink, yellow, or orange-red, not deep red or purple; those of *A. filiformis* are deep red or purple, with occasional petal laminae being purple centrally and white peripherally.
2. Petal lamina shape: *A. compacta* diamond, *A. filiformis* triangular
3. Petal lamina-claw junction: *A. compacta* 135 °, with lamina attenuate on claw; *A. filiformis* 90 ° and squared-off
4. Petal lamina appendages: *A. compacta* proximal 2/3 is the color of the lamina, distal 1/3 is black; the black portion is somewhat bulbous. *A. filiformis* is 90-100 % black and is sickle-shaped.
5. Sepals: *A. compacta* sepals may be green but often are a mottled red, sometimes on the same plant; *A. filiformis* sepals are bright green.

Fruits:

1. Mature fruit color: *A. compacta* red (immature are green), *A. filiformis* green
2. Fruit spines – size and pubescence: *A. compacta* <0.7 mm, with very short or absent hairs; *A. filiformis* 0.5-1.3 mm, with long, easily visible hairs
3. Fruit spines – color: *A. compacta* dark brown to black (even when fruit is green), *A. filiformis* green

This consistent combination of traits in plants of yellow/orange (*Ayenia compacta*) vs. purple (*A. filiformis*) flowers defines the two species. Naming the purple-flowered plants *A. filiformis* follows the original description of Watson (1889), who described the type, found in Sonora, Mexico, as “petals purple” and “fruit ... beset with numerous slender green processes.” Descriptions of *A. compacta* do not include the yellow/orange flower color except as “brownish” (Jepson 1925; Adams 1951) but do mention “short brown papillae” on the fruit (Rose 1905) and “capsule... muricate with black glands” (Adams 1951). Jepson (1925) noted that the type specimen of *A. californica*, now synonymized with *A. compacta*, was found “on the western edge of the Colorado desert”; photos of *A. compacta* from Anza-Borrego State Park and the surrounding desert in Southern California all show plants that are apparently the same as the plants with yellow/orange flowers in the WTM (e.g., CalFlora, SEINet websites).

These descriptions are of live plants in the field. In herbarium specimens, changes in color, shape, and other parameters in the plants’ minute structures due to drying, aging, and mounting create considerable impediments to their proper identification, though close examination may help to suggest which species they are. As though in confirmation of the difficulties of identifying older herbaria specimens, many such specimens in Arizona herbaria have over the years been renamed *Ayenia*

filiformis (and *A. insulicola*, as noted above) from *A. pusilla*, seemingly without regard to the possibility that *A. compacta* could be present.

Despite the uncertain identification of some herbarium specimens, it appears that *Ayenia compacta* is a species primarily of the lower Colorado desert, growing on both sides of the Colorado River and west into California and south into Baja California. Its easternmost distribution ends probably very near the WTM. *Ayenia filiformis*, on the other hand, occurs as far east as Texas but may have its westernmost distribution also ending near the WTM, though a small number have been identified in western Arizona. The two species meet and grow together in the WTM.

In summary, there are 2 species of *Ayenia* in the WTM (*Ayenia compacta* and *A. filiformis*), readily distinguished from each other by differences in flower color, petal lamina shape, petal appendage color and shape, and by the differences in fruit color and in the length, color, and pubescence of the fruits' spines, with supplemental support by other traits as described above and in the figures.

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Figures



Figure 1. *Ayenia compacta*. Features visible on the plant that may assist in identification are erect, decumbent, and procumbent branches; linear and lanceolate terminal leaves; small ovate basal leaves; numerous fruits turning from green to red; and orange flowers.



Figure 2. *Ayenia filiformis*. Visible are erect branches; linear and lanceolate terminal leaves, large ovate basal leaves, green fruit, and deep red/purple flowers.

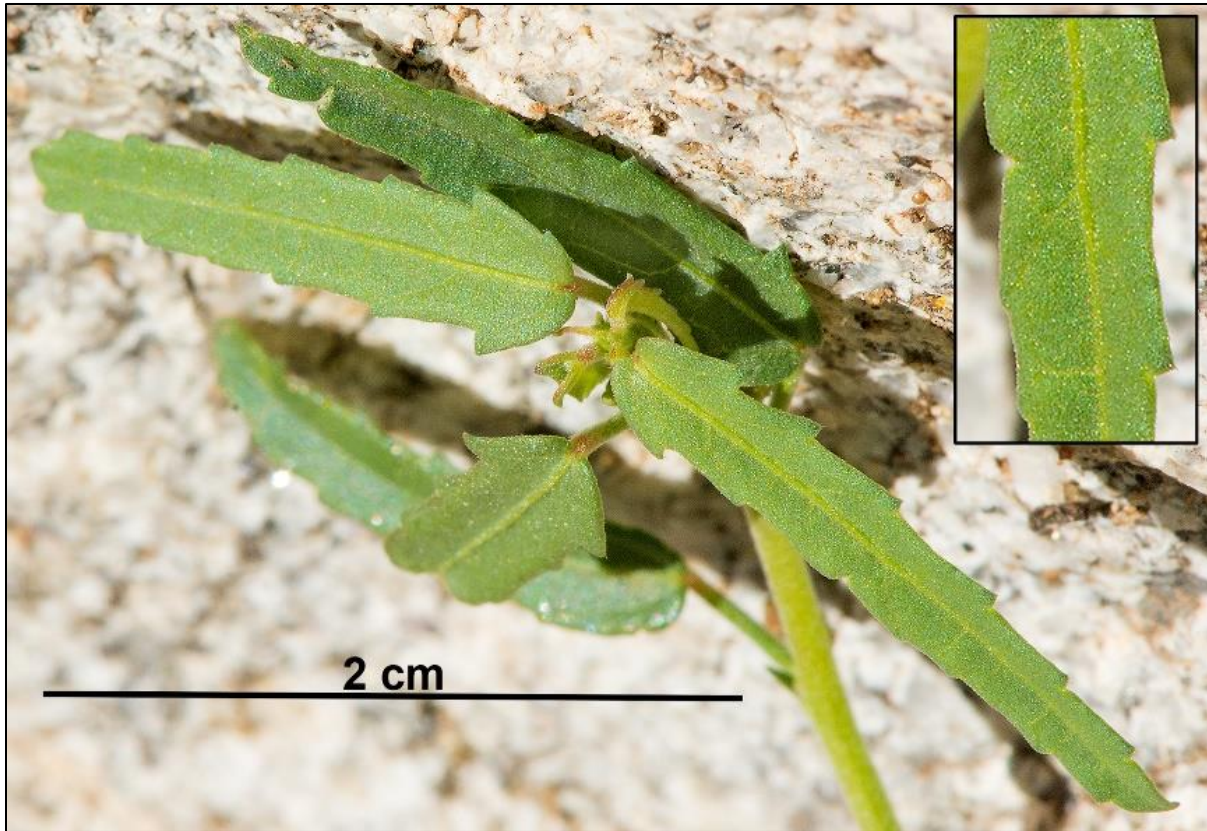


Figure 3. *Ayenia compacta*. A. Linear and lanceolate terminal leaves. Inset: lightly pubescent terminal leaf. B. Glabrous small ovate basal leaves plus ripening fruit.



Figure 4. *Ayenia filiformis*. A. Pubescent linear terminal leaves and one mature flower. Inset: pubescent terminal leaf. B. Pubescent small ovate basal leaves and ripening fruit.

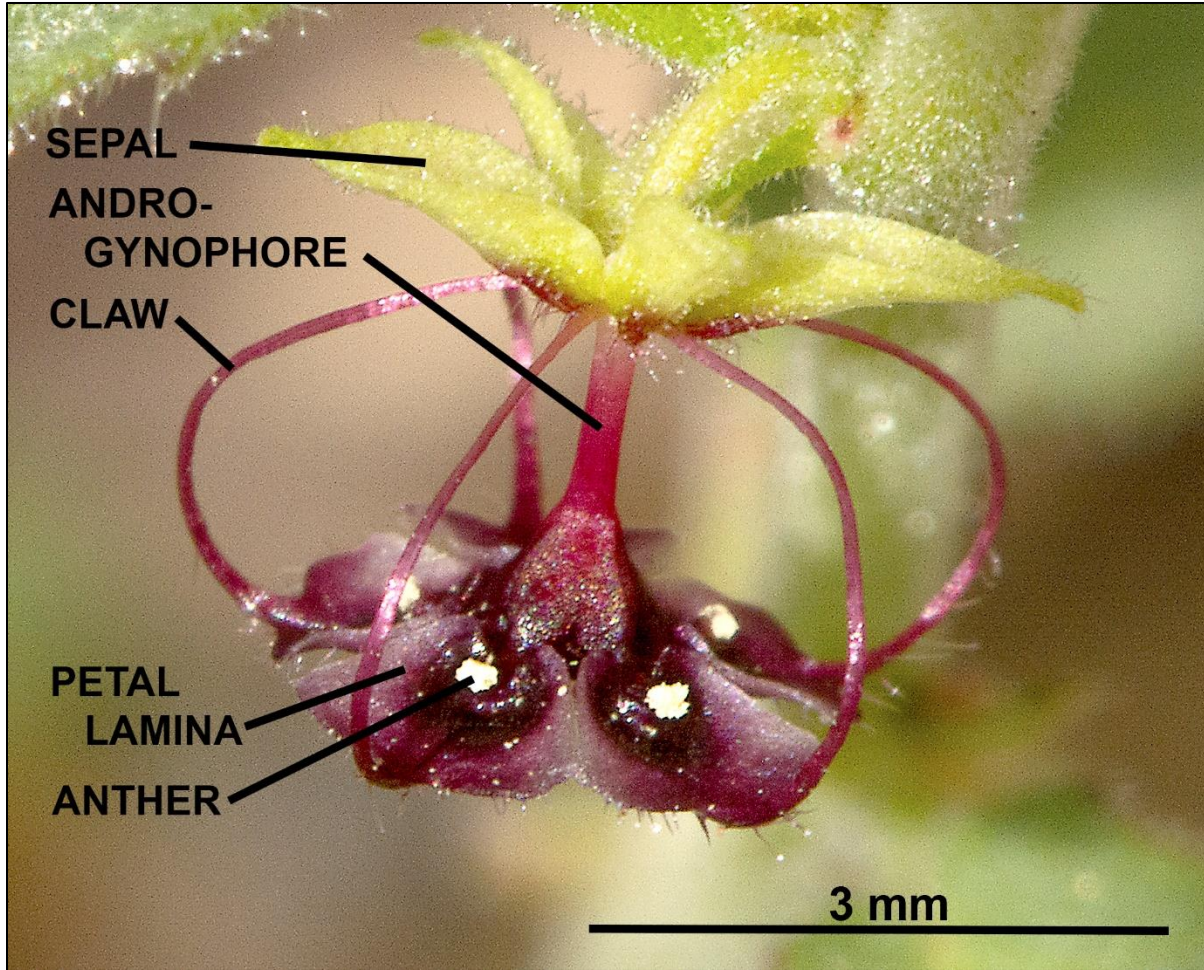


Figure 5. *Ayenia filiformis*. Flower, lateral view, annotated. Anthers on undersurface of laminae at proximal ends of clefts.

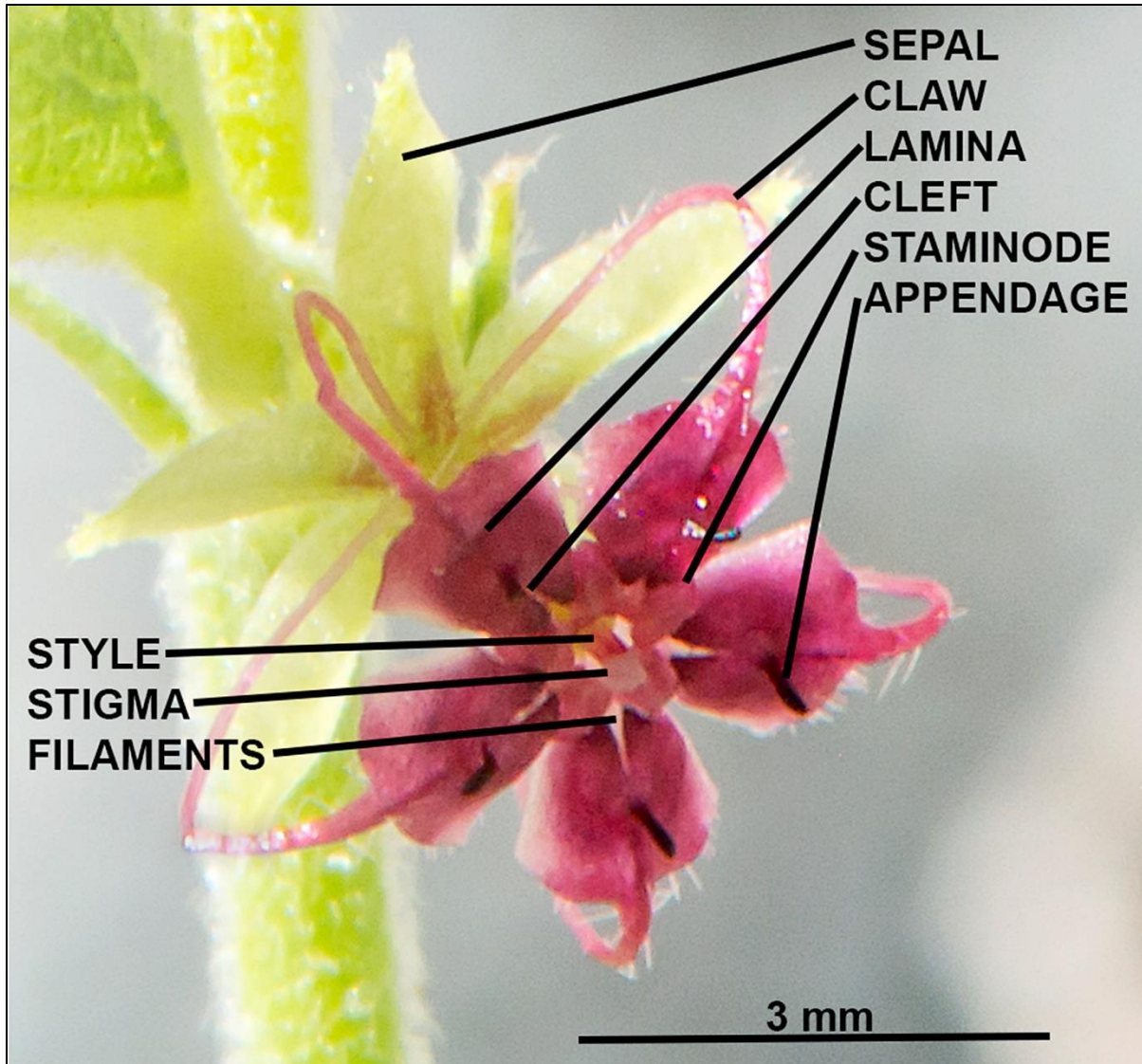


Figure 6. *Ayenia filiformis*. Flower, distal end view, annotated. Lamina attachments to staminodes visible.

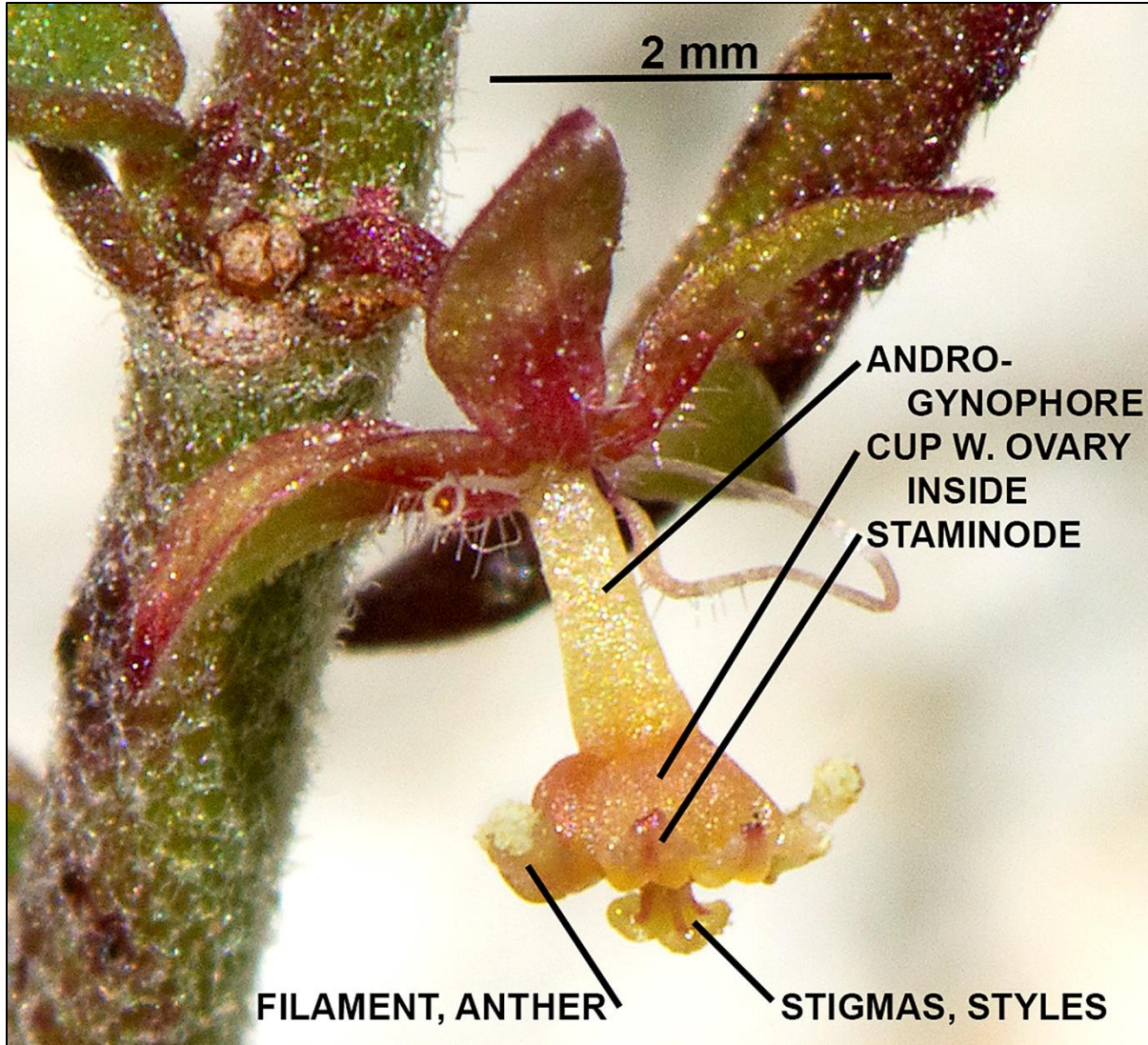


Figure 7. *Ayenia compacta*. Damaged flower with missing petals, exposing details of red sepals, androgynophore, pistils, and stamens.



Figure 8. *Ayenia compacta*. A. Immature green fruit with small dark brown spines having a few dark hairs. B. Mature red fruit with small dark spines having a few short hairs.



Figure 9. *Ayenia filiformis*. A. Green fruit with pubescent long green spines. One fruit has orange color on side facing sun. B. Green fruit with spine traits as in 9A. C. Reddish fruit turning brown (ripe seeds); note pubescent green spines.



Figure 10. *Ayenia compacta*. Flower lateral view.

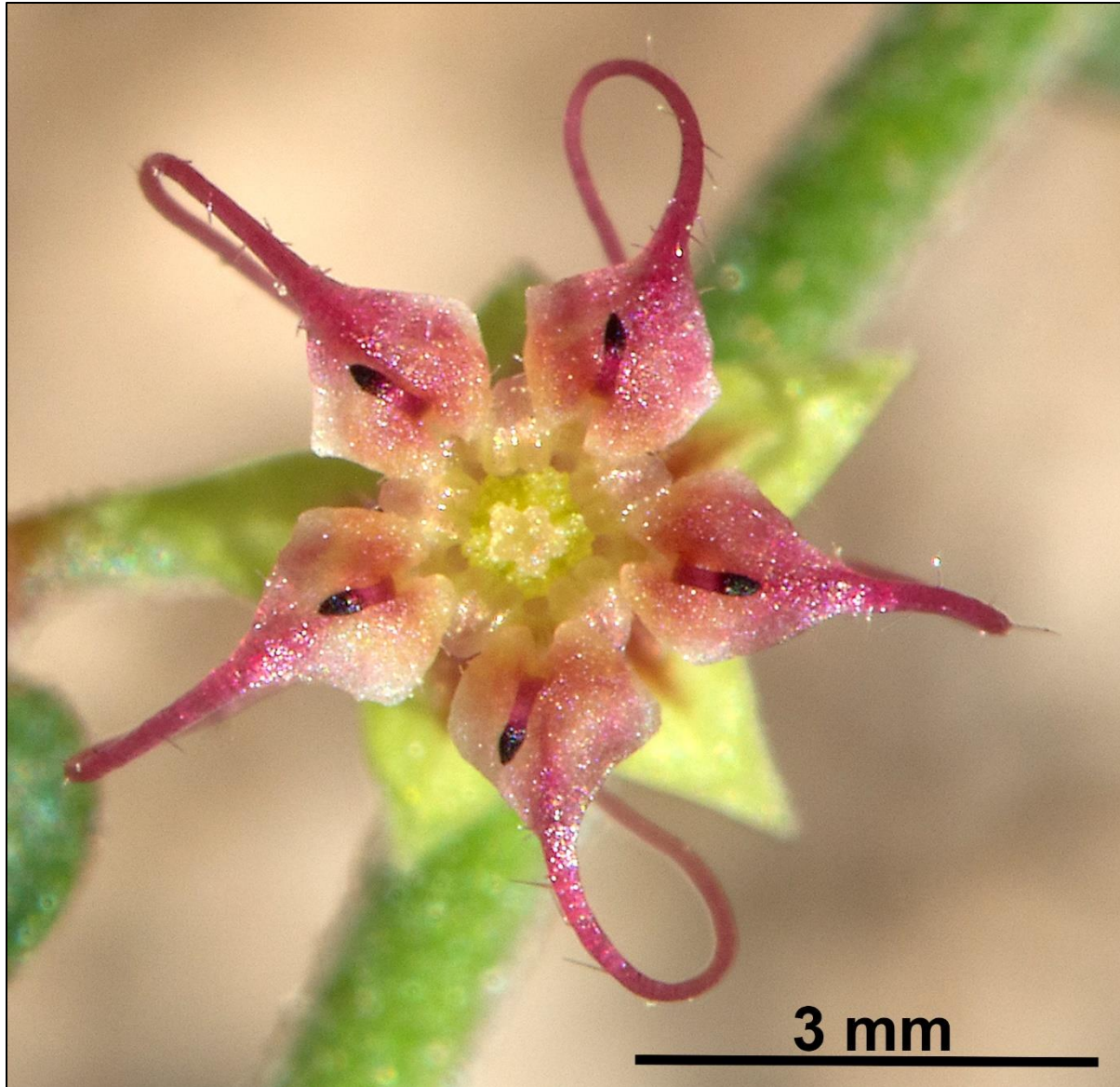


Figure 11. *Ayenia compacta*. Flower distal (end) view. Note diamond-shaped lamina attenuate on claw and the clear view of the laminas attaching to the staminodes.

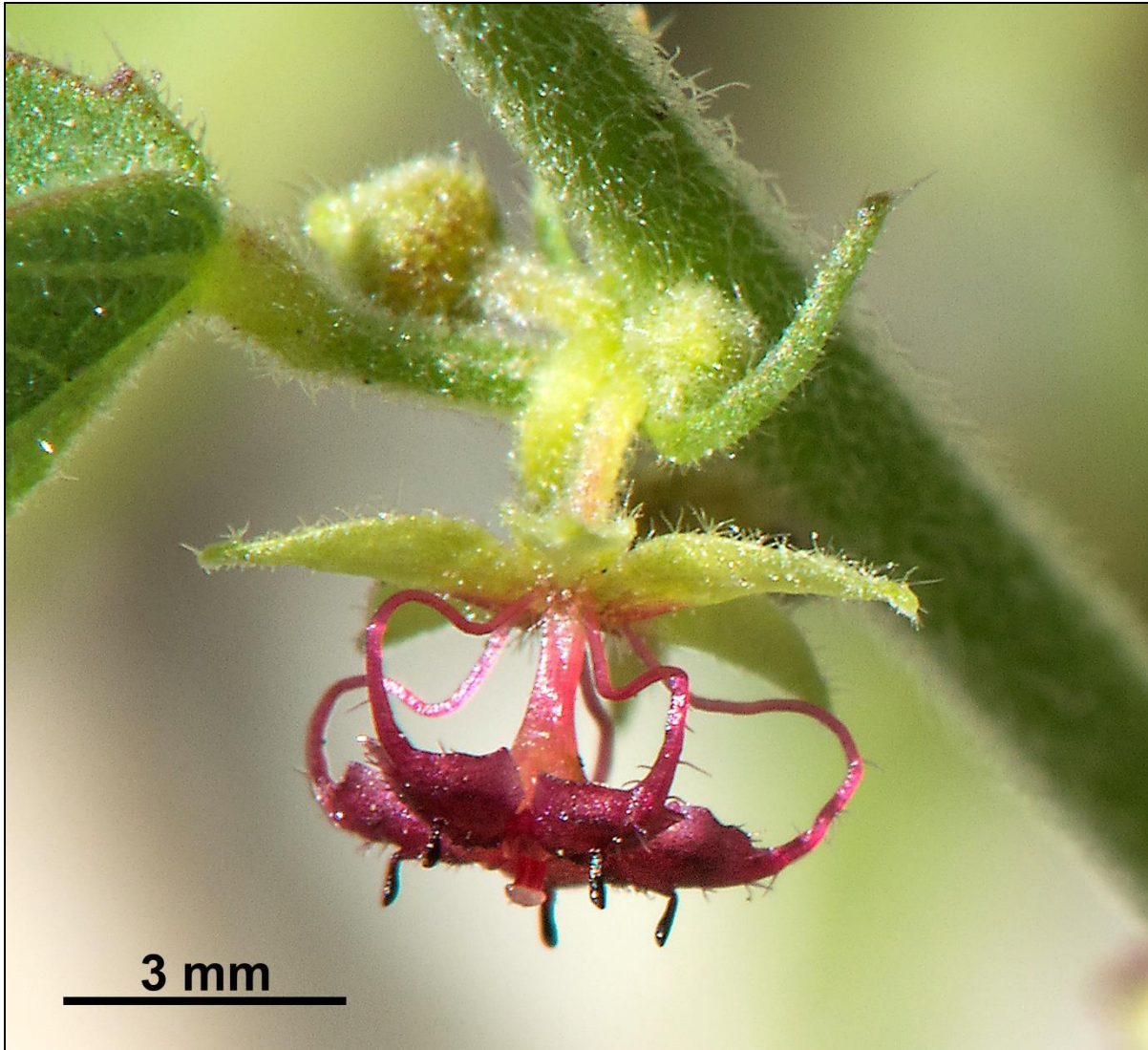


Figure 12. *Ayenia filiformis*. Flower lateral view.

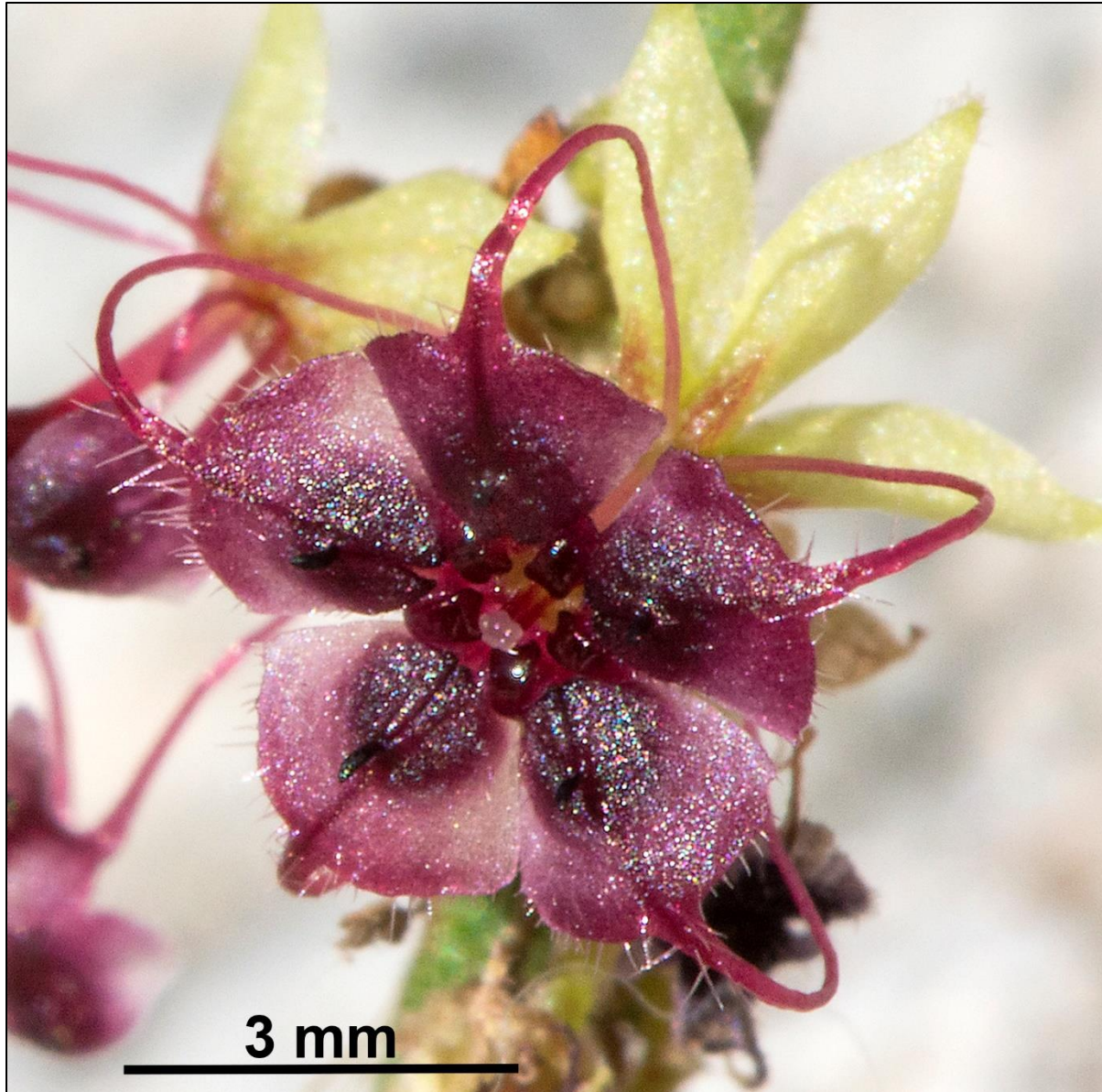


Figure 13. *Ayenia filiformis*. Flower distal (end) view. Note trapezoidal shape of lamina joining claw at a 90° angle and the clear view of the laminas attaching to the staminodes.



Figure 14. *Ayenia compacta*. Flower with 1 petal lamina attached to the undersurface of a sepal, one lamina just breaking away, one petal swinging freely, and one attached to staminodes. The petal lamina attaches to the staminodes and simultaneously attaches by means of its cleft to the stamen filaments, leaving the anther exposed on the lamina undersurface and the appendage on the external surface.

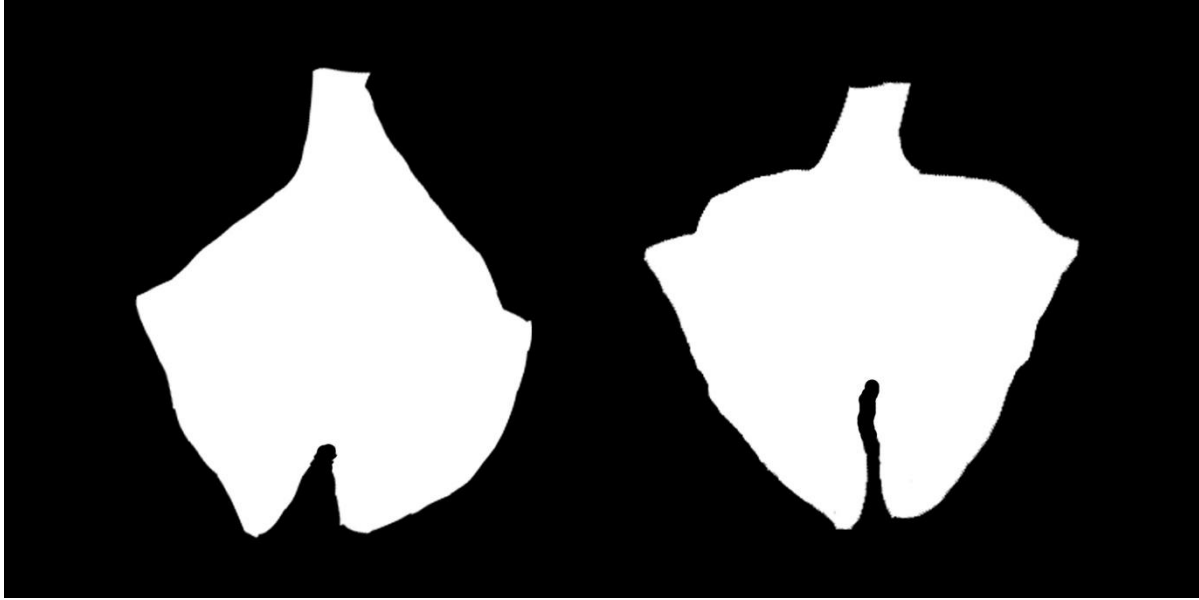


Figure 15. Petal lamina outlines. Left: *Ayenia compacta*. Right: *Ayenia filiformis*.



Figure 16. Seed and mericarp. Left: *Ayenia compacta*. Right: *Ayenia filiformis*. Note the nearly identical seed shapes and patterns of “wrinkles” on the seed surfaces. Note also the differences in color of the mericarp spines.