

A MORPHOLOGICAL AND ANATOMICAL
STUDY OF THE STEM INFLATION OF
THE WILD BUCKWHEAT, ERIOGONUM INFLATUM

by

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ABSTRACT

Eriogonum inflatum Torr. often exhibits enlargements of the lowest stem internode. These swellings are the basis for the specific epithet, and have been used as an identifying characteristic since the original description in 1845. These swellings are caused by cecidozoa of the Pyralidae and Mordellidae families of insects feeding in the stem pith, and are not a true species characteristic. E. inflatum can bloom either as an annual or as a perennial, and uninflated stems can occur in either form. The supposed variety E. inflatum var. deflatum and E. inflatum var. inflatum are identical, and the superfluous varietal names should be abandoned. In addition, care must be exercised in distinguishing annual flowering forms of E. inflatum from the similar but uninflated annual species Eriogonum trichopes Torr.

INTRODUCTION

Eriogonum inflatum Torr. is a striking roadside plant in many parts of the arid southwest. In favorable locations such as the gravel hills near Wickenburg, Arizona, it is the dominant species. E. inflatum, a perennial, is characterized by a cluster of glaucous grey-green scapelike, di-trichotomous stems from 15 cm. to 1 m. in height. These arise from a basal rosette of crisped hairy leaves varying in shape from obcordate to oblong. The involucre are few flowered, five-toothed, and about 1 mm. in diameter. The flowers are pale sulfur yellow. Dry stems from previous seasons are common on mature plants. The plant is popularly known as "Inflated Wild Buckwheat" or "Desert Trumpet" because of the large swellings which frequently occur on the lowest internode of the scape, and sometimes on the upper internodes as well. These enlarged stems are among the chief identifying characteristics in taxonomic keys, and have given the species its name.

Johnston (1924) distinguished E. inflatum var. inflatum from another variety, E. inflatum var. deflatum, only by its inflated stem. Stokes (1936) considered the two varieties to be synonymous, and thought that the fistulae failed to develop under extremely dry conditions.

The original description of E. inflatum Torr. (1845) is very similar to that of E. trichopes Torr. (1848). The outstanding

difference between the two being that in E. inflatum, "the lower part and sometimes the two primary divisions of the stem (are) much inflated and clavate" while those of E. trichopes are not described as being inflated in any fashion. He says the stem of E. trichopes is, "scape-like, verticillately and divaricately much branched"; that of E. inflatum "divides into three or more branches --- the subdivisions are dichotomous." He says that the involucre of E. inflatum are five-toothed, those of E. trichopes four-toothed. It appears, in fact, that the number of teeth on the involucre of E. inflatum occasionally varies to six or seven, but that the usual number is five.

A limited amount of cytological work has been done on E. inflatum. Stone and Raven (1958) have shown that the haploid number of chromosomes is sixteen. Raven (personal communication) reported that the chromosomes are extremely small, and that the microspore mother cells are quite large.

The purpose of this investigation was to determine the cause of the inflations of E. inflatum and to determine whether they are a valid character by which the variety inflatum can be segregated from the variety deflatum. Since these enlarged stems are also used in many keys to separate E. inflatum from E. trichopes, the study was also made to determine their validity as a species characteristic. Anatomical, cytological, and morphological aspects of the stem inflations were considered.

METHODS AND MATERIALS

A. FIELD STUDY

Eriogonum inflatum was studied in the field to determine the incidence of stem swellings. Plant populations were observed as far north as Walker Lake, Nevada, and in many areas of the state of Arizona. Five populations were studied in detail (Fig. 1). During three successive years, observations were made at all seasons on two of the populations.

The major flowering season is in the spring; however, in sheltered locations where moisture is available a few plants may bloom in the winter. All of the winter scapes that were seen are uninflated. The plant is a perennial, but may flower in the first year (Fig. 2). Such plants are sometimes extremely small and produce one delicate scape about 15 cm. tall. In more favorable locations the plants achieve considerable size within the first year (Fig. 3). The plants may persist for years, producing two to many stems each flowering season, and multiple rosettes of leaves on an extremely tough woody caudex (Fig. 4).

Specimens from populations 1, 2, and 3 (Fig. 1) were potted in the field and transferred to the greenhouse. All of these plants had some inflated stems which had grown in the field and several plants had both inflated and uninflated stems at the time of transplanting (Fig. 5).

Sixty-seven young stems from the population of Tortilla Flat (number 3 of Fig. 1) were examined in early spring during the development of the swellings. Most of the stems were in active growth at that time; the youngest stems had just begun to enlarge, and were growing very rapidly. Plants blooming for the first year had wiry, filiform stems with no swellings and no evidence of insect damage. All of the stems with inflations also showed insect damage 2 to 10 cm. above the base of the lowest internode of the scape, and 10 to 25 cm. below the bottom of the inflation. Minute larvae, visible only with the aid of a hand lens, were found in the stems about 2 cm. above the external lesion.

The population north of Wickenburg (number 5 of Fig. 1) was examined in the winter and in the summer. In a random sample of this population, 93% of the stems examined had stem enlargements. Of the inflated stems, 97% showed insect damage, and many contained insect larvae feeding in the pith of the lowest internode (Tables 1 and 2).

B. INSECT DAMAGE

In each of the populations of plants examined, many of the old inflated stems had small round openings, about 11 mm. in diameter, near the top of the inflation (Fig. 6). The cavities of these inflations were discolored, and contained strands of webbing, pupal skins, hair and feces. The discolorations probably were made by the adult insects before they left the cavities,

because only those cavities which have an open escape hole have discolorations of this type. A stem was found with a pupal case still attached to the inside of one of these unopened "portholes" (Fig. 7). The pupal case was attached to the walls of the cavity in several directions by single strands of webbing; there was no cocoon. The "portholes" from which the adult insects emerge are filled with a semi-translucent material, which is evidently an insect secretion. These plugs appear non-cellular and mucilaginous under the microscope.

In March, immature microlepidoptera larvae of the Pyralidae family were found feeding in the stem pith never far above the basal rosette. They were 1 to 2 mm. in length at this time. Larger Pyralidae larvae, collected in July, were feeding higher in the stem in the distended portion just below the fistula. These larvae were about the size of the pupa mentioned above. Dr. Werner suggested that it might be possible to rear the adult insects by sealing the larvae in small glass dishes to prevent desiccation during the maturation process. This was done, and one half of the larvae were maintained at room temperature, and the other half was refrigerated. Both groups were examined periodically. The refrigerated individuals were still alive but had not undergone metamorphosis by the following spring. Those which had been kept at room temperature were all dead by mid-winter. The refrigerated larvae died very shortly after they were returned to

room temperature, so that no mature individuals were obtained and it was not possible to identify the genus or species.

Many inflations had large, jagged holes in them which appeared to have been made by birds or small mammals. Such stems had no pupal skins in them, nor any soiling of the white cavity of the fistula, but sometimes had unopened "portholes", of the sort described above, and also exhibited evidence of larval habitation. Adult flies of the parasitic Bethylidae family were found in some stems with the larval or pupal remains of Pyralidae.

Those stems which had no injuries near the base of the stem, but only high on the lowest internode of the scape, had very small swellings and rarely contained live larvae (Table 2, Plant 10). Occasionally a stem had what appeared to be external insect injuries, but had no swellings and no internal evidence of insect habitation. These lesions were round sting marks with no raised wound tissue as was found where Pyralidae larvae had burrowed into the stem. Possibly they were made by fly parasites of the Bethylidae family which deposited their eggs within the stem tissues where they eventually infested the Pyralidae larvae, if any were present in the stem. These particular insect wounds evidently did not cause stem enlargement.

There were occasional stems with fistulae and no evident external insect lesions, which contained live larvae or internal evidence of insect habitation (Table 2, Plant number 3). In

these instances, it is possible that the larva entered the plant tissues below the attachment of the scape, between the nodes of the rosette of basal leaves.

Another type of larvae found in E. inflatum (Fig. 1, population number 2) is a species of beetle. These larvae are of the Mordellidae family, and feed actively through the winter. All of the live larvae noted in Tables 1 and 2 are of the Mordellidae type. In general, the swellings on stems which contained Mordellidae larvae were more slender than the swellings on dry stems which had been inhabited by Pyralidae during the previous summer. Specimens of plants which contained Mordellidae larvae were planted in the greenhouse in late January; by April these larvae had bored out of the stems, making fresh small holes of $\frac{1}{2}$ mm. to 1 mm. in diameter. These minute larvae disappeared, possibly to pupate in the soil. Apparently pupation did not take place in the stem, because there were no pupal remains in the cavities of the stems.

C. GREENHOUSE AND LABORATORY STUDIES

Achenes were obtained from populations 1 and 2 (Fig. 1), all of which were taken from plants with inflated stems. Several methods of germination were tried: planting in petri dishes at room temperature, and at 7°C; washing and then planting in petri dishes; and planting in pots of soil. In all cases it was necessary to remove adhering floral parts to prevent the development of fungi. Two groups of achenes were placed in petri dishes

between layers of damp filter paper. One dish was kept at room temperature and one was refrigerated at 7°C. Neither group germinated. A third group of achenes was washed for 24 hours in running tap water. Some of these seeds germinated within three or four days. The growth of the radicle was rapid; that of the epicotyl comparatively slow. Most of these root tips were used for cytological investigation (see below); six seedlings were potted in the greenhouse. The fourth group of achenes was planted in the greenhouse in pots which were watered copiously; the seeds germinated at irregular intervals over a period of several months.

Seedling plants were grown in the greenhouse for about four months before an attempt to induce flowering was carried out. To do this, two plants were allowed to dry out while the others were watered regularly. When watering of the dry plants was resumed, flower stalks were initiated in ten days to two weeks. All of the other seedlings reacted to a period of drouth in the same way. It was found that the perennial transplants could be induced to form a few flower stalks at any season, if watered after a period of neglect. These stalks were smaller and fewer in number than those produced in the normal spring season of bloom.

Eriogonum inflatum is difficult to transplant, but once established, does very well in the greenhouse. Plants were transferred to pots in the field, watered at once, and covered with

large plastic bags to retard wilting. Of the four groups of transplants the overall mortality rate was about 60%; slightly better results were obtained in the spring than in the fall.

All of the flower scapes which were grown in the greenhouse were uninflated, whether they grew on transplants which had produced inflated stems in the field, on seedlings from inflated plants, or on seedlings from uninflated plants. Seedlings produced uninflated scapes both the first and the second year (Figs. 5 and 8).

In spring and early summer, during the growth of scapes on greenhouse plants, an attempt was made to induce inflations by artificial means. Some stems were mechanically wounded by pricking, some by introduction of larval extract, others by application of growth substances. Of those which were mechanically wounded by pricking with a dissecting needle, none produced fistulae. When water extracts of the larvae were induced into other stems by micropipette, one stem, the youngest of those treated, showed a slight swelling. Later in the season, when another group of scapes had been produced, the induction of larval extract was repeated. No further swellings were produced. It was not possible to continue this line of research at the time, all the remaining larvae having died of starvation or desiccation. Later, when many meristematic scapes were available, some were treated with 1.0% IAA and others with 0.5% colchicine. In both instances the chemical was mixed with pure lanolin and applied to meristematic and basal areas of stems. On stems treated with IAA, abnormal

elongation and deformity were obtained when the chemical was applied to the meristematic portions. When applied to basal areas, no abnormal growth occurred. No inflations were produced in either situation. The stems which were similarly treated with colchicine showed no deviation from the normal morphological pattern.

Cytological investigations were carried out to determine whether somatic polyploidy, or endoploidy, was the cause of the inflations, and if so, whether this condition was a specific characteristic or was induced by external agents. Root tips were obtained by washing achenes in running water for 24 hours and then planting in petri dishes on damp filter paper. The root tips were squashed in aceto-carmin (Johansen, 1940). No major abnormalities were observed. The larger provascular cells and ground tissue cells which were found are not uncommon in higher plants. Thin sections of the stem apex were prepared by fixing young stems in Carnoy's (Johansen, 1940) and embedding them in paraffin by the alcohol method. They were sectioned on a rotary microtome, and stained with safranin and fast green. Sections from inflated stems contained large, thin-walled, multinucleate cells (Fig. 9).

To determine whether any abnormalities occurred in the process of pollen formation, buds were squashed in aceto-carmin (Johansen, 1940). Some of the tetrads disintegrate leaving empty thin-walled cases attached in the characteristic iso-bilateral tetrads, others mature to form viable pollen. Decussate tetrads

are also formed, but are much less numerous than the iso-bilateral type. The divisions are of the simultaneous type which is usual in dicotyledons (Maheshwari, 1950). The cell walls are formed by furrowing rather than by the formation of a cell plate. To determine the percent of viable pollen, pollen was placed on slides in a solution of Cotton Blue in lactophenol. Over 90% of the pollen was viable as indicated by this test.

Anatomical investigations were carried out using thin sections and cleared portions of stems. Mature fistulae were cleared in 5% NaOH for one week; tannins were then removed by two days immersion in Craf's A (Johansen, 1940). Chloral hydrate was used to complete the clearing. The material was then washed in water and stained in safranin in 50% alcohol (Arnott, 1959) (Fig. 6). These fistulae have an increase in number and volume of interfascicular cells which determine the diameter of each specimen. In the larger swellings, where the distance between vascular strands is greatly increased new vascular tissue develops from the interfascicular cambium. These strands are faintly visible between the normal vascular bundles (Fig. 6).

A series of thin sections across the end of the inflation in a very young stem disclosed pith cells which gradually increased in diameter as the cavity of the fistula was approached in successive sections. This stretching eventually ruptured a cell wall (Fig. 10), and in successive sections several cells were found to be torn until the open cavity was reached. In older stems, the center of

the stem is often hollow to the base, the cells having been eaten by insect larvae. Sometimes there is a hollow portion near the bottom occupied by the larva; above this is a solid portion, and above this is the open fistula. If the larvae reach maturity in the stem, the entire internode will be hollow and there may be some evidence of feeding in the lower half of the fistula.

DISCUSSIONS AND CONCLUSIONS

Field observations indicate that the ultimate size of the fistula depends on several interacting conditions. In the population at Tortilla Flat, for example, most plants were undergoing rapid stem growth, and the larger, more vigorous plants in the most favorable locations had the largest swellings. In other plants in the same location, or in different stems on the same plant, variance in fistula size appears to be related to the time of initial insect damage and to the duration of larval inhabitation (Tables 1 and 2). Beck (1953) observed a similar situation in the galls on Solidago, which apparently ceased to develop when the insect larvae died, and concluded that the ultimate size of the gall depended on the duration of stimulation. Barber (1938), and Lieby (1922), working with other types of galls, came to the same conclusion. Beck (1953) also found that the proliferation of tissue in Solidago stems was induced not only by the mechanical feeding activity of the larvae, but also by a chemical stimulus received from silk deposit on the inner surface of the stem by the feeding larvae.

In plants with several scapes, two sizes of fistulae may be found on the lowest internodes of the stems. The stems with the larger swellings usually contain live larvae, while smaller fistulae on the same plant will occur on stems which exhibit

evidence of insect damage, but which contain no live larvae (Tables 1 and 2). In a recent study of galls produced by sawflies (Hovanitz, 1959), it was shown that the abnormal growth began when the plant was wounded by the ovipositor of the adult fly. However, continued growth depended upon the stimulation by salivary secretions of the sawfly larvae. Microlepidoptera have no ovipositor, so this initial wound stimulus has to be discounted, and the abnormality in E. inflatum stems must result entirely from the larval feeding.

Eriogonum inflatum stems with injuries high on the first internode had very small swellings, if any, and rarely contained live larvae (Table 2). Thus, if the initial injury occurred when the first internode was nearing the end of meristematic activity, the swelling was small. Occasionally the swelling did not develop at all, probably because the injury occurred when growth of the lower internode had ceased. The experiments in which E. inflatum was treated with IAA also indicated that the net hormonal effect depended on the degree of meristematic activity at the time of treatment.

Swellings on the second or third internodes occur on both large and small plants and rarely exhibit larvae or insect damage. In the one plant where larvae were found in the upper internodes, feeding tunnels went through the nodes, and larval damage was found in both the upper and lower internodes. It appears that the upper inflations occur as the result of stimulation to the lower

internode during meristematic activity of the second or third internode. Cessation of larval feeding before the development of the upper portions of the stem would probably allow normal development to take place, larval feeding being necessary to stimulate in the plant the production of growth substances which are responsible for gall development (Leonian and Lilly, 1937). Evidently this substance is transported in the stem. Parasitic degradation of the larvae may terminate the stimulus before the upper internodes develop.

Leonian and Lilly (1937) found that in the case of crown galls, gall formation might be the result of excess production of growth substances by the plant rather than the result of substances furnished by the pathogen to the plant. Locke, Riker, and Duggar (1938) concluded that the chief growth substance in crown gall was of the auxin-a or auxin-b type rather than heteroauxin. On the other hand, IAA has been found to be the active cecidogenic principle in aphid saliva (Mani, 1964). In the present experiments, IAA produced no cecidogenic effects.

Although silk produced by the feeding larvae was found to stimulate growth of a gall of Solidago (Beck, 1953), it appears to have no cecidogenic effect in E. inflatum. Silk is produced by the Pyralidae larvae, but many inflated stems which contained evidence of larval feeding were entirely without silk. The silk was found in gall cavities in which the escape "portholes" had

been prepared, and thus appears to be part of the pupation preparation of the fully grown larvae.

In Solidago (Beck, 1953) it was found that the eggs of the gall-producing moth Gnorimaschema were deposited on the crown and on dead material near the crown of the plant. The eggs overwintered here, and in the spring the larvae hatched and burrowed into the soft meristematic tissues of the apical bud. Occasionally the larvae entered through other parts of the stem. Pyralidae larvae in E. inflatum pupate in the fistulae and emerge sometime in August. In March, recently hatched larvae are found in the stems, and as with Gnorimaschema, the eggs are evidently the overwintering stage of this Pyralidae.

The small "portholes" that are sometimes found in the fistula of E. inflatum are thin enough to admit light. Barber (1938) described this type of plug in Solidago as a thin ring of epidermis; Beck (1953) says that the plug is an insect secretion which is dissolved by the digestive juice of the adult, thus allowing it to leave the cavity. From the stains inside the cavity it is evident that pupation takes place within the fistula, and since the moth has no chewing mouth parts, it must dissolve the plug with saliva.

In Eriogonum inflatum, the fistula develops through an increase in the number and size of the interfascicular cells (Fig. 6), thus increasing the distance between vascular strands in the region of the swelling. The resulting increase in the circumference of the stem produces tensions on the large thin-walled cells of the

pith, eventually causing them to rupture, forming an initially schizogenous cavity (Fig. 10). Thin sections at the apex of the fistula showed the increased size of the central stem cells, then ruptured cells, and finally the main cavity.

The studies of the stem and root tips did not indicate a genetic cause of the inflations, but revealed histological characteristics which have been found to be conducive to gall formation, or to be the result of cecidogenesis. Tissue fusion is evidently a common feature of gall development (Mani, 1964); the cell walls of the host dissolve to form multinucleate, syncytial masses (Kuster, 1937). Cells with several nuclei are common in the meristematic stage of the fistula of E. inflatum. The observed columns of enlarged cells in the root tip, while not the cause of the inflations, possibly provide a favorable situation for cecidogenesis. The increased rate of growth of gall cells has been explained on the basis of tetraploidy (Winge, according to Beck, 1954). Mani (1964) says, "The factors which induce cecidogenesis arise within the plant cell itself and are specific to the plant, its organs, and its cells. Cecidogenesis is a highly specific and specialized type of plant reaction to the secretions of the cecidozoa and not every part of every plant exhibits this reaction always."

Members of the Polygonaceae are not particularly favored by the various cecidozoa; however, the four genera listed as host plants (Felt, 1940) are Eriogonum, Rumex, Coccolobis, and Polygonum.

All the cecidozoa listed for this group of larvae of Dipteran midges with the exception of the caterpillar of the moth Hexeris enhydris Grate.

The inflated stems of E. inflatum var. inflatum are not the normal morphogenetic condition of the plant, but are induced by cecidozoa including a Pyralidae and a Mordellidae. Therefore, the recognition of the varieties inflatum and deflatum is based not on a genetic characteristic, but on a monstrosity, and has no validity. In addition, care must be exercised in using the inflated stem as a characteristic to distinguish E. inflatum from E. trichopes, because the former may bloom as an uninflated annual.

SUMMARY

Plants of Eriogonum inflatum with inflated stems when collected in the field grew uninflated stems in the greenhouse for two successive years. Seeds from the plants with inflated stems produced plants with uninflated stems in both the seedling year and the second year in the greenhouse. Seeds which were collected from greenhouse grown plants germinated in pots and produced another generation of plants with uninflated stems.

Plants growing in populations containing primarily inflated individuals often have both inflated and uninflated stems on the same plant. Two insects, one a microlepidoptera of the Pyralidae family and the other a beetle of the Mordellidae family, have been found to inhabit 97% of the inflated stems, and it is probable that they induce cecidogenesis in E. inflatum. Multi-nucleate cells, characteristic of insect-induced galls, are found in the fistulae of E. inflatum. Since these fistulae are not a genetic characteristic of the plant, E. inflatum var. inflatum is the same as E. inflatum var. deflatum and the varietal distinction should be abandoned.

TABLE 1

Field Observations at Population #5, North of Wickenburg. January 26, 1966.

Plant Number	Inflated Stems	Uninflated Stems	Insect Lesions	No Insect Lesions	Larvae or Pupal Remains Present
1	2	0	2	0	0
2	6	0	5	1	0
3	2	0	2	0	0
4	small 4	0	4	0	0
5	10	1	10	1	10
6	4	0	3	1	1
7	2	0	1	1	0
8	1	2	1	2	1
9	3	0	3	0	0
10	large 3 small 5	0	8	0	3
11	2	0	2	0	1
12	6	0	6	0	3
13	7	0	6	1	4
14	large 5	0	5	0	5
15	8	0	8	0	8
	70	3	66	6	

(in the 3 large inflations)

TABLE 2

Field Observations at Population #5, North of Wickenburg. January 27, 1966.

Plant Number	Inflated	Uninflated	Insect Lesions or Damage	No Insect Damage	Larvae or Pupal Remains Present
1	4	1	3	1 + 1	1
2	9	0	9	0	5 larvae
3	3	0	2	1	3 pupal remains 2 (including stem with no observed lesions)
4	2	0	2	0	2 pupal remains
5	2	0	2	0	1 pupal remain
6	4	0	4	0	3 pupal remains
7	2	0	2	0	1 pupal remain
8	2	0	2	0	1 larva
9	5	0	5	0	0
10	3	1	4	0	3 (2nd internodes slightly inflated, lesions, very high on uninflated 1st node)
11	3	3	4	2	3 (lesions high on 1st internode of 1 uninflated stem)
12	3	0	1	2	1
13	2	0	2	0	1 (larva found in 2nd internode, hole bored through node)

TABLE 2 -- Continued

Plant Number	Inflated	Uninflated	Insect Lesions or Damage	No Insect Damage	Larvae or Pupal Remains Present
14	2	0	2	0	1 larva
15	4	1	5	0	3 larvae (lesions high on uninflated stems)
16	1	1	1	1	1 pupal remain
17	5	0	5	0	4 pupal remains
18	5	0	5	0	3 pupal remains
19	4	0	4	0	2 pupal remains
20	4	0	4	0	3 pupal remains
21	4	0	4	0	4 pupal remains
22	4	0	4	0	3 pupal remains
23	5	1	6	0	5 pupal remains (lesions high on uninflated stem)
	82	8	82	8	

Figure 1.

Distribution of Eriogonum inflatum Torr. in Arizona.

Numbered populations were studied in detail.

1. Mammoth, Arizona, 2½ miles south on Highway 77.
2. Yavapai County, east of Highway 93, and two miles south of Santa Maria River crossing.
3. Tortilla Flat, in Maricopa County, on slope above the Apache Trail.
4. Yuma County, at east base of Gila Mountains, south of Highway 80.
5. North of Wickenburg, west of Highway 93, at Date Creek crossing.

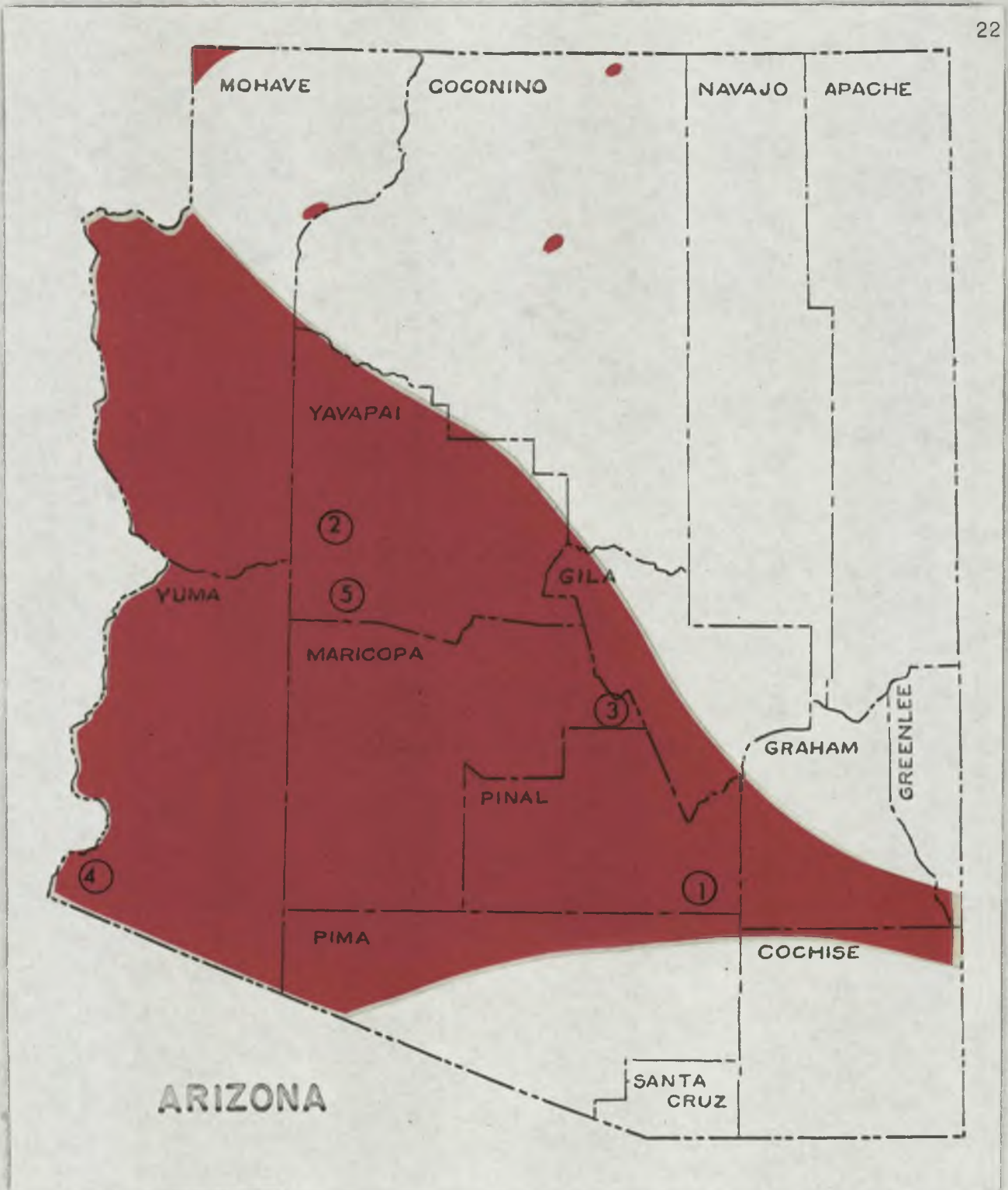


Figure 1. Distribution of *Eriogonum inflatum* Torr. in Arizona. Numbered populations were studied in detail.



Figure 2. Plants in the Mammoth Population #1; both annuals and perennials are producing flower scapes. The jackknife (7.5 cm long) is behind a tiny annual.

Figure 3. Examples of E. inflatum blooming as annuals:

a) Tortilla Flat population. (x0.28)

b) Mammoth population. (x0.28)

c) and d) Yuma population. (x0.28)



a



b



c



d

Figure 3. Examples of *E. inflatum* blooming as annuals.



Figure 4. Eriogonum inflatum blooming as a perennial. (x0.28)



Figure 5. A single plant from population #2, north of Wickenburg transplanted from field to greenhouse, showing:

- a) Inflated stems developed in the field.
- b) Uninflated stems developed in the field.
- c) Uninflated stems later developed in the greenhouse.

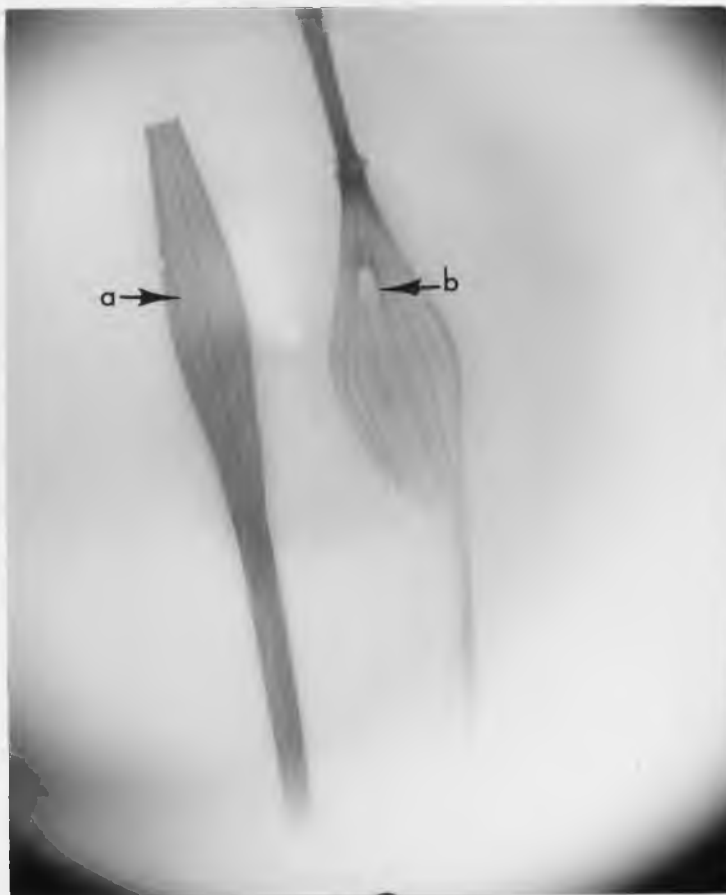


Figure 6. A cleared stem of *E. inflatum* (xl) showing:
a) Developing vascular bundles between mature darkly stained vascular strands.
b) An opening made by a larva.



Figure 7. A stem showing a pupal case attached near an opening filled with mucilaginous material. The dark object is the pupa. (x1)

Figure 8. E. inflatum parent and seedling:

a) E. inflatum, as transplanted, showing fistulae produced in the field.

b) E. inflatum, note uninflated stems of greenhouse seedlings from transplant shown above.



8a



8b

Figure 8. E. inflatum parent and seedling.

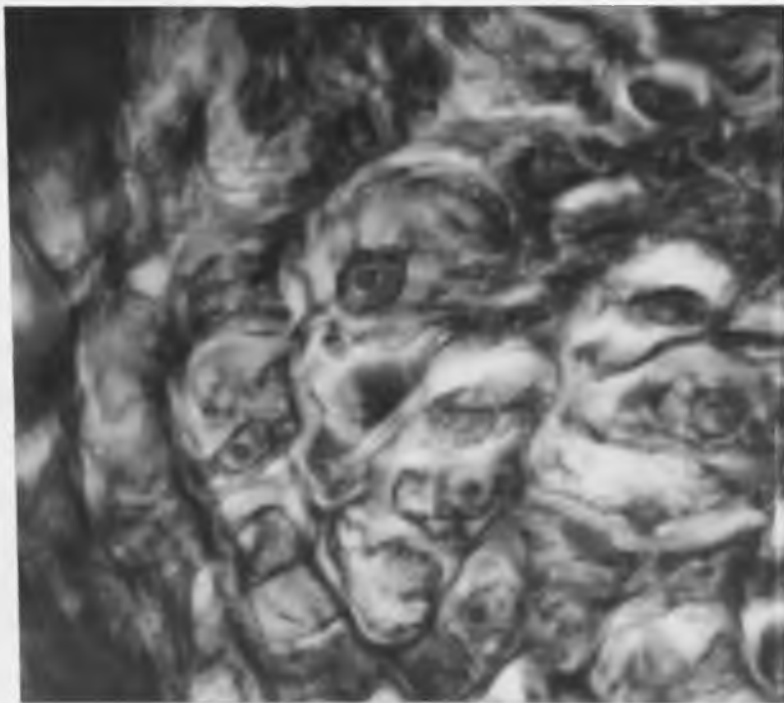


Figure 9. Coenocytic cells from the meristematic upper portion of a fistula. (x800)

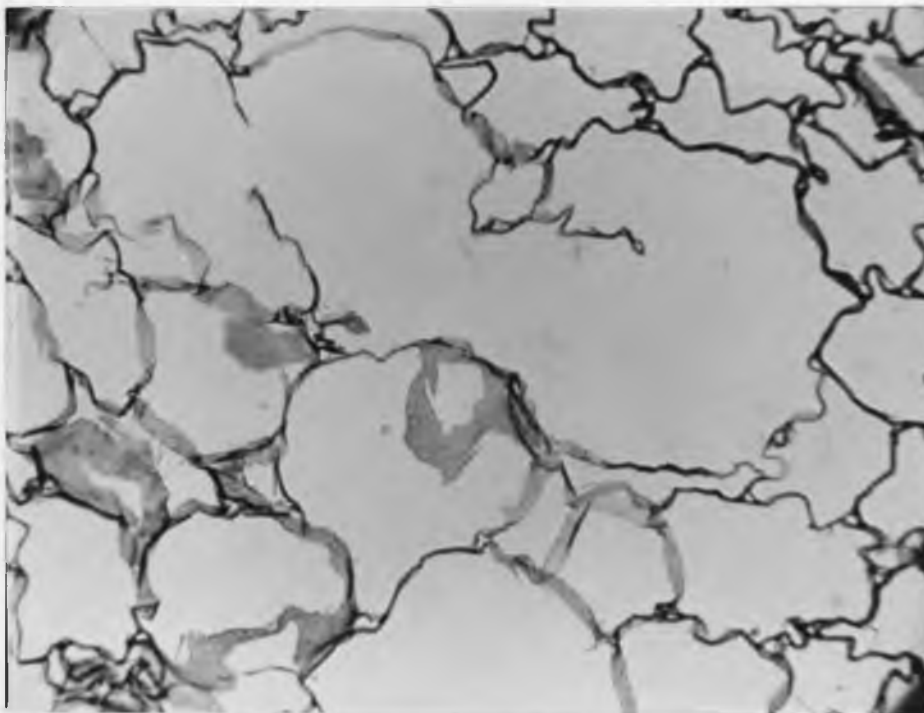


Figure 10. Pith cells of an inflated stem, at the point of inception of the cavity. Note the ruptured cell walls. (x800)

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