

FLORAL BIOLOGY AND SYSTEMATICS OF EUCNIDE (LOASACEAE)

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THE GENUS *Eucnide* presents a pattern of species differences somewhat unusual among flowering plants. The eleven species are very similar in all respects except floral morphology, in which they differ widely. For example, the corollas in several species are apopetalous while in others they are sympetalous, forming a long tube. Characters such as apopetaly and sympetaly are so well established as criteria for separating major families of flowering plants that it is difficult to determine their taxonomic importance when they occur as differences between otherwise similar species. We shall evaluate the taxonomic significance of floral morphology in *Eucnide* by two approaches. The gross features of floral morphology will be analyzed by determining their anatomical basis so that more refined comparisons between the species can be made. The biological importance of floral structures will be evaluated by considering their role in reproduction of the local populations. The assessment of the taxonomic importance of these characters will be independent of the correlations that they ultimately give in our classification.

Since the publication of *Monographia Loasacearum* (Urban & Gilg, 1900) the species of Loasaceae subfamily Mentzelioideae have been grouped into three genera: *Mentzelia*, *Eucnide*, and *Sympetaleia*. Although monographs of *Mentzelia* (Darlington, 1934) and *Eucnide* (Waterfall, 1959) have been published, no attention has been given to *Sympetaleia* since the turn of the century. Recent collecting activities in Baja California have greatly increased the material of *Sympetaleia* available for study, and this, along with the collection of the rare *Sympetaleia tenella* nearly 40 years after its discovery, has directed our attention to this group. Our initial examinations of *Sympetaleia* led us to the question of its generic limits and affinity to both *Eucnide* and *Mentzelia*. Consideration of all three genera has indicated the general importance of floral biology in this subfamily and has suggested the necessity for an entirely new evaluation of the specific differences. Our inescapable conclusion is that the differences between *Eucnide* and *Sympetaleia* are no greater than differences within *Eucnide*, and that these differences, when viewed against a background of the entire subfamily, make it clear that one genus with three sections is the most accurate representation of our concept of the affinities within the *Eucnide-Sympetaleia* complex.

Subfamily Mentzelioideae, to which *Eucnide* belongs, is distinguished from other Loasaceae by the numerous stamens not grouped in fascicles. Other Loasaceae either have only five stamens, as in subfamily Gronovioideae, or numerous stamens arranged in discrete fascicles opposite the

petals and accompanied by elaborate petaloid staminodia, as in subfamily Loasoideae. Within subfamily Mentzelioideae the genus *Mentzelia* is distinguished by its three parietal placentae (five only in *M. decapetala*) with the ovules inserted in two distinct vertical rows on each placenta and by the seeds, which are variously shaped but always large and not longitudinally grooved. The remaining species of this subfamily, which we consider to comprise the genus *Eucnide*, are characterized by five placentae, each with many rows of minute, longitudinally grooved seeds (FIG. 1). We recognize 11 species in *Eucnide* and arrange them in three sections as follows:

sect. EUCNIDE	series Eucnide	<i>E. bartonioides</i>
		<i>E. grandiflora</i>
		<i>E. lobata</i>
sect. MENTZELIOPSIS	series Tubiflorae	<i>E. cordata</i>
		<i>E. hypomalaca</i>
		<i>E. hirta</i>
		<i>E. xylinea</i>
		<i>E. urens</i>
		<i>E. aurea</i>
		<i>E. rupestris</i>
sect. SYMPETALEIA		<i>E. tenella</i>

MATERIALS AND METHODS

Much of our information about *Eucnide* comes from material of 17 populations, representing nine species, that we have been able to study in detail. TABLE 1 lists these collections and indicates how each was studied. Some have been observed as natural populations and some have been grown in the greenhouse at Los Angeles. All of these collections have been available in great quantity so that detailed morphological and anatomical studies could be made. Material was fixed in formalin-acetic-alcohol and then either cleared in lactic acid or embedded in paraffin, sectioned, and stained. Additional material from herbarium specimens of other species was restored by gentle boiling and cleared or sectioned, so that all species have been studied from both sectioned and cleared material. Meiosis has been examined with the usual method of fixing buds in 1:3 acetic-ethanol, squashing anthers in acetocarmine, and observing with a phase microscope. Meiosis was observed in at least three different individuals from most of the populations studied. Controlled pollinations were made in all populations grown in the greenhouse. The stamens were first removed and then the style and stigma were covered with a segment of plastic soda straw to prevent accidental pollinations. When the stigma became receptive the soda straw was removed momentarily while the desired pollen was applied to the stigma. In addition to our own collections we have studied the specimens in the following herbaria: A, BM, BR, CAS, CU, DS, E, F, GH, K, LA, M, MO, NY, POM, RSA, SMU, SRSC, TEX, UC, US.

TABLE 1. Collections of *Eucnide* of particular importance in this investigation.

COLLECTOR & LOCALITY		HAPLOID CHROMO- SOME NO.	GARDEN CULTURES	FIELD STUDY
Sect. <i>Eucnide</i>				
<i>E. bartonioides</i>	Thompson & Ernst 3283; Big Bend National Park, Texas	21	+	+
<i>E. cordata</i>	Chambers 1004; Cataviñá, Baja Calif., México	21	+	—
	Wiggins 15884; Puertecitos, Baja Calif., México	21	—	—
<i>E. grandiflora</i>	Ernst & Delgadillo 2475; NW of Nacaltepec, Oaxaca, México. Garden voucher, Thompson 3386	21	+	+
<i>E. hirta</i>	McVaugh 15108; Near Lake Chapala, Jalisco, México	21	+	—
<i>E. lobata</i>	King 4505; Ciudad Victoria, Nuevo León, México	21	+	—
	Waterfall 15324; Monterrey, Nuevo León, México	21	+	—
Sect. <i>Mentzeliopsis</i>				
<i>E. urens</i>	Thompson 3184; Panamint Valley, Inyo Co., Calif.	21	—	+
	Thompson 3182; Death Valley Buttes, Inyo Co., Calif.	21	—	+
	Thompson 3339, Raven 11784; Hoover Dam, Clark Co., Nevada	21	+	+
Sect. <i>Sympetaleia</i>				
<i>E. aurea</i>	Carter & Sharsmith 4160; Sierra Giganta, Baja Calif., México	21	+	—
	Carter & Sharsmith 4260; Isla Danzante, Baja Calif., México	21	+	—
	Carter & Ferris 3879; W of Loreto, Baja Calif., México	21	—	—
	Wiggins & Ernst 543; Santo Domingo, Sierra Giganta, Baja Calif., México	21	—	+
<i>E. rupestris</i>	Raven 14802; N of San Felipe, Baja Calif., México	21	—	—
	Thompson 3316; S of San Felipe, Baja Calif., México	21	—	+
<i>E. tenella</i>	Wiggins, Carter & Ernst 280; Misión Los Dolores, Baja Calif., México	—	—	+

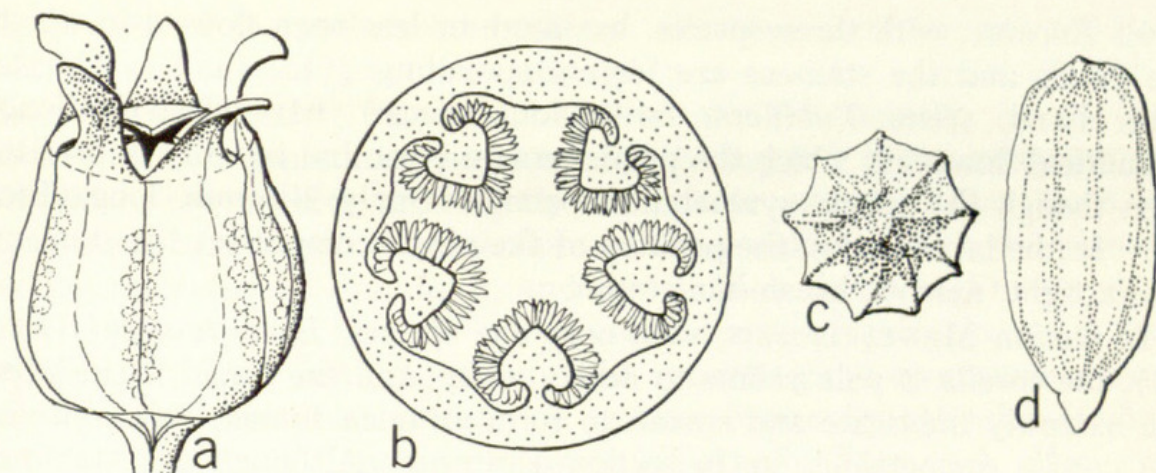


FIG. 1. Characteristic fruit, placentation, and seed in *Eucnide*. a, capsule, *E. tenella*, showing position of ovules, valves, and major veins, $\times 10$; b, ovary, *E. urens*, transverse section showing ovules and cordate placentae, $\times 4$; c, seed apex, *E. aurea*, $\times 70$; d, seed, *E. aurea*, longitudinal view, $\times 75$.

COMPARATIVE MORPHOLOGY

Morphological variation throughout *Eucnide* is somewhat unusual in that particular structures show either striking diversity or great uniformity. We have chosen to emphasize this aspect of the pattern of variation by discussing comparative morphology under two headings, considering first the morphological diversity, which occurs primarily in the flowers, and following this with the morphological similarities that occur throughout the remainder of the plant body.

Morphological diversity. Our three taxonomic sections are founded on morphological innovations in the conformation of the corolla and the spatial relationships of the anthers and stigma. The corollas are apopetalous or sympetalous anatomically, but this difference is bridged and made ambiguous by a peculiar condition of false sympetaly. Within either the apopetalous or sympetalous categories there are species with open, spreading corollas and species with narrow, tubular corollas. Among the species with spreading corollas and those with tubular corollas there are examples with included or exserted anthers and stigma. In our first two taxonomic sections, false sympetaly (i.e., apopetaly) is correlated with anthers that become two-locular at anthesis. In our third section, true sympetaly is correlated with anthers that become unilocular.

In section EUCNIDE, the corollas are white to yellow and are falsely sympetalous at the base. The staminal filaments are more or less filiform above but fused basally into a relatively very short tube (0.5–3 mm. long) to which the petals always are united. It is their union with this tube that holds the petals together when both stamens and petals abscise from the top of the ovary. We consider these corollas anatomically apopetalous but functionally slightly sympetalous by virtue of their union with the staminal tube. Two modifications are evident in this flower type. In either case, the anthers and the stigma are conspicuously exserted from the corolla and the anthers are two-locular at anthesis. On the one hand,

series *Eucnide*, with three species, has more or less open flowers in which the petals and the stamens are loosely spreading (FIG. 2a, b). On the other hand, series *Tubiflorae*, with four species, has relatively long, cylindrical flowers in which the petals remain erect and broadly imbricate, even though the falsely sympetalous portion is only 2–3 mm. long (FIG. 2c). In the latter series, the position of the petals compresses the stamens into a tight, narrow, brush-like cluster.

In section MENTZELIOPSIS, with only one species, *Eucnide urens* (FIG. 2d), the corolla is pale yellow to nearly white, and the broad, rigid lobes are narrowly imbricate and spread to form an open funnel. We consider the corolla apopetalous, as in section EUCNIDE. Although the staminal tube to which the petals are united is 5–8 mm. long, it is relatively short, being about a fifth the length of the corolla. The anthers and stigma are distinctly included and only a little more than half as long as the corolla. Above the staminal tube, the stout free filaments are slanted inward forming a kind of chamber around the style. The anthers are two-locular at anthesis. A few of the filaments, the outermost and longest, curve outward at the top, holding their anthers away from the stigma. The proximity of most of the anthers to the style, however, and their inwardly nodding position causes most of the pollen to be shed into the interstices of the filaments and into the chamber the filaments create around the style. The deposition of the pollen into this chamber is peculiar to this species of *Eucnide* but it recalls a very similar situation found in the genus *Mentzelia* section BICUSPIDARIA.

In section SYMPETALEIA, with three species, the corollas clearly are sympetalous anatomically, the stamens are epipetalous, and the anthers (to be discussed shortly) are unique. In *Eucnide tenella* (FIG. 2f), the whitish corolla (ca. 8 mm. long) with spreading narrow lobes, is united for about a third of its length into a narrow tube. The anthers are exposed on long filaments that equal or slightly exceed the stigma and corolla. In *E. aurea* (FIG. 2g), the yellow or brilliant reddish orange corolla (ca. 15–20 mm. long) is distinctly salverform, with broad, sometimes imbricate lobes, and is united for about two-thirds its length into a narrow tube. The nearly sessile anthers are included within the tube, and below them is a ring of upwardly curving hairs. In *E. rupestris* (FIG. 2e), the greenish corolla (to ca. 15 mm. long) with shadings of yellow or brown, is more or less cylindrical, with rigidly erect, valvate lobes, and is united into a tube for about three-fourths of its length. The anthers are included within the tube, the lower ones subsessile and the upper ones on short, stout, erect filaments. In the lower portion of the corolla beneath the stamens, as in *E. aurea*, there is a ring of upwardly curving hairs. The ring of hairs is absent in *E. tenella*. In this section the anthers are unilocular at anthesis.

The interesting differences in the structure of the anthers require explanation. The anthers vary in general external conformation, but more important, the original masses of sporogenous tissue, as well as the final pollen chambers (locules), differ both in shape and in number (FIG.

3a-q). All of the anthers are basifixed, and the microsporangia are lined with a well-defined tapetal-endothecial region. The anthers of section EUCNIDE and section MENTZELIOPSIS are divided medially by the connective, which sometimes projects slightly beyond the microsporangia; otherwise, the anthers are slightly emarginate apically (FIG. 3a, b, f). Transverse and longitudinal sections of these anthers (with the plane of section indicated in FIG. 3a, b, and the sections shown in FIG. 3c, d, e) clearly demonstrate that the sporogenous tissue of each occurs in four separate, straight, vertical masses. The two masses of sporogenous tissue on the same side of an anther are marked externally by a longitudinal groove (FIG. 3b, c) and are separated internally from each other only by the tapetal-endothecial layer. The paired masses of sporogenous tissue on one side of the anther are separated from those on the other side by the tissues of the connective. As the pollen matures, the tapetal-endothecial tissue breaks down joining the adjacent lateral pollen masses in a single locule on either side of the connective so that just before dehiscence, the anther becomes two-locular. The dehiscence is longitudinal at the lateral grooves. In the ovate to elliptical anthers of section EUCNIDE, the wall of the locule frequently becomes reflexed so that after dehiscence, the exposed portion of the anthers is the lining of the locule (FIG. 3f). In the linear-sagittate anthers of section MENTZELIOPSIS the wall of the locule usually does not reflex and the lining is less conspicuously displayed.

In section SYMPETALEIA, the anthers are reniform (FIG. 3g) and the connective never reaches the apex of the anther. Transverse and longitudinal sections (FIG. 3i-l; m-p) show the unusual nature of these microsporangia. In *Eucnide tenella* and *E. aurea* the sporogenous tissue occurs in two horseshoe shaped masses, for, although FIG. 3i shows four masses of sporogenous tissue, these are continuous over the apical portion of the anther (FIG. 3k, l). The nature of the sporogenous tissue in *E. rupestris* is particularly illuminating. In the portion of the anther facing the style (i.e., adaxially) the sporogenous tissue of the two sides of the anther is continuous apically (FIG. 3o) just as in *E. tenella* and *E. aurea*. In the portion of the anther toward the corolla (i.e., abaxially), however, the sporogenous tissue is not continuous, but occurs in two lateral masses separated apically by a thin septum (FIG. 3p).

Thus, in *Eucnide tenella* and *E. aurea* there are two masses of sporogenous tissue, while in *E. rupestris* there are three. When the pollen matures, the tapetal-endothecial tissues break down joining the pollen masses laterally so that in all three species the anthers have a single locule just prior to dehiscence. The anthers dehisce at the lateral groove (FIG. 3h), which, in section SYMPETALEIA, is continuous over the apex of the anther. After dehiscence, the anthers are peltate with the anther wall slightly cupped or opened out flat (FIG. 3q).

Morphological unity. The diversity in morphology and anatomy among the species of *Eucnide*, which permit the recognition of the species groups, is restricted to the flowers, i.e., corolla, stamens, and style. Underlying these striking differences, however, are many similarities in basic

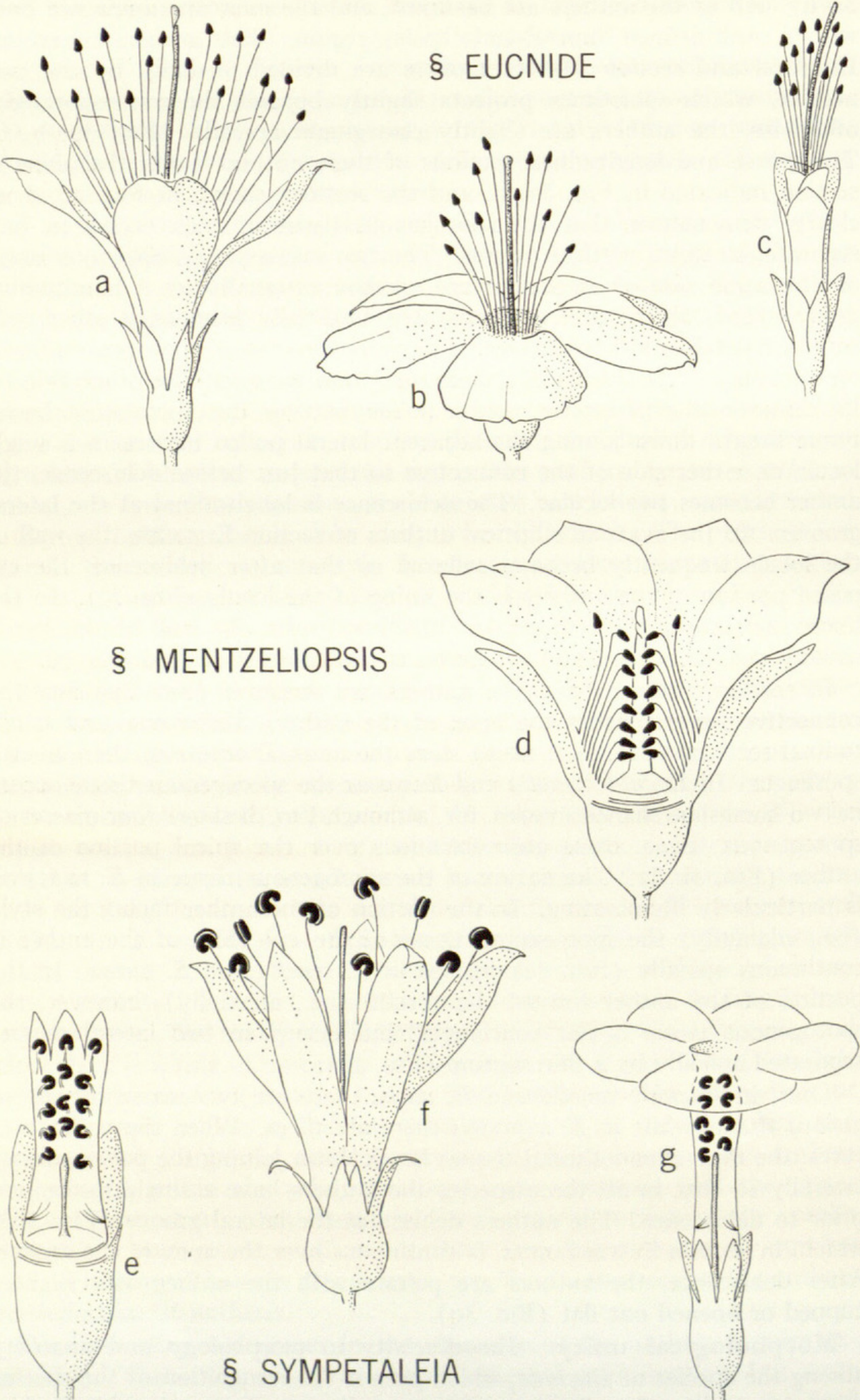


FIG. 2. Flowers of *Eucnide* reduced to nearly the same length, showing shape of corolla and position of stigma and stamens. a, *E. bartonioides*, $\times 1$; b, *E.*

floral and vegetative architecture which are unique to the genus and point out its morphological unity.

The plants are herbaceous, short lived perennials, often with the lower stems stout and appearing woody. Plants of *Eucnide aurea*, *E. bartonioides*, *E. cordata*, *E. hirta*, *E. lobata*, and *E. urens* all flowered about three months after the seeds were sown in a warm greenhouse in Los Angeles and seemed able to persist as perennials. Some species, such as *E. aurea*, *E. bartonioides*, and *E. rupestris*, also may be successful facultative annuals.

The leaves are alternate, simple, and of more or less characteristic appearance throughout the genus. They are petiolate, with the blades mostly cordate, orbicular to ovate with crenate, lobed or incised margins. The venation varies from nearly palmate in some species to quite pinnate in others; however, the general outline and appearance of the leaves remain very similar. In some species the upper surface of the leaves appears to be varnished.

The plants usually are densely pubescent with several kinds of trichomes that are characteristic of the family and often stinging to the touch. The trichomes are unicellular and either smooth or variously reflexly barbed; some are swollen at the base or rest upon multicellular epidermal platforms.

The ovary is inferior and unilocular, with each of the five parietal placentae alternate with the sepals. In transverse section the placentae are cordate in outline, intrude deeply into the locule of the ovary, and are densely covered with minute, horizontally radiating ovules (FIG. 1b).

The dry, dehiscent fruits are globular to obovoid and are surmounted by the persistent sepals (FIG. 1a). In contrast to the usually fragile walls of the fruit, the apex is hard and durable and divides into five valves which are attached opposite and interior to the sepals (i.e., alternate with the placentae). The valves open wide, permitting the sifting out of the seeds. Frequently, the style remains attached to the tips of the valves and is torn as they open.

The numerous seeds (FIG. 1c, d) are pale or straw colored, 0.5–1.25 mm. long, and usually acute at the attached end and rounded at the free end. They are conspicuously ribbed or grooved longitudinally with the parallel crests either straight or spirally twisted, both forms often occurring in the same capsule. In some instances, the seeds are slightly constricted near the middle. At the time of their dispersal, the seeds are filled by the embryo.

The pollen is oblate (shorter on the polar axis), tricolporate (each of the three narrow furrows with a median, round pore), and without prominent surface sculpturing.

The pedicels (or peduncles) in all species curve as the capsules mature

lobata, sepals removed, $\times 3$; c, *E. cordata*, $\times 1\frac{1}{4}$; d, *E. urens*, forward stamens, one petal, and two sepals removed, $\times 1$; e, *E. rupestris*, corolla shown as though transparent, forward two sepals removed, $\times 2$; f, *E. tenella*, $\times 5\frac{1}{2}$; g, *E. aurea*, corolla shown as though transparent, $\times 2\frac{1}{2}$.

and, in some species, elongate from a few millimeters at anthesis to as much as 33 cm. by the time the seeds are shed. In the plants grown in the greenhouse, the capsules always pointed north; from this we assume that the pedicels are negatively phototropic. Elongating pedicels are developed best towards the base of the plants, and, since these portions often are dry and broken in larger plants, they usually are not preserved on herbarium specimens and may not be noted by collectors.

The chromosome number has been determined for eight species representing all three sections of the genus. In each cytological examination, 21 pairs of chromosomes were observed in the meiosis of the pollen mother cells, and there were no cytological anomalies. The voucher specimens and collection data for these determinations are given in TABLE 1.

Another expression of the basic similarity of the flowers is found in vascular anatomy. In all species (whether apopetalous or sympetalous), the vascular pattern is fundamentally similar, differing only slightly in complexity from species to species and from specimen to specimen. The vascularization of a flower of *Eucnide cordata*, diagrammed in FIG. 4, may be taken as representative of the genus. Ten equally spaced primary traces (a, b) emerge from the pedicel and ramify, sending tracheary threads to the floral organs. Each of the five primary traces that is opposite a calyx lobe is called a sepal trace (a); each of the alternate five primary traces that is opposite a corolla lobe is called a petal trace (b). A sepal trace sends a small branch inward leading to stamens (c) and then becomes the median sepal vein (a'). A petal trace divides several times, first giving off lateral branches leading to stamens (c), then a pair of stouter veins (d) which become the adjacent marginal veins of adjacent sepals; the remaining median branch (b') becomes the petal vein. A sepal thus receives three veins, each of them originating from a different primary trace; the adjacent marginal veins of two sepals are derivatives of the same primary trace that provides the petal vein. In the complex petal trace, the veins leading to stamens are given off at the same or slightly lower level than the veins leading either to the sepals or petals. About eight stamens are vascularized from each petal trace but only about two stamens are vascularized from each median sepal trace. Inward branches from all ten primary traces toward the top of the ovary form a plexus (e) of tracheary tissue in the disc-like apex (i.e., the valves) of the ovary from which five veins emerge leading to the style (not shown).

The general pattern of flower vascularization is not altered by the degree of sympetaly and fusion of filaments with the corolla tube. The vertical diagrams in FIGURE 5 compare two sepal traces (a) and one petal trace (b) in the falsely sympetalous flower of *Eucnide cordata* and in the truly sympetalous flowers of the three species of section SYMPETALEIA. The vascularization of the most diverse flower types is fundamentally similar. The divergence of the stamen traces (c) from the petal trace (b) occurs at relatively the same level below the articulation of the corolla in all of the flowers regardless of the degree of petal-filament union. The petal trace (b) always is more complicated than the

sepal trace (a), and the vascular supplies to the placenta, valves, and style (e) all arise in the same way.

The differences between the sympetalous and apopetalous flowers concern the degree of relatively simple lateral fusion of nonvascular tissue without alteration of the tracheary tissue. It is noteworthy that in fresh material of *Eucnide aurea*, one of the most sympetalous examples in the genus with long salverform corollas with essentially sessile epipetalous anthers, the corolla tube readily can be stripped away leaving behind the anthers supported by the staminal tube. The corolla also can be torn from the staminal tube along a kind of cleavage plane in the apopetalous species with long filiform stamens. The differences, therefore, between the falsely sympetalous corollas (those actually apopetalous) and the truly sympetalous corollas seem to be relatively minor anatomically.

In respect to habit, leaves, hairs, fruits, pedicels, placentae, seeds, pollen, chromosome number, and pattern of floral vascularization, the species of *Eucnide* are remarkably similar. Quite the opposite is shown, however, with the corollas and stamens where there is great diversity in form, the differences being correlated to delimit three species groups, each with its own distinctive flower type.

BREEDING SYSTEM

The self-pollinations made in all of the greenhouse cultures listed in TABLE 1, representing six of the eleven species of *Eucnide*, resulted in full sets of viable seeds, while unpollinated flowers formed neither seeds nor mature capsules. In the absence of any indication of apomixis we take this to indicate that the plants tested were self-compatible. In these plants, therefore, the pollination system determines the inbreeding-outbreeding balance by controlling the amount of self- and cross-pollination. The main factors of the pollination system are the natural pollinators and floral morphology, in particular the position and developmental timing of the anthers and stigma. In *Eucnide* the morphology of the flowers is not only a convenient marker of the reproductively isolated units but is an important element in the operation of the populations, serving to adjust the populations to specific pollinators and to regulate the amount of inbreeding and outbreeding.

Section Eucnide. In all of the species of section EUCNIDE the flowers have yellow to pale yellow or nearly white petals and exserted stamens, and they open in the late afternoon. The species differ, however, in flower size, the degree of spreading of the petals, and in the timing of anther dehiscence so that there are three different floral forms. We have studied flowering in greenhouse cultures of *Eucnide bartonioides*, *E. cordata*, *E. grandiflora*, *E. hirta*, and *E. lobata*, representing all of the three types of flowers (FIG. 2). In *E. bartonioides* the flowers are large, with the yellow petals usually 3 cm. long and spreading away from the exserted stamens. The flowers first open in the late afternoon, at which time the already receptive stigma exceeds the anthers by a few millimeters

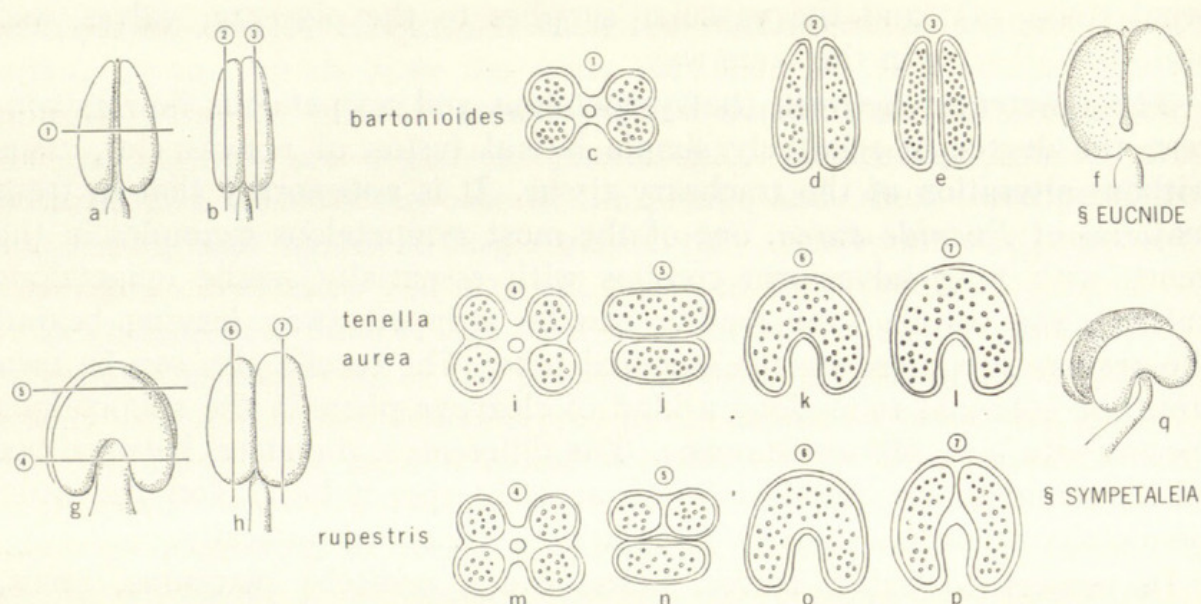


FIG. 3. Morphology of anthers in *Eucnide*. a-f, sect. *EUCNIDE*: a, adaxial view of anther, $\times 6$; b, same, lateral view; c-e, transverse section and longitudinal sections of "a" and "b" at positions indicated by numerals 1-3; f, lateral view of anther after dehiscence. g-q, sect. *SYMPETALEIA*: g, adaxial view of anther; h, lateral view; i-l, transverse and longitudinal sections of "g" and "h" at positions marked by numerals 4-7; m-p, same; q, abaxial view after dehiscence. Anthers of sect. *EUCNIDE* and sect. *MENTZELIOPSIS* (not shown), have four microsporangia and become two-locular at anthesis. Anthers of sect. *SYMPETALEIA* are unilocular at anthesis; *E. aurea* and *E. tenella* have two microsporangia, but *E. rupestris* has three. a-f, $\times 6$; g-q, $\times 19$.

(FIG. 2a), so that in completely undisturbed flowers there is no pollination and no seeds are formed. The anthers are sufficiently close to the stigma, however, so that even a slight jarring of a flower at anthesis results in some self-pollination. These observations on plants growing in the greenhouse indicate that in natural populations outcrossing would be encouraged by large insect visitors that would first touch the extended stigma as they approached the flower. The same pollinator would cause selfing by bending the stigma back into the anthers, as well as by visiting different flowers of the same plant. Thus, in natural populations the inbreeding-outbreeding balance must lie well toward the inbreeding extreme. Although we have not observed pollination of *E. bartonioides* in natural populations, we can make a reasonable prediction about its pollinator, since a model is available in the flowers of *Mentzelia laevicaulis* (sect. *BARTONIA*) which are very similar in general conformation, size, color, and opening time. We know that *M. laevicaulis* is pollinated by hawkmoths (Sphingidae), and the similarity of the flowers suggest that *E. bartonioides* also is hawkmoth pollinated.

In *Eucnide lobata* the flowers are small, with the deep yellow, rotate petals only 1 cm. long (FIG. 2b). The fully developed flowers have the stamens arranged in two distinct tiers: the shorter, outer stamens and the longer, inner stamens. The flower first opens in the late afternoon, at which time the outer stamens are fully expanded and release their pollen. The inner stamens, however, remain convolute around the base

of the style. The stigma is receptive at this time, but, because the outer stamens are shorter than the style and held away from it, no pollination can occur unless an insect visits the flower. On the following morning, the inner, longer stamens straighten out and release their pollen more or less directly onto the stigma, so that even completely undisturbed flowers in the greenhouse set a full complement of seeds. Thus the manner in which the flower matures presents an initial opportunity for insect visitors to effect some outcrossing, while automatic self-pollination follows the following morning. Populations of *E. lobata* probably have a somewhat greater range of outbreeding than the populations of its near relative, *E. bartonioides*. If pollinators are abundant, seed production and outbreeding would be very high; however, in the absence or shortage of pollinators seed production would remain high but the population would shift to maximal inbreeding. The breeding system is highly labile, responsive to conditions of the environment, and integrated by the natural pollinators. While the natural pollinators of *E. lobata* are unknown, the flowers of this size, form, and color in *Mentzelia* and other groups usually are bee pollinated.

A third line of flower development occurs in *Eucnide cordata*. The petals are very pale yellow, nearly white, about 2 cm. long, and tightly imbricated about the filaments of the exerted stamens (FIG. 2c). The style elongates first, while the petals are still tightly enclosing the anthers. The filaments then elongate, forcing the anthers out of the corolla, but they remain well below the stigma. The petals never spread, and flowers with stamens in various stages of emergence from the corolla can be seen throughout the day, making it difficult to say when the flowers open; the pollen, however, is released in the late afternoon. The stamens still are held together by the imbricated petals, and the pollen is shed well below the stigma. Some of the flowers in an inflorescence, particularly the first to mature, are held more vertically and in these self-pollination does not occur in undisturbed flowers. Other flowers in an inflorescence, particularly those that develop later, are held more horizontally or even point downward. In these flowers there is opportunity for pollen to fall on the stigma, and some of these flowers, even though undisturbed, form some viable seed. Self-pollination in undisturbed inflorescences is not very effective, since only about 25 per cent of the possible seed production is realized. Although no information about natural pollinators is available for *E. cordata*, the structure of the flower, along with the well exerted stigma, indicates dependence on a pollinator. Flower and inflorescence structure in *E. cordata* function to regulate the amount of inbreeding and outbreeding, the opportunity for inbreeding being more restricted in this species than in either *E. bartonioides* or *E. lobata*.

The flowers in *Eucnide hirta* have the same general structure as those of *E. cordata*, with one important exception. In *E. hirta* the style elongates somewhat less in proportion to the rest of the flower, and the stigma is surrounded by the anthers at the time pollen is shed. Thus, self-pollination always occurs, and every flower in undisturbed greenhouse plants

produces a capsule full of seeds. The natural pollinators of *E. hirta* are unknown but even with an active pollinator the populations must be primarily inbreeding.

The species of section *EUCNIDE* thus show striking differences in gross floral morphology. Without any modification of the basic floral structure, variation in relative lengths of stamens, styles, and corolla and position of the petals are harmoniously recombined to give three flower types the function of which is explicable in terms of the pollination system. All are probably insect pollinated. Within each flower type there are accommodations for flexibility in the amount of self- and cross-pollination, with this feature being most highly developed in *Eucnide lobata*.

Section *Mentzeliopsis*. In *Eucnide urens*, the only species of this section, the flowers are large, with the pale cream-colored petals about 5 cm. long. The stigma exceeds the anthers but does not extend beyond the petals. The stamens press inward around the style, the sturdy filaments forming a pollen chamber well below the stigma (FIG. 2d). Undisturbed flowers do not set seed, and natural populations must be highly dependent on insect visitors. We have studied pollination in two natural populations of this species, one on either side of the Panamint Mountains, Inyo Co., California. The population near Death Valley Buttes (*Thompson 3182*) was studied on 16 April, 1961, from 8:00 A.M. until 2:00 P.M. The population in Panamint Valley (*Thompson 3184* and *3187*) was studied on 6 May, 1961, from before sunrise until sunset. In addition, several other populations have been spot checked, and these observations confirm those made in more detail at the above localities. The flowers of *E. urens* open in bright sunshine at about 9:00 A.M., and pollen is released immediately into the pollen chamber. The flowers soon are visited by a melittid bee, *Hesperapis laticeps* Crawford, that remains active until early afternoon, when the desert winds usually increase in force. These pollinators alight on the exposed stigma and style and force their way head first into the pollen chamber. On backing out from the pollen chamber, they again touch the stigma. Although other insects occasionally are found in the corolla of *E. urens*, only *Hesperapis laticeps* enters the pollen chamber and affects pollination. The behavior of *Hesperapis laticeps* in the *E. urens* flowers results in both cross- and self-pollination.

This species is the only *Eucnide* with this type of flower and pollination system, but, in spite of its unique gross morphology, the basic architecture of the flower is the same as all of the other species of the genus. Flowers with the same gross morphology and the same pollinators occur in *Mentzelia* sect. *BICUSPIDARIA*, but in *Mentzelia* this flower type is developed from an entirely different basic flower structure. For example, the seeds, placentae, and floral vasculature in *Mentzelia* are entirely different from those in *Eucnide*.

Section *Sympetaleia*. The three species of this section show the greatest diversity in the features of gross floral morphology and corolla color that are associated with the pollination system. In all species, however, the flowers have tubular corollas and open in the morning. In

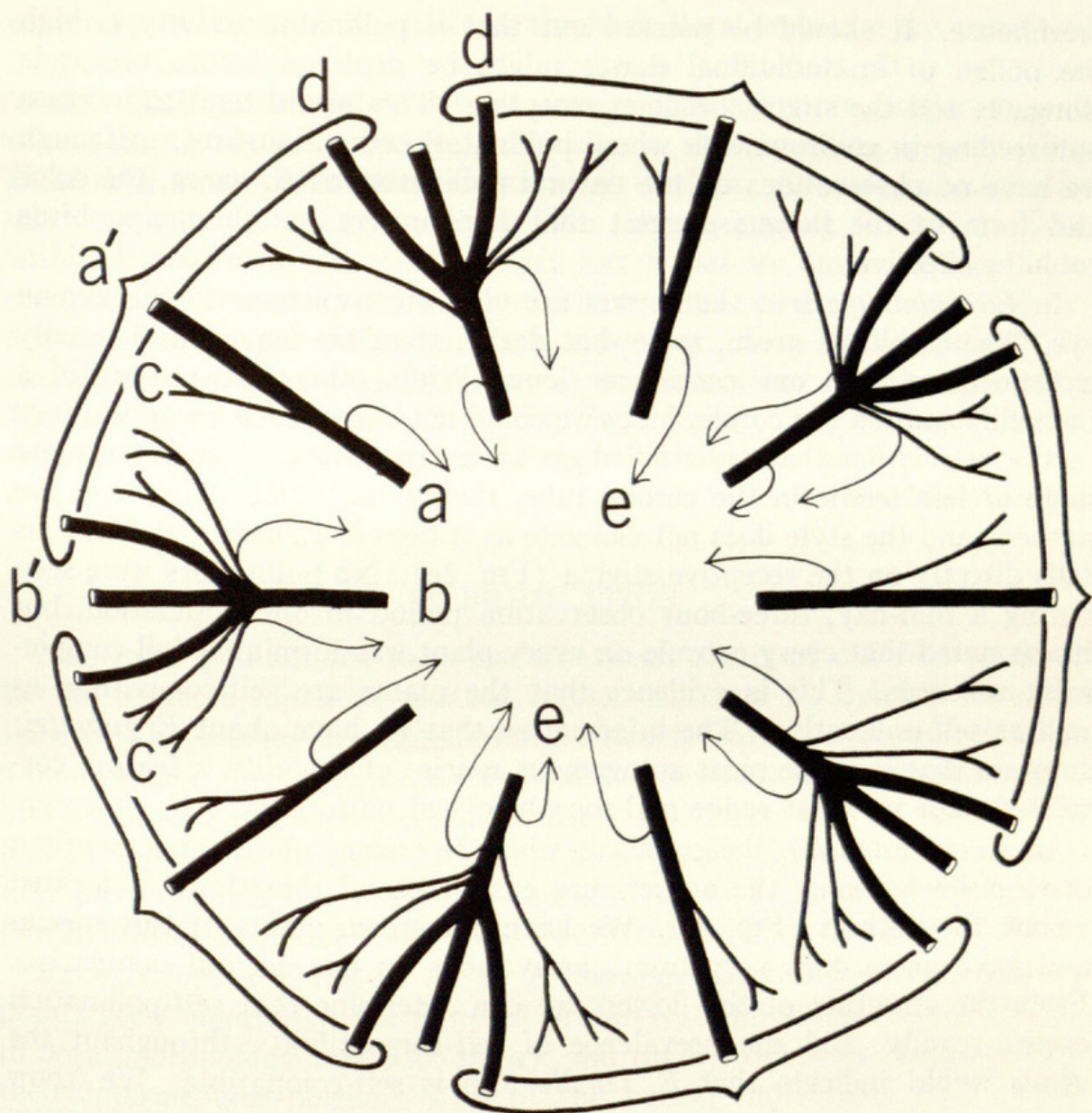


FIG. 4. Diagram of the major vascular traces and veins of the flower, in *Eucnide cordata*, transverse view from above. a, sepal trace; a', median sepal vein; b, petal trace; b', petal vein; c, staminal traces; d, lateral sepal vein; e, traces to valves and style.

Eucnide aurea the corolla is salverform and the anthers are sessile on the corolla tube (FIG. 2g), but the two populations represented in our cultures differ in flower color and size. The plants from Danzante Island (Carter & Sharsmith 4260) have strong reddish-orange corollas about 20 mm. long. When the anthers release their pollen, the stigma is at or just above the ring of hairs in the lower portion of the corolla tube below the stamens. About two days later, the style elongates until the now-receptive stigma is slightly exserted from the sympetalous corolla. In the plants from the Sierra Giganta (Carter & Sharsmith 4160) the flowers are smaller, with yellow corollas about 15 mm. long. Although the style elongates as it does in the Danzante Island plants, the elongation is relatively less, the stigma never being exserted at all and usually not exceeding the middle of the mass of anthers. Both the red and the yellow forms of *E. aurea* are self-compatible, and undisturbed flowers set seed in the

greenhouse. It should be pointed out that if pollinator activity is high the pollen of an individual flower might be depleted before the style elongates and the stigma becomes receptive. This would tend to increase outbreeding in environments where pollinators were abundant. Although we have no observations on the natural pollinators of *E. aurea*, the color and form of the flowers suggest that Lepidoptera and humming birds could be effective.

In *Eucnide rupestris*, the flowers are very inconspicuous to the human eye. The corolla is green, somewhat darker than the leaves, and usually a little more than one centimeter long. While others have recorded a metallic luster on the corolla lobes we could not detect such an appearance in the population that we studied on an overcast day. The anthers are more or less sessile in the corolla tube, the stigma is located among the anthers, and the style does not elongate as it does in *E. aurea*; pollen thus falls directly on the receptive stigma (FIG. 2e). No pollinators were seen during a mid-day, three-hour observation period in one population, but it was noted that every capsule on every plant was forming a full complement of seeds. This is evidence that the plants are self-compatible as well as self-pollinating. The information that we have about *E. rupestris* suggests that it is the most autogamous species of *Eucnide*, a feature correlated with its great range and morphological uniformity.

In *Eucnide tenella*, the corolla is white or cream colored and less than one centimeter long, the anthers are exserted, and the stigma is located among the anthers (FIG. 2f). We have not grown plants of this species and have made only very brief observations on one natural population. From the structure of the flowers we can determine that self-pollination occurs readily, and the prevalence of self-compatibility throughout the genus would indicate that *E. tenella* also is self-compatible. We know nothing of the natural pollinators, but the information on flower structure suggests a rather high degree of inbreeding for *E. tenella*.

Enough information is available about the breeding system of the species of *Eucnide* to allow us to outline the general pattern for the genus. The system is based on self-compatibility, with the inbreeding-outbreeding balance determined by the amounts of self- and cross-pollination permitted by the pollination system. The features of floral morphology involved in the pollination system are then important parameters of the entire breeding system. Each of the sections of *Eucnide* has distinctive features of floral morphology that are developed without alteration of the basic structure of the flower. The flowers in section EUCNIDE have yellow, cream or nearly white petals, exserted anthers, and open in the late afternoon. We speculate that this section is largely insect pollinated. In section MENTZELIOPSIS the flowers open in the morning, and the stamens form a pollen chamber that limits effective pollination to bees with a very special behavior. In section SYMPETALEIA the corollas are tubular, but otherwise the flowers are diverse, with corollas varying from inconspicuous green to highly conspicuous vermilion. We speculate that the latter is butterfly or hummingbird pollinated. Throughout the entire genus, and

especially in section SYMPETALEIA, the basic floral structure has permitted morphological adjustments to a wide range of pollinators. It is important to note that species pairs, that is, species that are more similar to each other than to any other species, may differ in their breeding system. Thus *E. hirta* is a self-pollinating version of *E. cordata*. *Eucnide rupestris*, the most autogamous species, is most like the outcrossing *E. aurea*. Even within *E. aurea* there are two flower forms that we have not seen fit to recognize in formal taxonomy but which differ in their floral biology, one being more self-pollinated than the other. It is also important to emphasize that species as dissimilar as *Eucnide urens* and the species of *Mentzelia* (sect. BICUSPIDARIA) can have nearly identical pollinating systems, although the basic morphology of the two groups is entirely different.

HYBRIDIZATION

Numerous pollinations were made between plants of different sections, but all of these failed to produce viable seeds and no hybrids were obtained. The crosses attempted were: *Eucnide aurea*, of section SYMPETALEIA, with *E. bartonioides*, *E. cordata*, and *E. lobata*, of section EUCNIDE, and reciprocals; *E. urens*, of section MENTZELIOPSIS, with *E. bartonioides* and *E. lobata*, of section EUCNIDE. Interspecific pollination within section EUCNIDE usually resulted in capsules full of viable seeds; plants of two hybrid combinations were grown and their fertility determined.

Eucnide lobata (3298-2) ♀ × *E. bartonioides* (3283-6) ♂. The F₁ plants grew vigorously and flowered profusely. The parents differ greatly in floral morphology (see FIG. 2b, a), and the hybrids were recognized by their intermediate flowers. Two of the hybrid individuals were tested for fertility and both produced less than two per cent good pollen. The large number of chromosomes made exact determination of chromosome pairing in most microsporocytes impossible, but 23 cells at metaphase showed 14 to 16 bivalents with the remainder of the chromosomes involved in multivalents or present as univalents. Heteromorphic bivalents were noted and unequal segregations at anaphase I of 20 to 22 and 19 to 23 were common. Although several flowers were self-pollinated, no viable seeds were obtained.

Eucnide cordata (3300-2) × *E. lobata* (3298-2) and reciprocal. The F₁ plants were vigorous and flowered profusely. The morphology of the flowers was intermediate between the very different flowers of the parents (see FIG. 2c, b). Five hybrid individuals were tested for fertility. All had less than five per cent good pollen. Meiosis in all five plants was irregular. Chromosome pairing was analyzed more or less completely in a total of 43 cells from all five of the F₁ plants. Most cells had about 15 bivalents, with the remainder of the chromosomes involved in multivalents or present as univalents. Heteromorphic bivalents were noted, and anaphase I cells with 21-21 segregations were less frequent than those with

unequal segregations. Self-pollinations on all five plants failed to produce seeds. There were no differences noted between the reciprocals.

The data from these cross-pollinations indicate a strong incompatibility between plants of different sections of *Eucnide* that operates at the level of crossability. Within section EUCNIDE hybrids are readily obtained between the most morphologically diverse species, but the F_1 plants, although easily obtained, are sterile.

DISTRIBUTION AND ECOLOGY

The genus *Eucnide* is distributed from the southwestern United States, through Mexico to Guatemala. Section MENTZELIOPSIS, with only one species, *E. urens*, occurs in the Death Valley region of California and in the lower Colorado River basin, with an outlying station in Baja California (MAP 1). *Eucnide urens* is the only species of the Mojave Desert area, and its distribution at elevations usually below 4000 feet does not overlap that of any of the other species of *Eucnide*. The three species of section SYMPETALEIA occur in Baja California, with *E. rupestris* extending into California, Arizona, Sonora, and Sinaloa (MAP 2). All are restricted to the Sonoran Desert region and do not occur above 3000 feet elevation. The species of this section apparently are allopatric — at least there are no data available to indicate that they ever occur as adjacent populations. Section EUCNIDE, with seven species, has the widest range of the three sections. *Eucnide cordata* and *E. hypomalaca* occur in the Sonoran Desert area of Baja California and Sonora (MAP 4). The remaining species of this section inhabit southern Texas, eastern and southern Mexico, and Guatemala (MAPS 3, 4). In the northern portions of this range, about latitude 29° north, the populations usually occur below 3000 feet. In southern Mexico, at latitude 18° north and in Guatemala, at latitude 15° north, the populations occur at elevations from 2000 feet to 8000 feet above sea level.

Some interesting relationships between the breeding system and distribution are found in *Eucnide*. The four species with long, narrow flowers, series *Tubiflorae*, replace each other geographically (MAP 4). In series *Eucnide*, the two species with large flowers, *E. bartonioides* and *E. grandiflora*, also are allopatric, but the third species, *E. lobata*, with small, rotate flowers, is at least geographically sympatric with *E. bartonioides* in part of its range (MAP 3). Species with different flower types, hence placed in different sections or series, often are sympatric. For example, *E. cordata*, of section EUCNIDE, is sympatric with each of the three species of section SYMPETALEIA, and, likewise, *E. xylinea*, of series *Tubiflorae*, is sympatric with both *E. lobata* and *E. bartonioides* of series *Eucnide*. Distribution and floral morphology in *Eucnide* are related through the generalization that species with similar flower types, and thus probably with similar pollination systems, are always allopatric; and conversely, sympatric species always have different flower types and presumably different

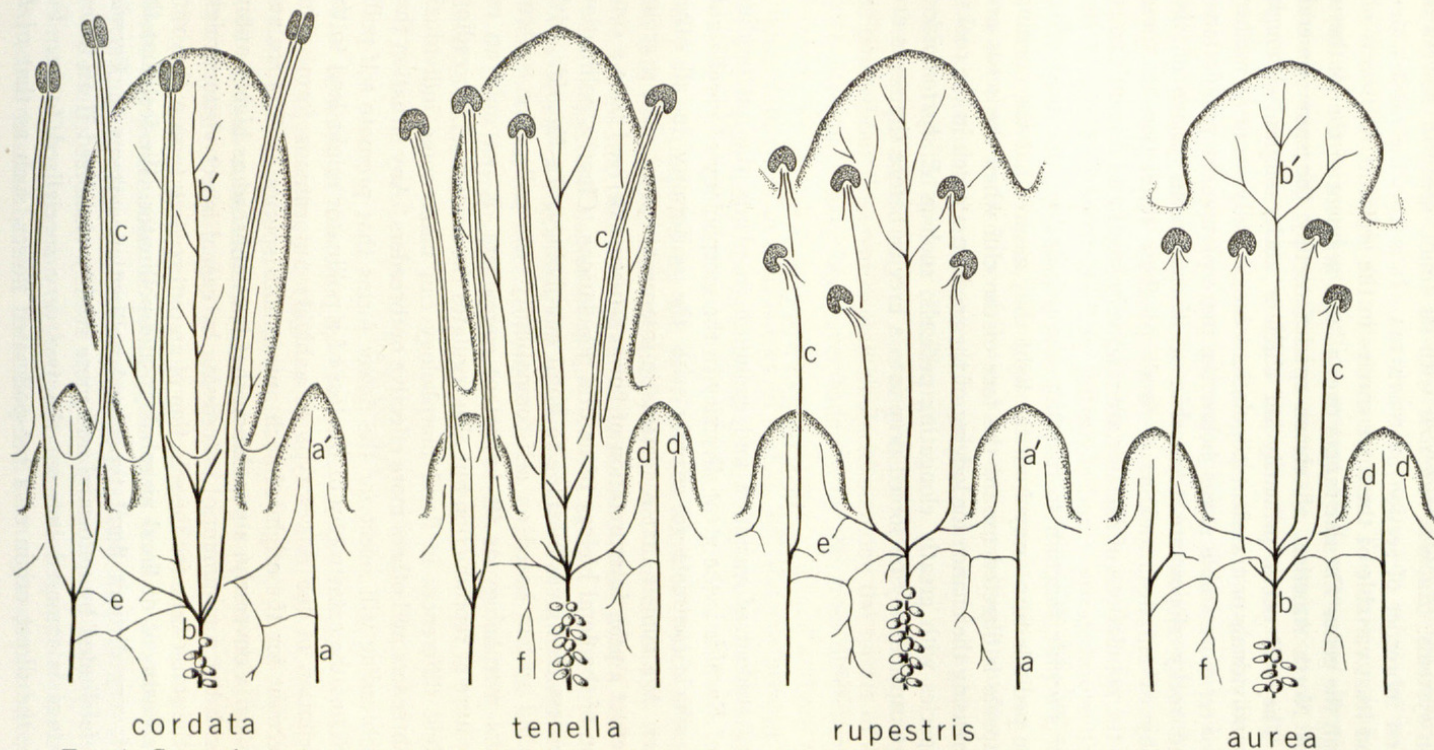


FIG. 5. Comparison of vasculature in two sepals and one petal in *Eucnide*, showing insertion of stamens and ovules for four species, adaxial view. a, sepal trace; a', sepal vein; b, petal trace (with ovules); b', petal vein; c, stamen traces; d, lateral sepal vein; e, traces to valves and style; f, peripheral veins of ovary wall.

pollination systems. *Eucnide rupestris* with its small, greenish flowers is the strictest inbreeder of section SYMPETALEIA. It is also the most widespread and least variable of the three species in the section.

Although the genus *Eucnide* ranges over a large segment of the southern portion of North America, all eleven species occupy the same general habitat. They all occur primarily on cliffs or rocky slopes, although scattered individuals or transient populations occasionally occur in washes and on lower, more stable slopes below the more permanent populations. Cliffs and rocky slopes are themselves a discontinuous phase of the topography of an area, and, as a result of their restriction to these habitats, the populations of *Eucnide* are relatively small and discontinuous. The negatively phototropic and elongating pedicels found in many of the species of *Eucnide* function to maintain the populations on steep cliffs. When the pedicels turn away from the light they assure that the opening of the capsule is directed toward the face of the cliff when the seeds are shed, increasing the chance for lodging of the seeds in a crack in the rocks. In the species with greatly elongating pedicels, such as *E. bartonioides*, the entire capsule may be forced deep into a crevice before the seeds are released.

TAXONOMIC RATIONALE

To any student of variation and evolution in plants the outstanding feature of *Eucnide* is the great diversity in the morphology of corolla and stamens which contrasts so sharply with the uniformity in all other characters. We submit that a systematic interpretation of such a group should reflect a prior interpretation of flower structure derived from a consideration of the floral biology of natural populations. Clearly, pollination is the process that gives meaning to floral morphology. In *Eucnide*, with its breeding system based on self-compatibility, the pollination system, with floral morphology as its important component, is not only an essential feature of reproduction but also regulates the amount of inbreeding. Even slight differences in floral morphology can make some individuals better inbreeders and others more effective outbreeders. Any situation that favors inbreeding will select for the flower forms that promote self-pollination. Thus the catastrophe of the loss of a pollinator might lead to the rapid evolution of the flower type of a highly autogamous form. This might account for the origin of such autogamous species as *E. hirta* and *E. rupestris*. Conversely, a population that is established as highly autogamous with but a minimum of outcrossing by casual insect visitors might provide the stable base for the selection of an outbreeding form with a very specific adjustment of floral morphology and pollinator. We feel that the origin of very distinct floral types and pollination systems in *Eucnide* may be facilitated by autogamy and more readily visualized if an autogamous stage is imposed between the two very specialized forms. For example, the direct origin of a bee-pollinated flower, such as that of *E.*

urens, from the hawk-moth flower of *E. bartonioides* by the occurrence of a "hopeful monster" in an *E. bartonioides* population is less probable than the transition through an autogamous stage. The striking similarity between the flowers and pollination system of *E. urens* and *Mentzelia involucrata* must be the result of evolutionary convergence. It is difficult for us to imagine either a single step or a series of steps, each with a specific pollinator, that could accomplish this convergence without any resort to autogamy. The autogamous species, therefore, may be phylogenetically very important in *Eucnide* and not merely evolutionary "dead ends." We speculate further that the architecture of the *Eucnide* flower with its fusion of petals and numerous filaments provides for a plasticity that allows for modification to different flower types without alteration of the basic anatomical structure and without incurring any modification of seeds, leaves, or fruits. It is important for us to present our speculations on these matters because they are the compelling thoughts we hold as we subjectively consider variation in *Eucnide* and make the taxonomic decisions required for our classification.

Our comparative study of the anatomical details of floral morphology has pointed out the great overall similarities among the species of *Eucnide* which previously have been overshadowed by the gross differences. Furthermore, we give less taxonomic weight than previous authors to these striking differences in morphology of corolla and stamens because we feel that as components of the pollinating system they are evolutionarily labile. We conclude that there are three coordinate groups in *Eucnide* rather than two as proposed by the previous classification which grouped the taxa into two genera, *Eucnide* and *Sympetaleia*. Our conclusion that these three groups are best considered sections rather than genera rests on our evaluation of their degree of affinity viewed against our understanding of generic levels in the remainder of the family. The differences and similarities between the three sections of *Eucnide* that we propose are equivalent to those between the sections of *Mentzelia*, the group of species most similar to *Eucnide*.

TAXONOMY

The revision of *Eucnide* by Waterfall (1959) has greatly simplified our task of presenting a formal taxonomy, for, although he excluded *Sympetaleia*, his treatment of the species that he did place in *Eucnide* basically is the same as ours. Accordingly, our comments on the classification and nomenclature of these species are limited primarily to presentation of additional information or to minor points of differences in opinion. We present the distribution of each species with detailed dot maps and cite only critical specimens. More extensive citations of specimens are given in Waterfall's revision, and we can provide on request a complete list of specimens. Our discussion of the species of section *Sympetaleia* are somewhat more detailed because these have not been monographed previously.

Eucnide Zucc. Del. Sem. Hort. Monac. 4th unnumbered page. 1844.¹

Microsperma Hook. Icon. Pl. pl. 234. 1839; not *Microspermum* Lag. Gen. et Sp. Nov. 25, 1816.

Sympetaleia A. Gray, Proc. Amer. Acad. 12: 161. 1877.

Loasella Baill. Bull. Soc. Linn. Paris. 1: 650. 1887.

Plants herbaceous, pubescent, potentially perennial (or annual), sometimes \pm woody at base, the stems usually less than 1 m. long. Leaves alternate, exstipulate, petiolate, the blades pinnately to palmately veined, broadly ovate (rarely obovate) to suborbicular, often cordate at base. Hairs smooth, needlelike, or variously reflexly barbed. Inflorescences \pm racemose, terminal or axillary, usually bracteate, of 1 to many flowers. Flowers pedicellate (or pedunculate), 5-merous, \pm regular, bisexual, epigynous. Sepals 5, free, persistent. Petals 5, yellow, \pm white, greenish or reddish orange, apopetalous, but united at base to staminal tube, or corolla sympetalous. Stamens few to many, maturing centripetally; filaments free above and \pm filiform but connate basally into a short tube (and united to base of free petals), or filaments epipetalous; anthers basifixed, exerted or included, oblong to ovoid and 2-locular at anthesis, with longitudinal dehiscence, or reniform peltate and 1-locular at anthesis, with apically confluent dehiscence; pollen oblate, 3-colporate. Gynoecium 5-carpellate; stigma exerted or included and equaling or exceeding the anthers, globular to linear and sometimes twisted, of 5 appressed (sometimes spreading) lobes (or stigma a small terminal tuft of hairs); style usually filiform (sometimes thick), usually elongating and somewhat persistent; ovary inferior, \pm spherical, obovoid to clavate, 1-locular, with 5 intruded, transversely cordate parietal placentae; ovules numerous on each placenta, anatropous. Fruits globular to narrowly obovoid, often nodding or reflexed on conspicuous pedicels (or peduncles), dehiscent apically by 5 centrifugally opening triangular valves interior to and opposite the persistent sepals. Seeds minute (usually less than 2 mm. long), numerous, \pm oblong, grooved or ribbed longitudinally, sometimes spirally twisted, pointed at the micropylar end, \pm rounded at chalazal end. Seedling cotyledons subreniform to ovate, short-petiolate. TYPE SPECIES: *E. bartonioides* Zucc. (Name from Greek, *eu*, pretty, and *knide*, nettle, "Schönnessel.")

¹ The place of publication for this name is "Delectus Seminum in Horto R. Botanico Monacensi Collectorum Anno 1844," a list of seeds offered by the Munich Botanical Garden. The name *Eucnide bartonioides* first appeared on the 2nd page with an asterisk which leads one to the 4th (last) page where both the generic and the specific characters are set forth in Latin. The description closes with "Zuccarini in Act. Monac. Acad. inedit," doubtless a reference to Abhandl. Bayer. Akad. Wiss. 4(2): 5. pl. 1. 1845, where the identity of this taxon is established by the plate. In the absence of other type material this plate ought to be accepted as the lectotype for *E. bartonioides*. The final printed line reads "Monachii, 28 Dec. 1844." The only original of this publication known to us is deposited in the library of the Conservatoire et Jardin Botaniques, Genève. We are grateful to C. E. B. Bonner and J. E. Dandy for locating this rare publication and for making a photocopy available to us.

The generic name *Microsperma*, first used in Loasaceae for *M. lobata* Hook. in 1839, is earlier than the generic name *Eucnide* Zuccarini, published at the end of 1844. In Loasaceae, *Microsperma* was used in original descriptions also for *M. rudis* Schauer (1847) and *M. grandiflora* Greenland (1861). Since *Microspermum* had been used in Compositae by Lagasca in 1816 the name *Microsperma* in Loasaceae was rejected as a homonym in 1900 by Urban & Gilg in favor of *Eucnide*. If the view of Urban & Gilg is regarded as contrary to Art. 75 (a subjective decision) then it will be necessary to conserve *Eucnide* or, failing this, to adopt the name *Microsperma* for this genus. We have submitted a proposal for the conservation of the well known name *Eucnide*.

The genus *Eucnide*, including 11 species, is divided into three sections. Two series are distinguished in section EUCNIDE on the basis of the form of the corolla. In series *Eucnide*, primarily of eastern Mexico, *E. bartonioides* and *E. grandiflora* are very similar, differing principally in size, color of the corolla, and in distribution. *Eucnide bartonioides* and *E. lobata* normally are strikingly dissimilar but a few specimens, ironically, almost seem to bridge the morphological gap, and the ranges of the two species overlap. Series *Tubiflorae* is widely distributed in Mexico. Three of the species, *Eucnide cordata*, *E. hirta*, and *E. hypomalaca*, are quite similar, differing mostly in corolla size, inflorescence, pubescence, elongation of the fruiting pedicels, and position of the stigma in relation to the anthers. As in series *Eucnide*, these species are isolated geographically from one another and from the more distinctive *E. xylinea*, also of series *Tubiflorae*.

The section MENTZELIOPSIS of the far southwestern United States, comprised of a single species, *E. urens*, is very different morphologically from all other species of the genus.

Section SYMPETALEIA, almost confined to Baja California, is composed of three species that are strikingly dissimilar from one another in morphology and color of the corolla.

KEY TO THE SPECIES

1. Corolla united for at least $\frac{1}{2}$ its length into a narrow, relatively long tube (8–10 mm.) with a ring of hairs below the \pm sessile, included anthers.
2. Corolla salverform, bright yellow or reddish orange; sepals half the length of the corolla tube or less; fruiting pedicels elongating greatly (to 27 cm.); southern Baja California. 9. *E. aurea*.
2. Corolla \pm cylindrical, with erect lobes, dark green with shadings of yellow and/or brown; sepals at least half as long as the corolla tube; fruiting pedicels reflexed, elongating only a few centimeters; Baja California, local in southern California, southwestern Arizona, Sonora, and Sinaloa. 10. *E. rupestris*.
1. Corolla united for $\frac{1}{4}$ or less of its length into a relatively short, \pm inconspicuous tube (1–8 mm.); ring of hairs lacking; all anthers on long filaments, exerted or included.
3. Anthers reniform (sporogenous tissue continuous over the connective),

- exposed, 1-locular and peltate at anthesis, the dehiscence confluent apically; corolla white or pale yellowish, to 10 mm. long; stigma among the anthers; fruiting pedicels elongating at least several centimeters; rare and local, eastern Baja California Sur. 11. *E. tenella*.
3. Anthers ovate to oblong (sporogenous tissue interrupted apically by the connective), 2-locular at anthesis, the dehiscence not confluent; flowers mostly larger.
 4. Stigma and stamens both distinctly included, about $\frac{1}{2}$ to $\frac{3}{4}$ as long as the open, funnelform, rigid corolla; filaments linear, stout, compressed around the style; fruiting pedicels 1–2 cm., not elongating; desert regions of California, Nevada, Utah, Arizona; local in north-eastern Baja California. 8. *E. urens*.
 4. Stigma and stamens exerted or clearly exposed; Texas, Mexico, Guatemala.
 5. Corolla open and stamens spreading (series *Eucnide*).
 6. Corolla rotate, to about 12 mm. long or 2 cm. wide; outer stamens shorter than stigma, inner stamens slightly exceeding the minute, subcapitate stigma; fruiting pedicels 1–2 cm., not elongating; northeastern Mexico to Puebla. . . . 3. *E. lobata*.
 6. Corolla open-funnelform and larger.
 7. Stigma \pm linear-truncate, to about 6 mm. long, less than 1 mm. broad, sometimes separating into 5 narrow lobes; sepals to about 2.2 cm. long; petals to about 4 cm. long; stamens to 5 cm. long; style to 5.5 cm. long; fruiting pedicels elongating up to 33 cm.; Texas, eastern Mexico south to San Luis Potosí. 1. *E. bartonioides*.
 7. Stigma obconical, to 2.5 mm. broad, 2–3 mm. long, 5-lobed; sepals 2.5–5 cm. long; petals 5.8–8 cm. long; stamens 8–11 cm. long; style 10–12 cm. long; Oaxaca and Guatemala. 2. *E. grandiflora*.
 5. Corolla \pm cylindrical, the petals broadly imbricate and holding the stamens in a long, narrow cluster (series *Tubiflorae*).
 8. Leaves small, to 15 mm. long, 10 mm. wide, villous-canescens; flowers solitary at ends of heavy branches; corolla to 25 mm. long, fruiting pedicels to 2.5 cm. long; rare, western central Coahuila and southwestern Tamaulipas near Nuevo León boundary. 7. *E. xylinea*.
 8. Leaves larger, 3–12 cm. long, 2.5–10 cm. wide, pubescent but not villous-canescens; flowers usually clustered; corollas 2–4 cm. long.
 9. Inflorescence many flowered, usually on a distinct peduncle, hence above the leaves; petals 1.5–2.5 cm. long; pedicels not elongating in fruit; Baja California, islands of the Gulf of California, and near Guaymas, Sonora. . . 4. *E. cordata*.
 9. Inflorescence few flowered, not on a distinct peduncle; petals 2–4 cm. long; pedicels sometimes elongating in fruit.
 10. Pubescence on pedicels with simple hairs conspicuously longer than the reflexly barbed hairs; pedicels greatly elongate in fruit; south-central Mexico and Guatemala. 5. *E. hirta*.

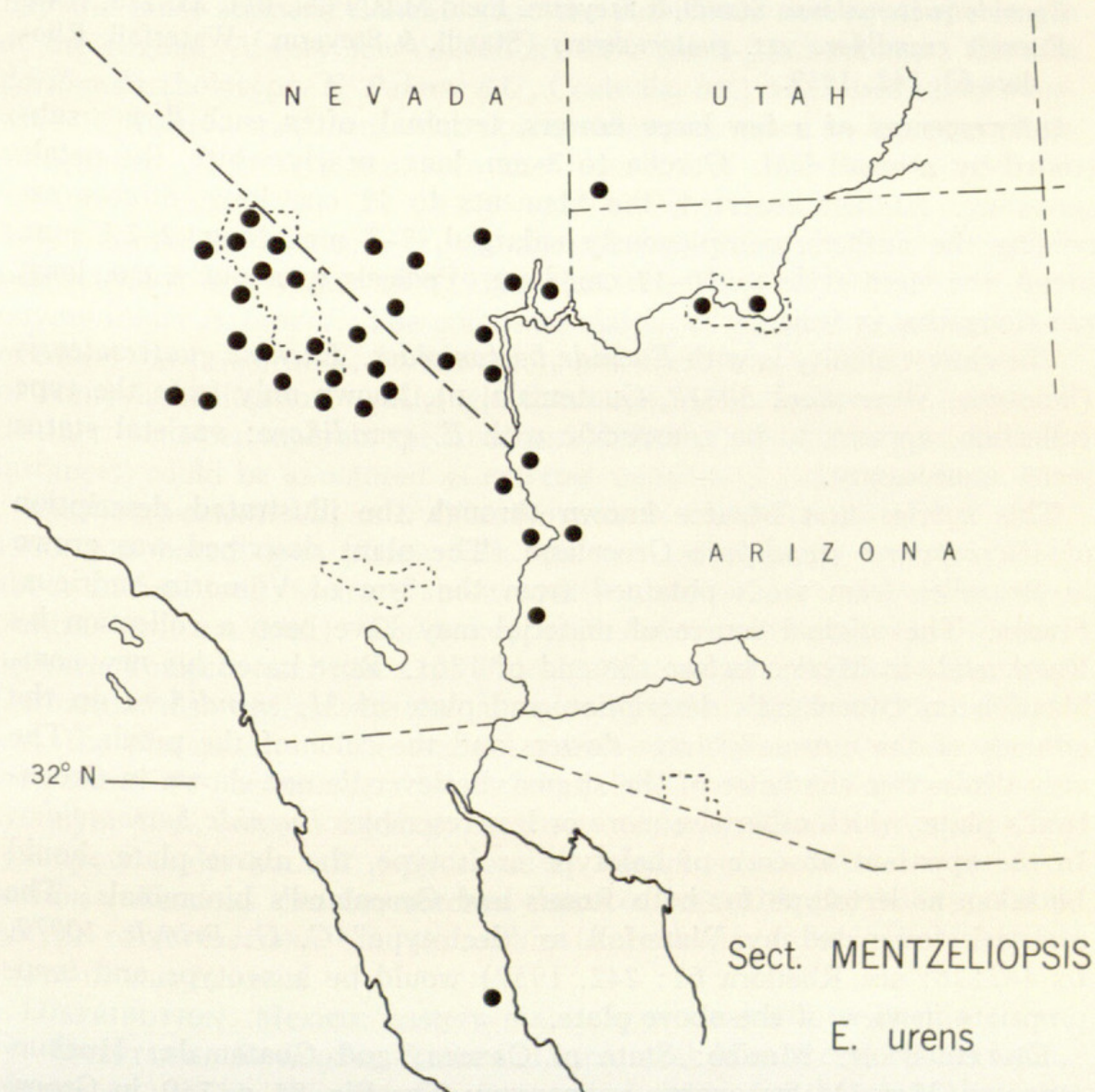
10. Pubescence on pedicels with reflexly barbed hairs at least as long as the simple hairs; fruiting pedicels unknown; Sonora, southwestern Chihuahua, and northern Sinaloa. 6. *E. hypomalaca*.

1. *Eucnide bartonioides* Zucc. Del. Sem. Hort. Monac. 4th unnumbered page. 1844.¹

Mentzelia gronoviaefolia Fisch. & Mey. in Fisch., Mey. & Ave-Lallemant, Index Sem. Hort. Petrop. 10: 54. 1845 (not before 3 Feb.).

Microsperma bartonioides Walp. Repert. Bot. 5: 777. 1845-46 (probably 1846).

Inflorescences of a few flowers, terminal, or the flowers axillary. Corolla 1-4 cm. long, yellow, paler below, the petals spreading. Anthers exserted, slightly exceeded by the linear (to 6 mm. long) stigma. Pedicels to 3-4 cm. long at anthesis, usually elongating to 15 cm. or more in fruit.



MAP 1. Distribution of section MENTZELIOPSIS in the southwestern United States and Baja California, Mexico.

The size of the corolla (and the leaves) is quite variable. The small flowered forms can be confusingly similar to depauperate plants of *Eucnide lobata* even though these two species normally are quite distinct. (See discussion of *E. watsonii* under *E. lobata*.)

DISTRIBUTION. United States: southwestern Texas; and Mexico: north-eastern states southward into San Luis Potosí (MAP 3). HOLOTYPE: The descriptions were based on plants grown in the Munich Botanical Garden from seeds probably collected by de Karwinski (perhaps number 285, gathered in Chihuahua, Mexico, in 1843; not seen by the present authors). Regarding the latter, Urban & Gilg (1900, p. 108) remarked: "Colitur in hortis Europaeis ab anno 1844 e seminibus Karwinskianus." At least 170 specimens have been annotated.

2. *Eucnide grandiflora* (Groenl.) Rose, Contr. U. S. Natl. Herb. 3: 317. 1895.

Microsperma grandiflora Groenl. Rev. Hort. 1861: 349. fig. 84. 1861.

Eucnide guatemalensis Standl. & Steyerl. Field Mus. Publ. Bot. 23: 178. 1944.

Eucnide grandiflora var. *guatemalensis* (Standl. & Steyerl.) Waterfall, Rhodora 61: 242. 1959.

Inflorescences of a few large flowers, terminal, often each flower subtended by a small leaf. Corolla to 8 cm. long, nearly white, the petals spreading. Anthers exserted, the filaments to 11 cm. long. Stigma exceeding the anthers, conspicuously enlarged, 2–3 mm. long, 2–2.5 mm. broad, the stout style to 10–12 cm. long. Pedicels to about 4 cm. long, not elongating in fruit.

The closest affinity is with *Eucnide bartonioides*. *Eucnide guatemalensis* (holotype, Steyermark 50818, Guatemala, F), known only from the type collection, appears to be conspecific with *E. grandiflora*; varietal status seems unnecessary.

This species first became known through the illustrated description of *Microsperma grandiflora* Groenland. The plant described was grown in Bruxelles from seeds obtained from the firm of Vilmorin-Andrieux, France. The original source of material may have been a collection by Roezl made in Mexico before the end of 1861. Rose based his new combination on Groenland's description and plate of *M. grandiflora* on the grounds of the unusually large flowers and the color of the petals. The very distinctive character of the stigma, however, is not shown in Groenland's plate, which otherwise more or less resembles *Eucnide bartonioides*. In the apparent absence of holotype or isotype, the above plate should be taken as lectotype for both Rose's and Groenland's binominals. The material designated by Waterfall as "lectotype" C. G. Pringle 10077, US 462126; see Rhodora 61: 242. 1959) would be a neotype and inappropriate in view of the above plate.

DISTRIBUTION. Mexico: State of Oaxaca; and Guatemala: Huehuetenango (MAP 3). SUGGESTED LECTOTYPE: The Fig. 84, p. 350, in Groenland, Rev. Horticole 1861: 349–351. 1861. At least 17 specimens have been annotated.

3. *Eucnide lobata* (Hook.) A. Gray, Boston Jour. Nat. Hist. 6: 192. 1857.

Microsperma lobatum Hook. Icon. Pl. 3: pl. 234. 1839, "*Microsperma lobata*."

Mentzelia lobata (Hook.) Walp. Repert. Bot. 2: 224. 1843.

Eucnide floribunda S. Wats. Proc. Amer. Acad. 17: 358. 1882.

Inflorescences of few to many flowers, usually more or less terminal (or flowers sometimes solitary, axillary). Corolla usually 6–12 (or 15) mm. long, rotate, the lobes broad. Anthers and stigma exerted and usually about equal. Stigma capitate (or sometimes about 1 mm. long, oblong). Pedicels short (rarely 2 cm. long) at anthesis, usually reflexed in fruit but not elongating conspicuously.

The stamens developmentally are in two ranks. The inner ones are convolute around the base of the style when the flowers first open and the outer ones are extended but shorter than the stigmas. On the second day the inner stamens elongate past the outer ones and equal the length of the stigma. A very few collections have giant-sized corollas. *Eucnide floribunda* (holotype, *E. Palmer* 832, Coahuila, GH) was based upon somewhat distinctive specimens with strict, elongated, more or less secund inflorescences. We have not seen the holotype of *Microsperma rudis* S. Schauer, Linnaea 20: 721. 1847 (presumably based upon *Aschenborn* 233, collected in Mexico); it was the opinion of Gray (1857), Urban & Gilg (1900), and Waterfall (1959) that this binomial belonged in synonymy under *E. lobata*. The northeast margin of distribution of *E. lobata* overlaps the range of *E. bartonioides*, and there would be the possibility of some hybridization. Although these species normally are strikingly distinct, some depauperate specimens are difficult to determine and, in some instances, could be annotated as extreme variants of either species.

Eucnide watsonii Urban & Gilg, Nova Acta Akad. Leop.-Carol. 7: 105. 1900, was based upon plants with few and rather small flowers (petals about 10 mm. long; stamens about equalling the petals) on relatively long pedicels (2–5 cm. long). The holotype, *E. Palmer* 1067 (K), was collected between Tampico and San Luis Potosí, Mexico. An isotype at the Gray Herbarium also agrees with the above description and confirms, more or less, the placement by the original authors of this material between *E. lobata* and *E. bartonioides*. Waterfall (1959) treated the binomial as a synonym of *E. lobata*. During our study we have placed it alternately in synonymy under both *E. lobata* and *E. bartonioides*. Several other herbarium collections can be matched more or less with the holotype and isotype of *E. watsonii* but we remain in doubt regarding the biological status of this material.

DISTRIBUTION. Mexico: eastern states from Coahuila to Puebla (MAP 3). HOLOTYPE: *Berlandier*, Santa Catarina, near Monterrey, Nuevo León, Mexico (K). This sheet has on it pencil sketches for the plate that appeared with the original description in *Icones Plantarum*. At least 142 specimens have been annotated.

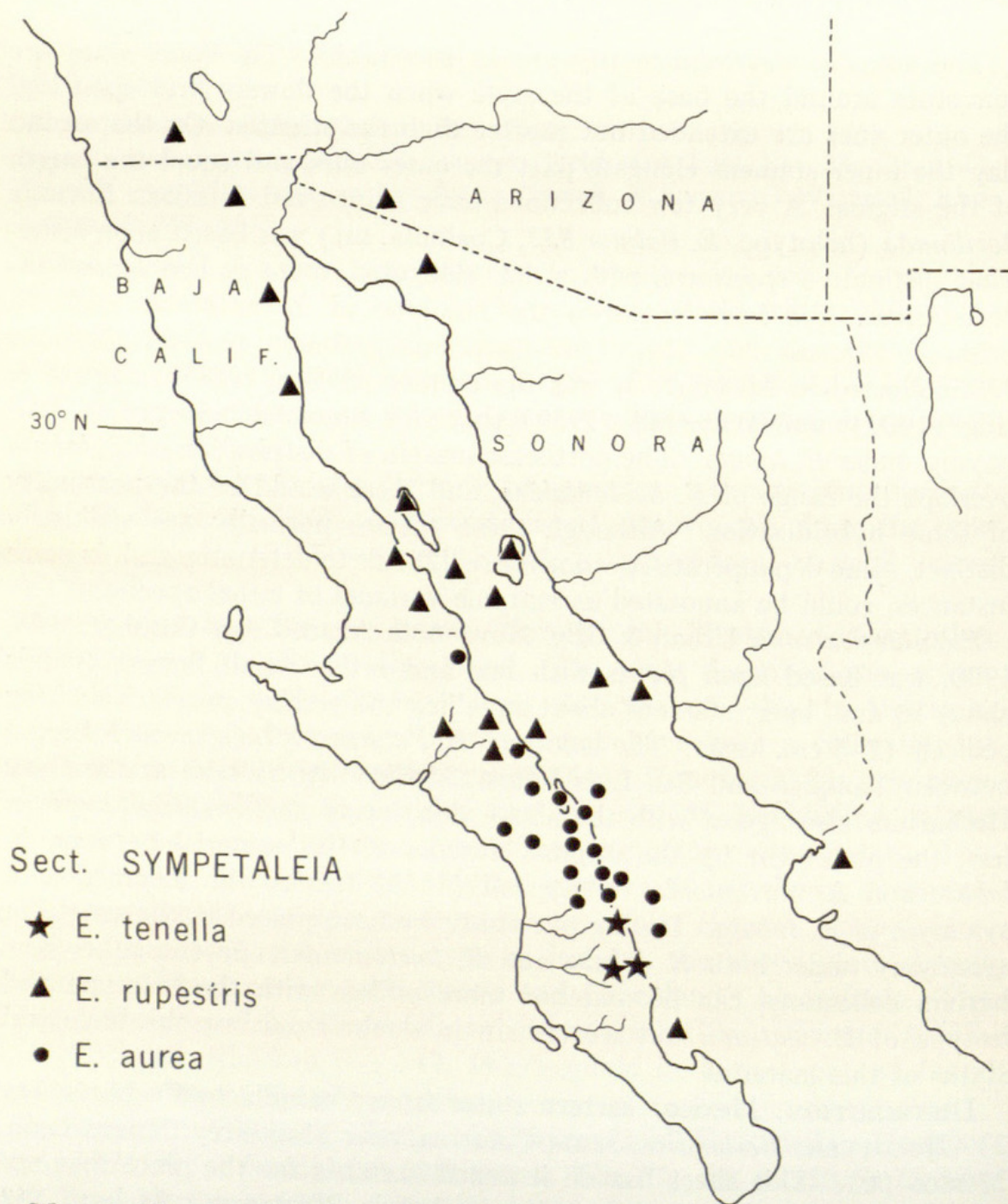
Series *Tubiflorae* Thompson & Ernst, ser. nov.

Series in sect. *Eucnide*, sed differt: corolla longe cylindrica, petala late imbricata, quasi tubus angustus, stamina in fasce angusto. Circa 4 species inclusae. *Typus*: *E. cordata* (Kell.) Kell. ex Curran.

4. *Eucnide cordata* (Kell.) Kell. ex Curran, Bull. Calif. Acad. 1: 137. 1885.

Mentzelia cordata Kell. Proc. Calif. Acad. 2: 33. 1860.

Inflorescences of many flowers, crowded, terminal, and much branched (sometimes elongating in fruit). Corolla about 1.5–2.5 cm. long, white



MAP 2. Distribution of section SYMPETALEIA in the region of the Gulf of California, Mexico.

(or yellowish), narrowly cylindrical, holding the stamens in a narrow cluster. Anthers exserted, well exceeded by the small, more or less clavate stigma. Pedicels short (rarely to 2.5 cm. long), not appreciably elongating in fruit.

This species most closely resembles *E. hirta*, of south-central continental Mexico, but is distinguished by its almost white corolla, very long exserted style, and pedicels which do not elongate.

DISTRIBUTION. Mexico: Baja California Norte and Sur (including Cedros Island and some islands in the Gulf of California) and near Guaymas, Sonora. (MAP 4). HOLOTYPE: *Dr. J. A. Veatch*, "Cedros Island." The species has been recollected on Cedros Island, its only insular station on the Pacific side of Baja California, by several botanists including Greene, Palmer, Anthony, and Mason. None of the original material seems to have survived at the California Academy of Sciences. An apparent isotype is preserved at the Gray Herbarium and probably this should be taken as the lectotype. At least 190 specimens have been examined.

5. *Eucnide hirta* (G. Don) Thompson & Ernst, comb. nov.

Mentzelia hirta G. Don, Gen. Syst. Gard. Bot. 3: 66. 1834.

Eucnide sinuata S. Wats. Proc. Amer. Acad. 17: 358. 1882.

Eucnide nelsonii Rose, Contr. U.S. Natl. Herb. 12: 286. 1909.

Eucnide pringlei Rose, Contr. U.S. Natl. Herb. 12: 287. 1909.

Inflorescences of few to several flowers, more or less terminal or axillary. Corolla about 2.5 (4) cm. long, yellow, narrowly cylindrical, holding the stamens in a narrow cluster. Anthers exserted. Stigma linear (or narrowly oblong), to 2 mm. long, more or less equalling the anthers (or sometimes exceeding them). Pedicels well developed, often 2 cm. long at anthesis, elongating in fruit to as much as 8 cm.

The holotypes of *Eucnide sinuata* (*Botteri* 266, GH) and of *E. nelsonii* (*E. W. Nelson* 6926, Michoacán, US 399295) are conspecific with *E. hirta*. *Eucnide pringlei* var. *pringlei* (holotype, *C. G. Pringle* 10077, Guerrero, US 462195; *H. E. Moore, Jr.*, 2122, Hidalgo, GH), known only from two collections, seems to be a robust form of *E. hirta* with larger flowers. *Eucnide hirta*, distinguished by its yellow corolla, shorter style, and elongating pedicels, appears to be a continental counterpart of *E. cordata*. (See also *E. hypomalaca*).

DISTRIBUTION. Mexico: south-central states, from San Luis Potosí to Guerrero; and discontinuously in Guatemala: Jalapa (MAP 4). HOLOTYPE: *Sessé & Mociño*, Mexico (BM). At least 57 specimens have been annotated, many of them as *E. sinuata*, but we now know that the correct name is *E. hirta*.

6. *Eucnide hypomalaca* Standl. Field Mus. Publ. Bot. 22: 41. 1940.

Eucnide pringlei var. *hypomalaca* (Standl.) Waterfall, Rhodora 61: 239. 1959.

Inflorescences of few flowers, terminal (or flowers axillary). Corolla

large, to about 4 cm. long, white, narrow, holding the stamens in a narrow cluster. Anthers and stigma exserted.

It is not known whether the pedicels elongate in fruit. The flowers suggest a giant-sized form of *Eucnide cordata*, perhaps with the petals slightly spreading. The species is known from only five localities. We find this material distinct from *E. hirta* (and also from *E. pringlei* var. *pringlei* which we consider an unusually large form of *E. hirta*). The species is distinguished by its distribution, the large, rather coarse flowers, the whitish, heavily veined corolla, and the prominent barbed hairs of the pedicels.

DISTRIBUTION. Mexico: northern and (discontinuously) southern Sonora and near the boundaries of adjacent northern Sinaloa and southwestern Chihuahua (MAP 4). HOLOTYPE: *H. S. Gentry 1315*, Sonora (F). OTHER SPECIMENS: Chihuahua: *Hartman 1016* (GH, UC); *Hewitt 272* (GH). Sinaloa: *Breedlove 1507* (LA); *Mason & Brewer 1855* (UC). Sonora: *Gentry 3021* (GH, MO); *Gentry 14445* (US); *Kaiser s.n.*, April 17, 1951 (CAS).

7. *Eucnide xylinea* C. H. Muller, Amer. Midl. Nat. 27: 487. 1942.

Flowers solitary, terminal on short leafy shoots. Corolla to 2.5 cm. long, yellow, narrowly cylindrical, holding the stamens in a narrow cluster. Anthers and stigma exserted. Pedicels 2–3 cm. long, not elongating in fruit.

This very distinctive species is distinguished by its solitary flowers, especially matted habit, and villous-canescient small leaves (to about 1.5 cm. long). It is known only from three stations.

DISTRIBUTION. Mexico: western central Coahuila and discontinuously in southwestern Tamaulipas near the southern Nuevo León boundary (MAP 4). HOLOTYPE: *C. H. Muller 3311*, Coahuila (US 2109944). OTHER SPECIMENS: Coahuila: *Johnston 9003* (GH); *Muller 3311* (GH, UC); *Stewart 1075* (GH). Tamaulipas: *Stanford, Lauber, & Taylor 2449* (DS, RSA).

Section *Mentzeliopsis* Thompson & Ernst, sect. nov.

Flores apopetali, sed petalis basi cum tubo filamentarum breviter coalitis. Antherae in anthesi biloculares. A sectione *Eucnide* differt: stigma antheraeque in corolla inclusae, staminum filamenta crassa interne obliqua, receptaculum pollinare circumstylare formantia. Species unica. TYPUS: *E. urens* Parry.

8. *Eucnide urens* Parry, Amer. Nat. 9: 144. 1875.

Mentzelia urens Parry ex Gray, Proc. Amer. Acad. 10: 71. 1874 (non Vell. Fl. Flum. 5: 97. 1825).

Eucnide synandra A. Nelson, Bot. Gaz. 47: 428. 1909.

Eucnide parryi House, Bull. N.Y. State Mus. 234: 67. 1922 (a substitute name for *E. urens*).

Inflorescences of several flowers, terminal (the flowers sometimes subtended by small leaves). Corollas about 5 cm. long, pale yellowish white, the petals rigid, spreading. Stamens included, the filaments somewhat thick, slanted inward around the stout style. Stigma included, slightly exceeding the anthers. Pedicels short, to about 1.5 cm. long, neither reflexed nor elongated in fruit.

DISTRIBUTION. United States: eastern California, southern Nevada, southwestern Utah, western Arizona, and discontinuously in Mexico: eastern Baja California Norte (MAP 1). LECTOTYPE: *C. C. Parry* 79, Utah (GH); see U. T. Waterfall, *Rhodora* 61: 236. 1959. At least 196 specimens have been annotated.

Section **Sympetaleia** (A. Gray), Thompson & Ernst, stat. nov. Basionym: *Sympetaleia* A. Gray, Proc. Amer. Acad. 12: 161. 1877.

Classes 2 morphologici: corollae tubus quam lobi longior, antherae inclusae, filamenta breviora (typo incluso); vel corollae tubus quam lobi brevior, antherae plus minusve exsertae, filamenta longa. Differt: corolla vere sympetala, antherae anthesin uniloculares, stamina quasi epipetala. Species 3 inclusae. TYPUS: *Sympetaleia aurea* A. Gray = *Eucnide aurea*.

9. **Eucnide aurea** (A. Gray) Thompson & Ernst, comb. nov.

Sympetaleia aurea A. Gray, Proc. Amer. Acad. 12: 161. 1877.

Inflorescences usually of many crowded flowers, terminal, sometimes



MAP 3. Distribution of section EUCNIDE, series *Eucnide*, in Texas, Mexico, and Guatemala.

elongating appreciably in fruit (or flowers sometimes solitary, axillary). Corolla 1–2 cm. long, bright yellow or strong reddish orange, salverform, the lobes broad and rounded. Stamens epipetalous, included, the anthers more or less sessile; a ring of upwardly curved hairs below the stamens. Style filiform, the stigma minute, situated among the anthers (or sometimes barely exposed in the mouth of the corolla tube). Pedicels usually short at anthesis but elongating conspicuously, sometimes to 27–33 cm. in fruit.

This species probably includes two taxa: one has smaller yellow corollas with stigma included; the other larger reddish orange corollas with stigma becoming slightly exposed.

DISTRIBUTION. Mexico: Baja California Sur, including some islands in the Gulf of California (MAP 2). HOLOTYPE: *Dr. Thomas H. Streets*, Pulpito Point (GH). At least 70 specimens have been annotated.

10. *Eucnide rupestris* (Baill.) Thompson & Ernst, comb. nov.

Loasella rupestris Baill. Bull. Soc. Linn. Paris 1: 650. 1887.

Sympetaleia rupestris (Baill.) S. Wats. Proc. Amer. Acad. 24: 50. 1889.

Inflorescences usually of many crowded flowers, terminal, sometimes elongating appreciably in fruit (or flowers sometimes solitary, axillary). Corolla 1–1.5 cm. long, mostly greenish with shadings of brown and/or yellow, narrowly cylindrical and inconspicuous on the plants, the lobes to 5 mm. long, rigid and erect. Stamens epipetalous, included, the anthers subsessile or on short, stout filaments, with a ring of upwardly curved



MAP. 4. Distribution of section EUCNIDE, series *Tubiflorae*, in Mexico and Guatemala.

hairs below the stamens. Style short and thick, the stigma not exceeding the lower anthers. Pedicels usually short at anthesis, sometimes reflexed in fruit and elongating up to 2 cm.

DISTRIBUTION. United States: Southern California and southwestern Arizona; and Mexico: Baja California Norte and Sur including some islands in the Gulf of California, also northwestern Sonora and discontinuously in northwestern Sinaloa (MAP 2). HOLOTYPE: *Thièbault 1099* (P); photograph (A) examined, courtesy of R. A. Howard. At least 55 specimens have been annotated.

11. ***Eucnide tenella*** (I. M. Johnst.) Thompson & Ernst, comb. nov.

Sympetaleia tenella I. M. Johnst. Proc. Calif. Acad. IV. 12: 1106. 1924.

Flowers few, small, mostly axillary. Corolla about 8 mm. long, white (? or yellowish), the tube inconspicuous, the lobes narrow and loosely spreading. Anthers exerted on filiform filaments, spreading. Stigma minute, terminal on the filiform style and equalling the staminal filaments in length; ring of hairs below the stamens lacking. Pedicels filiform, about 1.5 cm. long at anthesis, elongating in fruit to 8–10 cm. The corolla while distinctly sympetalous and short tubular, very closely approaches in form the corollas of sect. EUCNIDE, series *Eucnide*, thus differing conspicuously in form from the corollas of the other two species of sect. SYMPETALEIA. The species has been collected only three times.

DISTRIBUTION. Mexico: eastern Baja California Sur (MAP 2). HOLOTYPE: *I. M. Johnston 3091*, Agua Verde Bay (CAS 1239). Other specimens: *Wiggins 15546* (DS); *Wiggins, Carter & Ernst 280* (DS, LA, OKLA).

ACKNOWLEDGEMENTS

Many persons have helped us in the preparation of this paper. We are grateful to the curators of the herbaria where we have examined or borrowed specimens. The Latin descriptions were prepared by Robert C. Foster and additional scholarly assistance generously was provided by George K. Brizicky and Conrad V. Morton. In obtaining seeds for our use Annetta Carter, Roxanna Ferris, and Helen Sharsmith cheerfully risked life and limbs. Rogers McVaugh kindly led us to the lost name of *Eucnide hirta*. The insect pollinator of *Eucnide urens* was identified by Gerald I. Stage. Peter H. Raven corrected a final draft of the manuscript. A grant from the National Science Foundation provided financial support. It is an especial pleasure to acknowledge the faithful and competent assistance of Karen Bartholomew who has helped provide much of the technical information.

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Ernst, Wallace Roy and Thompson, Henry J. 1967. "Floral biology and systematics of Eucnide (Loasaceae)." *Journal of the Arnold Arboretum* 48(1), 56–88. <https://doi.org/10.5962/p.67866>.

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