

## SYSTEMATICS OF HENRYA (ACANTHACEAE)

Thomas F. Daniel  
Department of Botany  
California Academy of Sciences  
San Francisco, CA 94118

### INTRODUCTION

*Henrya* Nees ex Benthham is a genus of perennial herbs and shrubs occurring from the southwestern United States southward to western Costa Rica. In the only previous comprehensive revision of the genus, George Happ (1937) recognized 20 species and one variety. All of the taxa recognized by Happ have been combined into a single species, *H. insularis* Nees ex Benthham, in the present study. The only taxon described in *Henrya* since Happ's (1937) monograph, *H. tuberculosperma* T. Daniel (Daniel 1984), has been maintained as a distinct species. The monotypic genus *Solenoruellia* Baillon is included into the synonymy of *Henrya* for the first time.

Happ's treatment is particularly noteworthy for reestablishing *Henrya* as a genus distinct from *Tetramerium*. Happ (1937) studied a total of 77 collections from 15 herbaria. Among the 21 taxa that he recognized, 13 were newly described. Eight species were known only from a single collection.

Several floristic workers (Gibson 1974, Daniel 1984, Durkee 1986) have questioned the validity of some of the taxa recognized by Happ. Mutually exclusive, and thus diagnostic, characters are not readily evident among most specimens of *Henrya*. This situation is amply reflected in Happ's (1937) key to the species of *Henrya* where qualifying words such as "usually," "mostly," and "chiefly" are encountered 25 times and where only eight of the 20 pairs of contrasting leads offer at least one mutually exclusive character. Further, even among the mutually exclusive characters, imprecise terms (e.g., long vs. short, close vs. remote, rather loose vs. rather dense) are often utilized. The preponderance of weakly defined species recognized by Happ likely resulted from his reliance on a few, often plastic, characters and a taxonomic philosophy different from that adopted here and in my previous studies of Acanthaceae (see discussions in Daniel 1983, 1986).

The present study of *Henrya* is based on examination of more than 750 herbarium specimens representing some 325 collections, field observations in Mexico, and greenhouse and laboratory studies of *H. insularis*. A special effort is made to provide rationales for assigning the taxa recognized by Happ to *H. insularis*.

### TAXONOMIC HISTORY

Initial publication of *Henrya* dates from 1845 when an illustration of *H. insularis* appeared among the plates accompanying Benthham's *The botany of the voyage of H.M.S. Sulphur*. In the companion text of 1846, Nees provided descriptions of the genus, *H. insularis*, and *H. barclayana*. In 1847, Nees again treated both species; however, he included the type of *H. insularis* under a new combination, *H. scorpioides*, based on *Justicia scorpioides* L. The type of *J. scorpioides* is now

regarded as belonging to *Dicliptera* A. L. Juss. (Daniel 1989), a rather distant relative of *Henrya* in the Odontoneminae (Daniel 1986). Bentham and Hooker (1876) did not recognize *Henrya* and claimed that the genus consisted of a single species linked to *Tetramerium* Nees through an intermediate species, *T. polystachyum* Nees. Hemsley (1882) transferred *Henrya scorpioides* to *Tetramerium* and listed *H. barclayana* as a synonym. Lindau (1895) also treated *Henrya* as a synonym of *Tetramerium* in his influential monograph of the family. Baillon (1891) described the monotypic *Solenoruellia*, the type of which conforms to *Henrya*.

During the 55 years following Hemsley's treatment in 1882, six taxa pertaining to what is here recognized as *Henrya* were described in either *Henrya* or *Tetramerium*. Standley (1926) did not treat either genus in his monumental study of the ligneous flora of Mexico. Happ circumscribed and revised both *Tetramerium* and *Henrya* in 1937. In his treatment of the latter, he recognized 20 species and one variety. These consisted of the original species of Bentham and Nees (i.e., *H. barclayana* and including both *H. insularis* and *H. scorpioides* as separate taxa), five of the six taxa described subsequent to the work of Nees and prior to his own, and 12 species and one variety described as new. Happ (1937) made new combinations for two species originally described in *Tetramerium*. Gibson (1974) had reservations about, but largely followed, Happ's taxonomy in her treatment of *Henrya* in Guatemala. Daniel (1984) echoed Gibson's reservations, noted that *H. insularis* and *H. scorpioides* likely represented a single species, and described a new species in the genus.

#### INTRA-FAMILIAL RELATIONSHIPS

Nees (1847) included *Henrya* in his "suborder" Echmatacantheae, tribe Dicliptereae along with four other genera, including *Tetramerium*, with representatives in America. Among other characters, the genus was distinguished by having a fused involucre surrounding each flower and two seeds on retinacula that separate from the base of the capsule wall. Until Happ's (1937) monograph of the two genera, most systematists after Nees united *Henrya* and *Tetramerium* (see discussion of intrafamilial relationships of *Tetramerium* in Daniel, 1986). Happ (1937) noted the close relationship between the two genera but recognized *Henrya* on the basis of numerous characters, including: coalescence of the bractlets, two (vs. four ovules), and pubescent seeds. In the classificatory scheme of Bremekamp (1965), *Henrya* would be included in the subfamily Ruellioideae, tribe Justicieae, subtribe Odontoneminae. It has been shown to be allied with the morphologically and geographically similar assemblage of *Anisacanthus* Nees, *Aphanosperma* T. F. Daniel, *Carlowrightia* A. Gray, *Mexacanthus* T. F. Daniel, *Mirandea* Rzedowski, and *Tetramerium* (Daniel et al. 1984, Daniel 1986, 1988). *Henrya* and *Tetramerium* share several attributes (e.g., relatively large bracts and/or bractlets that conceal the calyx and separation of the septa from the capsule wall) that distinguish them from related genera.

My studies confirm the separation of *Henrya* and *Tetramerium*. *Henrya* appears to be a monophyletic lineage defined, in a cladistic sense, by at least two apomorphies: partial coalescence of the bractlets into an involucre and broad colpi of the pollen. These features are unique among the assemblage of Odontoneminae listed above. The genus can be distinguished from *Tetramerium* by the following couplet:

Bractlets fused along one side from base to near apex, forming an involucre; seeds 2 (rarely 1 by abortion) per capsule; pollen with colpi broad, much exceeding diameter of ora; lower-central lobe of corolla more or less flat with troughlike keel in center which partially encloses filaments only; leaf abscission occurring at base of petiole so that petiolar stubs are absent after abscission.

*Henrya*.

Bractlets fused, if at all, only at base for a distance up to 1 mm, not forming an involucre; seeds 4 (rarely fewer by abortion) per capsule; pollen with colpi narrow, not exceeding diameter of ora; lower-central lobe of corolla conduplicate, mostly enclosing stamens and style; leaf abscission occurring along petiole 0.1–2 mm from base so that petiolar stubs remain after abscission.

*Tetramerium*.

## MORPHOLOGY

*Habit.* Plants of *Henrya* vary in habit from sprawling, weak-stemmed herbs to robust, erect shrubs up to a meter or more in height. *Henrya tuberosperma* is always an erect shrub, whereas considerable variation exists in habit among individuals of *H. insularis*. This variation appears to have a genetic basis. Plants grown in a greenhouse from seed of *Daniel* 4072 and *Sanders et al.* 2613, both low and sprawling (i.e., with stems reclined for much of their length but ascending distally) herbs in their native habitats, retain the habit of their parents (Fig. 1a). Likewise, progeny of *Daniel & Bartholomew* 5027, an erect shrub in the wild, retains the habit of its parent when grown in the same greenhouse setting (Fig. 1b).

After germination, shoots arise from a slender taproot that soon becomes woody in texture. Additional roots subsequently arise near ground level resulting in a fibrous root system. An enlarged (up to 13 mm in diameter), sometimes somewhat contorted, portion of the stem at or near ground level becomes woody and likely serves as a caudex.

Plants of *H. insularis* grown in a greenhouse under more or less constant conditions of temperature and moisture lived for three years before being discarded. This persistence, the woody nature of the older stems and roots, and



FIG. 1. Habit variation in *Henrya insularis* cultivated at the San Francisco Conservatory of Flowers. a. *Sanders et al.* 2613. b. *Daniel & Bartholomew* 5027. Scale bar = 6 cm.

evidence of new and leafy growth from stems of the previous season on herbarium specimens indicate that herbs of *H. insularis* can have a perennial duration. It is not known whether plants in their native habitats persist primarily as perennial herbs or whether most individuals represent new plants from seeds.

The young stems are green and often have some maroon coloration at or near the nodes. The internodes are vertically banded with numerous, usually darker colored, striations. In cross section, the younger internodes vary from subterete to quadrate-alate. The older stems of *H. insularis* remain green or eventually the epidermis becomes coarse and gray, white, or light brown in color. In *H. tuberculosperra* the epidermis of the younger stems very soon becomes coarse and reddish or dark brown, obscuring the striations. The coarse epidermis of both species exfoliates from the older stems in thin, papery sheets. The older stems obtain diameters up to 8 mm.

*Leaves.* Leaves of *Henrya* are opposite and decussate. They usually consist of a well-defined petiole and blade. Petioles are canaliculate on the adaxial surface and vary in length from 2 to 78 mm. They are usually considerably shorter than the blades they subtend, however, in some individuals, especially those with broadly ovate to subcirculate blades, their length approaches or even equals that of the blades. Abscission occurs at the base of the petiole, without leaving a persistent petiolar stub. The blades are membranaceous, simple, and entire. Laminar shape and size are variable in both species. The margins vary from flat to undulate; the latter condition often results in a crenate appearance. Venation, like that of other members of Odontoneminae, is brochidodromous with up to five orders of veins readily observable on the abaxial surface. The major veins protrude conspicuously from the abaxial surface of the blade.

Happ (1937) placed considerable emphasis on characters of the leaf (e.g., pubescence, petiole length, blade outline, and venation) in defining species. During my studies, it became evident that these features vary on a seasonal basis (see Phenology). For example, *Daniel & Bartholomew 5027*, collected in full flower at the height of the dry season in southern Mexico, has very small leaves with few veins and abundant glandular trichomes. Plants grown in a greenhouse from seed of this collection initially had considerably larger leaves with more veins and mostly eglandular trichomes. By the time flowering had reached a peak, the greenhouse plants had dropped the large leaves and resembled their wild parent. Following flowering, a new flush of large, mostly eglandular leaves reappeared. Similarly, *Darrow & Haskell 2214* was collected in Arizona in October, 1944. This sterile specimen has large leaves and mostly eglandular trichomes. It was not recognized as *Henrya* until a fertile collection with considerably smaller leaves and abundant glandular trichomes was collected from the same locality in June of 1978.

*Inflorescence.* Inflorescences of *Henrya* consist of axillary and terminal spicate axes which together comprise a leafy, terminal panicle. The spicate axes are undoubtedly reduced thyrses (i.e., indeterminate main axes bearing determinate lateral axes). A thyrses, or various modifications by reduction of it, is common throughout the family. In *Henrya*, the determinate lateral axes (i.e., dichasia) are usually reduced to a single sessile flower subtended by two partially fused bractlets. These reduced dichasia, or involucre flowers, are sessile or subsessile (i.e., borne on a peduncle up to 2 mm long), solitary in the axil of a bract, and occur singly or paired at the inflorescence nodes. Occasionally, further development of the dichasia occurs with secondary bractlets forming in the axils between the flower and the primary bractlets (i.e., within the involucre). The secondary bractlets are reduced

in size and fused for only a short distance (ca. 1 mm) along one side. Typical flowers originate from within these secondary bractlets and emerge through the opening in the primary bractlets.

Happ (1937) often used the density of the spikes (i.e., the relative length of the internodes) in distinguishing species. Because internode length within the spikes usually decreases distally, it was consistently measured at or near the midpoint of the spike in my studies. Although spike density was found to have a genetic basis among individuals with long and individuals with short internodes grown for several generations in a greenhouse, it does not appear to correlate well with other characters.

The proximal bracts sometimes intergrade with the distal leaves. For consistency, only bracts (=cauline bracts sensu Happ) at or near the midpoint of the spikes were scored for characteristics in my studies. In all but a few specimens, the bracts are rather inconspicuous and exceeded in size by the bractlets. In those specimens conforming to *H. gualanensis*, the bracts are large and usually overtop the bractlets. The bracts have a short mucro borne at the apex or near it (i.e., arising from the abaxial surface a very short distance from the apex). A midvein is evident or prominent on the abaxial surface and 2 (to 4) lateral veins are commonly visible as well. The lateral veins arise from the base of the bract and are more or less parallel to the midvein.

The bractlets (=involucral bracts sensu Happ) are the single most characteristic feature of *Henrya*. Happ (1937) used features of the bractlets in defining most of the taxa he recognized and they thus play a dominant role in his key to species. They occur as pairs in the axils of, and oriented at right angles to, the bracts. Individual bractlets vary from oblanceolate to obovate and are concavoconvex with the two concave surfaces facing one another. The two bractlets of a pair are homomorphic and fused along that portion of their margins adjacent to the rachis (i.e., their adaxial margins) from the base to near the apex. Along their abaxial margins they are fused for only about 1 mm at the base. Because of the concave nature of the bractlets, the unfused edges meet, thereby forming a three dimensional obovoid involucre within which the flower bud develops and from which the mature flower emerges. The bractlets possess a usually conspicuous, straight mucro at or near their apex. The location of the mucro varies from apical (i.e., situated directly on and continuous with the apical margin of the bractlets) to dorsal (i.e., arising from the abaxial surface below the apex). It is useful to distinguish those dorsal mucros that are situated at a distance up to 0.3 mm from the apex (i.e., subapical) from those situated 0.3 to 1.2 mm from the apex (i.e., remote). Some variation of the direction in which the mucro points is evident among specimens of *Henrya*. Apical and remote mucros are generally erect (i.e., point directly upward), whereas subapical mucros are commonly somewhat divergent (i.e., point backward). Although the veins of the bractlets are often obscure on their outer surfaces, they are usually conspicuous on the inner surfaces. Five to seven prominent, more or less parallel veins traverse the length of each bractlet. Numerous cross-veins connect these primary veins.

*Flower.* The calyx is small, texturally thin, and completely enveloped by the subtending bractlets. Some of its functions are likely assumed by the bracteolar involucre. The fused basal portion of the calyx forms a short, cuplike tube. There are five triangular to lance-subulate to subulate lobes that are usually subequal in length. The posterior (i.e., adjacent to the rachis) lobe is usually reduced in size with respect to the other four lobes.

The mature corolla protrudes through the unfused side of the bracteolar

involucre in a more or less horizontal orientation. It consists of a cylindrical basal tube and a bilabiate limb. It varies in color from white to cream, often with yellow on one or both lips, or may be entirely yellow. The upper lip is marked with maroon, purple, yellow, and/or white nectar guides which vary in extent and colors. For example, *Sanders et al.* 2613 has a subcirculate patch (ca. 1 mm in diameter) of purple partially outlined and streaked with maroon in a dark yellow band on a pale yellow upper lip. In *Daniel & Butterwick* 3274, a white subcirculate patch (ca. 1 mm in diameter) is outlined in maroon in a broad, dark yellow band that is flanked by radiating maroon lines on a white upper lip. The nectar guides on the cream-colored upper lip of *Daniel & Bartholomew* 5027 consist solely of a broad, dark yellow band flanked by radiating maroon lines. All three collections are treated as *H. insularis* in this study. The upper lip varies from obovate to spatulate and comprises two nearly completely fused corolla lobes. It is shallowly bifid at the apex. The lower lip consists of three prominent lobes fused, if at all, only for a very short distance near their bases. The two lateral lobes are obovate and similar to one another in length. The lower-central lobe differs from the lateral lobes by its greater width and central keel. The keel, a trough about 0.5 mm deep running the length of the otherwise flat lower-central lobe, partially encloses the staminal filaments during anthesis. In other members of the Odontoneminae with corollas similar to those of *Henrya* (e.g., *Tetramerium* sect. *Tetramerium* and *Carlowrightia* sect. *Pseudopapilionaceae*) the lower-central lobe is conduplicate, enclosing the stamens and style during anthesis. The lobes are imbricate in bud with the lower-central lobe external and enveloping most of the others.

Corollas of *Henrya* are thin in texture and, unless carefully pressed, often are not well preserved on herbarium specimens. The corollas on many specimens are so shriveled and wrinkled that their shape and size is not apparent. For example, the best preserved corollas of *Sanders et al.* 2613 measure up to 12 mm in length, whereas carefully pressed corollas from plants cultivated from seeds of this collection vary from 14 to 16 mm in length.

The androecium consists of two stamens emerging from the corolla at or near the mouth of the tube. They can extend up to several millimeters beyond the distal tip of the lower-central lobe. The filaments are white and proximally scabrous with downward pointing, eglandular trichomes. They curve upward distally, raising the anthers slightly above the level of the lower-central lobe of the corolla. They are geniculate in the developing bud but straighten at the onset of anthesis. The anthers are bithecal with maroon (or yellowish) thecae. The thecae are parallel and equally inserted or very slightly superposed on the filament. They are subequal in length with one up to 1.4 times longer than the other. Each theca is rounded to subacute at both apex and base. Pollen of *Henrya* is prolate and tricolporate (Fig. 2). The grains vary in shape from ellipsoid to hour-glass shaped and are 1.2 to 3.4 times longer (i.e., polar diameter) than wide (i.e., equatorial diameter) in wet preparations. The colpi are broad, much exceeding the diameter of the centrally positioned, circular ora, and elliptic in outline. Both colpi and ora are covered with wartlike tubercles. The colpi are flanked on each side by a very narrow pseudo-colpus. The intercolpal surfaces are reticulate.

The gynoecium consists of a bicarpellate, superior ovary, a compound style, and two short stigma lobes. The ovary contains four ovules and sits atop a fleshy nectar disc. The style is white and filiform. Like the filaments, it is geniculate in bud but straightens as soon as the bud opens. Where it emerges from the mouth of the corolla tube, the style is oriented roughly parallel to the lower-central lobe of the

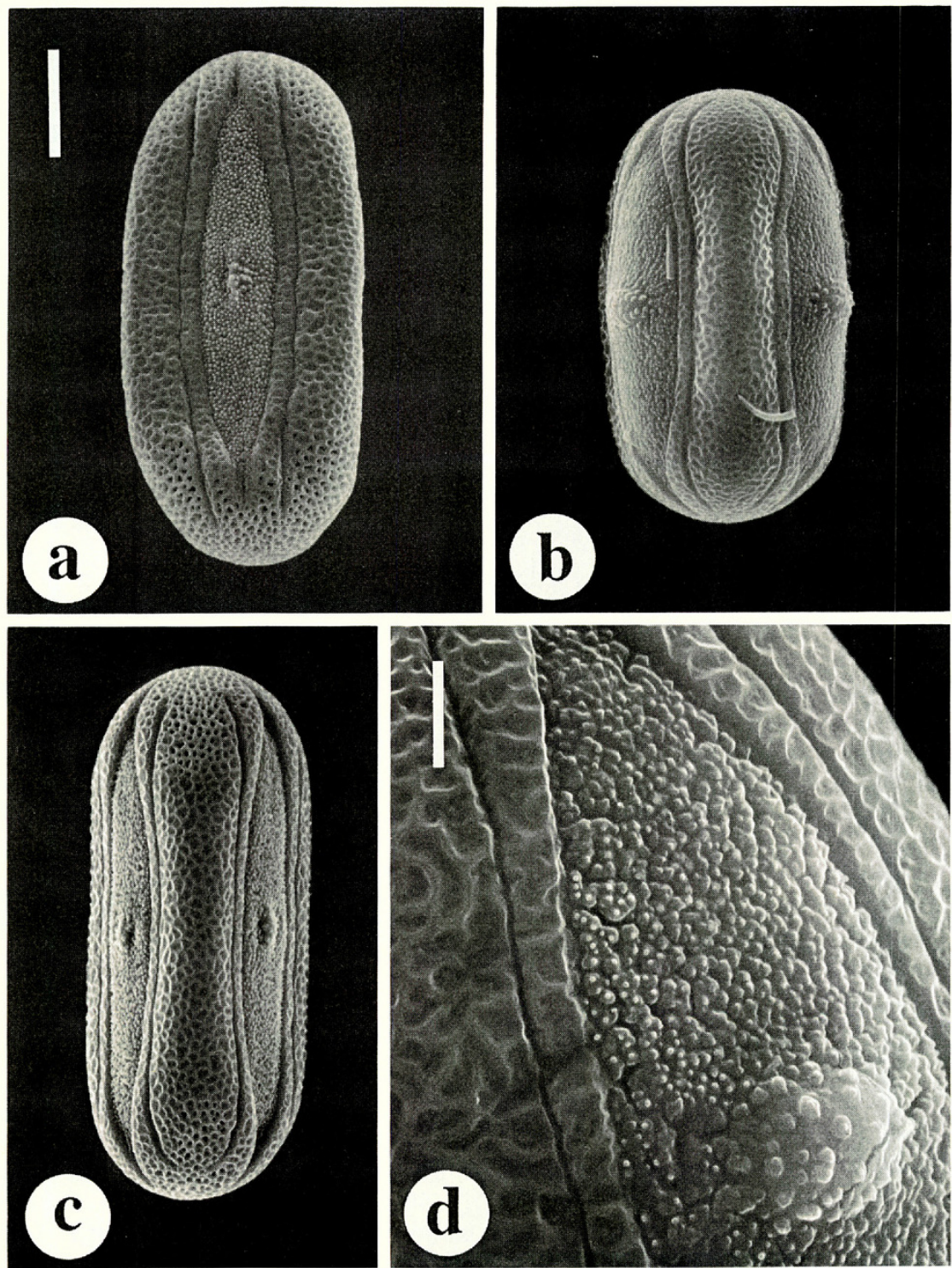


FIG. 2. Pollen of *Henrya*. a. *H. insularis* (Daniel 4731), colp view. b. Pollen of *Henrya* removed from *Lepidanthrax* visitor to plants of Daniel & Bartholomew 4822. c. *H. tuberculosperra* (Daniel 4868), intercolpal view. d. *H. insularis* (Daniel & Bartholomew 4822), enlargement of portion of colpus and os. Scale: for a–c, bar = 11.5  $\mu$ m; for d, bar = 3  $\mu$ m.

corolla. The distal portion, however, curves upward, bringing the stigma lobes to a position level with, but extended slightly beyond, the anthers.

*Capsule and seeds.* Following fertilization the ovary matures into an indurate, two-valved, loculicidal capsule. The capsule is green when immature but turns light brown before dehiscing. It consists of a solid stipe and a subspherical to broadly

ellipsoidal, chambered head that contains the seeds. The head can be slightly shorter than, equal to, or slightly longer than the stipe. It is terminated by a short, solid, and pointed beak. Upon dehiscence, the two valves of the capsule split apart, opening the bracteolar involucre along the unfused side and sometimes tearing it along the fused side. Two hooklike retinacula are borne along the septa (1 per septum) near the base of the head. The septa, with the attached retinacula, break slightly from the inner capsule wall on dehiscence.

Although there are four ovules per ovary, a maximum of two seeds develop in each capsule. Occasionally only one seed develops. The mature seeds (Fig. 3) are brown, often mottled with a darker brown or black, and subcirculate to broadly elliptic in outline. Characters of the seed provide the primary means for distinguishing the two species of *Henrya*. The light colored, immature flat seed surface of both species is covered with stout tubercles. In both species the flat surface of the mature seed is relatively smooth or somewhat bumpy with low, rounded protrusions (Fig. 3b, e). These protrusions appear to be the remains of the tubercles. The convex surface and margin of seeds of *H. insularis* are covered with flexuose-appressed, hygroscopic trichomes (Fig. 3a, c). When moistened, these become erect and radiate from the seed surface. In seeds of *H. tuberculosperma*, the convex surface and margin are covered with stout, branched or barbed tubercles (Fig. 3d, f).

*Vesture and cystoliths.* Trichomes can occur on the vegetative and reproductive shoots, calyces, filaments, capsules, and seeds of individuals of *Henrya*. They are unbranched. Both glandular and eglandular trichomes are present in the genus. The eglandular trichomes consist of from 1 to 12 uniseriate cells and taper to a pointed tip. They vary in orientation from appressed to retrorse to flexuose to straight to antrorse. The flexuose-appressed trichomes on seeds of *H. insularis* are hygroscopic. The glandular trichomes consist of a straight to flexuose stalk with an apical, multicelled gland. They can be absent or so dense as to render a surface viscid. The viscid shoots of most individuals of *Henrya* emit a strong odor, especially when touched. It appears that exudate from the glands is responsible for this odor, which is not present on the eglandular growth of otherwise viscid individuals (see Phenology). The odor has been variously described by collectors as skunklike, mephitic, musty, and fetid. To my sense of smell, the odor is similar or identical to that described for various species of *Tetramerium* (Daniel 1986), i.e., somewhat lemony or citruslike. Some of the variation in pubescence utilized by Happ to distinguish species was found to have a seasonal basis in my studies (see Phenology).

Surfaces of both vegetative and reproductive shoots are covered with inconspicuous or prominent cystoliths. These are greenish or whitish, straight to slightly curved, and linear formations that are especially evident on glabrous or glabrate surfaces. They vary from 0.2 to 0.4 mm in length and usually taper at one end. They sometimes give the appearance of appressed eglandular trichomes.

### CHROMOSOME NUMBERS

Daniel et al. (1984) reported a chromosome number of  $n=18$  for *H. insularis* (Daniel 2055, ASU). Recent counts (Daniel et al., 1990) of  $n=18$  for *H. tuberculosperma* (Daniel & Bartholomew 4868, CAS) and four additional individuals of *H. insularis* (Daniel 3363, CAS; Daniel & Bartholomew 4814, CAS; Daniel & Bartholomew 5027gh, CAS; Sanders et al. 2613gh, CAS), representing three different forms of the species, further document this number in the genus. All close

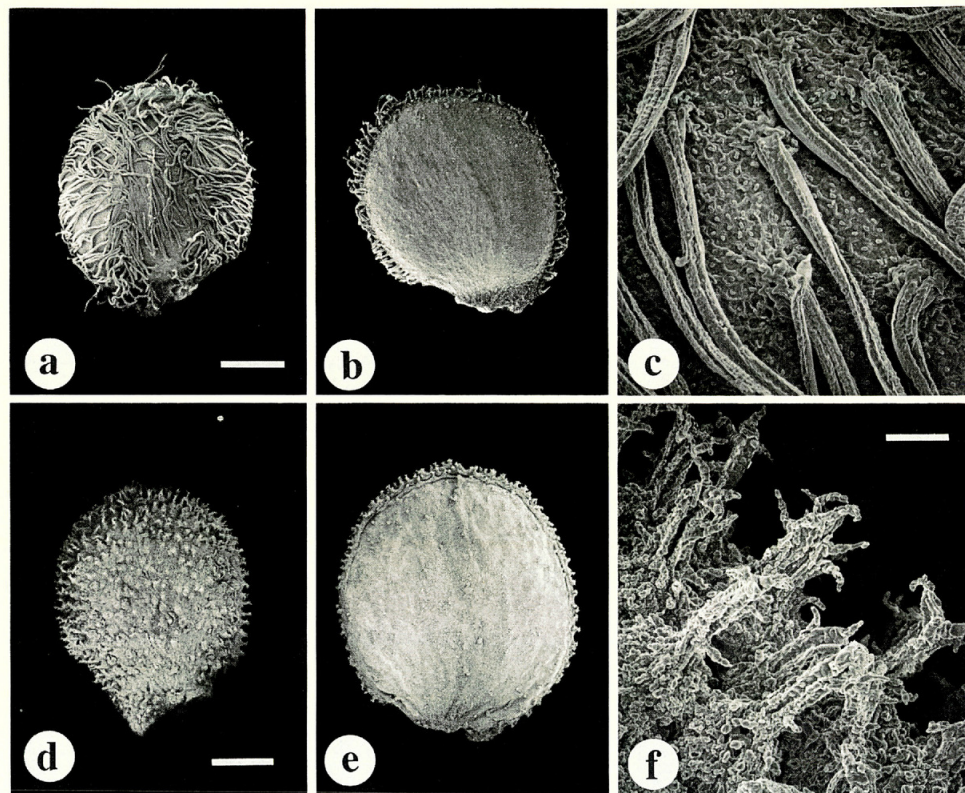


FIG. 3. Seeds of *Henrya*. a. *H. insularis* (Daniel 2055), convex surface. b. *H. insularis* (Daniel 2055), flat surface. c. *H. insularis* (Daniel 2055), enlargement of hygroscopic trichomes on convex surface. d. *H. tuberculosperma* (Daniel 2123), convex surface. e. *H. tuberculosperma* (McVaugh 11946), flat surface. f. *H. tuberculosperma* (Daniel 2123), enlargement of tubercles near margin. Scale: for a, b, bar = 0.5 mm; for c, f, bar = 43  $\mu$ m; for d, e, bar = 0.7 mm.

relatives of *Henrya* in the Odontoneminae have also been shown to have chromosome complements of  $n=18$  (Daniel et al. 1984; Daniel et al., 1990). Like their counterparts in other genera of Odontoneminae, chromosomes of *Henrya* are small (Fig. 4).

### DISTRIBUTION AND HABITATS

The geographic range of *Henrya* extends from about latitude  $31^{\circ} 20'N$ , longitude  $111^{\circ} 07'W$  in the southwestern United States (southern Arizona) southward and eastward through much of Mexico and northern Central America to about latitude  $9^{\circ} 56'N$ , longitude  $84^{\circ} 31'W$  in western Costa Rica (southern Alajuela). [The only collection from Costa Rica (Alajuela: Desamparados de San Mateo, Quirós 671, F) was studied and cited by Durkee (1986) but has been misplaced and was not seen by me.] The plants are usually found in regions of tropical deciduous or subdeciduous, oak, and pine-oak forest at elevations from 30 to 2000 meters. Plants occur on rocky cliffs and slopes, in flat areas, and in a variety of naturally and artificially disturbed habitats (e.g., along streams, fences, and roadsides) on igneous (e.g., basalt) and sedimentary (e.g., limestone) substrates.

The distribution of *H. insularis* is similar to that of *Tetramerium nervosum* Nees in the northern hemisphere. These two weedy species often grow near one another. For the most part, *H. insularis* occurs in dry regions, although, unlike *T. nervosum*, it does not occur in desert scrub. The Mexican distribution of *H. insularis* corresponds rather well with regions of nondesertic dry forest as shown on Rzedowski's (1978) map of the vegetation of Mexico. The isolated occurrences of *H. insularis* in Yucatán and central Veracruz correspond to the isolated regions of tropical dry forest there. The altitudinal range of *H. insularis*, like that of *T. nervosum*, extends from the relatively low dry forests upward in elevation into the oak and eventually the pine-oak zones. In Central America occurrences of *H. insularis* are concentrated along the Pacific coast in the dry or mixed evergreen forests there. *Henrya tuberculosperma* is known only from west-central Mexico, within the range of *H. insularis*, where individuals can grow within a few meters of *H. insularis* (e.g., Daniel 2121 and Daniel 2123 from Jalisco).

Happ (1937: 542) noted that the "center of geographic distribution, as well as the relative abundance of individuals, appears to be located in west-central Mex-

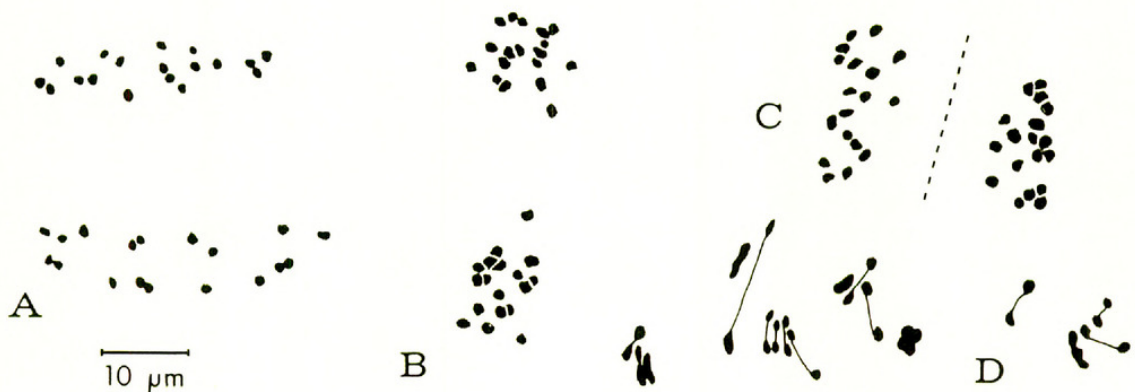


FIG. 4. Camera lucida drawings of meiotic chromosome preparations of *Henrya*. a. *H. insularis* (Sanders et al. 2613gh), telophase I. b. *H. tuberculosperma* (Daniel & Bartholomew 4868), telophase II (only  $\frac{1}{2}$  of cell shown). c. *H. insularis* (Daniel & Bartholomew 4814), telophase I (halves of cell shown artificially close). d. *H. insularis* (Daniel & Bartholomew 5027gh), metaphase I.

ico." Indeed, this is the only region in which both of the species recognized in my study occur. More forms of *H. insularis* occur in west-central Mexico (i.e., southern Sinaloa through Guerrero) than in any other portion of the range of the species. This same region is particularly rich in species of *Tetramerium* and in forms of *T. nervosum*.

## PHENOLOGY

Flowering and fruiting of *Henrya* occurs during the tropical dry season. Although plants have been collected in flower from October into June, the vast majority of flowering collections were made in February, March, and April, the months corresponding to the height of the dry season in Mexico and Central America (Shelford 1963). Observations from herbarium specimens and plants grown in a greenhouse reveal that flowering individuals often lack most or all of their foliage. Late in the flowering season new vegetative growth often arises from the woody stems, sometimes overtopping the withering reproductive growth. The pubescence of these flushes of new stems and leaves is sometimes mostly eglandular, unlike that of the flowering shoots. These vegetative shoots can persist into the next flowering season during which time many or most of the leaves will fall away.

## REPRODUCTIVE BIOLOGY

Aspects of the reproductive biology of *H. insularis* were studied in the field and greenhouse. Procedures similar or identical to those described for study of *Carlowrightia* (Daniel 1983), *Tetramerium* (Daniel 1986), and *Aphanosperma* (Daniel 1988) were utilized. cursory observations were made on populations of *Henrya* throughout Mexico. A population north of Guadalajara, Jalisco, (Daniel & Bartholomew 4822) was studied in more detail in March of 1987. At this site, floral visitors were photographed and captured, nectar samples were obtained, distances between anthers and stigmas were measured, and presence of pollen on stigmas was determined with a hand lens (10 $\times$ ). Seeds from three Mexican populations (Daniel 4072 from Sinaloa, Daniel & Bartholomew 5027 from Chiapas, and Sanders et al. 2613 from Sonora) were gathered and subsequently grown in a greenhouse at the San Francisco Conservatory of Flowers from 1987 to 1989. These plants, indicated by the field numbers followed by "gh", were utilized for additional observations and measurements, compatibility experiments, and cross-pollinations. In order to test for self-compatibility, autogamy, and autonomous agamospermy, 10 flowers of each plant were marked for each of the following treatments: control (no treatment), emasculation (anthers excised prior to dehiscence), and self-pollination (stigmas manually dusted with pollen). Fruit-set was used as a measure of fertilization. Seeds resulting from self-pollinations were grown to maturity. Pollen stainability of both greenhouse generations was determined by examining the contents of one anther from each of five flowers in aniline blue in lactophenol stain (methodology outlined by Daniel 1983). Artificial cross-pollinations among plants representing the three populations cited above were attempted in the following manner: unopened anthers were removed from flower buds prior to anthesis; during anthesis, pollination of the emasculated flowers was effected by rubbing dehiscent anthers from unmanipulated flowers across their stigmas several times; the cross-pollinated flowers were tagged and subsequently monitored for fruit-set. Ten pollinations were made

for each of the three crosses and reciprocal crosses. Mature fruits were removed and allowed to dehisce in small envelopes in order to capture the seeds. Seeds were subsequently grown to maturity. Pollen stainability was determined for the cross-pollinations as described above. Results of the self- and cross-pollinations were compared. Voucher specimens of the parents, self-pollinated progeny, and cross-pollinated progeny are deposited at CAS.

In both the field and the greenhouse, corollas of *Henrya* open in midmorning, by which time or very soon after which the anthers dehisce. No floral fragrances were detected. Prominent nectar guides (i.e., colored markings) are present on the upper lip of the corolla and a relatively small quantity of nectar (see below) is located at the base of the corolla tube. During anthesis the staminal filaments are partially enclosed in the keel of the lower-central lobe of the corolla. They arch upward distally, exposing the anthers. The style extends past the anthers situating the stigma 1–4 mm beyond them. The positioning of the anthers and stigma would appear to prevent autogamy during most of anthesis. It would allow for cross-pollination or geitonogamy by insect visitors transporting pollen which, if approaching the nectar guides, would first contact the stigma and then the anthers when seeking either pollen or nectar. Some autogamy would be likely among otherwise unpollinated flowers as the corollas fall, sometimes bringing the anthers and stigma into contact with each other.

The greenhouse studies confirm that *H. insularis* is self-compatible. Ninety percent of the self-pollinated flowers set fruit (*Daniel 4072gh* =  $\frac{9}{10}$ , *Daniel & Bartholomew 5027gh* =  $\frac{10}{10}$ , *Sanders et al. 2613gh* =  $\frac{9}{10}$ ). The lack of any fruit-set among emasculated flowers reveals that autonomous agamospermy does not occur among these individuals of *H. insularis*. Autogamy appears to be limited with only 16.6% of the control flowers setting fruit (*Daniel 4072gh* =  $\frac{2}{10}$ , *Daniel & Bartholomew 5027gh* =  $\frac{3}{10}$ , *Sanders et al. 2613gh* =  $\frac{1}{10}$ ). Interestingly, all capsules of *Daniel & Bartholomew 5027* resulting from control and self-pollinated flowers aborted prior to maturity. Many other capsules resulting from autogamy of unmarked flowers in this individual likewise aborted whereas others attained maturity.

During anthesis numerous visitors to flowers of *H. insularis* were noted at the site north of Guadalajara. These included halictid bees, butterflies, and bombyliid flies. Both pollen and nectar were gathered. Bombyliid flies were the most prevalent visitors. They exhibited territorial behavior by chasing away other bombyliids as well as other insect visitors. Six individuals (all females) representing three undetermined species of *Lepidanthrax* Osten-Sacken were captured at this site. Pollen identical to that of *H. insularis* (Fig. 2b) was removed from the bodies of three individuals (representing two of the species). Pollination efficiency by insects at this site is high; of 10 stigmas examined with a hand lens, all had adhering pollen.

Nectar quantity was determined for the three individuals of *H. insularis* grown in a greenhouse using the technique of Baker (1979). Five spots were measured for each of the following: *Daniel 4072gh* ( $\bar{x}$ =0.194  $\mu$ l), *Daniel & Bartholomew 5027gh* ( $\bar{x}$ =0.204  $\mu$ l), and *Sanders et al. 2613 gh* ( $\bar{x}$ =0.281  $\mu$ l). An average nectar volume per flower of *H. insularis* based on this sampling is 0.226  $\mu$ l. This quantity is similar to, although slightly greater than, the average amount of nectar produced by species of *Tetramerium* sect. *Tetramerium* ( $\bar{x}$ =0.19  $\mu$ l), which have similar flowers that are pollinated by similar insects, including *Lepidanthrax*. It is considerably greater than the average amount of nectar recorded for *Carlowrightia arizonica* A. Gray

( $\bar{x}$ =0.09  $\mu$ l, six samples from a population in southern Arizona) which also has similar flowers that are pollinated by *Lepidanthrax* (Daniel 1986).

Nectar sugar composition of four individuals of *H. insularis* (Daniel 4072gh, Daniel & Bartholomew 4822, Daniel & Bartholomew 5027gh, and Sanders et al. 2613gh) was analyzed by Dr. C. E. Freeman. The mean percentages (range, standard deviation) of fructose, glucose, and sucrose for this species are 23.4 (13.4, 5.4), 45.3 (23.5, 8.5), and 31.2 (28.1, 10.7) respectively. In all greenhouse samples, glucose was the most abundant nectar sugar. In Daniel & Bartholomew 4822, sucrose was the dominant sugar. The overall dominance of glucose in most samples of *Henrya insularis* is similar to that found in species of *Tetramerium*, *Carlowrightia*, and *Aphanosperma* with similar flowers.

Because flowers of *H. tuberculosperra* are very similar to those of *H. insularis*, it is likely that pollination biology of the former species parallels that of the latter.

Artificial intraspecific crosses among the three collections of *H. insularis* cited above were all successful in producing at least some fruit (table 1). The most successful crosses in terms of percent fruit-set resulted when Daniel & Bartholomew 5027gh served as the female parent. Abortion among maturing capsules resulting from cross-pollinations of this collection was high, just as it was for many capsules resulting from self-pollinated flowers. Abortion (i.e., a decrease in size accompanied by a change from green to brown coloration prior to maturity) was encountered only when this collection served as the female parent. It is perhaps noteworthy that, in spite of the abortion evident among crosses involving Daniel & Bartholomew 5027gh, crosses with this collection resulted in greater fruit-set than crosses between the two morphologically and geographically more similar collections from northwestern Mexico.

Seeds resulting from the cross-pollinations were viable and readily germinated. Pollen stainability of the resulting progeny (table 2) was similar to that of both the parental plants and the  $F_1$  generation of self-pollinated individuals in most instances.

Although *H. insularis* and *H. tuberculosperra* can occur in close proximity to one another, no evidence of hybridization between them was found.

TABLE 1. Percentages of capsule formation of parents and intraspecific crosses of *Henrya insularis*. (Maternal parent listed first in crosses.)

Collection(s)	Percent capsule formation
Parents (control)	
Daniel 4072gh	20
Daniel & Bartholomew 5027gh	30 (100% abort)
Sanders et al. 2613gh	0
Parents (self-pollinated)	
Daniel 4072gh	90
Daniel & Bartholomew 5027gh	100 (100% abort)
Sanders et al. 2613gh	80
Intraspecific Crosses	
4072gh $\times$ 5027gh	80
4072gh $\times$ 2613gh	20
5027gh $\times$ 4072gh	100 (40% abort)
5027gh $\times$ 2613gh	90 (44% abort)
2613gh $\times$ 4072gh	30
2613gh $\times$ 5027gh	40

TABLE 2. Percentages of pollen stainability of parents, F<sub>1</sub> generation of self-pollinated parents, and progeny of intraspecific crosses of *Henrya insularis*. (Maternal parent listed first in crosses.)

Collection(s)	Percent Pollen Stainability
Parents	
<i>Daniel 4072gh</i>	74
<i>Daniel &amp; Bartholomew 5027gh</i>	76
<i>Sanders et al. 2613gh</i>	97
F <sub>1</sub> generation of self-pollinated parents	
<i>Daniel 4072gh</i>	99
<i>Daniel &amp; Bartholomew 5027gh</i>	99
<i>Sanders et al. 2613gh</i>	93
F <sub>1</sub> generation of intraspecific crosses	
<i>4072gh</i> × <i>5027gh</i>	85
<i>4072gh</i> × <i>2613gh</i>	87
<i>5027gh</i> × <i>4072gh</i>	47
<i>5027gh</i> × <i>2613gh</i>	98
<i>2613gh</i> × <i>4072gh</i>	84
<i>2613gh</i> × <i>5027gh</i>	62*

\* This figure includes both fully (31%) and partially (31%) stained pollen. The partially stained pollen resembles unstained grains by its generally smaller size. Partially stained pollen was not observed in other samples.

## INTRAGENERIC RELATIONSHIPS

Happ (1937) provided an intuitive diagram showing perceived interspecific relationships of *Henrya*. Unfortunately, the diagram was presented without explanation and the relationships depicted do not always concur with the discussions of relationships in the text. For example, in his discussion of *H. yucatanensis*, Happ (1937) noted that the species is most closely allied to *H. insularis*, yet his diagram shows it linked only to *H. scorpioides*.

The two species recognized in my study are undoubtedly closely related. Using *Tetramerium* as an outgroup, character polarity can be established for two (i.e., seed pubescence and mature stem color) of the three primary characters used to distinguish these two species in the key. Calyx length in *Tetramerium* is too variable to permit polarity determination of this character in *Henrya*. Seeds of *H. tuberculosperma* are glabrous and have a similar superficial ornamentation to some species of *Tetramerium*. The hygroscopic trichomes on seeds of *H. insularis* are not encountered in *Tetramerium* and therefore likely represent a derived condition in *Henrya*. The reddish or dark brown color of mature stems in *H. tuberculosperma* likewise appears to be a derived feature. Both species can thus be defined by autapomorphies.

## TAXONOMY

**Henrya** Nees ex Benth, Bot. voy. Sulphur t. 49. 1845.—TYPE: *Henrya insularis* Nees ex Benth.

*Solenoruellia* Baillon, Hist. pl. 10: 445. 1891.—TYPE: *Solenoruellia galeottiana* Baillon.

Erect or spreading perennial herbs or shrubs up to 2 m tall, arising from a woody base. Young stems green, often with maroon at or near nodes, subterete to quadrate-alate in cross section, striate with numerous longitudinally parallel, usually dark bands, variously pubescent with glandular (rarely absent) and eglandular (often absent) trichomes or, rarely, glabrous, the trichomes, when present, usually evenly distributed or sometimes concentrated in 2 vertical lines. Leaves opposite, subsessile to petiolate; petioles canaliculate on adaxial surface, detaching at junction with stem; blades simple, membranaceous, lance-ovate to ovate to broadly ovate to elliptic to subcirculate, attenuate to acute to rounded to truncate to cordate at base, acute to acuminate at apex, the margin entire, flat to undulate. Inflorescences of axillary and terminal, stout to lax, spicate axes up to 5 dm long, these forming leafy, terminal panicles; flowers borne in reduced dichasia (often reduced to a single flower) in axils of bracts, each flower subtended by 2 bractlets; dichasia sessile or short pedicellate, solitary or paired at nodes. Bracts sessile, linear to lanceolate to elliptic to oblanceolate to obovate, submucronate to mucronate at or near apex. Bractlets isomorphic, oblanceolate to obovate, concavoconvex, fused from base to near apex along side adjacent to rachis, rounded to acute at apex, mucronate with straight, apical or dorsal, erect or divergent projection; secondary bractlets, if present, much reduced, 1.5–5 mm long. Calyx 5-lobed; tube shorter than lobes; lobes triangular to subulate, homomorphic or heteromorphic with posterior lobe reduced in size. Corolla of 5 partially fused petals, white, cream, or yellow with maroon, purple, yellow, and/or white markings on upper lip, glabrous; tube subcylindric to cylindric, 0.8–1.3 mm in diameter, shorter than limb; limb bilabiate, the upper lip obovate to spatulate, bifid, the lower lip trilobate with lateral lobes obovate and lower-central lobe obovate to broadly obovate and keeled. Stamens 2; filaments emerging at or near mouth of corolla tube, white, proximally scabrous; anthers bithecal, the thecae maroon or yellowish, parallel, equally inserted or slightly superposed, subequal, rounded to subacute at apex and base; pollen prolate, tricolporate with broad colpi, hexapseudocolpate, 59–83  $\mu\text{m}$  long (polar diameter), 20–34  $\mu\text{m}$  wide (equatorial diameter) (measured in wet preparations), the exine reticulate. Disc fleshy, ca. 0.5 mm high. Ovary ovoid, ca. 1 mm long, 4-ovulate; style filiform, white, glabrous; stigma bilobed with triangular lobes. Capsule stipitate, glabrous, pubescent over entire external surface, or pubescent only near apex, the trichomes eglandular and/or glandular; head subspherical to broadly ellipsoidal, terminating in a short (up to 0.5 mm) beak; retinacula 1 per valve, hooklike; septa separating from capsule wall just below retinacula upon dehiscence. Seeds 2 (or 1 by abortion) per capsule, planoconvex, subcirculate to subelliptic in outline, the flat surface smooth to bumpy, the convex surface and margin either pubescent with hygroscopic trichomes or covered with stout, branched or barbed tubercles.

The name *Henrya* honors Aimé Constant Fidèle Henry (1801–1875), artist, lithographer, and co-author with T. F. L. Nees von Esenbeck of *Das System der Pilze*.

#### KEY TO THE SPECIES OF HENRYA

1. Seeds glabrous, the convex surface and margin covered with stout, conical tubercles bearing barbs; mature stems reddish or dark brown; calyx 2.5–5 mm long. 1. *H. tuberculosperma*.

1. Seeds pubescent, the convex surface and margin covered with slender, flexuose-appressed, hygroscopic trichomes lacking barbs; mature stems green, gray, white, or light brown; calyx 0.8–2.5 mm long. 2. *H. insularis*.

1. ***Henrya tuberculosperma*** T. F. Daniel, Madroño 31: 88. 1984.—TYPE. MEXICO. Jalisco: 24–29 km SW of Autlán, 9 Apr 1951, *McVaugh 11946* (holotype: MICH!; isotypes: MEXU! US!).

Shrub to 1.5 m tall. Stems subquadrate to quadrate, the younger internodes nearly glabrous or evenly pubescent with straight, glandular trichomes 0.05–0.2 mm long and flexuose, eglandular trichomes (sometimes sparse) 0.2–0.5 mm long, the latter type trichomes sometimes becoming more prominent and antrorse to retrorse and often restricted to 2 lines on mature internodes, the mature internodes reddish or dark brown and sometimes glabrate. Leaves subsessile to petiolate; petioles to 36 mm long; blades lance-ovate to ovate to ovate-elliptic, 17–87 mm long, 9–55 mm wide, 2–3.8 times longer than wide, rounded to acute to truncate at base, acute to acuminate at apex, the margin flat, the surfaces pubescent with straight to antrorse, eglandular (and occasional glandular trichomes on younger leaves) trichomes 0.05–0.9 mm long. Branches of inflorescence (rachises) evenly pubescent with straight, glandular trichomes 0.05–0.5 mm long; dichasia sessile or borne on peduncles up to 1 mm long, opposite at the inflorescence nodes, 3.5–9 mm distant near midspike; bracts near midspike linear to lanceolate to lance-elliptic, 4–7 mm long, 0.9–1.6 mm wide, mucronate at apex, pubescent like rachis and occasionally with a few scattered, straight to flexuose, eglandular trichomes to 0.3 mm long as well, the midvein prominent and 2 lateral, submarginal veins usually evident; bractlets oblanceolate to obovate, 9–14 mm long, unfused for 3–4.5 mm along side adjacent to rachis, pubescent like bracts, the mucro apical, 0.2–0.8 mm long, erect. Calyx 2.5–5 mm long, pubescent with glandular and eglandular trichomes 0.05–0.3 mm long, the lobes subulate, 1–4.5 mm long; corolla cream to pale yellow with a white eye outlined with red veins on upper lip, 14–19 mm long, the tube 5–7 mm long, 1.1–1.3 mm in diameter, the upper lip spatulate, 9–12 mm long, 2.5–4.5 mm wide, the lower lip 10–13 mm long with lateral lobes obovate, 9–12 mm long, 5–5.5 mm wide, and lower-central lobe obovate, 8.5–11 mm long, 5–7 mm wide; stamens 9–10 mm long, the thecae maroon, 1.7–2.2 mm long, subequal with one 0.2 mm longer than the other; style 13–15 mm long, stigma lobes 0.2–0.5 mm long. Capsule 7–11 mm long, pubescent over entire surface or mostly near apex with straight to flexuose, glandular and eglandular trichomes 0.05–0.3 mm long, the stipe 3–5 mm long, the head 4–6 mm long, 3–4 mm in diameter, the retinacula 1.5–1.7 mm long. Seeds subelliptic in outline, 2–3.4 mm long, 1.7–2.6 mm wide, 0.7 mm thick, the flat surface more or less smooth or with scattered tubercles on immature seeds, these sometimes remaining as more or less rounded bumps on mature seeds, the convex surface covered with retrorsely barbed tubercles with swollen bases (sometimes with mostly only swollen bases present forming a bumpy surface on mature seeds), the margin with tubercles up to 0.2 mm long. Fig. 5.

Distribution and habitats. Western Mexico from southern Sinaloa through north-central Guerrero (Fig. 6). The plants occur on slopes and in stream valleys at elevations from 750 to 1500 m in regions of tropical deciduous and subdeciduous forest (with *Inga*, *Lysiloma*, and *Brosimum*), oak forest, and pine-oak forest. Plants are frequently encountered in disturbed situations. Abundance varies from uncommon to very abundant.

Phenology. Flowering and fruiting from February through April.

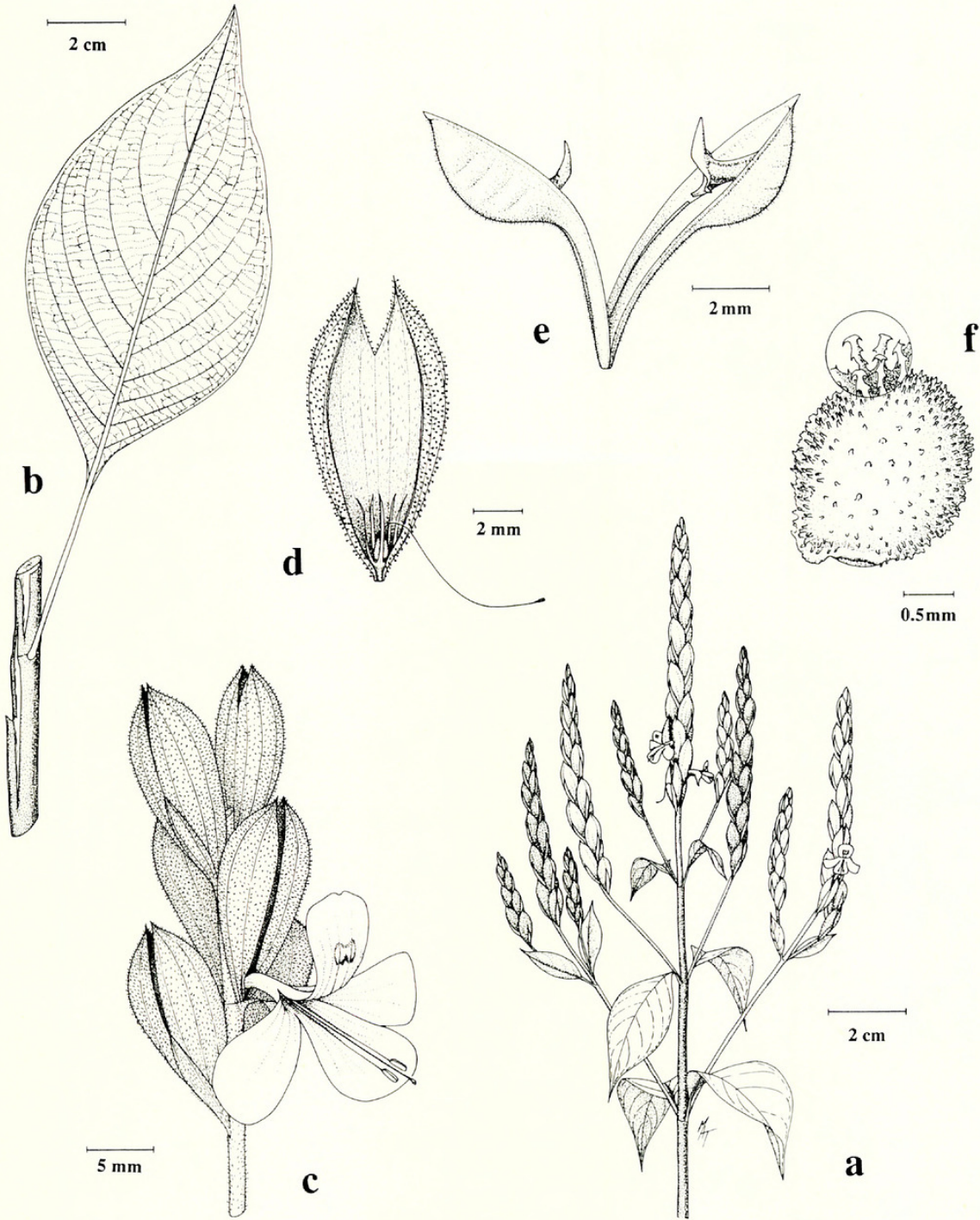


FIG. 5. *Henrya tuberculosperma*. a. Habit of distal portion of plant. b. Segment of shoot from proximal portion of plant. c. Portion of inflorescence with flower. d. Bractlets opened to show calyx and gynoecium. e. Capsule. f. Seed with enlargement of tubercles. (a, f, Lott *et al.* 1978; b, Daniel & Bartholomew 4868; c, Daniel 2123; d, Marin M76-79; e, McVaugh 11946.)

ADDITIONAL SPECIMENS EXAMINED. MEXICO. Guerrero: Taxco, Abbott 101 (ENCB, GH), 523 (ENCB).—Jalisco: 23.7 mi NE of La Huerta and 11.9 mi SE of turn to Ahuacapan S of Autlán on Hwy 80, Daniel 2123 (CAS); along Hwy 80 between Autlán and La Huerta, 10.8 mi S turn to Ahuacapan, Daniel & Bartholomew 4868 (CAS, K, MEXU); Mpio. Talpa, entre Cumbre del Tejamanil y Caule, González T. 97 (MICH); 21.2 km al SW de Atenquique, Lott *et al.* 1978 (ASU, CAS, MEXU).—Sinaloa: 15 mi NE of Concordia, Marin M76-79 (ARIZ).

In addition to the diagnostic characters noted in the key, several character tendencies are sometimes useful for further distinguishing *Henrya tuberculosperma*

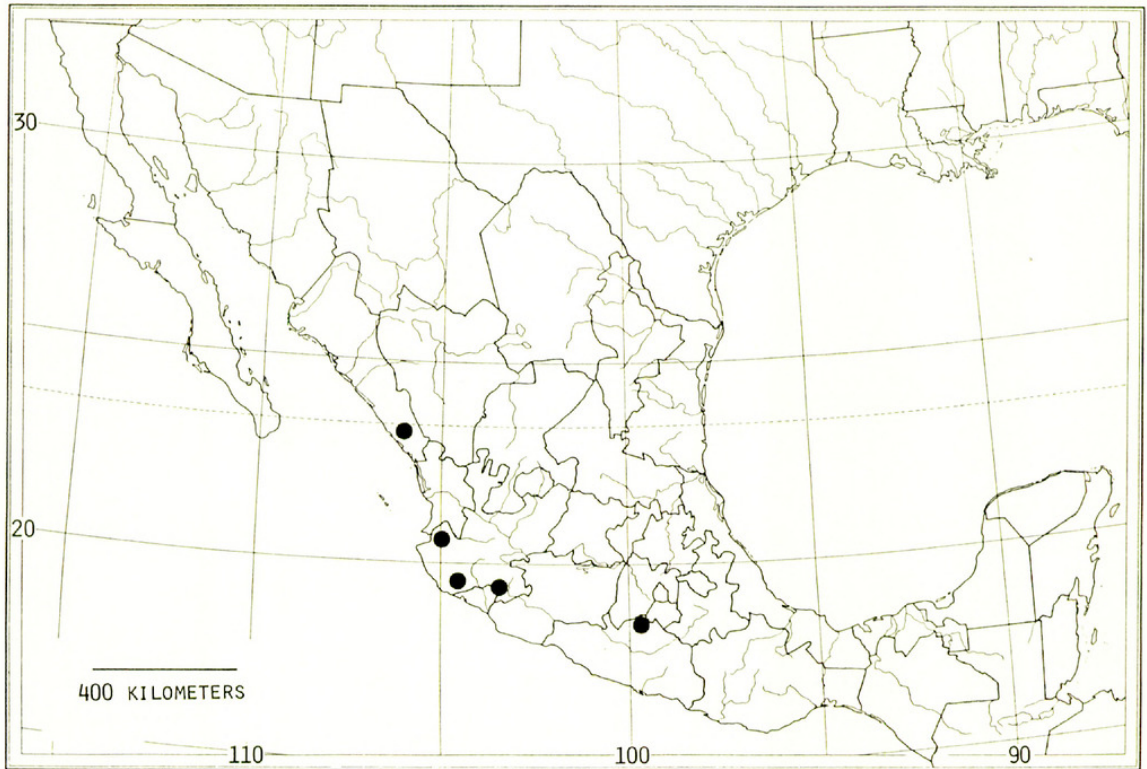


FIG. 6. Distribution of *Henrya tuberculosperma*.

from most specimens of *H. insularis*. *Henrya tuberculosperma* is always an erect shrub with relatively dense spikes (i.e., with the bractlets always imbricate near midspike) and with larger and more pubescent capsules containing slightly larger seeds than usually encountered in *H. insularis*.

Some variation was noted among collections of *H. tuberculosperma*. In *Marin M76-79*, the stems are glabrous or nearly so and the capsular trichomes are mostly glandular. In the other collections, the stems are conspicuously pubescent and the capsular trichomes are primarily eglandular.

**2. *Henrya insularis*** Nees ex Benth, Bot. voy. Sulphur t. 49. 1845.—TYPE: plate 49 of Benth's *The botany of the voyage of H.M.S. Sulphur*.

*Henrya barclayana* Nees in Benth, Bot. voy. Sulphur 149. 1846.—TYPE: MEXICO. Colima: Manzanillo Bay, without date, *Barclay s.n.* (holotype: K!).

*Henrya costata* A. Gray, Proc. Amer. Acad. Arts 21: 406. 1886. *Tetramerium costatum* (A. Gray) Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 47. 1895.—TYPE: MEXICO. Chihuahua: near Batopilas, Aug–Nov 1885, *Palmer 211* (holotype: GH!; isotypes: K! LE! MEXU! NY! PH! US!).

*Solenoruellia galeottiana* Baillon, Hist. Pl. 10: 445. 1891.—TYPE: MEXICO. Veracruz: without specific locality, 1840, *Galeotti 7039* (holotype: P!).

*Henrya imbricans* J. D. Smith, Bot. Gaz. (Crawfordsville) 16: 198. 1891.—TYPE: GUATEMALA. Amatitlán: Laguna Amatitlán, *Smith 1923* (holotype: US!; isotypes: G! GH! K! NY! PH! US!).

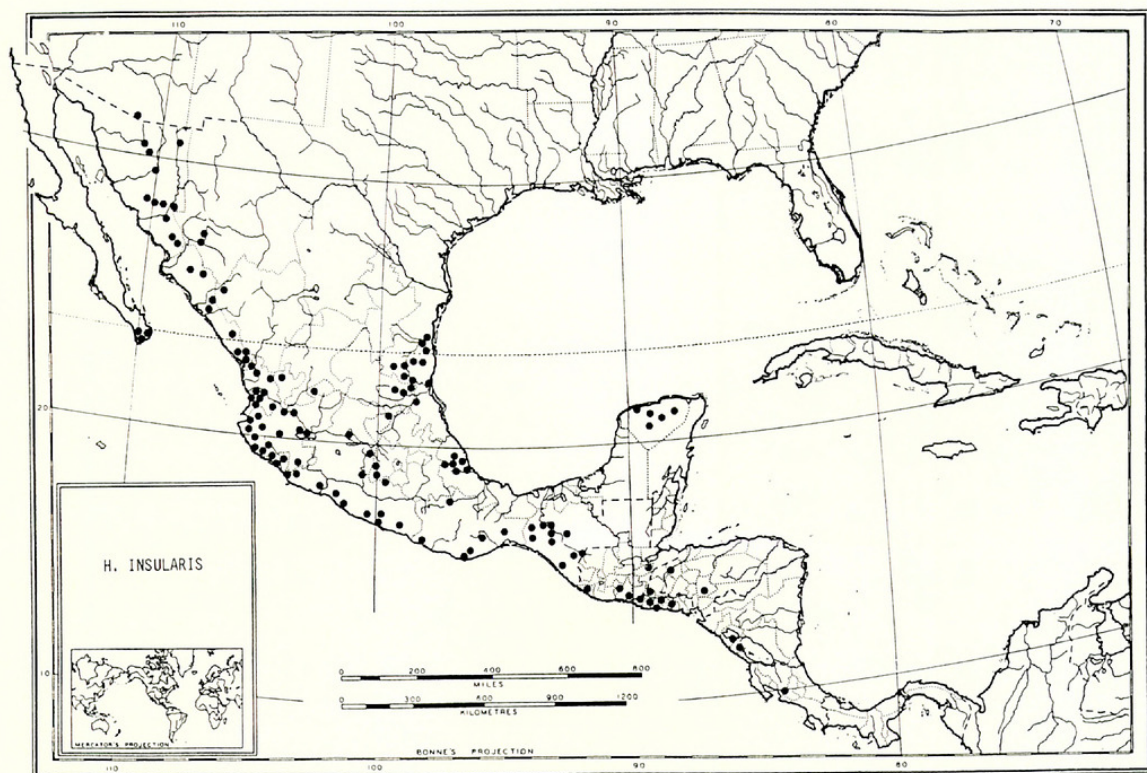
*Henrya grandifolia* Fernald, Bot. Gaz. (Crawfordsville) 20: 537. 1895.—TYPE: MEXICO. Sinaloa: Esquinapa, Jan 1895, *Lamb 505* (holotype: GH!).

*Henrya costata* var. *glandulosa* T. Brandegee, Zoe 5: 171. 1903.—TYPE: MEX-

- ico. Baja California Sur: Cape Region, Santa Anita, 1901, *Purpus* 266 (lectotype, designated here: UC!; isolectotypes: ARIZ! MO! US!).
- Tetramerium gualanense* Robinson & Bartlett, Proc. Amer. Acad. Arts 43: 58. 1907. *Henrya gualanensis* (Robinson & Bartlett) Happ, Ann. Missouri Bot. Gard. 24: 553. 1937.—TYPE: GUATEMALA. Zacapa: Gualán, 18 Jan 1905, *Deam* 397 (holotype: GH!; isotype: MICH!).
- Tetramerium flavum* Eastwood, Proc. Amer. Acad. Arts 44: 608. 1909. *Henrya flava* (Eastwood) Happ, Ann. Missouri Bot. Gard. 24: 550. 1937.—TYPE: MEXICO. Durango: San Ramón, 21 Apr–18 May 1906, *Palmer* 75 (holotype: GH!; isotypes: F! GH! K! MO! NY! UC! US!).
- Henrya brevifolia* Happ, Ann. Missouri Bot. Gard. 24: 547. 1937.—TYPE: MEXICO. Sonora: Las Durasnillas, 18 May 1892, *Brandege* s.n. (holotype: UC!; isotypes: DS! GH! NY! PH! US!).
- Henrya konzattii* Happ, Ann. Missouri Bot. Gard. 24: 560. 1937.—TYPE: MEXICO. Oaxaca: Distr. Pochutla, Cerro de Apango de Hualulco, 20 Apr 1917, *Konzatti, Reko & Makrinus* 3152 (holotype: US!; isotype: MO!).
- Henrya donnell-smithii* Happ, Ann. Missouri Bot. Gard. 24: 563. 1937.—TYPE: GUATEMALA. Santa Rosa: Río de Los Esclavos, Feb 1893, *Heyde & Lux* 4559 (holotype: MO!; isotypes: F! G! GH! K! NY! US!).
- Henrya laxa* Happ, Ann. Missouri Bot. Gard. 24: 557. 1937.—TYPE: MEXICO. Guerrero: Acapulco and vicinity, Oct 1894–Mar 1895, *Palmer* 575 (holotype: MO!; isotypes: F! GH! K! POM! UC! US!).
- Henrya longipes* Happ, Ann. Missouri Bot. Gard. 24: 549. 1937.—TYPE: EL SALVADOR. San Salvador, 1925, *Calderón* 2283 (holotype: F!; isotype: US!).
- Henrya mephitica* Happ, Ann. Missouri Bot. Gard. 24: 562. 1937.—TYPE: MEXICO. Jalisco: San Sebastián, trail to Las Mesitas, 17 Mar 1927, *Mexia* 1864 (holotype: CAS!; isotypes: NY in part! US!).
- Henrya ortegana* Happ, Ann. Missouri Bot. Gard. 24: 552. 1937.—TYPE: MEXICO. Sinaloa: Sind. San Juan, San Ignacio, Mar 1931, *Ortega* 6868 (holotype: MO!; isotypes: CAS! F! MIN!).
- Henrya pilosa* Happ, Ann. Missouri Bot. Gard. 24: 556. 1937.—TYPE: MEXICO. Colima: near Manzanillo, 2–18 Mar 1891, *Palmer* 1330 (holotype: US!; isotypes: GH! K! NY! US!).
- Henrya puberula* Happ, Ann. Missouri Bot. Gard. 24: 559. 1937.—TYPE: GUATEMALA. Amatitlán: Amatitlán, Feb 1928, *Morales R.* 911 (holotype: F!; isotype: US!).
- Henrya reticulata* Happ, Ann. Missouri Bot. Gard. 24: 566. 1937.—TYPE: EL SALVADOR. Ahuachapan: vicinity of Ahuachapan, 9–27 Jan 1922, *Standley* 20221 (holotype: US!; isotypes: GH! NY!).
- Henrya rupicola* Happ, Ann. Missouri Bot. Gard. 24: 564. 1937.—TYPE: MEXICO. Jalisco: San Sebastián, trail to Las Mesitas, 17 Mar 1927, *Mexia* 1864 (holotype: MO!; isotypes: A! DS! F! GH! MICH! MIN! NY in part! UC!).
- Henrya scorpioides* var. *latifolia* Happ, Ann. Missouri Bot. Gard. 24: 556. 1937.—TYPE: MEXICO. Veracruz: Barranca de Panoaya, Dec 1919, *Purpus* 8495 (holotype: MO!; isotypes: GH! NY! UC! US!).
- Henrya yucatanensis* Happ, Ann. Missouri Bot. Gard. 24: 551. 1937.—TYPE: MEXICO. Yucatán: vicinity of Ixamal, Jan–May 1895, *Gaumer* 368 (holotype: MO!; isotypes: A! CAS! DS! F! GH! K! LE! MICH! NY! PH! UC! US!).

Bushy, erect or sprawling perennial herb or shrub to 2 m tall. Stems subterete to quadrate to quadrate-alate, the younger internodes evenly pubescent with straight, glandular (sometimes inconspicuous, rarely absent) and straight to subflexuose to antrorse, eglandular (sometimes inconspicuous or absent) trichomes 0.05–1.1 mm long or rarely nearly glabrous, the mature internodes green, gray, white, or light brown, becoming glabrate or pubescent mostly with eglandular trichomes (sometimes concentrated in 2 vertical lines). Leaves petiolate; petioles to 78 mm long; blades ovate to elliptic to subcirculate, 12–155 mm long, 5–90 mm wide, 1.1–2.9 (–4) times longer than wide, attenuate to acute to rounded to truncate to cordate at base, acute to acuminate at apex, the margin flat to undulate, the surfaces of young leaves usually pubescent like young internodes, the surfaces of mature leaves usually pubescent with mostly eglandular trichomes (often restricted to major veins) or glabrate. Branches of inflorescence (rachises) pubescent with a mixture of straight to subflexuose glandular (sometimes inconspicuous, rarely absent) and eglandular (sometimes absent) trichomes 0.05–1 mm long; dichasia sessile or borne on peduncles up to 2 mm long, solitary or opposite at inflorescence nodes, 2.5–23 mm distant near midspike; bracts near midspike linear to elliptic to oblanceolate to obovate, 2–12 mm long, 0.5–6 mm wide, mucronate at or near apex, pubescent like rachis, the midvein usually prominent and 2 (–4) lateral, submarginal veins often evident; bractlets elliptic to oblanceolate to obovate, 6–13 mm long, unfused for 1–5 mm along side adjacent to rachis, acute to rounded at apex, pubescent with glandular (rarely absent) and eglandular (sometimes absent) trichomes, the trichomes usually like those of the rachis, the abaxial surface sometimes becoming purplish and venose, especially toward apex, the mucro (rarely absent) 0.1–2.2 mm long, apical to dorsal (i.e., 0.05–1.2 mm distant from the apex), erect or divergent. Calyx 0.8–2.5 mm long, the abaxial surface pubescent with straight to flexuose, glandular (sometimes absent) and eglandular trichomes 0.05–0.3 mm long, the lobes triangular to lance-subulate to subulate, 0.5–2 mm long; corolla cream to yellowish with maroon, purple, and yellow markings on upper lip, 8.5–18 mm long, the tube 2.5–8 mm long, 0.9–1.3 mm in diameter, the upper lip spatulate to obovate-spatulate, 4.5–10.5 mm long, 1.5–4 mm wide, the lower lip 6–12.5 mm long with lateral lobes obovate, 5–12 mm long, 2.5–6.5 mm wide, and lower-central lobe obovate to widely obovate, 5.5–11 mm long, 3.5–9 mm wide; stamens 6–12 mm long, the thecae yellowish to maroon, 1.2–2.5 mm long, subequal with one 0.2–0.6 mm longer than the other; style 7.5–17 mm long, stigma lobes 0.1–0.4 mm long. Capsule 4.5–9.5 mm long, glabrous or pubescent near apex (occasionally over entire surface) with straight to flexuose, eglandular and/or glandular trichomes 0.05–0.2 mm long, the trichomes often sparse, the stipe 1.5–4.5 mm long, the head 2.7–5 mm long, 1.7–3.6 mm in diameter, the retinacula 0.7–1.8 mm long. Seeds subcirculate to elliptic in outline, 1.6–2.8 mm long, 1.3–2.2 mm wide, 0.6–1 mm thick, the flat surface smooth to bumpy, the convex surface covered with dense, appressed, flexuose, hygroscopic trichomes 0.3–0.7 mm long.

Distribution and habitats. Southwestern United States (Arizona) southward throughout Mexico, Guatemala, El Salvador, Honduras, and Nicaragua to western Costa Rica (Fig. 7). Flats and rocky slopes, from about 30 to 2000 meters in regions of tropical deciduous forest (with *Acacia*, *Bursera*, *Caesalpinia*, *Ceiba*, *Cordia*, *Gliricidia*, *Haematoxylon*, *Ipomoea*, *Lemaireocereus*, *Lysiloma*, *Pachycereus*, *Prosopis*, *Pseudobombax*, and *Tabebuia*), tropical subdeciduous forest (with *Brosimum*), evergreen forest (with *Pinus* and *Quercus*), and riparian forests (with *Celtis*, *Ficus*, *Guazuma*, *Platanus*, *Salix*, and *Taxodium*). The species is common, or

FIG. 7. Distribution of *Henrya insularis*.

often a dominant element, in second growth and disturbed situations (e.g., fencerows and roadsides).

**Phenology.** Flowering and fruiting from October through June although peak flowering occurs from February through April.

**Ethnobotany.** *Bye 3514* notes that a tea from the herbage is used to treat malaria. *Chemin B. 104* records, "El cocimiento tomado contra la diarrea." Labels on several collections note that this species is eaten as a pasture plant by domesticated animals in Mexico. The following local names have been noted for *H. insularis*: "hierba del toro" or "yerba del toro" or "yerba de toro" (*Bye 3514* and 3600 from Chihuahua, *González Ortega 85* and 6868 from Sinaloa, *Pennington 323* from Chihuahua, and *Martínez 1979*), "hierba del zopilote" (*Soto Nuñez 469* from Michoacán), "k'an-sahil-xiu" (a Mayan name from Yucatán, *Martínez 1979*), "mayorquilla" (*Puga 44* from Jalisco), "ohasin (?)" (*Rea 1052* from Sonora), "rama del toro" (*Pérez 20* from Sinaloa), "siáctica" (*Gentry 8057* from Chihuahua), "hierba del olotito" (*Chemin B. 104* from San Luis Potosí), and "s-kokmak bibiogam" (*Rea 1052* from Sonora).

**REPRESENTATIVE SPECIMENS.** EL SALVADOR. Ahuachapán: vicinity of Ahuachapán, *Standley & Padilla V. 2582* (F); 2743 (F). Chalatenango: along Tejutla creek, hwy to La Palma, *Molina R. & Montalvo 21584* (F). La Libertad: ca. 2 km W of La Libertad, *Wilbur et al. 16365* (F, MICH, MO). San Salvador: vicinity of San Salvador, *Standley 20449* (GH, NY, US), 23103 (NY, US). San Vicente: vicinity of Ixtepeque, *Standley 21424* (GH, NY, US); vicinity of San Vicente, *Standley & Padilla V. 3358* (F), 3583 (F, UC, US). Sonsonate: vicinity of Izalco, *Standley 21801* (NY, US).—GUATEMALA. Guatemala: Lake Amatitlán between Santa Catarina and Tsanjuju, *Artamanoff s.n.* (F); Laguna (Amatitlán), *Kellerman s.n.* (MEXU, MICH); Amatitlán, *Kellerman s.n.* (US); El Cerrito, between La Laguna and Amatitlán, *Pittier 125* (US); near Amatitlán, *Standley 61327* (F), 61345 (F); 61364 (F, US); vicinity of Lago de Amatitlán, *Standley 89445* (F). Retalhuleu: near Nueva Linda, halfway between Retalhuleu and Champerico, *Standley 88432* (F, US). Department undetermined: *Kellerman 5215* (US); *Heyde 687*

(US); *Friedrichsthal* s.n. (K); Morazán, *Johnston* 1160 (F).—HONDURAS. Morazán: Río Guarabuequi, terrenos de los indios Xicaques de la Montaña de La Flor, *Molina* R. 3017 (F, GH). Santa Bárbara: on hwy to Copán at double S curve, *Dickson* 1443 (US).—MEXICO (see the appendix for additional collections examined that are not listed here). Aguascalientes: Mpio. Calvillo, Arroyo de Malpaso, *de la Cerda* L. & *García* R. 602; Mpio. Calvillo, Malpaso, Guerra 58 (MEXU). Baja California Sur: Sierra de Laguna, *Brandege* s.n. (GH, PH, UC); Cape Region, trail above la Burrera, *Moran* 7454 (ARIZ, CAS, DS, ENCB, GH, MEXU, UC, US); west slope of Sierra de la Victoria between La Burrera and La Laguna, *Thomas* 7931 (ARIZ, CAS, DS, GH, MEXU, MICH, UC, US). Chiapas: Road to El Sumidero, 20 km N of Tuxtla Gutiérrez, *Breedlove* 9047 (DS, F, MICH, US); Mpio. Chiapa de Corzo, El Chorreadero, 5.6 mi E of Chiapa de Corzo along Hwy 190, *Breedlove* 9102 (DS, ENCB, F, MICH, US), *Laughlin* 179 (DS, ENCB, F, US); Mpio. Arriaga, 13 km N of Arriaga along Hwy 195, *Breedlove* & *McClintock* 23734 (DS, LL, MEXU, MICH, MO, NY, RSA); Mpio. Cintalapa, logging road to Cerro Baul and Colonia Figaroa, *Breedlove* & *Smith* 31276 (DS, MEXU); 16 mi W of Tuxtla Gutiérrez, *Carlson* 2063 (F, MICH, NY, UC), Cañón El Sumidero, near Km 19 in vicinity of Mirador El Roblar, *Daniel* & *Bartholomew* 5027 (CAS, K, MEXU, MICH); Mpio. Venustiano Carranza, Rancho Nacimiento between Chiapilla and San Lucas, *Laughlin* 283 (DS, MICH, US); Escuintla, *Matuda* 133 (MEXU, MICH, US); Fraylesca, near Siltepec, *Matuda* 5216 (F, MEXU, MO); Cañada Carretera Villa Flores, SE Suchiapa, *Miranda* 6831 (MEXU). Chihuahua: Mpio. Batopilas, S side of Barranca de Batopilas, W of La Bufa near Arroyo Bakosiachi, *Bye* 3600 (CAS); Mpio. Batopilas, Arroyo Guimivo, between Batopilas and Guimivo, *Bye et al.* 9228 (ASU, MEXU, TEX); Sierra Charuco, Arroyo Hondo, *Gentry* 8057 (ARIZ, DS, MEXU, MICH, UC, US). Colima: Mpio. Ixtlahuacán, ca. 8 km. al NE de Las Conchas, camino a Las Tunitas, *Lott* & *Magallanes* 924 (ASU, CAS, ENCB, MEXU, MO); 15–25 km NW of Santiago, *McVaugh* 23028 (ENCB, MICH); Manzanillo, *Palmer* 1330a (US). Durango: Corral de Piedra above Río Piaxtla, *Lundell* 13004 (LL, MICH). Guanajuato: Mpio. Valle de Santiago, 5 km S de Charco de Pantoja, *González* L. 42 (CAS, CHAPA, MEXU). Guerrero: Taxco, *Abbott* 101a (GH); along road from Petatlán to Camalotito, 1.0–6.1 mi SW of Camalotito, *Daniel* & *Bartholomew* 4922 (CAS, MO), 4924 (CAS, MEXU, TEX); Distr. Galeana, Atoyac-Mescaltepec, *Hinton* 11217 (GH, K, MICH, NY, US); Distr. Montes de Oca, Vallecitos, *Hinton* 11779 (ARIZ, F, GH, K, MO, NY, UC, US); Mpio. San Luis Acatlán, Atotonilco, a 8 km al NW de Horcasitas, *Martínez* S. *et al.* 3527 (MEXU); Sierra Madre del Sur, Distr. Adama, Temisco, Los Cajones, Río Achotla, *Mexia* 8939 (ARIZ, CAS, F, GH, K, MO, NY, UC, US). Jalisco: vicinity of "Las Canoas," Río Cuale, Puerto Vallarta, *Carter* & *Chisaki* 1180 (GH, MEXU, MICH, TEX, UC); between Tomatlán and Talpa de Allende, ca. 5 mi N of Tomatlán, *Daniel* 2085 (CAS); near Hwy 80, 20.9–23.7 mi NE of La Huerta, *Daniel* 2116 (CAS), 2121 (ASU, CAS), 2124 (ASU, CAS); along road from Tequila to microondas on Volcán Tequila (Montaña Azul), *Daniel* & *Bartholomew* 4789 (CAS, ENCB); along road between Tesistán and San Cristóbal de la Barranca, 3.4 mi S of Río Santiago, *Daniel* & *Bartholomew* 4814 (CAS, K, MEXU, MICH); along Hwy 54, ca. 21 km N of Guadalajara, *Daniel* & *Bartholomew* 4822 (CAS, MO, NY, TEX); between Autlán and La Huerta, ca. 1.2 mi S of summit (Puerto Los Mazos), *Daniel* & *Bartholomew* 4856 (CAS); El Tigre, along Hwy 80, 14.6 mi S turn to Ahuacapan, *Daniel* & *Bartholomew* 4876 (CAS, ENCB); between Tepalcatepec and Tecalitlán, 22.5 mi SE of Jilotlán, *Daniel* & *Butterwick* 3274 (ASU, CAS, MEXU, MICH); Mpio. La Huerta, Est. Biol. Chamela, Camino Antiguo, cerca del Pozo Antiguo, *Lott* 914 (CAS, CHAPA, F, MEXU, TEX); 9–10 km N of La Cuesta, below the pass to Talpa de Allende, *McVaugh* 23382 (ENCB, MICH); roadside between San Sebastián and Las Palmas, *Nelson* 4125 (GH, US); Mpio. Talpa de Allende, base del Cerro Don Pedro, *Palafox* T. 7 (CHAPA, ENCB, MEXU, MICH); vicinity of San Juan Cosalá, N of Lake Chapala, *Puga* 44 (MICH); canyon of Río Santiago, 10 mi N of Guadalajara, *Rinehart* 7312 (LL, MICH, MO); 4 km SE de Puerto Vallarta *Rzedowski* 16586 (CAS, ENCB, MICH). México: Distr. Temascaltepec, Nanchititla, *Hinton* 3410 (GH, K, NY, US); Distr. Temascaltepec, Tejupilco, *Hinton et al.* 5756 (F, GH, K, MO, NY, US); Distr. Temascaltepec, Nanchititla, *Hinton et al.* 7611 (K, US). Michoacán: along Hwy 200, 2.4 mi NW turn to Aguila, *Daniel* & *Bartholomew* 4890 (CAS, MEXU); Km 322 carretera Playa Azul-Arteaga, antes Uruapan, *Germán et al.* 391 (ASU, CAS, ENCB, MEXU); Coalcomán, *Hinton et al.* 13606 (DS, NY, US), 13608 (GH), 13639 (ARIZ, DS, F, MO, NY, US); Distr. Coalcomán, Carmen, *Hinton et al.* 15918 (ENCB, NY, US); Guanoro, 18–19 km SW de Zitácuaro, carr. a Huetamo, *Soto Nuñez* 469 (MEXU, TEX, WIS), *Soto Nuñez* & *D. Ramos* T. 1393 (CAS). Nayarit: Jalisco, *Beechey* (Lay & Collie) s.n. (K); along Hwy 200 between Tepic and Puerto Vallarta, 33 mi S of Tepic, *Croat* 45368 (CAS, MEXU, MO); along Hwy 54 between Hwy 15 and San Blas, ca. 2 mi W of Hwy 15, *Daniel* 2041 (ASU, CAS, K, MEXU, MICH, NY); along Hwy 200 S of Tepic, 7.0 mi S of Compostela, *Daniel* 2055 (ASU, CAS, ENCB, K, MICH, NY); along Hwy 66 from Tepic to Miramar, 1.8 mi E turn to Mecatán, *Daniel* & *Bartholomew* 4731 (CAS, MICH); Acaponeta, Tiger Mine, *Jones* 23049 (F, POM, UC); La Barranca, *Jones* 23188 (MO, POM,

UC); Mpio. El Nayar, El Pinito, 8 km SO de Arroyo Santiago, *Magallanes* 3536 (CAS); Acaponeta, *Rose* 3125 (NY, US); Ixtlán, *Viereck* 1139 (US). Oaxaca: between Pochutla and Summit (near Puerto Angel), *Ernst* 2649 (MEXU, US); "Lacs de Tutepeque", *Galeotti* 510A (GH, NY, UC, US); Distr. Yautepec, ca. 140 km SW (sic) de Oaxaca a Tehuantepec, *Lorence & Cedillo* T. 2992 (CAS, F, MEXU); Tehuantepec, Las Animas, *MacDougall* s.n. (ENCB, F, NY); Distr. Pochutla, Zacatal San Rafael, *Makrinius* 517 (US); Distr. Pochutla, vicinity of Concordia, *Makrinius* 746 (US), 817 (US); Cerro Concordia, *Morton & Makrinius* 2673 (DS, F, K, MICH, PH, US), 2734 (US); Tomellin Canyon, *Pringle* 4634 (GH, K, LE, MEXU, MO, NY, PH, UC, US); Pochutla, Cerro del Machete, *Reko* 6220 (F). Querétaro: Mpio. Pinal de Amoles, La Cuesta, 3 km S de Escanelilla, *Fernández N.* 2380 (MEXU, NY). San Luis Potosí: Mpio. Tamasopo, Rincón de Ramírez, *Chemin B.* 104 (MEXU); Sierra Tanchipa, E edge of El Abra, 6.4 mi E of Cd. Valles on Hwy 110, *Hansen et al.* 3847 (LL, MEXU, MICH, RSA, WIS); Las Palmas, *Pringle* 3506 (F, GH), 5947 (MO); 7699 (ARIZ, F, GH, MICH, US); Km 280 de la carretera S.L. Potosí-Antiguo Morelos, *Rzedowski* 7329 (DS, ENCB, LL, MICH, TEX). Sinaloa: Cañón Tarahumare, below Jolla in Sierra Surotato, *Breedlove* 15615 (DS, ENCB, US); ca. 30 mi E of Culiacán along rd between Presa López Mateos and Tamazula, Dgo., *Breedlove* 24468 (CAS, MEXU, MICH, MO); Microondas El Tule, ca. 3 mi W of Hwy 15 and 7 mi S of Culiacán, *Daniel* 4072 (CAS); Sindicatura de San Javier, San Ignacio, Cerro de la Silla, *Ortega* 85 (MEXU); Balboa, *Ortega* 5128 (US); Mazatlán, *Ortega* 5699 (US); Mpio. Sinaloa de Leyva, Isleta de la Cana de Audon C., Agua Caliente de Zevada, *Pérez* 20 (CAS, CHAPA, ENCB, MEXU, MO); vicinity of Mazatlán, *Rose et al.* 13845 (F, US); Sierra Madre Occidental, along Hwy 40 between La Guayanera and El Cantil, ca. 21 mi NE of Concordia, *Sanders et al.* 4986 (CAS, UC). Sonora: along road between Hwy 16 E of Tonichi and Onavas, 0.5 mi S jct. Hwy 16, *Daniel* 3352 (CAS); along road between Rosario de Tezopaco and Nuri, 7.1 mi S of turnoff to Nuri, *Daniel* 3363 (ASU, CAS); 9 mi from Imuris in Magdalena River canyon, *Ferris* 8783 (DS, US); 16.2 mi E of turnoff to Tonichi along Mex. Hwy 16, *Gallagher et al.* 294 (ASU, CAS, NY); Alamos, Río Fuerte, *Gentry* 2200 (ARIZ, F, GH, K, MEXU, MO, UC, US); Rancho Agrimincor, Río Mayo, *Gentry* 3043 (ARIZ, F, GH, K, MEXU, MO, UC, US); Curohui, Río Mayo, *Gentry* 3639 (ARIZ, F); ca. 4 mi NE of Santa Rosa on road to Yécora, *Lehto & Reeves* L18746 (ASU); Sierra de Alamos, *Rose et al.* 12829 (NY, US); Río Cuchujaqui, ca. 7 mi ESE of Alamos, *Sanders et al.* 2573 (ARIZ, ASU, RSA); NW side of Sierra de Alamos along road from Alamos-Navajoa road at Rancho Las Lomas to Promontorios, *Sanders et al.* 2613 (ASU); 20–25 mi NE of Ures, *Straw* 2118 (RSA, UC); ca. 17 mi SSE of Magdalena in Cerro Cinta de Plata (=Sierra Babiso), *Van Devender* s.n. (ARIZ), *Van Devender et al.* s.n. (ARIZ, NY); 13 mi E of Imuris, *Wiggins* 11665 (DS, MEXU, MICH, TEX, UC, US). Tamaulipas: Sierra de Tamaulipas, Ejido Las Yucas, ca. 40 km NNW of Aldama, *Dressler* 2426 (GH, MEXU, MICH, MO); pass above El Abra, ca. 11 mi S of Cd. Mante, *Fryxell & Magill* 2267 (CAS, ENCB, MICH, MO); Rancho Buenos Aires, outskirts of Ocampo, *Johnston & Crutchfield* 5189 (TEX, MICH, US); Bernal, *Karwinski* 547 (LE); Mpio. Ocampo, 1 km N de Flores Magón, *Medrano & Valiente B.* 12122 (ARIZ, ENCB, MEXU); Soto la Marina, *Viereck* 1061 (US); Tampico, *Viereck* 1087 (US); near Gómez Farías, *Walker* 72030 (ARIZ). Veracruz: 10 km de Tempoal, hacia Panuco, *Chiang* 402 (ENCB, F, K, MEXU, MO); près V. Cruz, *Galeotti* 7028 (G); La Purga, *Greenman* 224 (F, GH, NY, US); Mirador, *Linden* 190 (K, LE, MICH); Mpio. Puente Nacional, Baños de Carrizal, 5 km SE of Emiliano Zapata, *Nee & Taylor* 26612a (ENCB, F, MO, NY); Zacuapan and vicinity, Río de Santa María, *Purpus* 2261 (F, GH, MO, UC, US); Remulatero, *Purpus* 8663 (ARIZ, DS, UC), s.n. (DS, POM, UC); Rancho Remudadero, *Purpus* 11155 (A, DS, F, K, MO, NY, PH, US), 11166 (F, NY, PH), 15235 (A), s.n. (MO); Puente Nacional, *Purpus* 11155 (MO, NY); San Francisco, near Vera Cruz, *Smith* 1330 (F, GH, MICH); Mpio. Dos Ríos, Palo Gacho, Carretera Xalapa-Veracruz, cerca de la desv. Actopán, *Ventura A.* 3032 (DS, ENCB, MICH, TEX); Mpio. Paso de Ovejas, La Pasa, *Ventura A.* 15770 (CAS, MEXU). Yucatán: Thien-Welden Dzibilchaltun Survey, roadside near stele, *Bradburn & Darwin* 1161 (F, MEXU, MO, NY); Silam, *Gaumer* 1712 (F, GH, MO, NY, US); Calotmul, *Gaumer* 1713 (CAS, F, K, LE, US); Colonia San Cosme, *Greenman* 350 (F, GH, NY, US); Izamal, *Greenman* 391 (F, GH); Chichén Itzá, *Paray* 1521 (ENCB, MEXU); ruins of Mayapán, *Seler & Seler* 3875 (F, GH, NY); Izamal, *Seler & Seler* 3922 (F, GH, NY, US).—NICARAGUA. Carazo: vicinity of Jinotepe, *Standley* 8561 (F). Managua: Sierra de Managua, *Garnier* 126 (F), 522 (US). Department undetermined: *Oersted* 46 (K); *Wright* s.n. (GH, US).—U.S.A. Arizona: Santa Cruz Co., Sycamore Canyon near Ruby, *Darrow* 2214 (ARIZ, CAS); Pajarito Mountains, Sycamore Canyon, ca. 4.5 mi S of Hank & Yank Spring, *Toolin* 1 (ARIZ).

Daniel (1989) presented an argument for recognizing Bentham as the author of this species. Plate 49 of Bentham's *The botany of the voyage of H.M.S. Sulphur* is

the only element in the protologue of *H. insularis* and must therefore serve as its type. In the companion text published 13 months after the plate, Nees (1846) cited a Sinclair collection from an "Island off the coast of Veragua" which concurs with the data provided on a specimen in Bentham's herbarium at K. Numerous islands occur near the Pacific coast of Veragua, a name given by Columbus to the western portion of the Isthmus of Panama. *Henrya* is not currently known to occur south or east of the province of Alajuela in Costa Rica. Sinclair's specimen has apically mucronate bractlets, erect mucros, relatively small bracts (3–3.7 mm long and 0.38–0.43 times as long as the bractlets), and sparse glandular and eglandular understory trichomes and sparse glandular overstory trichomes on the bractlets. Plants with this combination of attributes are common in western and southern Mexico and in Yucatán, but are not presently known from Central America. Although the sole collection from Costa Rica is not available for study (see under Distribution above), Durkee (1986) described it as having bractlets with subapical mucros. I therefore question whether the Sinclair specimen of *H. insularis* was indeed collected in Panama. I suspect that it was collected elsewhere during the voyage of *H.M.S. Sulphur*, likely at one of the many localities visited along the Pacific coast of Mexico.

The name *H. scorpioides* has figured prominently in the history of the genus since its introduction by Nees (1847). Although Nees (1847) included the type of *H. insularis* within his circumscription of *H. scorpioides*, Happ (1937) chose to recognize both *H. insularis* and *H. scorpioides*. He treated the latter as having been newly published by Nees and indicated one of the collections cited, *Linden 190*, as the type. It is clear that in 1847 Nees was, in effect, making a new combination for the plant he had earlier described as *H. insularis*. He cited his description and the figure of that species from *The botany of the voyage of H.M.S. Sulphur* as well as the Sinclair collection noted above. He also cited the basionym, *Justicia scorpioides* L., from which his new combination was derived. The type of *H. scorpioides* is therefore that of the basionym, not *Linden 190* or any of the other collections cited by Nees (1847). Daniel (1989) has shown that *J. scorpioides* pertains to a species of *Dicliptera* and the name *H. scorpioides*, the most commonly encountered name on herbarium specimens of *Henrya*, must be excluded from the genus. If *H. scorpioides* sensu Happ were to be accepted as a species, another name would have to be applied to it.

Baillon (1891) described the monotypic genus *Solenoruellia* and noted the two fused "bracteis" which form an involucre around the flower. His brief description conforms well to *Henrya* with the exception of "staminia 4, didynama." Baillon did not cite a collection; however, there is a fragmentary specimen (*Galeotti 7039*) labelled as *S. galeottiana* at P. A label on this specimen notes that the flowers were yellow but neither flowers nor fruits are now present on the specimen. The fragments of *Galeotti 7039*, including bracteolar involucre with subapical mucros, reveal this specimen to be *H. insularis*. The reference to four didynamous stamens is inexplicable.

In his description of *H. costata* var. *glandulosa*, Brandegee did not cite a type or any specific collections from which to choose one. In the introductory comments of his article, he noted that his information was based on plants collected by C. A. Purpus in 1901, himself in 1902, and unspecified collectors in previous years. There are two collections at UC that were in Brandegee's herbarium at the time he described *H. costata* var. *glandulosa*: Purpus 266 and Brandegee s.n. 26 Jan. 1890. Both concur equally with Brandegee's very brief diagnosis. The former collection is chosen as the lectotype, because it is a more fully fertile collection that bears the

name, *H. costata* var. *glandulosa* in Brandegee's handwriting. Brandegee's collection of 1890 lacks fruit, and the label (in Brandegee's hand) does not include the epithet *glandulosa*.

In this study, *H. insularis* is treated as a widely distributed and morphologically variable species, much like *Carlowrightia arizonica* A. Gray (Daniel 1983) and *Tetramerium nervosum* Nees (Daniel 1986). These three species commonly occur alongside one another in disturbed habitats. Figure 8 illustrates some of the variation in characteristics of the bracts and bractlets throughout the range of *H. insularis*. These characters were of prime importance in Happ's (1937) classification of the genus.

Happ's (1937) key divides *Henrya* into two readily recognizable groups, those plants with apical mucros on the bractlets and those with dorsal (i.e., subapical or relatively remote from the apex) mucros. Seven species (*H. brevifolia*, *H. costata*, *H. flava*, *H. insularis*, *H. longipes*, *H. ortegana*, and *H. yucatanensis*) recognized by Happ in the former group are quite similar. Based on his intuitive diagram portraying putative interspecific relationships within *Henrya*, Happ (1937) considered *H. insularis* to occupy a central position in the genus. He distinguished this species (Happ 1937: 547) by "the rather loose inflorescence and by the mucro, usually erect, situated directly on and continuous with the apical margin of the acuminate-apiculate involucre bracts, which are also relatively long." Happ distinguished *H. brevifolia* from *H. insularis* on the basis of leaves obovate to ovate (vs. ovate), bracts 3–5 mm long (vs. 2–3 mm long), anterior corolla lobes 7–8 mm long and 3–4 mm wide (vs. 4.2 mm long and 2 mm wide), and capsules slightly puberulent near apex (vs. glabrous). *Henrya brevifolia* was known to Happ from only two collections from Sonora, Mexico. With the extensive collections now available from northwestern Mexico, none of these distinctions remains viable. Indeed, several of the collections cited by Happ as representative of *H. insularis* (e.g., *Ortega 5128*, *Purpus 266*) have apically pubescent capsules; and the dimensions provided for the corolla lobes of *H. insularis* by Happ were likely taken from a poorly preserved corolla (see discussion under Morphology). Of the nine collections cited by Happ under *H. insularis*, only four (*Jones 23188*, *Ortega 5128*, *5699*, and *Rose et al. 13845*) have corollas with measurable features. Most of the corollas are conspicuously shriveled and measurements of the lobes of the lower lip are approximately 4 mm long. However, lobes of well-preserved corollas on the two Ortega collections from Sinaloa, Mexico, measure up to 7.5 mm in length and 4 mm in width. Furthermore, *Daniel 4072* from Sinaloa which otherwise matches Happ's circumscription of *H. insularis* has corolla lobes up to 10 mm long and 5 mm wide.

Happ (1937: 549) recognized *H. costata* and noted "that the close-costate condition, particularly at the base of the leaves continuing curvinerved and somewhat parallel to the margin towards the apex, together with the broad ovate to elliptical outline and comparatively small size of the leaves, is characteristic of the species." The species was known to Happ solely by the type from western Chihuahua, Mexico. During my studies, features of leaf venation, shape, and size were found to be variable among specimens from northwestern Mexico without any noticeable correlation with other characters. Rather, phenological phenomena and position on the plant appear to be important factors regulating some of these characteristics of the leaves (see discussion under Morphology). In his key to species, Happ distinguished *H. costata* from *H. brevifolia* partly on the basis of glandular petioles in the latter and eglandular petioles in the former species. Examination of the holotype of *H. costata* reveals the presence of glands on most petioles.

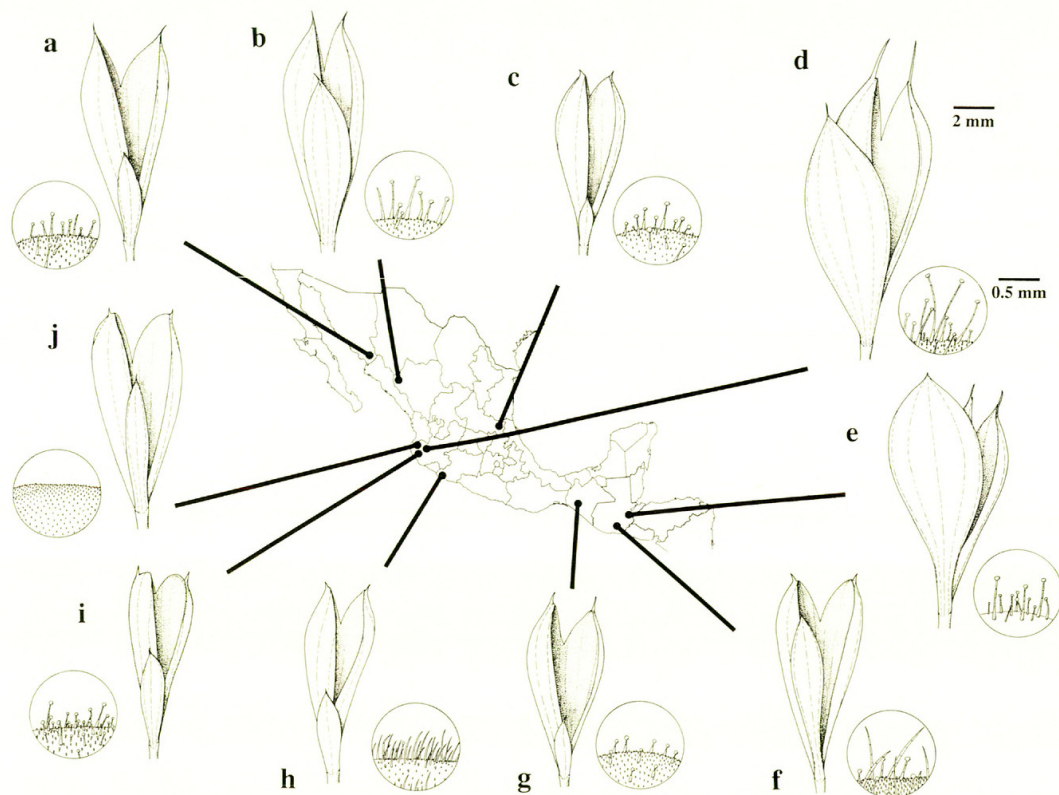


FIG. 8. Some of the variation in bract form, bractlet form, and pubescence of *Henrya insularis* throughout the range of the species. See text for discussion. a. Daniel 3377. b. Palmer 75. c. Pringle 7699. d. McVaugh 23382. e. Deam 397. f. Kellerman s.n., 20 Jan 1966. g. Ton 3897. h. Daniel & Bartholomew 4890. i. Daniel 2071. j. Rzedowski 16586.

Happ described another taxon from northwestern Mexico, *H. ortegana*, which he distinguished from the other taxa there by its longer bracts, bractlets, corollas, and capsules. In spite of some overlap in length, these organs indeed tend to be somewhat longer in specimens attributed by Happ (1937) to *H. ortegana* (i.e., 3.5–10 mm, 9–13 mm, 18–20 mm, and 7–9 mm respectively) than in those attributed by him to *H. insularis*, *H. brevifolia*, and *H. costata* (i.e., 2–5 mm, 6–9 mm, 10–12 mm, and 6–7 mm respectively). When measurements from recent collections from northwestern Mexico are considered, discontinuities are no longer evident. For example, corollas 13–16 mm in length are now known for plants occurring in this region.

Happ (1937: 551) noted that *H. flava* (Fig. 8b), known to him only by the type from Durango, Mexico, was “a distinct species of the genus” by virtue of the “large yellow corolla-lobes, the closely imbricated inflorescence, the rather large involucre bracts, the prominent nerves on the under side of the leaf with the close pubescence especially on the midrib and nerves, and the rather consistently acute angles of the four-sided stem . . .” Various combinations of these characteristics are now known to occur throughout the range of the genus.

*Henrya yucatanensis* was described (Happ 1937: 552) from Yucatán, Mexico, and distinguished from *H. insularis* “in having larger, broader, and more conspicuously nerved bracts of the inflorescence, a larger corolla, and a more densely glandular pubescence.” The range of variation in these characters in plants now known from the Yucatan Peninsula, all of which have apical mucros, is nearly identical to that now known for plants with apical mucros occurring in northwestern Mexico (e.g., Sonora, Sinaloa, and western Chihuahua) that were treated by Happ as *H. brevifolia*, *H. insularis*, and *H. costata*. For example, bract length varies from 2.5 to 6.5 mm among plants in northwestern Mexico and from 3.3 to 5.5 mm among plants in the Yucatan Peninsula; bract width varies from 0.7 to 1.8 mm in northwestern Mexico and from 1.3 to 2 mm in the Yucatan Peninsula; bractlet length varies from 7 to 12 mm in northwestern Mexico and from 8 to 11 mm in the Yucatan Peninsula; and corolla length varies from 10 to 16 mm in northwestern Mexico and from 11 to 15 mm in the Yucatan Peninsula.

Happ (1937) described collections from El Salvador with similarities to those from Mexico with apical mucros as *H. longipes*.

Plants with bracts conspicuously shorter than the bractlets and apical bracteolar mucros (i.e., the following taxa as recognized by Happ: *H. insularis*, *H. brevifolia*, *H. costata*, *H. flava*, *H. yucatanensis*, *H. ortegana*, and *H. longipes*) constitute a form of the species occurring from Arizona southward through western Mexico to El Salvador and in the Yucatan Peninsula (Fig. 8a). It appears that the plants from the northwestern portion of this range tend to be sprawling perennial herbs whereas those in the southern portion tend to be erect shrubs. Although these tendencies were observed in the field, the exact habit is often difficult to determine from herbarium specimens.

Happ (1937) treated a collection from Guatemala with unusually large bracts as *H. gualanensis* (Fig. 8e). Although he noted that the mucros of the bractlets were apical, examination of the type collection reveals that the mucros vary from apical to subapical. Since Happ's (1937) monograph, at least six additional collections from Honduras and western Mexico with similarly sized bracts have been made. In four of these collections (*Daniel 2116*, *Daniel & Bartholomew 4856*, *4876*, *McVaugh 23382*, Fig. 8d), all from Jalisco, Mexico, the mucros are dorsal (subapical to relatively remote from the apex). In *Dickson 1443* from Honduras and *Lehto &*

Reeves L18746 from Sonora, Mexico, the mucros are apical. It is perhaps noteworthy that the collection from Sonora has mucros of the same type as all other collections of *Henrya* from that state and that *Daniel & Bartholomew 4876* with remote mucros is from the same region as other collections of *Henrya* with remote mucros. Given the variation in micro position among these large-bracted collections, a taxon based solely on size of the bracts seems unwarranted. This is especially so considering the overlap in bract length (9–12 mm vs. 2–10 mm) and width (3–6 mm vs. 0.4–3 mm) between specimens referable to *H. gualanensis* and those pertaining to other species recognized by Happ. Thus, plants referable to *H. gualanensis* using Happ's key are treated here as a sporadic, large-bracted form of *H. insularis*.

Happ's key divided the 12 species with mucros "situated more or less below the apical margin" of the bractlets into those with the bractlets "acuminate, acute at apex" (i.e., *H. konzattii*, *H. imbricans*, *H. laxa*, *H. pilosa*, *H. puberula*, and *H. scorpioides*) and those with the bractlets "obtuse to rounded at the apex" (i.e., *H. barclayana*, *H. donnell-smithii*, *H. grandifolia*, *H. mephitica*, *H. reticulata*, and *H. rupicola*). In the former group, *H. scorpioides* was represented by the greatest number of collections. Happ (1937: 556) noted that the "rather loose spikes, comparatively small acuminate involucre bracts, and the recurved micro, located slightly below the apical margin, render it of ready recognition." He recognized *H. scorpioides* var. *latifolia* on the basis of specimens with broader, rotund-ovate leaves and longer petioles that occur throughout the range of the nominate variety. Although specimens cited by Happ under *H. scorpioides* var. *latifolia*, and several more recent collections with similar leaves, are noteworthy for their exceptionally broad leaves (i.e., with length:width ratio 1.1:1.8) with long (up to 70 mm) petioles, specimens either treated by Happ as, or conforming to his circumscriptions of, *H. pilosa* (e.g., *Palmer 1330*), *H. gualanensis* (e.g., *Deam 397*), *H. puberula* (e.g., *Rzedowski 16586*), *H. reticulata* (e.g., *Standley 20221*), and *H. insularis* (e.g., *Darrow & Haskell 2214*), possess similar leaves as well. Gibson (1974) placed *H. scorpioides* var. *latifolia* into the synonymy of *H. scorpioides*.

Specimens referable to *H. scorpioides* sensu Happ tend to separate into two forms: those with young shoots, rachises, bracts, and bractlets pubescent mostly with straight, glandular trichomes (Fig. 8c, g) and those with these same structures pubescent with a mixture of straight to subflexuose (to antrorse), eglandular trichomes (sometimes inconspicuous) and glandular trichomes (sometimes inconspicuous and rarely absent) (Fig. 8h). Both forms occur widely in Mexico and Central America. Some specimens, however, are not readily assignable to either. Several collections of *Purpus* from Veracruz (e.g., 8863 at DS, s.n. at MO) contain sprigs of both forms. *Purpus 8863* at ARIZ shows a dominance of eglandular trichomes on proximal portions of the new growth and a dominance of glandular trichomes on the distal portions. *Hinton 11779* from Guerrero, Mexico, has numerous eglandular trichomes on the stems but relatively few in the inflorescence.

In most of those collections with a mixture of eglandular and glandular trichomes, the trichomes are straight to subflexuose. In several collections from Mexico and Guatemala (i.e., *Daniel 2124*, *Hinton et al. 7611*, *Kellerman s.n.* (Fig. 8f), *Makrinius 517*, 817, *Morton & Makrinius 2673*, 2734, and *Reko 6220*), glandular trichomes are mostly or entirely absent on cauline and foliar surfaces and present on the rachises, bracts, and bractlets. Furthermore, in these collections the eglandular trichomes on the stems are antrorse.

*Palmer 1330*, the type of *H. pilosa*, has foliage similar to *H. scorpioides* var.

*latifolia* and, except for the longer (up to 1.8 mm vs. up to 1 mm) eglandular trichomes, resembles specimens of *H. scorpioides* with a preponderance of eglandular trichomes.

Happ (1937: 558) described *H. laxa* and contended that the "long lax spikes, the loosely imbricated involucre bracts, and the extremely glandular pubescence definitely characterize this species." Known only from the type, this collection closely resembles other exclusively glandular specimens of *H. scorpioides*.

*Henrya imbricans* was distinguished by Happ (1937: 559) on the basis of "the close imbrication of the spikes, the acute rather long bracts, and the slightly recurved mucro." Gibson (1974) distinguished this species from *H. scorpioides* by its longer bracts (mostly 5–8 vs. 2–4 mm) and longer bractlets (9–11 vs. 7–9 mm). She noted, however, that in *Johnston 1160* from Guatemala, some of the bracts are only 3 mm long, as in *H. scorpioides*, whereas others are 6 mm long. She concluded that *H. imbricans* might be only a form of *H. scorpioides*. Because length of the bracts is often a function of their location (i.e., distal bracts are usually smaller than proximal ones), for purposes of comparison in my study bract length was measured only at or near the midpoint of the spike. Length of the bracts near midspike varies from 5.5 to 7.5 mm among specimens of *H. imbricans* cited by Happ and from 5 to 9 mm among more recent collections that would fall within the circumscription of Happ's taxon. Length of the bracts near midspike among specimens that would be treated as *H. scorpioides* using Happ's key varies from 2 to 7 mm. This overlap, and an even greater overlap in bractlet length (7–11 vs. 6–10.5 mm) among specimens attributable to the two taxa as recognized by Happ, is suggestive of variation within a single taxon. Plants generally treated as *H. imbricans* appear to differ from those treated as *H. longipes* only by the subapical (vs. apical) mucro of the bractlets. In fact, Gibson (1974) synonymized the latter species with the former.

Happ distinguished *H. puberula* and *H. konzattii* from the assemblage of taxa having apically acute bractlets with subapical mucros by their puberulent (i.e., *H. puberula*) or glabrous (i.e., *H. konzattii*) bractlets. Examination of the type, and only known collection, of *H. konzattii* reveals that the abaxial surface of the bractlets is covered with inconspicuous eglandular trichomes up to 0.05 mm long. Scattered flexuose trichomes up to 0.3 mm long are sometimes present as well. Bractlet pubescence as seen on the type (i.e., *Morales R. 911*) of *H. puberula* from Guatemala is denser and more conspicuous than that of *H. konzattii*. Some specimens (e.g., *Standley 88432*) have bractlets with a puberulence intermediate in density between *H. puberula* and *H. konzattii*. Bractlets of other specimens collected since Happ's monograph, including some from near the type locality of *H. puberula* (e.g., *Standley 61345, 61364*) are puberulent like *Morales R. 911* and, in addition, possess scattered flexuose eglandular trichomes to 0.6 mm long and rare, stipitate glands to 0.3 mm long. Certain specimens resemble *H. puberula* in bractlet pubescence but also have irregular patches of glandular and/or eglandular trichomes (e.g., *Kellerman s.n., Matuda 133, 5216*). Understory puberulence consisting of trichomes similar to those described above for *H. konzattii* and *H. puberula* is present, although often inconspicuous, on the bractlets of most forms of what is here treated as *H. insularis* from throughout the range of the species. Plants treated as *H. konzattii* and *H. puberula* (Fig. 8j) appear to represent forms of the species in which the usual overstory of glandular and/or eglandular trichomes is largely or nearly absent.

Among the six species recognized by Happ (1937) with apically obtuse to rounded bractlets with dorsal mucros, four (i.e., *H. barclayana*, *H. grandifolia*, *H.*

*reticulata*, and *H. rupicola*) resemble one another by their relatively remote (up to 1.2 mm from the apex) mucros. Nees (1846) described *H. barclayana* from western Mexico and noted that it differed from *H. insularis* by its more densely glandular bractlets with rounded apices. Fernald (1895) described *H. grandifolia* from western Mexico without reference to its distinctive attributes. Happ (1937: 561) maintained *H. grandifolia* and noted that the "usually large leaves, rather loose inflorescence, and the large involucre bracts with inconspicuous subapical mucro are distinctive characteristics of the species." The type of *H. grandifolia* differs from *H. barclayana* only by its larger (up to 130 mm long and 55 mm wide) leaves.

The remaining four taxa with subapical mucros and apically obtuse to rounded bracts were newly described by Happ (1937). *Mexia* 1864 from Jalisco, Mexico, forms the basis both for *H. mephitica* and *H. rupicola*. Specimens at CAS, NY (in part), and US were attributed to the former species whereas duplicates at DS, F, MICH, MO, NY (in part), and UC were attributed to the latter. The species were distinguished primarily by the shorter (6–7 vs. 9–10 mm long) bractlets and the longer (0.5 vs. 0.2 mm long), more remote (0.8–1.0 vs. 0.1–0.2 mm below apex) mucros of *H. rupicola*. In my study, measurements (rounded to the nearest whole number) for five characters used by Happ (1937) to distinguish *H. barclayana*, *H. mephitica*, and *H. rupicola* were taken from all specimens cited in his monograph. All available specimens referable to these species from Nayarit, Jalisco, and Colima collected since Happ's study were also scored. The measurements were plotted on frequency histograms (Fig. 9). The histograms reveal that discontinuities are largely absent in these quantitative characters, both among specimens studied by Happ and among more recent collections not studied by him. The discontinuity in internode length was apparently not taxonomically significant to Happ, because he treated specimens with internode lengths of 2 mm and 19 mm both as *H. barclayana*.

*Henrya reticulata* was described from El Salvador and noted to combine features of *H. scorpioides* var. *latifolia* and *H. imbricans*. The type is indistinguishable from glandular-pubescent plants of western Mexico with apically rounded bractlets and remote mucros.

Happ (1937) described *H. donnell-smithii* from southern Mexico and Central America and included it among species with rounded bractlet apices. Examination of the type and other specimens cited by Happ reveal that the apex of the bractlets varies from somewhat rounded to acute. Since the mucro is only up to 0.2 mm from the apex, these specimens more closely resemble those considered by Happ to represent *H. scorpioides*. In fact, Gibson (1974) included *H. donnell-smithii* within the synonymy of that species.

Other collections also exhibit variation in the conformation of the bractlet apex. *Standley* 21801 from El Salvador, cited and annotated by Happ as *H. reticulata*, has bractlets with rounded, subacute, and acute apices. Some specimens collected since Happ's study have bractlets with similarly variable bractlet apices (e.g., *Standley & Padilla* V. 2743, 3583).

Plants from western Mexico with apically rounded bractlets and remote mucros certainly appear distinctive (Fig. 8i). Because other plants with apically rounded bractlets possess subapical mucros and still other plants possess bractlets with both rounded and acute apices, it would be inconsistent to formally recognize this distinctive form.

Variation in the stance of bracteolar mucros was observed by Happ (1937). He noted that apical mucros usually were erect, whereas dorsal mucros sometimes were divergent. This correlation is generally, although not universally, applicable.

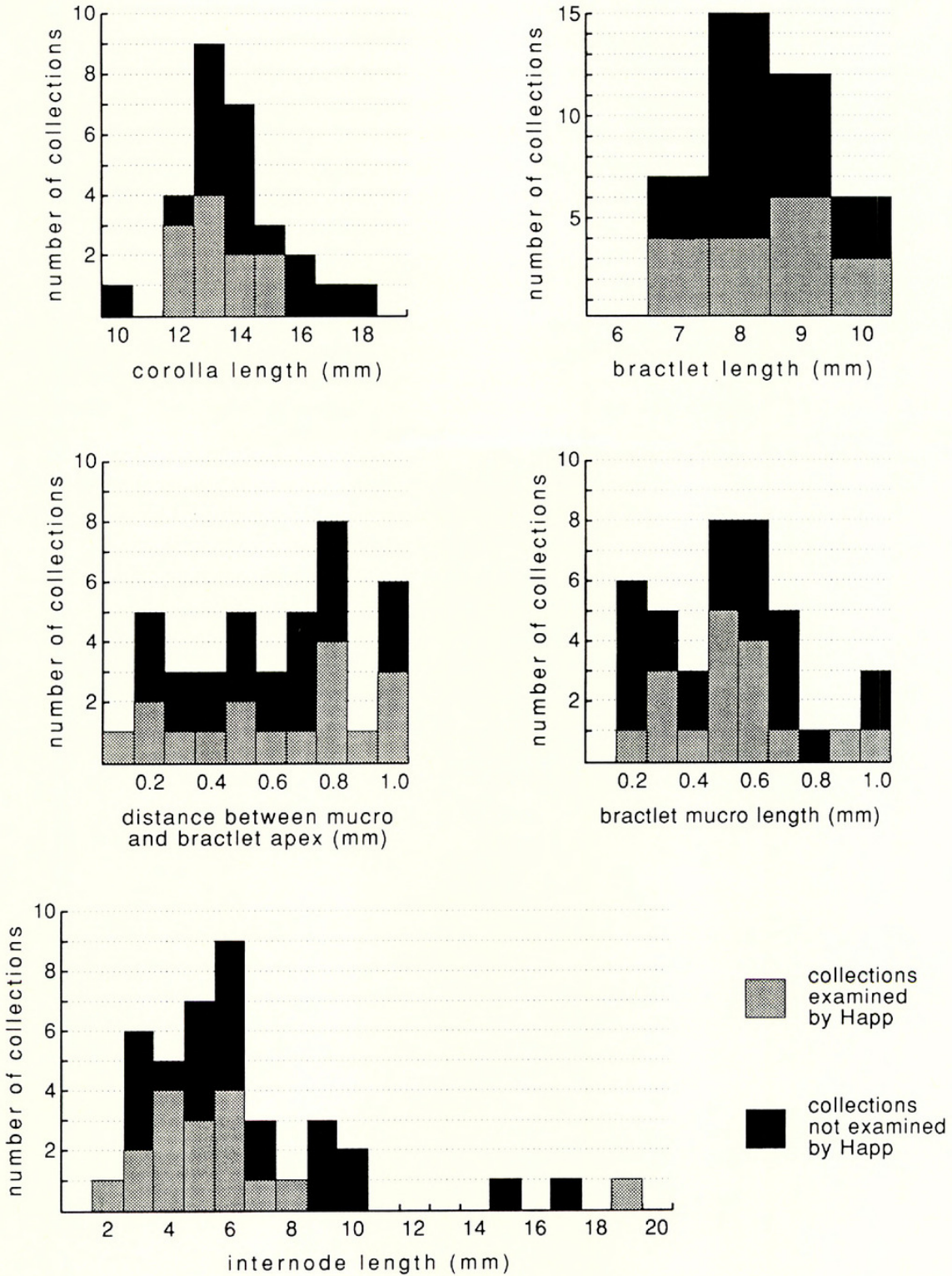


FIG. 9. Frequency histograms showing numbers of collections (from Nayarit, Jalisco, and Colima) per size class for five characters used by Happ in distinguishing *H. barclayana*, *H. mephitica*, and *H. rupicola*.

Figure 8 illustrates some of the variation in both stance and position of the mucro relative to other characters.

The character resulting in the major division among taxa in Happ's (1937) key is position of the bracteolar mucro, apical vs. dorsal. There appears to be no other

morphological difference between plants traditionally recognized as *H. insularis* (apical) and *H. scorpioides* (dorsal). There are some geographic correlations with mucro position. Only plants with apical mucros occur in the southwestern United States, northwestern Mexico, and the Yucatan Peninsula. Only plants with dorsal (i.e., subapical) mucros are known from northeastern and east-central Mexico. In west-central through southern Mexico, and in Central America, however, plants with apical mucros and those with dorsal mucros both occur. Plants with remotely dorsal mucros occur only in west-central Mexico and El Salvador.

Although position of the mucro is consistent and readily apparent in most collections, in some (e.g., *Breedlove* 9047, *Lott & Magallanes* 924, *Hinton* 11217, *Martínez S. et al.* 3527, *Breedlove & Smith* 31276) either both apical and subapical mucros occur on the same individual or it is not possible to determine whether the mucros are apical or subapical with a dissecting microscope. Happ (1937) distinguished *H. longipes* of El Salvador from *H. imbricans* of Guatemala largely by its apical, erect (vs. subapical, divergent) mucro. When Gibson (1974) united these taxa, the resulting species possessed both apical and dorsal mucros. Among specimens conforming to *H. gualanensis* on the basis of bract form, both apical and dorsal (varying from 0.05 to 0.5 mm below the apex) can be found. Furthermore, some bractlets of specimens (e.g., *Daniel & Bartholomew* 4731, *Pérez* 20) with mostly or entirely rounded bractlet apices lack mucros altogether. Because of this lack of consistency in the single character used to distinguish *H. insularis* and its relatives from *H. scorpioides* and its relatives, mucro position does not appear to be a suitable diagnostic character for recognizing species in *Henrya*. As a consequence of the information presented above, I propose treating all of the species recognized by Happ (1937) as a single, variable species, *H. insularis*.

### EXCLUDED NAMES

*Henrya scorpioides* (L.) Nees in A. DC., Prodr. 11: 491. 1847. *Justicia scorpioides* L., Sp. pl. 1: 21. 1762. *Dicliptera scorpioides* (L.) A. L. Juss. Ann. Mus. Natl. Hist. Nat. 9: 269. 1807. *Tetramerium scorpioides* (L.) Hemsley, Biol. Centr. Amer. Bot. 2: 526. 1882. *Tetramerium scorpioides* (Nees & Benth.) Lindau, Bull. Herb. Boissier 5: 679. 1897; nomen nudum.—TYPE: MEXICO. Veracruz: without locality, *Houstoun s.n.* in Sloane Herbarium, vol. 292, fol. 69 (neotype: BM!, designated by Daniel, 1989).—The basionym pertains to *Dicliptera sexangularis* (L.) A. L. Juss.

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## APPENDIX

Additional Mexican collections of *Henrya insularis* examined.

Avina 981; Baker 1108, 1119; Balogh 929; Bamps 5534; Barkley 17M277; Barr & Mason 62-324; Bauml & Voss 1460; Bowers et al. 2813; Breedlove 19146, 23924, 49626, 50183, 50304, 50470; Breedlove & Almeda 56896; Breedlove & Smith 31276; Breedlove & Thorne 30233; Bye 3514, 8584; Calzada 5287; Carlson 2879; Carter & Ferris 3388; Cobián O. 276; Crockett 95; Daniel 2029.5, 2033, 2049, 2071, 2099, 2105, 3377; Daniel & Bartholomew 4765, 4838; Daniel et al. 3304; Delgado S. et al. 972; Donohue et al. 101; Dorantes 519; Dorantes et al. 5163; Duke M3606; Feddema 2595; Fernández N. 1533; Gallagher et al. 290; Gentry s.n.; Gilley et al. 20; Goldman 590; González M. 1005; Gregg 1017, 1159; Guevara F. 1527; Hahn s.n.; Henze & Henze s.n.; Hernández A. & Figueroa N. 21; Hess & Hall 567; Hill 59; Jurgensen 101; Kimnach & Brandt 925; Koelz 34248; Kruse 997; Lane & Fryxell 2325; Langman 3151; Lehto 24240, 24269, 24273B; León de la Luz 1052; Long 3193, 3213; Lott 2416; Martin s.n.; Martin & O'Rourke s.n.; Martínez S. et al. 3527; Martínez 547; Mason et al. 3294; McGill & Pinkava 6491; McVaugh 11878, 22568, 25124, 26084; Medrano 1005; Medrano et al. 2713; Mell 2255; Millspaugh 65, 1161; Narváez M. & Salazar 293; Neill 5514; Ortega 1250, 7184, 7186; Pennington 323; Pérez de la Rosa 52; Pérez J. 258, 1761; Pérez J. & Petroga 1703; Perkins & Hall 3340; Purpus 8235; Rea 1052; Reko 5048; Rzedowski 12301, 37746; Sanders et al. 2668; Saunders 47; Schmidt & Davis s.n.; Spaulding 75-3-22; Starr & Palzkill 363, 368; Stone 244; Taylor & Taylor 7286; Thompson & Davis 82-46; Ton 3897; Toolin 289, 297; Van Devender et al. 82-61, 84-146, s.n.; Ventura A. 7179, 9427, 10802, 10895, 12187, 12288, 13732, 18128, 19324; Viereck 1177; Walker BAN 7.



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