

Systematic Anatomy of *Hesperomannia*

SHERWIN CARLQUIST¹

THE GENUS *Hesperomannia* (Compositae, tribe Mutisieae) has attracted interest because of its arborescent habit, its restriction to certain of the Hawaiian Islands, and its rarity in the locations in which it is found. The purpose of the present paper is to survey the anatomical diversity which exists in the genus and relate it to gross morphological characters in an attempt to achieve an acceptable classification. The affinities of *Hesperomannia*, as suggested particularly in terms of anatomical characters, are to be discussed in later studies. Within the genus, however, anatomical features seem illuminating in demonstrating the most natural taxonomic groupings.

ACKNOWLEDGMENTS

The writer wishes to express appreciation to the curators of the herbaria named below for loan of specimens. Dr. Harold St. John of the University of Hawaii kindly conducted a field trip on which the writer was able to collect material of *Hesperomannia*. Acknowledgment is offered to Dr. Reed C. Rollins and Dr. Grady Webster for reading the manuscript and suggesting improvements.

MATERIALS AND METHODS

Vegetative material of the writer's collection of *H. arborescens* subsp. *Swezeyi* was fixed in a Carnoy's solution (3 parts absolute ethyl alcohol: 1 part glacial acetic acid). All other material was prepared from herbarium specimens as follows. Vegetative and floral parts

were treated with warm 2.5 per cent aqueous NaOH to remove cell contents and expand structures to their original condition. Further clearing was achieved by treatment with a 250 per cent chloral hydrate solution. After washing, whole mount preparations of flowers and leaves were made by dehydration in an ethyl alcohol series, staining in a 1 per cent safranin solution in absolute ethyl alcohol, transferring to xylene, and mounting in xylene-soluble synthetic resin. Portions of both the Carnoy's-fixed material and the "revived" herbarium material were prepared for sectioning according to the tertiary butyl alcohol schedule of Johansen (1940: 130-131). Treatment with hydrofluoric acid prior to infiltration was necessary for softening woody structures. Sections were stained with a safranin-fast green combination corresponding to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen 1940: 92-93). All of the collections for which anatomical data were assembled are represented in the Bernice P. Bishop Museum in Honolulu, except where otherwise noted. Duplicates of many of these specimens are in other herbaria.

ANATOMY

The Leaf

Examination of young leaves near the shoot apex of *Hesperomannia arborescens* subsp. *Swezeyi* showed them to be densely covered with uniseriate nonglandular hairs (Fig. 1). Interspersed among these are biseriate glandular trichomes. At such an early stage, virtually every epidermal cell on both surfaces

¹ Rancho Santa Ana Botanic Garden, Claremont, California. Manuscript received February 9, 1956.

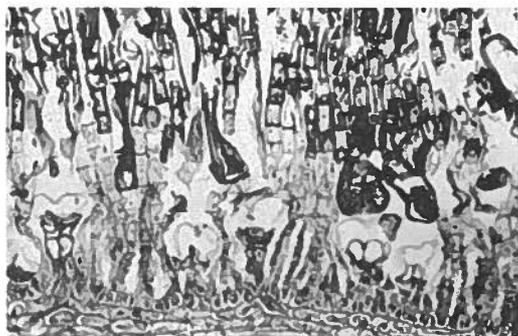


FIG. 1. Longitudinal section of young petiole of *Hesperomannia arborescens* subsp. *Swezeyi* (Carlquist H3), $\times 170$. Short biseriate glandular hairs may be seen near the epidermis (below), interspersed among crowded uniseriate nonglandular hairs, which cover most of the photograph.

of the leaf bears a trichome of one of these types. This condition is true of all of the species. A preparation of the most glabrous species, *H. Lydgatei*, showed an identical situation. During enlargement of the young leaf of *H. arborescens* subsp. *Swezeyi*, there is a tendency for the uniseriate trichomes to degenerate and slough off. In Figure 1, the uniseriate trichomes already show an accumulation of dark-staining resinous contents, indicating the beginning of their decline relatively soon after formation. Upon maturation of the leaf of this plant (Fig. 2), uniseriate hairs have disappeared altogether, except for occasional persistent basal cells. Simultaneously, the biseriate glandular trichomes increase in size and become sunken into pockets as the mesophyll expands.

Differences in leaf indument, which are treated here as important characters of the species, may be explained on the basis of differential elimination of trichomes during maturation of the leaf. In *H. arbuscula* subsp. *oahuensis*, for example, uniseriate hairs are retained, particularly on the young stems and lower surfaces of leaves (Fig. 3). In this species, uniseriate hairs, particularly the terminal cell of each, become sclerified, corresponding with their persistence. Biseriate glandular hairs are also present on the mature leaf of

H. arbuscula subsp. *oahuensis*. Although less numerous, both types of trichomes may also be found on mature leaves of *H. arbuscula* subsp. *arbuscula*. *Hesperomannia arbuscula* is the only species in which uniseriate trichomes are retained on the mature leaf.

In *H. Lydgatei*, *H. arborescens* subsp. *arborescens*, subsp. *Bushiana*, and some populations of subsp. *Swezeyi* (Judd 1244, for example), both types of trichomes disappear early in leaf ontogeny. In leaves of these taxa, a heavy cuticle is formed on both adaxial and abaxial epidermis.

Variations in leaf thickness occur in all the species, and cannot be considered as a constant taxonomic character.

Peduncle

Among the taxa recognized here under *H. arbuscula* and *H. arborescens*, little variation in

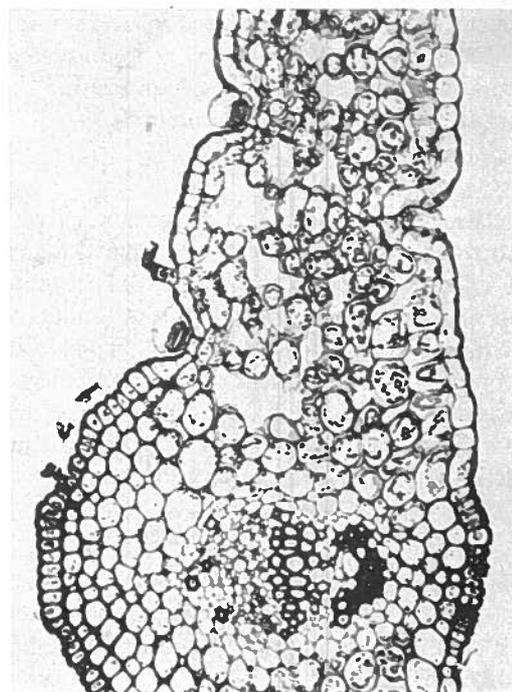


FIG. 2. Transection of a mature leaf of *Hesperomannia arborescens* subsp. *Swezeyi* (Carlquist H3), $\times 130$. Abaxial epidermis at left. Note vein, accompanied by sclerenchyma, remnants of uniseriate hairs on the abaxial surface, and sunken glandular hairs.



FIG. 3. Lower surface of mature leaf of *Hesperomannia arbuscula* subsp. *oahuensis* (Hillebrand 1871), $\times 140$. Numerous sclerified hairs may be seen above the vein reticulum.

peduncle size or structure occurs. A peduncle of *H. arborescens* subsp. *Bushiana*, shown in Figure 4A, is typical in its numerous bundles and sclereid nests. Trichomes are persistent on the epidermis of peduncles in these two species. *Hesperomannia Lydgatei*, on the contrary, shows peduncles much smaller in diameter. This smaller stature is reflected anatomically in the fewer bundles present in the vascular cylinder and in the much smaller size of the pith (Fig. 4B). In addition, no hairs are present on the peduncle epidermis of *H. Lydgatei*, which is covered by a prominent cuticle.

Involucral Bracts

As in peduncle anatomy, the involucral bracts of plants belonging to *H. arbuscula* and *H. arborescens* are comparatively uniform in anatomical structure. As shown for *H. arborescens* subsp. *Swezeyi* in Figure 4C, a thick region of subhypodermal fibers occurs near the outer face of the bract in these species. Epidermal and hypodermal cells on this sur-

face remain thin-walled. This zone of fibers may be as many as 14 cells in thickness. On the interior face of the bract, a thinner band of fibers is present. The adaxial epidermis is most heavily sclerified, with decreasing wall thickness on the two or three cell layers interior to it. Between the fibers on the inner and outer faces of the bract, a region of thin-walled parenchyma is present. A single series of vascular bundles occurs in this region. The thickness of this central parenchyma band is greatest near the base of the bract and decreases toward the apex.

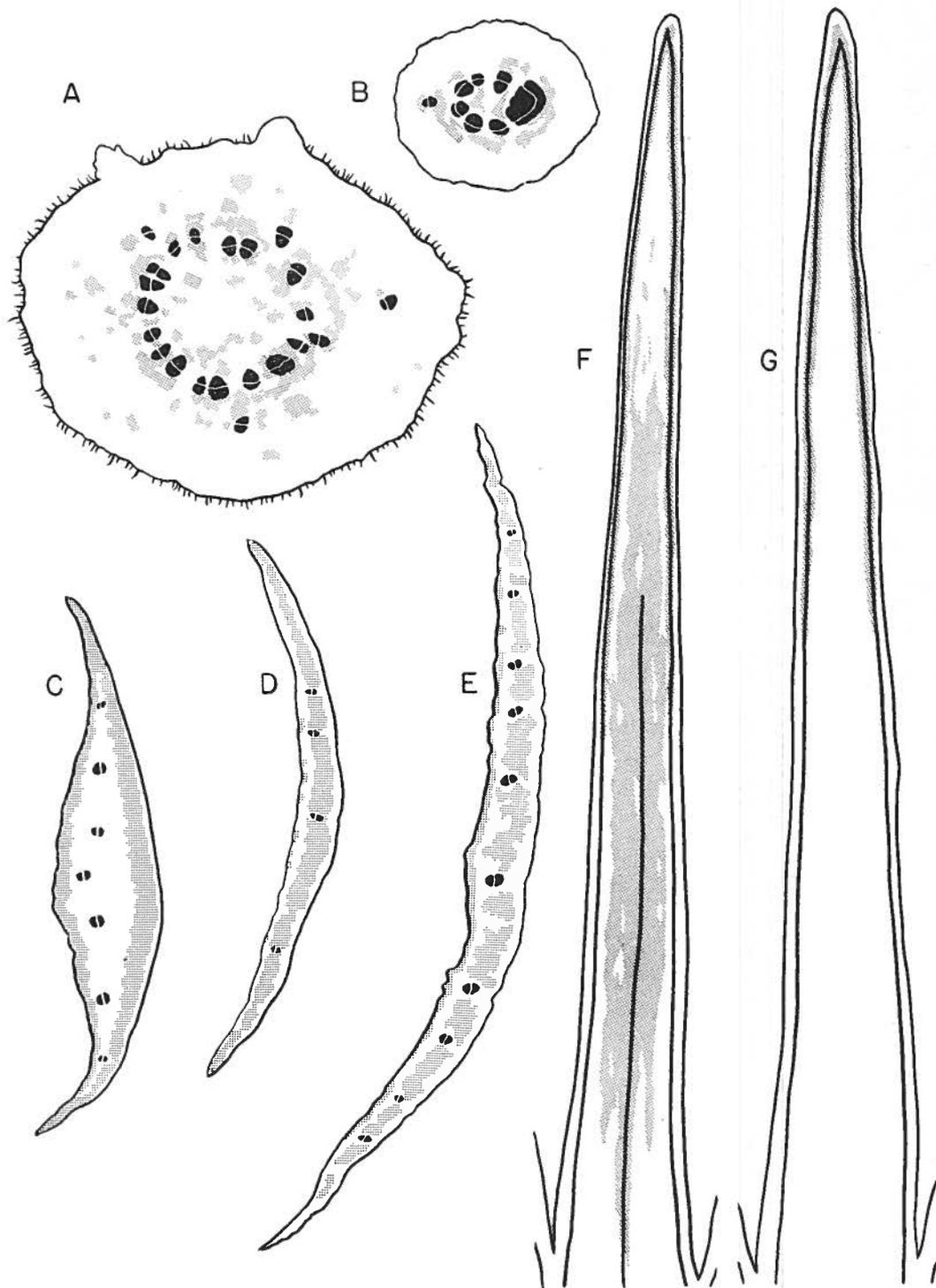
Inner involucral bracts show an altered form of this structure in the two species, as the bract of *H. arborescens* subsp. *Bushiana* in Figure 4D demonstrates. In such a bract, the region of parenchyma between the two bands of fibers is greatly narrowed. The bundles occur at points within the outer band of fibers, rather than in the parenchyma. The outer band of fibers is continuous, or nearly so, and encases most of the bundles.

The involucral bracts of *H. Lydgatei* show a structure comparable only to the inner involucral bracts of the other species. Bundles occur only in interstices between the strands of fibers, which never form a continuous band as they do in the bract of *H. arborescens* subsp. *Bushiana* described above.

Corolla

As is typical for Compositae, a pair of lateral veins, which fuse beneath each sinus, is present in each corolla lobe in *Hesperomannia* flowers. In addition, median veins, such as shown in Figure 4F, were found to be present in both subspecies of *H. arbuscula* as well as in *H. arborescens* subsp. *Swezeyi*. Such median veins are present in one to three of the larger corolla lobes of a flower in these taxa, or are absent in some flowers. Where present, they extend for varied distances in the lower portion of the lobe. No median veins were found in the taxa not mentioned.

Fibers encase the upper extent of the lateral veins of corolla lobes (Fig. 4F, G) in all



species. In addition, subepidermal cells interior to the lateral veins of the lobe may become sclerified; such diffuse sclereids were found in all the subspecies of *H. arborescens* and *H. arbuscula*. The extent of these sclereids is shown diagrammatically in Figure 4F for *H. arborescens* subsp. *Swezeyi*, in which they were abundant. They were least abundant in *H. arbuscula* subsp. *arbuscula*, and altogether lacking in *H. Lydgatei* (Fig. 4G). Sclereids of this type appear in the young flowers, and increase in size until the corolla withers. As shown in Figure 5, these sclereids become impacted against each other, forming blunted ends and distorted shapes. Because of the presence of such sclereids, median veins in corolla lobes can be detected with certainty only in cleared preparations. Although sclereids of this nature have never been reported in the Compositae before, they have been found by the writer in a number of Mutisieae.

EVOLUTION WITHIN THE GENUS

Characters of gross morphology alone give few suggestions concerning presumed evolutionary advancement within *Hesperomannia*. One feature which deserves mention is the tendency toward aggregation of heads. In most Mutisieae, particularly putatively primitive genera, the heads are solitary and terminal. In *Hesperomannia*, they may be solitary, but are more frequently in clusters of 2 to 10. Where fewer peduncles are present, they are borne coordinately at the end of an axis. Where more numerous peduncles form a cluster, some peduncles may branch from others. If more than one head is present, no leaves or bracts subtend the additional heads. In view of the fact that clusters of heads are present in all of the taxa except *H. arborescens* subsp. *Bushiana*, which would appear to be derived on other grounds, such clusters may

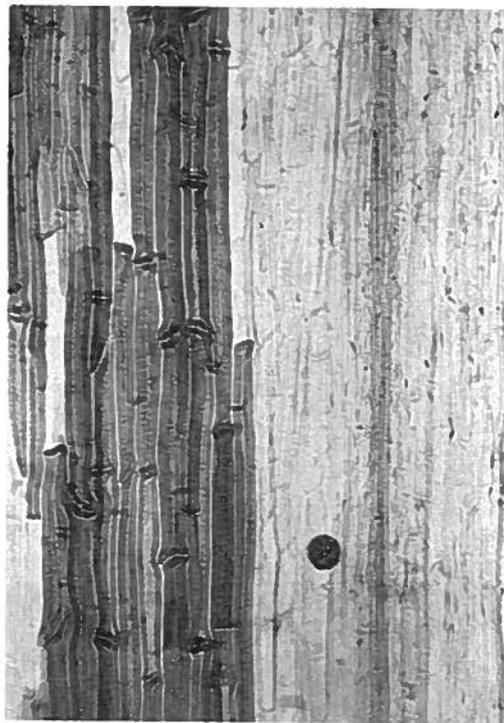


FIG. 5. Portion of cleared corolla-lobe of *Hesperomannia arborescens* subsp. *Swezeyi* (Judd 1244), $\times 175$. Margin of lobe at right; inward from the margin may be seen the lateral vein, a glandular hair (out of focus), and a number of subepidermal sclereids, left.

have been primitively present in *Hesperomannia*, despite the solitary condition elsewhere in the Mutisieae.

Anatomical characters seem to offer more reliable criteria of primitiveness, though few features can be cited in this regard. The caducous hairs on herbage and peduncles may be interpreted in this connection. One would expect the development of mature trichomes to be more primitive than the condition where they are lost at an early stage. In this case, *H. arbuscula* shows the most primitive expression of this character. *Hesperomannia Lydgatei* shows the most advanced condition,

←FIG. 4. A, B, transsections of peduncle near base, $\times 30$. A, *Hesperomannia arborescens* subsp. *Bushiana* (Degener 11927a); B, *H. Lydgatei* (Forbes 190K). C–E, transsections of involucre bracts, midway along length of bract, $\times 21$. C, *H. arborescens* subsp. *Swezeyi* (Judd 1244), outer bract; D, *H. arborescens* subsp. *Bushiana* (Degener 11927a), inner bract; E, *H. Lydgatei* (Forbes 190K), outer bract. F, G, corolla lobes, $\times 15$. F, *H. arborescens* subsp. *Swezeyi* (Judd 1244); G, *H. Lydgatei* (Forbes 190K). Outlines and veins shown in black, sclerenchyma shaded.

since it lacks trichomes on both mature leaves and peduncles. *Hesperomannia arborescens* shows intermediate stages, since uniseriate hairs are present on peduncles, though lacking on mature leaves. Biseriate glandular trichomes have likewise disappeared from mature leaves in some populations of this species.

The involucral bracts of *H. Lydgatei* may be interpreted as advanced in their structure. Likewise, the lack of median veins in corolla lobes of this species, despite optimal lobe-width, would seem to be an advanced characteristic. Absence of median veins in flowers of *H. arborescens* subsp. *arborescens* and subsp. *Bushiana* may similarly be interpreted as reductions, if the generally-accepted tenet of Koch (1930: 940) that median veins are primitively present in the family is correct.

Thus, *H. arbuscula* would seem to possess the more primitive characteristics. *Hesperomannia arborescens* shows somewhat more advanced features, while *H. Lydgatei* is differentiated from the other species by characters which seem best interpreted as the most advanced condition in the genus.

SYSTEMATIC TREATMENT AND DISCUSSION

The writer has had the privilege of studying type or isotype material of all of the species of *Hesperomannia*. In addition, the collections of the three largest assemblages of specimens of this genus, those of the Bishop Museum, the Gray and Arnold herbaria at Harvard, and the Herbarium of the University of California, Berkeley, have been examined. This comparatively large amount of material has permitted a more comprehensive picture of species variability than has previously been available. The descriptions of Degener (1946) are adequate for indicating some of the extremes of variation, particularly in the complex recognized here as *H. arborescens*. These descriptions do not incorporate the intermediate expressions of characters that are found in many specimens, however, and the discussions following each of the taxa below

emend these descriptions where necessary, suggesting the most constant characters for each taxon recognized.

KEY TO SPECIES AND SUBSPECIES

- 1A. Peduncles 1.8 mm. in diameter or less, glabrous; inner involucral bracts 3.5 to 5 cm. long; corolla lobes without diffuse sclereids *H. Lydgatei*
- 1B. Peduncles 3 mm. in diameter or more, bearing hairs even at maturity; inner involucral bracts 3.3 cm. long or less; corolla lobes with diffuse sclereids in subepidermal layers 2
- 2A. Leaves elliptic, the lamina base acute; abaxial surface of mature leaf covered with numerous uniseriate sclerified hairs 3. (*H. arbuscula*)
- 3A. Straggling shrub; hairs on abaxial surface of leaf relatively sparse; diffuse sclereids in corolla lobes infrequent; West Maui *H. arbuscula* subsp. *arbuscula*
- 3B. Tree; abaxial surface of leaf densely coated with hairs; numerous diffuse sclereids present in corolla lobes; Waianae Mts., Oahu *H. arbuscula* subsp. *oahuensis*
- 2B. Leaves lanceolate to oblanceolate or obovate, the lamina base acuminate; no uniseriate hairs present on mature leaves 4. (*H. arborescens*)
- 4A. Achenes at maturity 12-14 mm. long; no median corolla veins present; Lanai *H. arborescens* subsp. *arborescens*
- 4B. Achenes at maturity 12 mm. or less in length; median corolla veins present or not; Koolau Mts., Oahu 5
- 5A. Heads solitary or in clusters of 2 to 10; heads containing 30 or more flowers; median veins present in some corolla lobes *H. arborescens* subsp. *Swezeyi*
- 5B. Heads solitary, containing approximately 25 flowers; no median veins in corolla lobes *H. arborescens* subsp. *Bushiana*

1. *Hesperomannia Lydgatei* Forbes

Hesperomannia Lydgatei Forbes, Bernice P. Bishop Mus., Occas. Paper 4: 220, 1909.

This species is the most distinct in the genus, by virtue of its geographic isolation (endemic to Kauai) and numerous morphological and anatomical features. As shown above, the peduncles are glabrous and markedly narrower than those of the other species. The long, lanceolate involucre bracts are distinctive both in size and shape and in their anatomy. The lack of diffuse sclereids in corolla lobes has been mentioned earlier. In features of vegetative anatomy, however, no differences can be found between *H. Lydgatei* and the other species. The leaves and stems were found to be identical in shape and anatomy to some plants referred here to *H. arborescens* subsp. *Swezeyi* (Judd 1244, for example). Consequently, the difference in these respects suggested by Forbes (1909: 220) cannot be maintained. Although it has not been collected since 1910, this species may still be extant.

Representative specimens—Kauai, Waiawa Mts.: *Lydgate*, May 1908 (type, BISH²), *Forbes* 190K (A, BISH, UC).

2. *Hesperomannia arbuscula* Hillebrand

Hesperomannia arbuscula Hillebr., Fl. Hawaii. Is., 232, 1888.

Compared with *H. Lydgatei*, the remaining taxa are remarkably uniform. *Hesperomannia arbuscula* has been maintained as distinct here because of its geographical distribution and the constancy of the leaf shape and indument characters. In addition, the occurrence of slightly different plants on Oahu and West Maui respectively suggests that if the two populations are to be recognized as separate subspecifically, they are best grouped as a species separate from *H. arborescens*.

² Abbreviations of herbaria according to J. Lanjouw and F. A. Stafleu, Index Herbariorum, Part I, 1954, Utrecht.

2A. *Hesperomannia arbuscula* subsp. *arbuscula*

This taxon is known only from the type collection. Since repeated exploration of West Maui has failed to rediscover this plant, it may be extinct. Because the type at Berlin is apparently destroyed and the sterile type fragment at the Bishop Museum is inadequate, the isotype material in the Gray Herbarium remains the only usable material.

Representative specimens — West Maui: *Bishop*, 1871 (type fragment, BISH; isotype, GH).

2B. *Hesperomannia arbuscula* subsp. *oahuensis* (Hillebr.) comb. nov.

Hesperomannia arborescens var. *oahuensis* Hillebr., Fl. Hawaii. Is., 232, 1888.

Hesperomannia oahuensis (Hillebr.) Degener, Flora Hawaiiensis. 1938.

Hesperomannia oahuensis, like the earlier variety of Hillebrand, was erected on the basis of material from Mt. Kaala, Oahu. Since Degener copied the description of *H. arbuscula* from that of Hillebrand, did not illustrate *H. arbuscula*, and cited the type only as "before 1888," it seems likely that Degener did not study the fertile specimens of *H. arbuscula* (mentioned above) extant at that time. Examination of both Oahu and Maui material reveals the small differences noted in the key above, but close identity in all other characters. Contrary to Degener's description of *H. oahuensis*, leaves with dentate margins may be found in this taxon.

Representative specimens—Oahu, Mt. Kaala and vicinity: *Hillebrand*, 1871 (GH), *Degener and Salucop* 11200 (BISH, GH).

3. *Hesperomannia arborescens* Gray

Hesperomannia arborescens Gray, Amer. Acad. Arts and Sci., Proc. 6: 554, 1886.

The type specimen of *H. arborescens* was collected on Lanai. Subsequent to Gray's description of this species, the first in the genus,

various authors have found difficulty in separating specimens collected later on Oahu from the Lanai material. Rock (1913: 507) and Skottsberg (1944: 512) find considerable similarity. Examination of the type specimens of all the taxa treated here as *H. arborescens*, as well as the numerous specimens which have been collected at various stations in the Koolau Mts., Oahu, reveals that considerable variability exists in this species. The descriptions of Degener for taxa in this group do not allow for this variability, as the comments below will indicate. The characters used by Degener in separating the species of this group have been found to have frequent exceptions and various degrees of intermediacy. For this reason the writer has found it inadvisable to maintain the species proposed by Degener.

3A. *Hesperomannia arborescens* subsp. *arborescens*

The Lanai population of *H. arborescens* has not been encountered since a single tree was seen in 1931, and may now be assumed to be extinct. It is only dubiously separable from Oahu material. As the type specimen and the collection *Munro 492* show, clusters of fewer heads, pubescent involucre bracts, and glandular trichomes on the achenes, thought by Degener to be characteristic only of Oahu plants, may be found in the Lanai material. The latter is maintained as a subspecies here because of its geographical isolation and seemingly slightly longer achenes, although it is possible that longer achenes may be found in future collections of mature Oahu material. The leaves do not match those of a particular Oahu population in that they combine a broad shape with a prominently toothed margin and are glabrous. These leaf characters, however, may all be found in Oahu plants.

Representative specimens—Lanai, near summit: *Mann and Brigham 357* (type and isotype, GH), *Hillebrand, 1874* (GH), *Munro 492* (A, BISH).

3B. *Hesperomannia arborescens* subsp. *Bushiana* (Degener) comb. nov.

Hesperomannia Bushiana Degener, *Flora Hawaiiensis*. 1933.

The small population found at the crest of Halawa ridge, Koolau Range, Oahu, is the most distinctive in the *H. arborescens* complex. The type specimen and the collection *Degener 11927a* show that the heads are uniformly solitary and smaller than in subsp. *Swezeyi*. The smaller head size, however, is not so pronounced as Degener's description indicates. Heads with as few as 30 flowers may be found in specimens of subsp. *Swezeyi* such as *Degener 10007*; *H. Bushiana* was described by Degener as having "approximately 25 flowers" per head. Solitary heads are occasional or frequent in populations treated here as subsp. *Swezeyi*. The combination of narrow leaves with toothed margins is not represented in other populations, but equally narrow leaves and leaves with toothed margins may be found independently in various localities, so the combination of these two characters in subsp. *Bushiana* is not surprising. In view of the closeness of this plant to some populations of subsp. *Swezeyi*, it has seemed preferable to recognize it as a subspecies in this complex, rather than a species coordinate with *H. arborescens*.

Representative specimens—Oahu, Koolau Range, Halawa: *Bush et al. 9981* (type, BISH), *Degener 11927a* (BISH).

3C. *Hesperomannia arborescens* subsp. *Swezeyi* (Degener) comb. nov.

Hesperomannia Swezeyi Degener, *Flora Hawaiiensis*. 1933.

Hesperomannia Bushiana var. *Fosbergii* Degener, *Flora Hawaiiensis*. 1937.

Within this subspecies are included all the populations of the Koolau Range except *H. arborescens* subsp. *Bushiana*. This group has been previously divided by Degener into *H. Swezeyi* and *H. Bushiana* var. *Fosbergii*. He

regards the latter as intermediate between *H. Swezeyi* and *H. Bushiana*. While this variety could be interpreted as being intermediate in number of heads per cluster, it has entire leaves, which are not characteristically found in either *H. Bushiana* or the plants regarded by Degener as *H. Swezeyi*. The type of *H. Swezeyi* is based upon material from the northern end of the Koolau Range. Other similar plants may be found midway along this range, in Kipapa and Halawa canyons, for example, as well as at the east end, on Mt. Konahuanui. While the type of *H. Bushiana* var. *Fosbergii* comes from the middle portion of the range (Kalauao ridge), plants which would have to be referred to this variety by virtue of limited numbers of heads and entire leaves may also be found at the north end of the range (e.g., Fosberg 9419), separated from the Kalauao populations by what could only be interpreted as *H. arborescens* subsp. *Swezeyi*. Thus, *H. Bushiana* var. *Fosbergii* has no geographical unity. Moreover, a number of specimens show intermediacy, as indicated below. It seems best to refer all the Koolau Mts. material except the extreme variant treated here as *H. arborescens* subsp. *Bushiana* to *H. arborescens* subsp. *Swezeyi*. *Hesperomannia arborescens* would seem to be an instance in which a species is broken up by the severe topography found in the Hawaiian Islands into small colonies in which various characters attain degrees of stabilization independently. Taxonomic recognition of portions of such a polymorphic complex does not seem advisable in most instances, since the essential continuity of the variation pattern is then lost.

Representative specimens—Oahu, Koolau Range. Specimens typical of "*H. Swezeyi*": Pupukea-Kahuku trail: Degener and Swezey

4398 (type, BISH), Degener and Shear 3397 (GH); Anahulu trail: Degener et al. 10079 (BISH); S. Opaulea ridge: Suehiro, Sept. 1933 (BISH); Kipapa trail: Hosaka 619 (BISH), Fosberg 9820 (BISH), Degener et al. 10007 (BISH); Halawa trail: Degener 11927 (BISH), Carlquist H3 (BISH, UC); Mt. Konahuanui: Rock 1910 (A), Rock 1912 (GH). Specimens typical of "*H. Bushiana* var. *Fosbergii*": Laie-Waimea trail: Fosberg et al. 9419 (BISH); Waimalu-Hanaiki trail: Judd 1244 (BISH); Waimalu-Kalauao trail: Fosberg 9470 (type, BISH). Specimens showing intermediacy between the above two types: Waimea ridge: Forbes 2035.0 (BISH); Pupukea-Kahuku trail: Degener 7445 (BISH), Degener 7448 (BISH); Wahiaua gulches: Forbes 1703.0 (BISH, UC).

REFERENCES

- DEGENER, OTTO. 1946. *Flora Hawaiiensis* (as a unit; parts published variously). Privately printed.
- FORBES, CHARLES N. 1909. Some new Hawaiian plants. *Bernice P. Bishop Mus., Occas. Paper* 4: 213-223.
- JOHANSEN, DONALD A. 1940. *Plant Micro-technique*. xi + 523 pp. McGraw Hill, New York.
- KOCH, MINNA F. 1930. Studies in the anatomy and morphology of the composite flower. I. The corolla. *Amer. Jour. Bot.* 17: 938-952.
- ROCK, JOSEPH F. 1913. *The Indigenous Trees of the Hawaiian Islands*. 518 pp. Privately printed. Honolulu.
- SKOTTSBERG, CARL. 1944. Vascular plants from the Hawaiian Islands. IV. *Göteborgs Bot. Trädg., Meddel.* 15: 275-531.