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A BIOSYSTEMATIC REVISION OF HAWAIIAN TETRAMOLOPIUM
(COMPOSITAE: ASTEREAE)¹

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INTRODUCTION

Tetramolopium Nees (Compositae: Astereae) is a genus of shrubby perennials that occurs in New Guinea and the Hawaiian Islands. Approximately 25 species are recognized in New Guinea (van Royen, 1981) and eleven species are found in Hawaii. None of the species occurs in both areas. The New Guinean species grow in submesic to mesic habitats in the high mountains above 2,000 m. and are small caespitose or decumbent alpine shrubs. In contrast, the Hawaiian species occur in specialized xeric to submesic habitats ranging in elevation from sea level to 3,300 m. The Hawaiian taxa vary in habit from prostrate rosette perennials to tall upright shrubs. Despite their broad altitudinal range, all but one are considered to be rare and endangered, and several are probably extinct (U.S. Fish and Wildlife Service, 1980).

Previous authors have considered that *Tetramolopium* originated in New Guinea and was later dispersed to the Hawaiian Islands (Fosberg, 1948; Smith, 1977). Smith (1977) considered the genus to be the descendant of late Tertiary immigrants into New Guinea from Australasia. He further suggested that *Tetramolopium* arose as a neo-endemic in New Guinea during the Pleistocene and was later dispersed to the Hawaiian Islands. The affinities of *Tetramolopium* clearly support this contention. *Tetramolopium* is most closely related to Australian genera of Compositae, notably *Vittadinia* A. Rich. and *Camptacra* N. Burb. All three genera possess subulate style appendages, prominent barbellate pappus bristles, and several similar achene features. *Vittadinia*

occurs in Australia and New Zealand; *Camptacra* occurs in New Guinea and Australia (Burbidge, 1982).

Whereas New Guinea originated as part of the Australian continental land mass, with a geologic history reaching back to the Paleozoic (Loffler, 1980), the Hawaiian Islands are an oceanic chain of volcanoes that, as regards their major components, are of quite recent origin. The major Hawaiian Islands, beginning with the oldest island, Kauai, become progressively younger to the southeast, ending with the youngest island, Hawaii (Dalrymple et al., 1973). Kauai is approximately 5.6 million years old, and Hawaii is less than 0.7 million years old. As emphasized by Carlquist (1980), since the Hawaiian Islands have always been oceanic, their biota has resulted from chance immigrations from areas throughout the Pacific Basin.

Chance immigrants to the Hawaiian Islands have developed into a flora long noted for its exceptional diversity. The few recent biosystematic studies of Hawaiian plants have contributed much important new information concerning the evolutionary history and diversity of the flora. These studies have been especially important in view of the past and continuing devastation of the native Hawaiian flora (Lamoureux, 1971). Although the number of Hawaiian plant genera monographed or revised in the past 60 years is relatively high, much of the work is woefully inadequate, with the exception of certain recent biosystematic investigations. Gillett (1972, 1975) emphasized the lack of field studies in the preparation of many early monographs; the use of strictly traditional methods, without adequate field studies, does not permit an accurate assessment of variation patterns.

Previous studies of Hawaiian *Tetramolopium* clearly illustrate Gillett's remarks. In the most recent revision (Sherff, 1935), the circumscription of taxa is based entirely on studies of scanty herbarium material; several taxa are described on the basis of a single collection each. One result of past reliance only on herbarium specimens for taxonomic studies of *Tetramolopium* is that the generic limits of the Hawaiian taxa have been subject to widely differing opinions. The taxa have been lumped into *Vittadinia* (Gray, 1861), split between *Vittadinia* and *Tetramolopium* (Bentham, 1873), unified into *Tetramolopium* (Hillebrand, 1888), and recently split again between a new genus, *Luteidiscus*, and *Tetramolopium* (St. John, 1974).

In view of the differences of taxonomic opinion on generic limits, the great but largely undocumented morphological and ecological diversity, the precarious existence of the extant taxa, and the presumed progenitor-derivative relationship to the disjunct New Guinean species, biosystematic studies of the Hawaiian species were undertaken as a first step toward understanding their evolutionary relationships. The objectives of the studies were: (1) to provide a classification for Hawaiian *Tetramolopium* based on field, laboratory, and greenhouse investigations, and (2) to document the biological and ecological diversity of the taxa and determine whether they constitute a natural assemblage derived from a single ancestral colonization.

ACCEPTED TAXA OF HAWAIIAN TETRAMOLOPIUM

A. Sect. *Alpinum* Lowrey, sect. nov. (including all New Guinean taxa)

1. *T. humile* (A. Gray) Hillebr.

a. subsp. *humile*

i. var. *humile*

ii. var. *sublaeve* Sherff

b. subsp. *haleakalae* Lowrey, subsp. nov.

- B. Sect. *Tetramolopium*
2. *T. capillare* (Gaud.) St. John
 3. *T. filiforme* Sherff
 - i. var. *filiforme*
 - ii. var. *polyphyllum* (Sherff) Lowrey, comb. et. stat. nov.
 4. *T. remyi* (A. Gray) Hillebr.
 5. *T. rockii* Sherff
 - i. var. *rockii*
 - ii. var. *calcisabulorum* (St. John) Lowrey, comb. et. stat. nov.
 6. *T. sylvae* Lowrey, sp. nov.
 7. *T. tenerrimum* (Less.) Nees
- C. Sect. *Sandwicense* Lowrey, sect. nov.
8. *T. lepidotum* (Less.) Sherff
 - a. subsp. *lepidotum*
 - b. subsp. *arbusculum* (A. Gray) Lowrey, comb. et. stat. nov.
 9. *T. conyzoides* (A. Gray) Hillebr.
 10. *T. arenarium* (A. Gray) Hillebr.
 - a. subsp. *arenarium*
 - i. var. *arenarium*
 - ii. var. *confertum* Sherff
 - b. subsp. *laxum* Lowrey, subsp. nov.
 11. *T. consanguineum* (A. Gray) Hillebr.
 - a. subsp. *consanguineum*
 - b. subsp. *leptophyllum* (Sherff) Lowrey, stat. nov.
 - i. var. *leptophyllum*
 - ii. var. *kauense* Lowrey, var. nov.

MORPHOLOGY

Floral morphology was studied using florets preserved in FAA from rehydrated herbarium specimens, and from living plants grown under uniform conditions. Dried florets were rehydrated by soaking in modified Pohl's softening agent (1% solid aerosol OT, 74% distilled water, 25% ethanol). The corollas, stamens, and styles were mounted in Hoyer's mounting medium. Measurements and observations of microscopic characters were made using a compound binocular microscope fitted with an optical micrometer.

Plants grown from field-collected seed were kept in a greenhouse at the University of California Botanical Garden. Achenes were selected at random from mass lot collections and were planted in 1-inch peat pots containing U.C. potting soil mixture. Four achenes per pot were planted and placed in the greenhouse under ambient light. Individual seedlings were separated when approximately 3 cm. tall and transplanted into 4-inch plastic pots also containing U.C. soil mix. The pots were maintained in the greenhouse under ambient temperature and light conditions. They were watered twice daily. The plants were collected and pressed in the same manner as field-collected material, to serve as vouchers for these experimental studies.

Detailed measurements were made on 100 herbarium specimens (borrowed from other herbaria) representing 30 populations, from personal field collections representing 18 populations, and from seeds collected from these same 18 populations and grown in the greenhouse. Seventeen vegetative and 38 reproductive characters were measured. These measurements were made to assess the phenetic relationships in Hawaiian *Tetramolopium*. A minimum of 20 measurements per character was made for each population. The measurements were made on organs from approximately

equivalent positions obtained from the broadest and/or longest point of the organ. A total of 500 herbarium specimens (detailed measurements were not made on all of these), 42 field collections, and 18 greenhouse populations has been studied. Specimens of all New Guinean taxa were examined for comparison with the Hawaiian species.

HABIT, BRANCHING PATTERN, AND STEM

The habit of *Tetramolopium* varies from caespitose, decumbent, prostrate, or dwarf shrubs in sects. *Tetramolopium* and *Alpinum* to upright shrubs in sect. *Sandwicense*. The habit is determined, to a large extent, by branching pattern and shoot orientation. All species have axillary branching, i. e., sympodial branching related to the development of a terminal capitulescence. This development results in continuation of the longitudinal growth of shoots from one or more of the uppermost axillary buds. Capitulescence development leading to sympodial branching occurs repeatedly on the plant. The uppermost axillary buds expand into shoots and give the false impression (depending on the number of buds involved) that branching is dichotomous or even verticillate. The number of buds that develop at any one point is variable but usually is two or three. Several species may produce adventitious roots along the stem.

The length of the main stem that develops before the first capitulescence is formed plays an important role in determining adult habit. Those species having a short main axis (less than 5 cm.) are basally branched, and those having a long axis are apically branched. Basal branching coupled with plagiotropic (horizontally oriented) shoots produces a decumbent or prostrate shrub. This situation characterizes sects. *Tetramolopium* and *Alpinum*. Apical orthotropic (vertically oriented) shoots with apical branching characterize upright shrubs as in sect. *Sandwicense*.

The basal portions of the stems are woody in all species. Species of sect. *Tetramolopium* tend to have lesser amounts of secondary growth than do those in the other sections. *Tetramolopium tenerrimum* has very thin and delicate branches.

LONGEVITY

Individuals of *Tetramolopium* are probably not long-lived. It is difficult to determine the longevity of plants in the field, but individuals showing signs of great age were not detected during field study. Individuals of taxa cultured in the greenhouse have survived for three years. They do exhibit marked dieback or senescence in the second year. Demographic studies of field populations are needed to determine the population structure of the different species. Such studies might provide a clue as to why most of the species are so rare.

LEAVES

Phyllotaxy is alternate-spiral. The leaf internodes are very short; as a result, leaves are very congested on the shoots and may form rosettes or appear to be whorled in some species. As the stems elongate and mature, the lower leaves senesce and die. This senescence pattern produces mature plants having leaves on the distal portions of the branches only, imparting a brushlike appearance to upright plants or a rosette form to prostrate or decumbent plants.

The leaf is usually differentiated into blade, petiole, and leaf base. The demarcation between blade and petiole is not sharply marked. The blade is attenuated into the petiole with the petiolar region retaining wings of laminar tissue. In taxa having linear or filiform leaves the boundary between blade and petiole is not readily discernible. Such leaves are deemed sessile. After the leaves fall, the decurrent leaf bases persist. The mature stems have a tuberculate surface due to the persistent leaf bases.

Leaf shape varies from filiform or linear to oblanceolate or spatulate. Strictly spatulate leaves are found only in species of sects. *Alpinum* and *Tetramolopium*. In *T. remyi* and *T. capillare* of sect. *Tetramolopium*, the adult leaves are linear-oblanceolate but are strongly involute, thus appearing linear or filiform. However, the juvenile leaves are not involute and are obviously oblanceolate or spatulate.

All species have simple leaves. The margin may be entire or dentate. The dentation of leaves is a very plastic character both within a taxon and even on the same plant. *Tetramolopium lepidotum* is the only species having prominently dentate adult leaves. The populations of this species on Oahu have exclusively dentate leaves with two-six prominent teeth. The number and length of the teeth differ among populations, but these characters are maintained when plants are grown under uniform conditions. Populations of *T. lepidotum* on Lanai have a mixture of dentate and entire leaves on single individuals or entire leaves only. *Tetramolopium consanguineum* subsp. *leptophyllum* has dentate juvenile leaves but entire adult leaves. This heteroblastic leaf development is also present in one population of *T. sylvae* and perhaps in *T. conyzoides* and *T. arenarium* (as judged from herbarium specimens). Leaf length and width have also been found to be very plastic, depending on the environmental conditions. Greenhouse plants exhibited great variability depending on the light and moisture regime. In view of this variability, leaf dentation and size are not accepted as reliable taxonomic characters, despite their use in past treatments.

Leaves are pinnately veined in all species. There is a difference in the surface conspicuousness of the veins that is useful in recognizing sections. The venation pattern is prominent in sect. *Sandwicense* but obscure in the other two sections. The reasons for this difference are discussed in the section on leaf anatomy.

Leaves of several taxa exhibit specialized morphologies that may reflect adaptation to particular habitats. The involute or filiform leaves of *Tetramolopium remyi*, *T. capillare*, and *T. filiforme* are indicative of xeromorphy. *Tetramolopium sylvae* has succulent leaves that may be a response to salt spray present in its maritime environment. The dense pubescence exhibited by some taxa may be important in regulation of temperature and light intensity.

INDUMENT AND TRICHOMES

The herbage of *Tetramolopium* exhibits great diversity in indument. These patterns are useful in delimiting taxa at both specific and infraspecific levels. The pubescence characters are genetically controlled. Thus, the patterns observed in the field are maintained with little change in plants grown under uniform environmental conditions. The range in variation is illustrated by the nearly glabrous condition of *T. sylvae* as contrasted with the densely pubescent species *T. rockii*.

The trichomes of *Tetramolopium* consist of two types: glandular (type I) and nonglandular (type II). Both types are usually multicellular and show diversity in size and shape. All taxa possess both types but in differing amounts. The different mixtures

TABLE 1. DISTRIBUTION OF TRICHOME TYPES IN TETRAMOLOPIUM

	stem	leaf blade	peduncle	phyllaries
sect. <i>Tetramolopium</i>				
<i>T. capillare</i>	I	I	*I, II	I
<i>T. filiforme</i> var. <i>filiforme</i>	I	*I, II	I	I
<i>T. filiforme</i> var. <i>polyphyllum</i>	*I, II	*I, II	*I, II	*I, II
<i>T. remyi</i>	*I, II	I	II	I
<i>T. rockii</i> var. <i>rockii</i>	*I, II	*I, II	*I, II	*I, II
<i>T. rockii</i> var. <i>calcisabulorum</i>	I, *II	I, *II	I, *II	I, *II
<i>T. sylvae</i>	I	*0 or (I, II)	I	I
<i>T. tenerrimum</i>	II	*I, II	II	I
sect. <i>Alpinum</i>				
<i>T. humile</i> subsp. <i>humile</i> var. <i>humile</i>	I, *II	I, *II	I	I
<i>T. humile</i> var. <i>sublaeve</i>	*I, II	*I, II	I	I
<i>T. humile</i> subsp. <i>haleakalae</i>	I, *II	I, *II	I	I
sect. <i>Sandwicense</i>				
<i>T. arenarium</i>	I, *II	I, *II	I, *II	I, *II
<i>T. consanguineum</i> subsp. <i>consanguineum</i>	I, *II	*I, II	I, *II	I
<i>T. consanguineum</i> subsp. <i>leptophyllum</i> var. <i>leptophyllum</i>	I	*I, II	*I, II	I
<i>T. consanguineum</i> var. <i>kauense</i>	I	*I, II	I	I
<i>T. conyzoides</i>	I, *II	I, *II	I, *II	0
<i>T. lepidotum</i>	I, *II	*I, II	I, *II	I

I = glandular trichomes; II = non-glandular trichomes; * = dominant trichome type; 0 = glabrous.

are responsible for the various observable indument patterns. Different parts of the same plant often have different pubescence patterns (TABLE 1).

POLLEN

Pollen grains of *Tetramolopium* are tricolporate. The exine is densely echinate. The diameter of the lumen ranges from 35 to 65 μm . but most species have grains 40–50 μm . in diameter. *Tetramolopium humile* has the largest pollen grains, with lumen diameters of 55–65 μm .

CAPITULESCENCE

Capitulescence is a term used to denote the arrangement or grouping of heads on a branch. The capitulescence is terminal in *Tetramolopium*. It may appear to be lateral due to sympodial branching.

Both simple (monocephalous) and compound (polycephalous) capitulescence types are present. The simple capitulescence consists of a well-developed peduncle supporting the head. The peduncle is sparsely bracteate, with the bracts reduced acropetally. The bracts are generally subulate or filiform, but in *Tetramolopium rockii* they are spatulate. The length of the peduncle may be a useful taxonomic character at the specific level. A simple capitulescence occurs only in sects. *Alpinum* and *Tetramolopium*.

Compound capitulescences are corymbose-paniculate or rarely subumbellate. The corymbose-paniculate type is restricted to sect. *Sandwicense* and *Tetramolopium humile* subsp. *humile*. The subumbellate condition occurs only in *T. filiforme*. This species usually has a simple capitulescence, but under optimal growth conditions it may produce two–four heads per branch. No individual of *T. filiforme*

has been observed to possess entirely compound capitulescences. Within sect. *Sandwicense* each species has a characteristic range in number of heads per capitulescence; this is a useful taxonomic character.

CAPITULA

The shape of the involucre varies from cylindrical in *Tetramolopium humile*, campanulate or turbinate in sect. *Sandwicense*, to broadly hemispheric in sect. *Tetramolopium*. There is a wide range in capitulum size from 2.5 mm. wide in *T. conyzoides* to 15 mm. wide in *T. remyi*. The size of the head is correlated with capitulescence type. Those species with compound capitulescences have much smaller heads than do the species with simple capitulescences. Head size is genetically controlled. Hybrids between large-headed taxa and those with small heads have intermediate-sized capitula.

All capitula are erect at anthesis. The heads of *Tetramolopium remyi* are deflexed prior to anthesis and become erect at anthesis.

PHYLLARIES

The phyllaries are imbricated in three-four series and are free. The bracts in the outermost series are very much shorter and usually much more pubescent than the inner ones. The margins are usually scarious-hyaline and may be entire or variously lacerate or dentate. *Tetramolopium consanguineum* can be distinguished on the basis of its prominently denticulate phyllary margins. Phyllary shape varies from lanceolate to nearly linear. The apex is generally acute or acuminate, rarely obtuse, as in *T. consanguineum*. The phyllary tips are often purplish.

RECEPTACLE

The receptacle is uniformly flat or slightly convex, naked, and alveolate. The diameter of the receptacle varies in conjunction with the head size.

RAY FLORETS

The ray florets are pistillate. The style morphology is uniform throughout the genus. The style has two penicillate branches devoid of external papillae. The corolla is distinctly divided into lamina and tube. The lamina is linear or rarely filiform and is either 2- or 3-lobed apically. The lamina is conspicuous in species of sects. *Tetramolopium* and *Alpinum*, being longer than 3 mm., while sect. *Sandwicense* has a much reduced lamina, generally less than 3 mm. long. This reduction is carried to the extreme in *T. conyzoides*, which has filiform ligules resembling those of *Conyza*.

DISK FLORETS

The disk corollas of *Tetramolopium* are either yellow or a variation of maroon. Each species has a dominant color; however, the maroon-flowered species may produce yellow-flowered individuals. It is interesting that no individuals with maroon disk corollas are known to be produced by those species with yellow disk corollas. Apparently the species that produce yellow floral pigments do so exclusively, while those that have maroon pigments have the ability also to produce yellow ones.

The corolla color is under genetic control. The color observed in an individual in

the field is maintained in progeny grown from seed in the greenhouse. Crosses between yellow- and maroon-flowered plants all produced F_1 hybrids with yellow corollas. It is not known whether this is simple dominance or is due to epistasis.

In past treatments of *Tetramolopium* much emphasis has been placed on the color of disk floret corollas. St. John (1974) proposed a new genus, *Luteidiscus*, for those species with yellow disk florets. Although there is a tendency for disk floret corolla color to be correlated with sectional boundaries, significant variability invalidates the establishment of a genus solely on this basis. Species in sect. *Tetramolopium* have yellow corollas except *T. filiforme*, which, though it has mostly maroon disk corollas, does produce plants with yellow corollas. Sections *Alpinum* and *Sandwicense* consist of species with maroon corollas, but in each taxon a few individuals with yellow corollas are produced.

The disk corollas are strictly pentamerous. The apices of the corolla lobes are abaxially papillate. With the exception of *Tetramolopium humile* all species have infundibular corollas. *Tetramolopium humile* has tubular corollas that are very similar to those of several New Guinean species. The length of the corollas ranges from more than 7 mm. in *T. humile* to 2.2 mm. in *T. conyzoides*. The corollas of species in sect. *Sandwicense* are distinctly shorter than those in the other two sections. This length difference is also reflected in corolla tube length (that portion of the corolla from the base to point of attachment of the filaments).

Disk florets are either hermaphrodite or functionally staminate. Functionally staminate florets, though possessing both styles and ovaries, produce only pollen and have sterile achenes. The sexual condition of the florets is constant within a species and generally follows sectional boundaries with the exception of *Tetramolopium humile* in sect. *Alpinum*. Section *Tetramolopium* has functionally staminate disk florets exclusively, as do the New Guinean taxa in sect. *Alpinum*. The sole Hawaiian species of sect. *Alpinum*, *T. humile*, and all taxa in sect. *Sandwicense* have hermaphrodite disk florets only.

STAMENS

Shape of the anthers is similar in all taxa. There are differences in length of the anther sacs which positively correlate with the length of disk corollas. *Tetramolopium humile* has the longest anthers (1–1.5 mm.) and the longest corollas (6.5–7.5 mm.); *T. conyzoides* and *T. consanguineum* have the shortest anthers (0.5–0.8 mm.) and the shortest corollas (2.2–3 mm.).

The anthers of all taxa have an apical appendage that differs in both size and shape from species to species. The shape varies from deltoid or linear to lanceolate. The length of the appendage includes only that portion beyond the anther thecae.

STYLES

The shape of the style branches, regardless of the sexual condition of the disk floret, is linear-lanceolate or, rarely, linear. Each branch has a prominent apical appendage. These appendages are ornamented externally with long papillate "pollen collecting hairs". The shape of branches does not change with respect to the sexual condition of the floret. There is, however, a difference in the length of the branch covered by the collecting hairs. Perfect florets generally have collecting hairs only on the upper half of the branches, while the functionally staminate florets have collecting hairs along their

entire length. This condition is similar to that found in several Australian genera (Grau, 1977). Style branches of the functionally staminate florets lack stigmatic lines. *Tetramolopium humile* has exceptionally long style branches that are extruded from the anther tube and become divaricate. The other taxa never have the style long-exserted or with divaricate branches.

At the base of the style is a nectarium which produces large quantities of nectar, considering the small size of the floret. In the early morning, droplets of nectar may be seen in the mouth of the corollas. All species have been observed to produce some nectar. The ability to produce nectar is not affected by the sexual condition of the disk floret.

ACHENES

The achenes of *Tetramolopium* are strongly compressed laterally with prominently thickened margins. The compressed faces of the achenes are usually 1- or 2-nerved but show a great deal of variability among taxa. The achenes of *T. humile* are obsoletely or obscurely 1-nerved, while those of *T. consanguineum* subsp. *leptophyllum* may have as many as seven nerves per face. The number of nerves per achene may vary within a population or even within one head. Despite this variability each taxon has a predominant number and configuration of nerves.

The achene is generally obovate, oblanceolate, or obconic in outline. *Tetramolopium humile* is exceptional in having fusiform-cylindric achenes. Achenes are usually pubescent but may be glabrous as in *T. sylvae*, *T. filiforme* var. *polyphyllum*, and *T. tenerrimum*. The degree of pubescence seems to be positively correlated with the amount of foliage pubescence. When the leaves are densely pubescent, the achenes are also densely pubescent. This phenomenon is particularly well illustrated by the varieties of *T. rockii*. *Tetramolopium rockii* var. *calcisabulorum* is both glandular and sericeous with correspondingly greater achene pubescence than *T. rockii* var. *rockii*, which has only glandular-pubescent foliage.

Achene pubescence consists of varying combinations of the typical Compositae "zwillingshaare" and capitate glands. The twin hairs are often attached basally to a single-celled gland. The achenes of *Tetramolopium humile* are unusual in having large, spherical, stalked glands filled with a sticky substance.

The main source of variability in achene width is largely due to the sex expression of the disk florets. Those species with functionally staminate disk florets have linear, sterile, disk achenes. Those species with perfect disk florets produce disk achenes identical in shape to the ray achenes.

PAPPUS

The pappus consists of barbellate bristles. The bristles may be in one or two series. Section *Tetramolopium* has exclusively a uniseriate pappus. *Tetramolopium humile* has a biseriate pappus with the outer bristles slightly shorter and less stout. The pappus in *T. consanguineum* is also biseriate, with an outer row of very short bristles. The remaining species in sect. *Sandwicense* have a uniseriate pappus.

There are distinct differences in overall pappus length and pappus color. *Tetramolopium humile* has very long bristles (up to 6 mm. long or more). The bristles are an unusual yellowish or fulvous color. The pappus bristles of species in sect. *Tetramolopium* are from 2.1 to 4 mm. long and are white. Pappus bristle length in sect.

Sandwicense varies from 1.6 to 4 mm. long, and the bristles are generally brownish or off-white. The short pappus in *T. consanguineum* subsp. *leptophyllum* and *T. conyzoides* is brittle, easily breaking off from the achene. The brittleness and shortness of the bristles in these taxa would seem to be an example of the precinctiveness seen in many island taxa (Carlquist, 1974).

LEAF ANATOMY

Leaf anatomy was studied using slides prepared from preserved collections and from rehydrated herbarium specimens. Field material was collected as whole branches from several different individuals in a population. They were fixed in standard FAA fixative. The fixed specimens were later transferred from FAA to 70% ethanol for prolonged storage.

Both temporary hand sections and permanent microtome sections were utilized. The hand-sectioned material was stained in 1% aqueous Toluidine Blue O. Fixed plant material stored in 70% ethanol was dehydrated in a standard tertiary-butyl alcohol series (Berlyn and Miksche, 1976) and embedded in paraffin blocks. The blocks were sectioned on a rotary microtome to a thickness of 15 μ m. The sections were stained in safranin-fast green (Johansen, 1940) and then mounted in Permount.

Major features of leaf anatomy that are of diagnostic value are listed in TABLE 2. The leaf epidermis of *Tetramolopium* is uniseriate. The stomata of all species are anomocytic (ranunculaceous). Substomatal chambers are well developed (FIGURE 1A, B). Druses or raphides are present in the epidermal cells of most species.

The mesophyll of all species is isolateral. The palisade parenchyma is generally one-two cell layers thick and compact, but in *Tetramolopium sylvae* (FIGURE 1E) and *T. rockii* the palisade parenchyma is three-four cell layers thick and less compact. Nonphotosynthetic "storage" parenchyma tissue is present in species of sect. *Tetramolopium*; it is rare or absent in the other sections. The storage parenchyma is especially prominent in *T. sylvae* (FIGURE 1E). Leaves of all species have bundle sheaths one-two cells thick. Section *Sandwicense* is distinctive in having bundle sheath extensions (FIGURE 1B, D). Bundle sheath extensions are associated only with major veins. Due to these bundle sheath extensions the veins are visible in intact leaves. In leaves without sheath extensions, the veins are obscured by the palisade parenchyma.

TABLE 2. SELECTED LEAF ANATOMICAL FEATURES IN HAWAIIAN TETRAMOLOPIUM

	storage parenchyma	bundle sheath extension	secretory cavities	brachysclereids
sect. <i>Alpinum</i>				
1. <i>T. humile</i>	-	-	+	rare
sect. <i>Tetramolopium</i>				
2. <i>T. filiforme</i>	+	-	+	+
3. <i>T. remyi</i>	+	-	+	+
4. <i>T. rockii</i>	++	-	+	++
5. <i>T. sylvae</i>	++	-	few	+
6. <i>T. tenerrimum</i>	N.A.	-	+	+
sect. <i>Sandwicense</i>				
7. <i>T. consanguineum</i>	-	+	++	+
8. <i>T. conyzoides</i>	-	+	++	+
9. <i>T. lepidotum</i>	-	+	++	+

Symbols: ++ = abundant; + = frequent; - = lacking; N.A. = information not available from material.

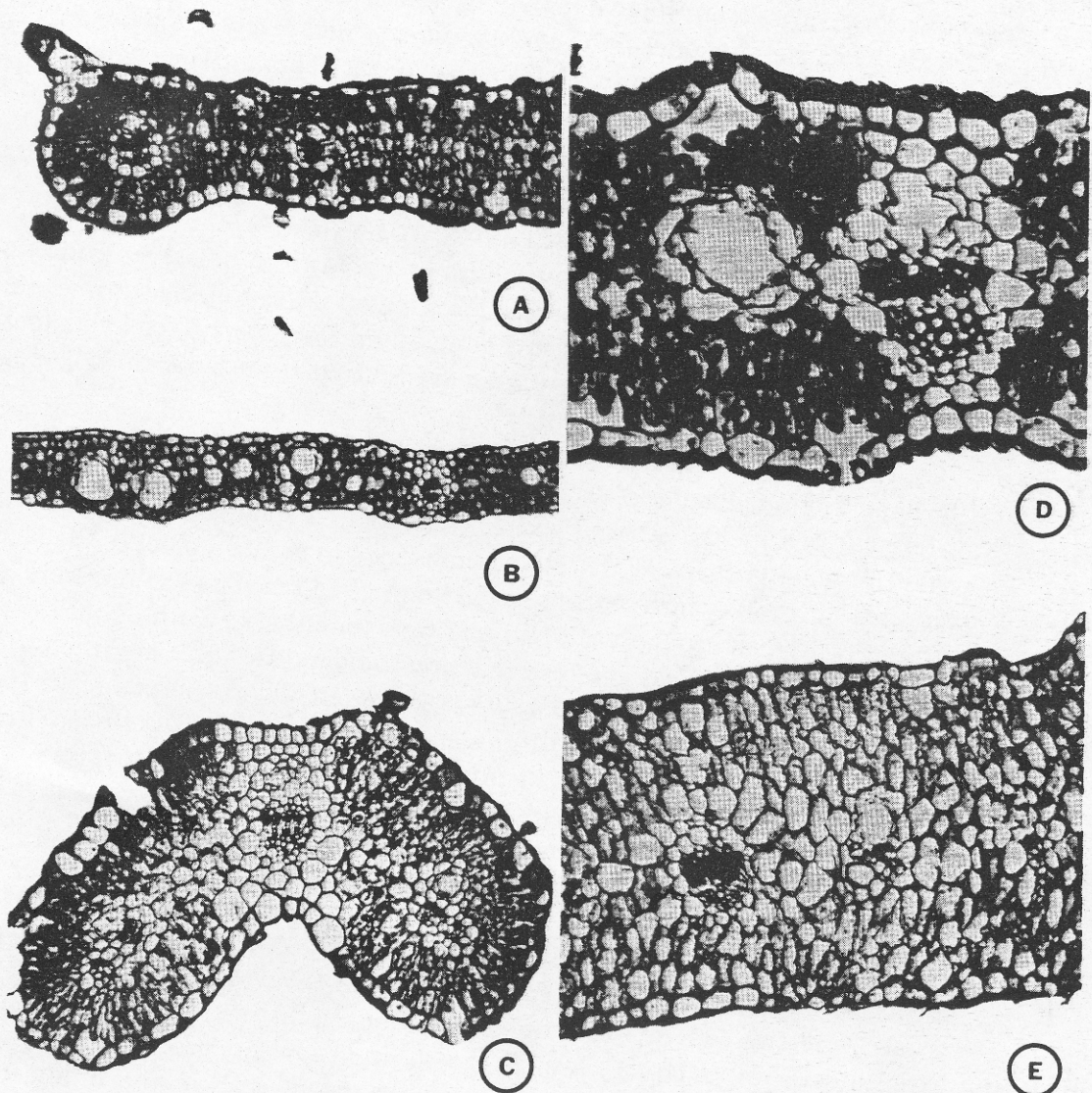


FIGURE 1. Leaf transections of *Tetramolopium* with abaxial surface toward top of page. Micrographs A, B, C, and E $\times 92$; micrograph D $\times 184$. A, Lowrey 437 (*T. humile* var. *humile*), showing compact isolateral mesophyll and large substomatal chambers. B, Lowrey 416 (*T. lepidotum* subsp. *lepidotum*), with thin lamina, large secretory cavities, and bundle sheath extensions. C, Lowrey 415 (*T. remyi*), whole leaf showing involute margins and small surface-to-volume ratio. D, Lowrey 414 (*T. consanguineum* var. *leptophyllum*), showing bundle sheath extensions and prominent secretory cavity. E, Lowrey 418 (*T. sylvae*), with thick lamina and prominent nonphotosynthetic storage parenchyma.

The sheath extensions are responsible for the prominent appearance of the major veins in leaves of sect. *Sandwicense*.

Secretory cavities are a prominent feature of *Tetramolopium* leaves. All species have secretory cavities abaxial to some or all veins, but species of sect. *Sandwicense* may have secretory cavities positioned laterally to the bundles (FIGURE 1D). The cavities are particularly well developed in sect. *Sandwicense*, where they may extend to nearly the entire thickness of the mesophyll (FIGURE 1D).

Brachysclereids occur in most leaves of *Tetramolopium*; however, they are rare in *T. humile*. The sclereids are found only in the median portion of the leaf, between the

two palisade layers. Leaves of *T. rockii* contain the most prominent concentrations of sclereids. Collenchyma tissue is associated with the midveins of leaves in all species. Bundle sheath fibres are rarely found in the midveins of leaves of *T. humile*. The relatively small size of *Tetramolopium* leaves precludes the need for pronounced development of mechanical support tissue.

As suggested by Anderson and Creech (1975), leaf anatomy often reflects environmental adaptation. The environmental conditions encountered by extant species of *Tetramolopium* closely match those that might be predicted by the leaf anatomy. Thick leaves and abundant water storage tissue often occur in plants of saline or extremely xeric habitats (*T. rockii* and *T. sylvae*). Isolateral mesophyll is characteristic of leaves subjected to high light intensities (all species). Thin leaves and bundle sheath extensions may be indicative of increased moisture availability (sect. *Sandwicense*). Thick cuticle, small surface-to-volume ratio, and involute leaf margins indicate xeromorphy (FIGURE 1C) (*T. remyi*, *T. capillare*, and *T. filiforme* var. *filiforme*). Although these features represent environmental adaptations, they are all maintained in plants grown under uniform conditions, indicating not only that they are genetically controlled but also that they are expressed regardless of the ambient environmental conditions.

Several features of the leaf anatomy are useful in delimiting the sections of *Tetramolopium* (TABLE 2). *Tetramolopium* sect. *Sandwicense* is characterized by having bundle sheath extensions, thin leaves, prominent secretory cavities, and little water storage tissue. Section *Tetramolopium* possesses water storage tissue, thick leaves, and prominent brachysclereids. Section *Alpinum* (FIGURE 1A) is distinctive in that it lacks bundle sheath extensions, storage parenchyma, and prominent brachysclereids, all features of the latter two sections. Various features of the leaf anatomy may be distinctive at the species level as noted above.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

The past distribution and ecology of Hawaiian *Tetramolopium* are difficult to ascertain, due to the recent extinction of many specific and infraspecific taxa. Even the extant taxa have undergone severe restriction in their distributions. This unfortunate circumstance in Hawaii is not unique to *Tetramolopium*. The Hawaiian flora in general has been severely devastated (Lamoureux, 1971). For reasons that are not entirely known, most species of *Tetramolopium* have probably always been rare (based on herbarium collection data). They are, then, particularly vulnerable to extirpation.

There is a notable lack of information available from previous collectors. Specimen labels often lack specific locality and habitat data. As a result, the former distributions and habitat preferences of extinct taxa must be inferred from knowledge of extant taxa and from anecdotal accounts of the past natural history of the Hawaiian Islands made before extensive disturbance by animals or man. Information concerning the distribution and ecology for each recognized taxon follows. The taxa are grouped according to sectional affinity.

TETRAMOLOPIUM SECT. ALPINUM

Section *Alpinum* in Hawaii is restricted to alpine areas. The alpine zone in Hawaii includes those regions above 1,900 m. in elevation (Carlquist, 1980). Only the islands of

Maui and Hawaii have areas that are high enough to qualify for this designation. These regions include the slopes and crater of Haleakala (volcano) on East Maui and the slopes of and saddle areas between the volcanos of Mauna Kea, Mauna Loa, and Hualalai on Hawaii. The distribution of *Tetramolopium humile*, the sole Hawaiian species in the section, includes all these alpine areas (FIGURE 2). Exceptionally, this species also occurs at 1,300 m. near Kilauea on Hawaii. Though this area is technically out of the alpine zone, it is climatically and edaphically similar to the true alpine areas (Carlquist, 1980).

Tetramolopium humile has two subspecies, each of which occurs on different islands. *Tetramolopium humile* subsp. *humile* grows in alpine zones on the island of Hawaii and *T. humile* subsp. *haleakalae* is restricted to similar zones on Haleakala on East Maui. Both subspecies are densely pubescent, caespitose dwarf shrubs typical of alpine vegetation.

The altitudinal range of the species is from (1,300–) 1,900 m. to about 3,300 m. At the upper end of its range *Tetramolopium humile* occurs on xeric barren cinder slopes or in rock crevices. It is found in more mesic habitats having denser (but still open) vegetation at the lower end of its range. Here the species occurs in open patches of the community, often in rock crevices. It does not tolerate shading well. Occasional individuals have been observed growing in very shaded areas among rocks, but they show obvious signs of etiolation and have somewhat wider and longer leaves than plants in full sun.

Tetramolopium humile is the most common species of the genus in Hawaii. This is perhaps largely due to its ability to tolerate a wide range of environmental conditions. Its occurrence in pioneer habitats at high elevations also makes it less vulnerable to disturbance by animals or man.

TETRAMOLOPIUM SECT. TETRAMOLOPIUM

Section *Tetramolopium* consists of six species that occur on Oahu, Molokai, Maui, and Lanai (FIGURE 3). The taxa are prostrate, decumbent, or dwarf shrubs. They usually inhabit xeric exposed habitats below 1,000 m. Morphological and ecological variation within this section is the greatest in the genus. The only known coastal species occur in this section, and examples of edaphic endemism and xeromorphy are also present.

Tetramolopium capillare is known only from a small area on West Maui. The few collections of the species were obtained from the mountain slopes between Lahainaluna and Wailuku at about 400 m. This area is very dry and is occupied by dry forest scrub. This vegetation type is dominated by *Dodonaea* and *Sida*. *Tetramolopium capillare* has a decumbent or sprawling habit and strongly involute leaves. The involute leaves are probably a xeromorphic adaptation to the dry habitat. My several attempts to locate the species were unsuccessful. It very likely has been extirpated due to extensive overgrazing throughout its distributional range.

The second species in the section, *Tetramolopium remyi*, occupies a habitat similar to that of *T. capillare*. It occurred historically on both western Maui and Lanai. The distribution on Maui extended from Lahaina to Wailuku and on Lanai from Kahinahina Ridge to Awalua Ridge. The species now survives only on Lanai. The altitudinal range of *T. remyi* is 150–770 m. Its habitat in this zone on Maui was similar to that of the preceding species. On Lanai it occurs on nearly barren red lateritic soils in a highly

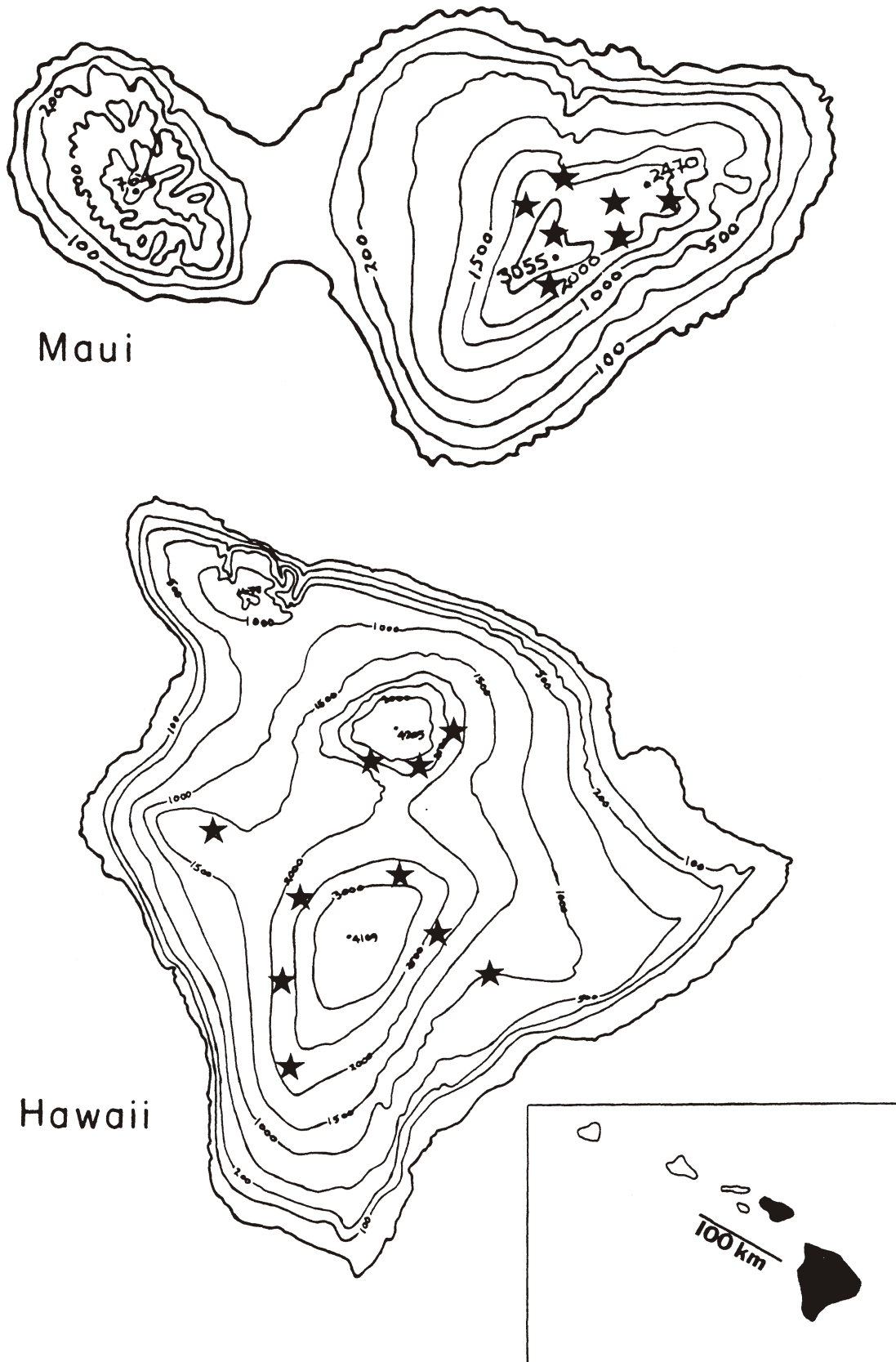


FIGURE 2. Distribution map of species in *Tetramolopium* sect. *Alpinum*. ★ = *T. humile*.

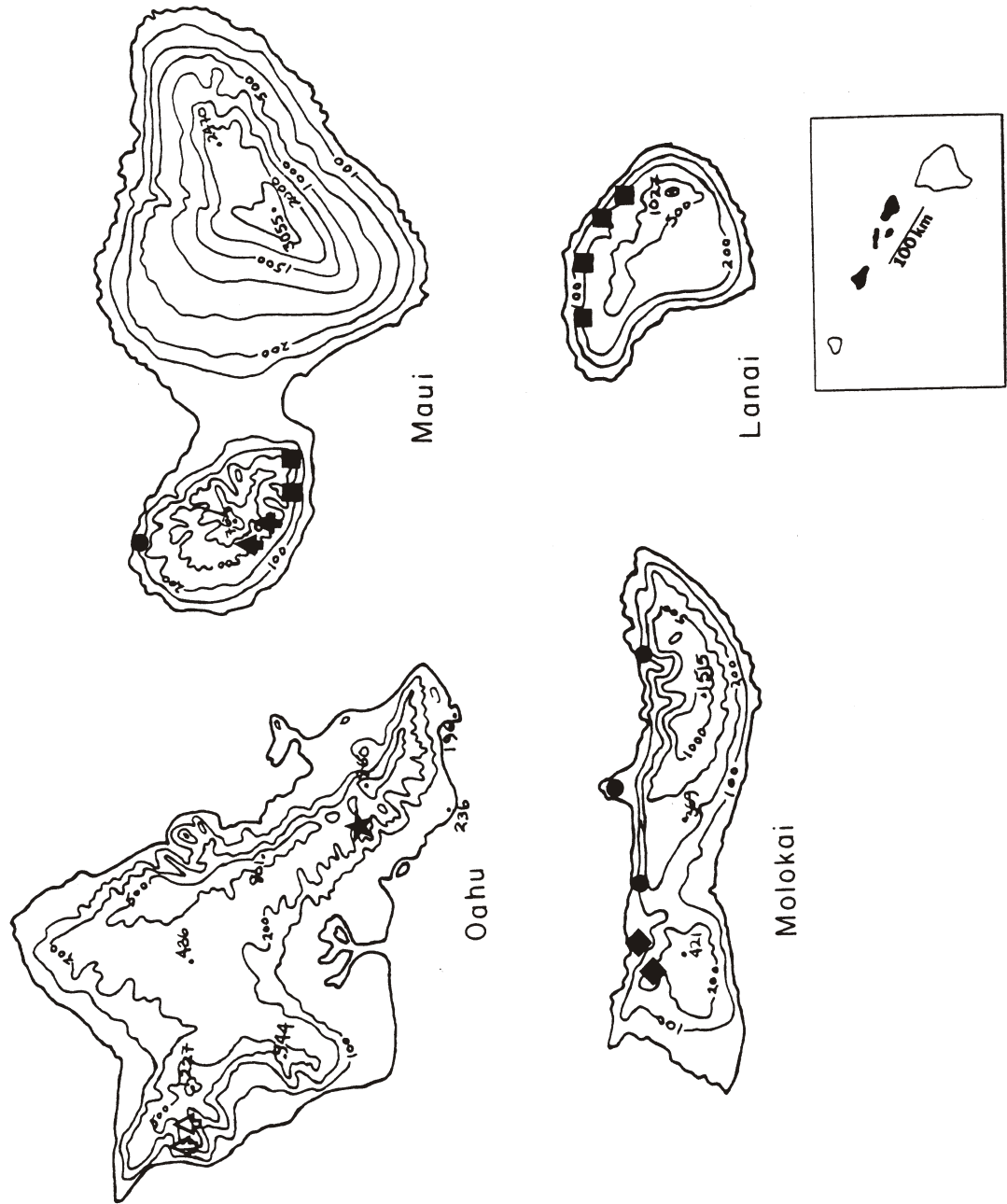


FIGURE 3. Distribution map of species in *Tetramolopium* sect. *Tetramolopium*. ● = *T. sylvae*, ■ = *T. remyi*, ★ = *T. tenerrimum*, ŷ = *T. filiforme*, † = *T. capillare*, ◆ = *T. rockii*.

overgrazed area. The leaves of *T. remyi* also have the xeromorphic feature of being involute. Field observations suggest that the population size of the species can be profoundly affected by variability in annual precipitation. The only known extant population (on Awalua Ridge) was visited in the summers of 1978 and 1979. In 1978, after a very dry spring, the population consisted of seven living individuals and numerous dead plants. In the following year, which had a very wet spring, ten adult plants and over 200 seedlings were counted. Although the adult plants may succumb to prolonged drought, apparently there is a seed bank in the soil that can replenish the population during favorable conditions.

The third member of sect. *Tetramolopium* is *T. sylvae*, a newly discovered species inhabiting seacliffs along the north coast of Molokai and the northwestern coast of Maui. It is a small, prostrate, rosette, woody perennial with glabrous succulent leaves. The succulent condition is probably an adaptation to frequent salt exposure in the maritime habitat.

Tetramolopium rockii is the other coastal species in this section. It grows only in a small area in northwestern Molokai called the "desert strip". The desert strip is a zone of lithified or calcareous dunes extending four miles inland from Moomomi Beach (Macdonald and Abbott, 1970). The species occurs only on the lithified portions of dunes. The substrate is exceptional in the islands in that it is sedimentary and not igneous in origin. It is the only species of the genus in Hawaii to grow on this substrate. The dune soil has a pH of 8 as contrasted to the pH range of 5-7 for the volcanic soils occupied by all other species of the genus. This appears to be a clear example of edaphic endemism.

Tetramolopium rockii is a decumbent or prostrate shrub that often is a dominant component of the vegetation on the lithified dunes. The species consists of two morphological races (here accorded varietal status) that occupy different portions of the desert strip area. These races are *T. rockii* var. *calcisabulorum*, a variety having sericeous foliage and slightly involute leaves, and *T. rockii* var. *rockii*, which has glandular-pubescent foliage and noninvolute leaves. The latter variety occupies the coastal foredunes and hybridizes with var. *calcisabulorum* in a narrow zone of contact somewhat more inland. Beyond this zone, var. *calcisabulorum* extends inland to the boundary of the desert strip. The morphological differences seen under field conditions are maintained in uniform culture. This type of morphological differentiation may indicate the same kind of underlying physiological variability observed in the mainland desert shrub *Encelia* by Ehleringer et al. (1976). Comparative physiological studies of photosynthesis rates and water use efficiency of the two varieties of *T. rockii* are needed.

The fifth species in this section is *Tetramolopium tenerrimum*. It is a small decumbent perennial found only on Oahu. Very little is known about the distribution and habitat of this species; it has not been collected in this century and is probably extinct. At least some specimens collected by Anderson give reference to their collection site on the mountains of Oahu. Thomas Nuttall apparently collected the species on cliffs of the Nuuanu Pali in the Koolau Mountains (St. John, 1979). It can be deduced that *T. tenerrimum* probably grew in submesic open sites on the lower areas of the Koolau Mountains on Oahu.

The final member of the section is the dwarf shrub *Tetramolopium filiforme*. The species comprises two varieties confined to the same ridge in the Waianae Mountains

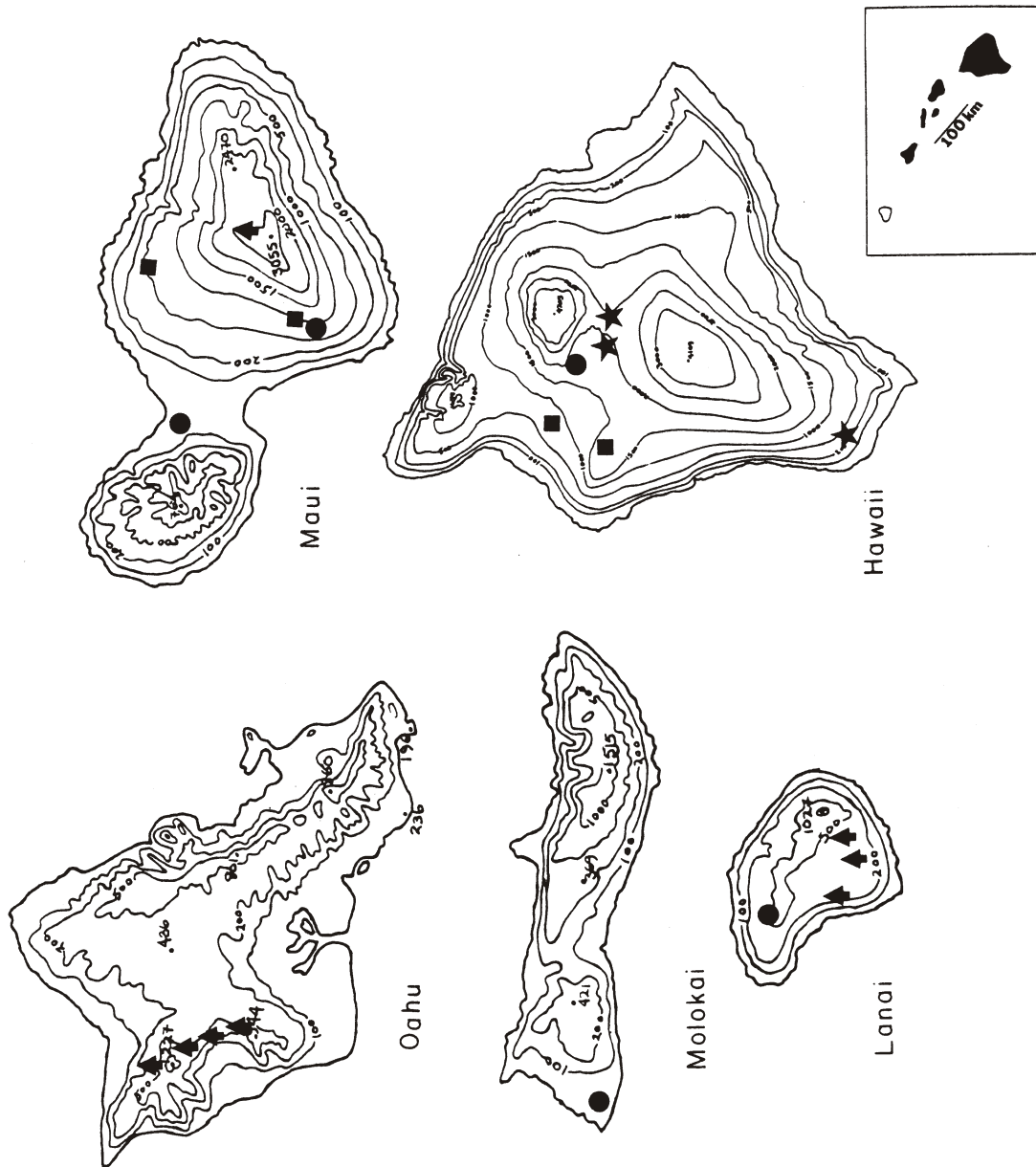


FIGURE 4. Distribution map of species in *Tetramolopium* sect. *Sandwicense*. ■ = *T. arenarium*, ★ = *T. conyzoides*, ● = *T. consanguineum*, ▲ = *T. lepidotum*.

on Oahu. *Tetramolopium filiforme* var. *filiforme* occupies xeric sites on the ridge crest of Ohikilolo Ridge or in rock crevices on cliff faces. The plants occur at elevations of 500–700 m. The leaves are filiform or slightly involute. *Tetramolopium filiforme* var. *polyphyllum* grows at the summit of the ridge at 900–1,000 m. The habitat is submesic, vegetated mainly by low grasses and herbs. The foliage of var. *polyphyllum* is more lush than in the former variety and the leaves are linear-oblongate and toothed. *Tetramolopium filiforme* var. *filiforme* flowers two to three weeks in advance of var. *polyphyllum*, probably due to elevational influences. Both varieties occur on areas with a northern exposure, although the portion of the ridge where var. *polyphyllum* occurs receives substantially more moisture from the trade winds. The distributions of the two varieties were probably contiguous in the past but have become separated recently due to heavy erosion. This erosion is largely the result of overgrazing by feral goats in the last 30–50 years.

TETRAMOLOPIUM SECT. SANDWICENSE

Species of this section have been collected on five of the six major Hawaiian Islands (FIGURE 4). Unfortunately, two of the four species in sect. *Sandwicense* probably have been extirpated: *Tetramolopium conyzoides* and *T. arenarium*. The two remaining species have extinct infraspecific taxa and the remaining populations of the extant taxa have very restricted distributions. Most of the taxa in this section occurred in the lower dry forest or dry scrub communities. The great amount of extinction in sect. *Sandwicense* is probably due to the overgrazing and clearing of these plant communities. Carlquist (1980) states, “areas of lower dry forest are now so few that we have difficulty in constructing a picture of this vegetation”. Thus many features of the distribution and ecology of this group of species will never be known.

Tetramolopium consanguineum is a rather tall upright shrub 1–2 m. high. The species consists of two subspecies, one of which contains two varieties. *Tetramolopium consanguineum* subsp. *consanguineum* is known only from the type collection. Its distribution is given as the “mountains of Kauai”. Nothing is known concerning its exact locality or its habitat. It is presumed to be extinct. If the label information is to be believed, *T. consanguineum* subsp. *consanguineum* was the only member of the genus to occur on Kauai. The other subspecies, *T. consanguineum* subsp. *leptophyllum*, consists of two varieties that differ mainly in head size and floret number. They are both restricted to the island of Hawaii. *Tetramolopium consanguineum* var. *leptophyllum* occurs in the saddle area between Mauna Kea and Mauna Loa on Hawaii; var. *kauense* occurs in the Kau district of southwestern Hawaii. Both taxa are understory plants of *Metrosideros* dry forest communities. *Tetramolopium consanguineum* var. *leptophyllum* grows in forested a’a lava flows at 1,600 m. under a moderately closed canopy. Variety *kauense* grows in a more sparsely vegetated area at 200 m. The substrate at this site consists of either a’a or pahoehoe lava with the plants occupying the crevices in the flows.

The disjunct distribution of the two subspecies of *Tetramolopium consanguineum* is an extremely unusual one for the Hawaiian flora. Not only is the disjunction unusual, but the occurrence of *Tetramolopium* on Kauai is exceptional. The type materials for *T. consanguineum* subsp. *consanguineum* and subsp. *leptophyllum* were both collected during the same period. It is very possible that both taxa were actually collected on Hawaii and that an error was made during preparation of the label. This

problem unfortunately may never be properly resolved because of the probable extinction of subsp. *consanguineum*.

The second species in the section is *Tetramolopium arenarium*, now known only from herbarium specimens. Its former distribution included the islands of Maui and Hawaii. *Tetramolopium arenarium* consisted of two subspecies differing in capitulescence and pubescence characters: subsp. *arenarium* occurred on Hawaii and Maui and subsp. *laxum* was found only on Maui. These taxa were upright shrubs, probably inhabiting dry forest communities on both islands. *Tetramolopium arenarium* subsp. *arenarium* was collected at two different localities on Hawaii: the slopes of Hualalai at 1,850 m. and on Nohonaohae at about 800 m. The latter collection has been recognized as var. *confertum* on the basis of its smaller heads and fewer florets. The Maui localities are rather vague. These localities on Maui and Hawaii were dominated by dry forest vegetation (Rock, 1913), and remnants of such vegetation can still be found there today.

Tetramolopium conyzoides is an upright shrub with copious pubescence and floral features similar to those found in the genus *Conyza*. The species has been collected on Maui, Molokai, Lanai, and Hawaii, but it is probably now extinct. The Maui localities include Kula and "the sandhills of Maui" (perhaps near Waiehu). On Molokai *T. conyzoides* is known from only one locality in the southwestern portion of the island, near Kumikaipo. The Hawaii distribution is based on one collection made by Hillebrand on the "central plateau." Information concerning the distribution of the species on Lanai is lacking. The species was probably a component of the dry forest community.

The final species in sect. *Sandwicense* is *Tetramolopium lepidotum*, consisting of subsp. *lepidotum* from Oahu and Lanai and subsp. *arbusculum* from Maui. *Tetramolopium lepidotum* subsp. *lepidotum* is now found only on Oahu, where it occurs in the Waianae Mountains. *Tetramolopium lepidotum* subsp. *lepidotum* is a low upright shrub less than 1 m. tall. The taxon formerly grew in the Miki Basin and Honopu Uplands on Lanai. It was presumably extirpated on Lanai due to overgrazing and pineapple cultivation. Populations of *T. lepidotum* on Oahu occur on open, east-facing ridge tops and cliffs. The elevational range is from 600 to 900 m. The plants grow only on sites with eastern exposures that face into the trade winds. In the late afternoons these areas are often shrouded in fog. The fog is an important source of moisture in these areas, which otherwise receive only 30–40 inches of annual rainfall. The vegetation is short submesic scrub dominated by *Metrosideros* and *Bidens*. The populations on Lanai occurred at much lower elevations (300–400 m.) and in drier sites (15–25 inches of annual precipitation) than the Oahu populations. The pre-European vegetation probably consisted of low scrub with an understorey of grasses.

Tetramolopium lepidotum subsp. *arbusculum* is somewhat of an enigma, being known only from the type collection. The locality was given by Gray (1861) as "On the Great Crater of the eastern part of Maui," meaning it was collected somewhere on Mt. Haleakala. Extrapolating from what is known about the habitat occupied by subsp. *lepidotum*, subsp. *arbusculum* probably occurred on submesic cliff faces of the western part of Haleakala Crater. The specimens indicate that it was a larger shrub than subsp. *lepidotum*, with linear leaves. It was probably driven to extinction by feral goats and pigs in this area.

TABLE 3. MEIOTIC CHROMOSOME NUMBERS IN HAWAIIAN TETRAMOLOPIUM

taxon	haploid number	voucher or reference
1. <i>T. consanguineum</i> subsp. <i>leptophyllum</i> var. <i>leptophyllum</i>	9	Lowrey 414, 459.
2. <i>T. filiforme</i> var. <i>filiforme</i>	9	Carr, 1978; Lowrey 419, 441.
3. * <i>T. filiforme</i> var. <i>polyphyllum</i>	9	Lowrey 420, 442.
4. <i>T. humile</i> subsp. <i>haleakalae</i>	9	Carr, 1978; Lowrey 424, 425, 426, 427, 428, 429, 430; Solbrig et al., 1964.
	(7) ^a	Carlquist, 1956.
5. <i>T. humile</i> subsp. <i>humile</i> var. <i>humile</i>	9	Lowrey 436, 437; Solbrig et al., 1964.
6. * <i>T. lepidotum</i> subsp. <i>lepidotum</i>	9	Lowrey 416, 421, 443.
7. * <i>T. remyi</i>	9	Lowrey 415, 450.
8. * <i>T. rockii</i> var. <i>rockii</i>	9	Lowrey 417, 455.
9. * <i>T. rockii</i> var. <i>calcisabulorum</i>	9	Lowrey 435, 456.
10. * <i>T. sylvae</i>	9	Lowrey 431, 444, 418, 451, 454.

*First report for taxon;^a count probably in error, see discussion in text.

CHROMOSOME NUMBER

All chromosome counts were obtained from preparations of meiotic stages of microspore mother cells. Floral buds for chromosome counts were fixed and stored in modified Carnoy's fixative (4 : 3 : 1, chloroform: 95% ethanol; glacial acetic acid). Anthers were macerated, squashed, and stained in a 1 : 1 mixture of Hoyer's mounting medium and acetocarmine.

The chromosome number of Hawaiian *Tetramolopium* is uniformly $n = 9_{II}$ at meiosis (TABLE 3). Meiotic chromosomes exhibited normal bivalent pairing and subsequent normal disjunction. The configuration of the chromosomes at diakinesis and metaphase I consist predominantly of ring bivalents with only one or two rod bivalents.

The first reported chromosome count for *Tetramolopium* was $n = 7$ for *T. humile* subsp. *haleakalae* (formerly var. *humile*) (Carlquist, 1956). This report has been cited as an unusual example of aneuploidy and of intraspecific chromosome variation (Grau, 1977; Solbrig et al., 1964; Solbrig et al., 1969), but the report has not been substantiated in subsequent studies (Carr, 1978; Solbrig et al., 1964), including the present one. I collected chromosome material from eight populations of *T. humile* subsp. *haleakalae* throughout its elevational range. One of these was from same altitude and area as that of the Carlquist (1956) collection. All eight populations are uniform in having $n = 9$ chromosomes. Only two species of New Guinean *Tetramolopium* have been counted and both are $n = 9$ (Borgmann, 1964). The $n = 7$ report must be presumed to be the result of technical error or aberrant plant material and should therefore be discounted.

HYBRIDIZATION STUDIES

Experimental pollinations were performed in all possible combinations among 16 populations of *Tetramolopium* to obtain hybrid progeny. In most cases the parental greenhouse population consisted of 20 individuals, except for *T. consanguineum* subsp. *leptophyllum*, in which case only one plant was available for use. All plants

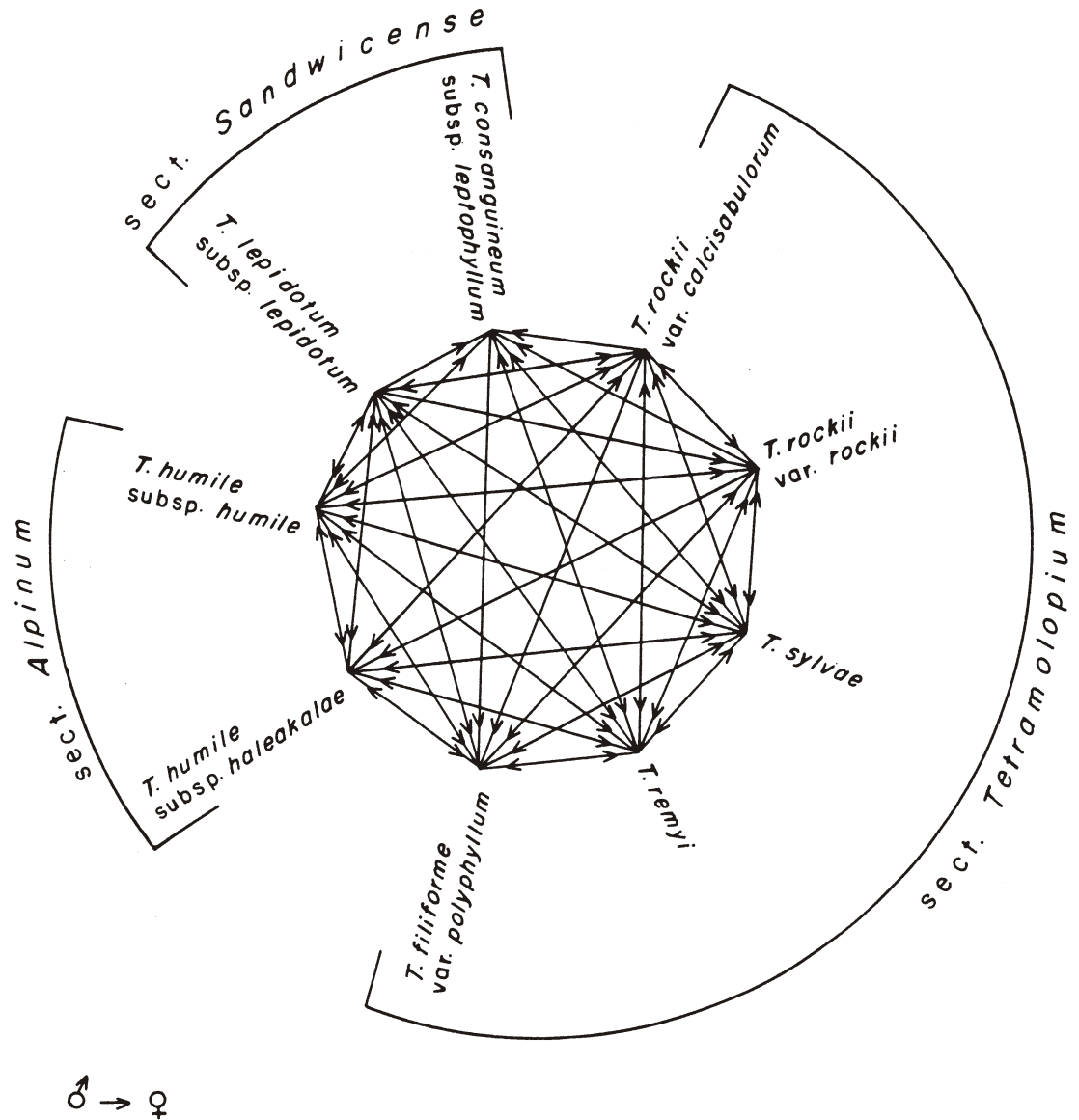


FIGURE 5. Polygon summarizing successful crosses obtained from artificial hybridizations attempted among taxa of Hawaiian *Tetramolopium*. Arrows indicate the direction of cross.

within a population were used. Pollen grain viability, as estimated by stainability in cotton blue-lactophenol, was measured for each parent used. A minimum of 500 grains per slide was counted. The slides were allowed to stand for 24 hours before the pollen grains were counted. Lightly stained or abnormally stained grains were scored as non-fertile.

Pollen was transferred by removing disk florets at anthesis from the pollen parent and applying their pollen to receptive styles of ray florets on the seed parent. The disk florets from each head used on the seed parent were removed to prevent selfing. Some crosses were repeated without removing the disk florets. This was done to test for any damage caused by floret removal. The heads were bagged with glassine envelopes and marked with string tags. Crosses that did not yield fertile achenes on the first trial were repeated. Mature heads were collected and the numbers of fertile and sterile achenes

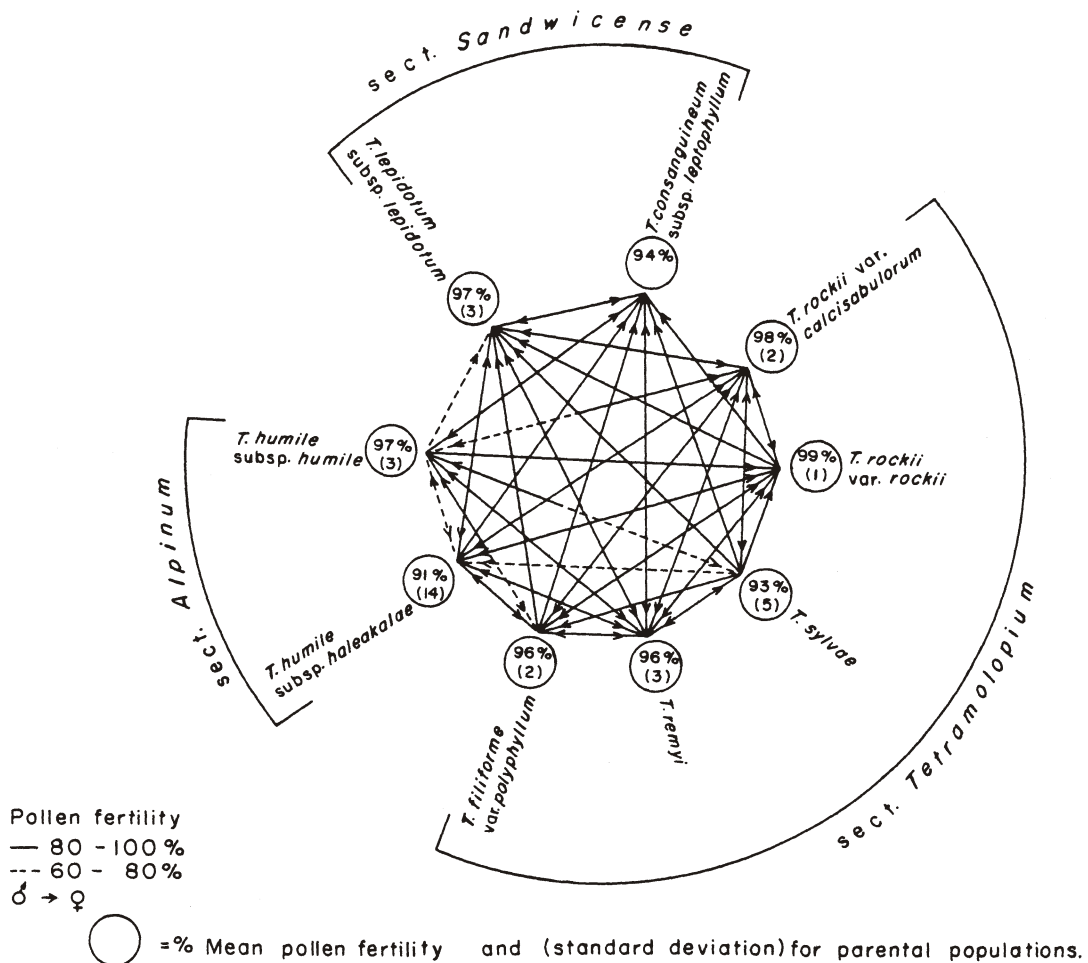


FIGURE 6. Crossing polygon summarizing mean pollen viabilities of F_1 progenies obtained from artificial hybridizations among taxa of Hawaiian *Tetramolopium*. Absence of lines indicates hybrid was not tested.

were counted. The F_1 hybrids from the successful crosses were then grown and tested for pollen fertility in the same manner as the parental pollen. Bud material was also collected from those hybrids showing reduction in pollen viability. Voucher specimens of progeny from each cross are deposited in the UC herbarium, along with vouchers of other companion studies.

Over 360 artificial inter- and intraspecific hybridizations were attempted, involving 16 populations belonging to seven species. Fertile F_1 achenes were obtained from over 60% of the crosses attempted. Hybrids were produced among all taxa regardless of taxonomic rank (FIGURE 5). The hybrid achenes germinated readily, most within six days. The percentage of germination was extremely high, approaching 99%. All hybrids were vigorous and flowered normally.

The morphology of the F_1 hybrids was intermediate to the parents in most respects. This is particularly evident in such features as height, floret number, head size, pappus length, pubescence, and leaf shape. Two important characters not exhibiting intermediacy in the hybrids were disk floret achene sterility/fertility and capitulescence type. Female sterility and compound capitulescences appear to be epistatically controlled. The exact number of genes involved has not been determined. The color of the

disk may also be under epistatic control, but the results are not clear-cut. All hybrids between maroon-flowered and yellow-flowered plants are yellow, but some are tinged with maroon, suggesting either polygenic control or partial dominance. The inheritance patterns need further study in the F_2 generation. It is notable that both disk achene fertility and capitulescence type are important facets of the sex expression syndrome in *Tetramolopium*. In fact, the female fertility of the disk florets determines which particular mode of sex expression is exhibited.

The mean pollen viability of the parental plants was greater than 90% in all cases. However, there was a wide range of variability in pollen viability, with some individuals having a viability as low as 75%. Mean pollen viabilities of the F_1 hybrids were strikingly high regardless of the taxonomic rank or ecological diversity of the parent (FIGURE 6). In most instances the values of the hybrids were as high as or higher than those of the parents. The only hybrid combinations exhibiting lowered viabilities were those involving either of the two subspecies of *Tetramolopium humile*. Perhaps the most interesting result was the lowered fertility exhibited by hybrids between the *T. humile* subspecies. This was a totally unexpected result, in view of the fact that most other interspecific crosses showed such high pollen viability. Upon examination of pollen viability values obtained from crosses between different populations of these two taxa, it appears that only crosses involving plants from a particular population of *T. humile* subsp. *humile* have low values, yet hybrids obtained from interpopulational crosses within subsp. *humile* exhibit high pollen viability. The reason for this lowered viability is unclear and deserves further study.

Examination of meiotic chromosome pairing showed normal bivalent pairing and normal disjunction regardless of pollen viability. This is true even for the hybrids within *Tetramolopium humile*. All F_1 hybrids produced fertile achenes. The production of F_2 hybrids was so great that seedlings became greenhouse weeds. F_2 achenes from several selfed F_1 plants were grown. The F_2 plants grew vigorously. Plants from two different F_2 hybrids tested had pollen viabilities greater than 90%. There is no evidence of hybrid breakdown or inviability in the F_2 generation.

The results of the artificial hybridization program clearly show the absence of any significant genetic barriers to hybridization. Even those hybrids showing lower pollen viabilities than their parents are still highly fertile and within the range of parental variability. This phenomenon was not unexpected, based on information provided by the few previous biosystematic studies of Hawaiian groups. Artificial hybridization studies in *Bidens* (Gillett and Lim, 1970) and in *Lipochaeta* (Rabakonandrianina and Carr, 1981; Rabakonandrianina, 1980) have revealed the lack of internal reproductive barriers to hybridization even between those species exhibiting great morphological and ecological diversity. This phenomenon is not limited to plants in Hawaii, but in fact many trees, shrubs, and perennials in areas other than Hawaii often lack or have only poorly developed internal barriers to hybridization (Raven, 1976). This is particularly true for insular plants (Rattenbury, 1962).

NATURAL HYBRIDIZATION

Although natural hybridization is known to be a widespread and important phenomenon in the Hawaiian flora (Carr and Kyhos, 1981; Gillett, 1972), it does not appear to be so in *Tetramolopium*. There are no previous reports of naturally occurring hybrids nor is there any discernible evidence in herbarium collections. During the

field work for the present study I detected only one example of hybridization among extant taxa (between two varieties of the same species) and one possible occurrence of past introgressive hybridization (at the specific level).

The first example involves *Tetramolopium rockii* var. *rockii* and *T. rockii* var. *calcisabulorum*. These two varieties intergrade in a narrow zone of sympatry. The plants within the zone exhibit variability in the diagnostic characters of leaf pubescence and leaf size. Outside the approximately 50 m. wide zone of intergradation the parental phenotypes are expressed homogeneously. Plants within the zone exhibit variability in the leaf characters which is not seen in progeny of plants just a short distance away from the area of overlap. The occurrence of hybridization between these two taxa might be expected, due to their similar morphology and habitat, their sympatric distributions, and their demonstrated lack of internal reproductive barriers. The containment of the hybrids within such a narrow zone suggests that there must be intense selection against hybrid genotypes.

A possible instance of past introgressive hybridization may explain the anomalous occurrence of several diagnostic characters of *Tetramolopium* sect. *Sandwicense* in *T. filiforme* of sect. *Tetramolopium*. These characters include purple disk corollas, nonspatulate dentate leaves, and occasionally compound capitulescences. Incorporation of these characters into *T. filiforme* may have resulted from hybridization with *T. lepidotum* of sect. *Sandwicense*, which occurs in the same general area on Oahu. The two species do not now occur sympatrically but may have in the past, since populations of both can be found within a few kilometers of each other. Further studies are needed to investigate this hypothesis.

The virtual absence of naturally occurring hybrids between taxa of any rank in *Tetramolopium*, despite the lack of genetic barriers to prevent them, is mainly due to geographical and ecological isolation. The distributions of all species (and in many cases their infraspecific taxa) are totally allopatric. Habitat preferences of many of the species also enforce this isolation. These same factors also appear to be important in *Lipochaeta* (Rabakonandrianina, 1980), where only one instance of natural hybridization has been detected. The importance of strong selectional pressure against survival of hybrids also must be taken into consideration. It is difficult to say with total assurance that hybridization has always been a rare event in *Tetramolopium*, especially with the fairly recent disruption of the Hawaiian flora. Yet, as discussed earlier, the species of *Tetramolopium* probably have always been rare and localized. The recent range reductions and extinctions will serve to prevent hybridization from occurring in the future.

FEATURES OF THE BREEDING SYSTEM

INTRODUCTION

The influence of different sexual systems on flowering plants with respect to their taxonomic diversity, population variability, and evolutionary potential has been widely recognized by botanists (Ornduff, 1969; Raven, 1979). One of the features of these systems, sex expression, has received particular attention in recent evolutionary and botanical literature (see Bawa and Beach, 1981, for a review). However, despite the demonstrated existence of different sexual classes (e. g. monoecy or dioecy) in the Compositae, the diversity and importance of sex expression classes have been largely unstudied in this group (Heywood and Humphries, 1977). The analyses of the remark-

TABLE 4. SELECTED CHARACTERS ASSOCIATED WITH SEX EXPRESSION IN TETRAMOLOPIUM TAXA

	Ray floret/ head		Disk floret/ head		Ray/disk floret ratio		capitulum-lescence type	disk corolla color	Ray floret lamina length		habit
	mean	s.d.	mean	s.d.	mean	s.d.			mean	s.d.	
sect. <i>Tetramolopium</i>											
<i>T. remyi</i>	173	31	81	5	2.2	0.4	simple	yellow	5.0	0.8	decumbent**
<i>T. rockii</i> var. <i>rockii</i>	84	16	40	11	2.0	0.2	simple	yellow	3.7	0.6	decumbent
<i>T. rockii</i> var. <i>calcisabulorum</i>	77	11	44	10	1.6	0.3	simple	yellow	3.8	0.5	decumbent
<i>T. sylvae</i>	67	9	29	4	2.3	0.2	simple	yellow	3.1	0.4	prostrate
<i>T. filiforme</i> var. <i>polyphyllum</i>	48	21	27	2	1.8	0.1	simple*	maroon	3.2	0.5	dwarf shrub
<i>T. filiforme</i> var. <i>filiforme</i>	43	2	20	1	2.2	0.1	simple*	maroon	3.4	0.1	dwarf shrub
<i>T. capillare</i>	39	3	24	1	1.6	-	simple	yellow	3.9	0.3	decumbent
<i>T. tenerrimum</i>	29	4	17	-	1.7	-	simple	yellow	2.9	0.3	decumbent
sect. <i>Alpinum</i>											
<i>T. humile</i> subsp. <i>haleakalae</i>	31	6	17	3	1.5	0.04	simple	maroon	3.1	0.1	caespitose
<i>T. humile</i> subsp. <i>humile</i>	25	5	9	2	2.7	0.2	compound	maroon	3.0	0.1	caespitose
sect. <i>Sandwicense</i>											
<i>T. arenarium</i> subsp. <i>arenarium</i>	40	3	6	2	7.4	0.9	compound	maroon	2.1	0.2	upright
var. <i>arenarium</i>											
<i>T. arenarium</i> var. <i>confertum</i>	24	1.4	4.6	0.1	5.2	0.2	compound	maroon	2.1	0.1	upright
<i>T. arenarium</i> subsp. <i>laxum</i>	N.D.		7	1	N.D.		compound	maroon	1.7	0.2	upright
<i>T. lepidotum</i> subsp. <i>lepidotum</i>	31	2	6.8	2	5.2	0.3	compound	maroon	1.9	0.4	upright
<i>T. lepidotum</i> subsp. <i>arbusculum</i>	31	1	5.3	0.6	5.7	0.7	compound	maroon	1.7	0.2	upright
<i>T. consanguineum</i> subsp. <i>consanguineum</i>	22	-	4.5	0.6	4.9	-	compound	maroon	1.5	0.2	upright
<i>T. consanguineum</i> subsp. <i>leptophyllum</i> var. <i>leptophyllum</i>	33	4	7.8	2	4.2	0.3	compound	maroon	1.2	0.1	upright
<i>T. consanguineum</i> var. <i>kauense</i>	23	1	4.1	0.8	5.0	0.5	compound	maroon	0.9	0.1	upright
<i>T. conyzoides</i>	18	5	2	0.7	10.2	1.2	compound	maroon	0.7	0.2	upright

N.D. = no data; * = rarely compound; ** = rarely upright; s.d. = standard deviation.

ably diverse sex expressions in *Cotula* (Anthemideae) by Lloyd (1972a, b; 1975a, b) have provided the only extensive studies in the Compositae to date.

Sex expression systems in the Compositae span the entire range of possibilities from strict monoecy (hermaphroditism) through gynodioecy, monoecy, subdioecy, gynodioecy, to complete dioecy. Nearly the entire series may be present within a single genus, as in *Artemisia* (Heywood and Humphries, 1977) and *Cotula* (Lloyd, 1972a). Besides the obvious changes in floral form attendant to development of different gender classes, there often are major differences among a number of morphological characters (mainly reproductive). These characters may or may not be associated directly with distribution of the various classes. Particular states of these characters may be highly correlated with specific modes of sex expression. These character sets or syndromes have proven to be taxonomically valuable (Ornduff, 1969) and have important implications for the reproductive biology and evolutionary history of those plants in which they occur.

Preliminary analyses of the sexual system of Hawaiian *Tetramolopium* have revealed the existence of previously unrecognized diversity in sex expression. What follows provides a general account of the sex expression, which includes important aspects of the plants' sexual systems and their taxonomic distribution. Present theories regarding the evolution and direct function of sex expression systems in plants are discussed in relation to *Tetramolopium*.

SEX EXPRESSION

Hawaiian *Tetramolopium* species have two different classes of sex expression: monoecy and gynodioecy. These two classes differ with respect to the sexual condition of the disk florets. Both forms have pistillate ray florets, but the monoecious species have functionally staminate disk florets, while the gynodioecious species have perfect disk florets (cf. prior discussion of disk florets).

Each sex expression class has a particular set of associated characters (TABLE 4). The associated morphological features are both qualitative and quantitative. The qualitative characters include differences in capitulescence type, disk corolla color, and habit; the quantitative characters include the numbers of ray and disk florets per head, the ratio of ray to disk floret number per head, and the ray floret lamina length (ligule length). Comparison of the character values for each taxon reveals several interesting features.

Perhaps the most striking feature is the broad range in numbers of disk and ray florets (TABLE 4). These numbers vary from an average of two disk and 18 ray florets in gynodioecious *Tetramolopium conyzoides* to 81 disk and 173 ray florets in monoecious *T. remyi*. It is obvious upon inspection of the data that a continuum of values for both characters exists between these two extremes. Correlation analysis of the two floret number characters (comparing the number of ray florets to the number of disk florets), utilizing the mean values of each taxon, indicates an extremely high correlation between them (Pearson Product-Moment Correlation Coefficient value of $r = 0.96$, $p \leq 0.01$; FIGURE 7). This relationship also is maintained in plants grown under uniform conditions, indicating that the relative numbers of each floret type are genetically controlled. Comparisons of disk floret number vs. ray floret lamina length and ray floret number vs. ray floret lamina length show similar trends and are significantly

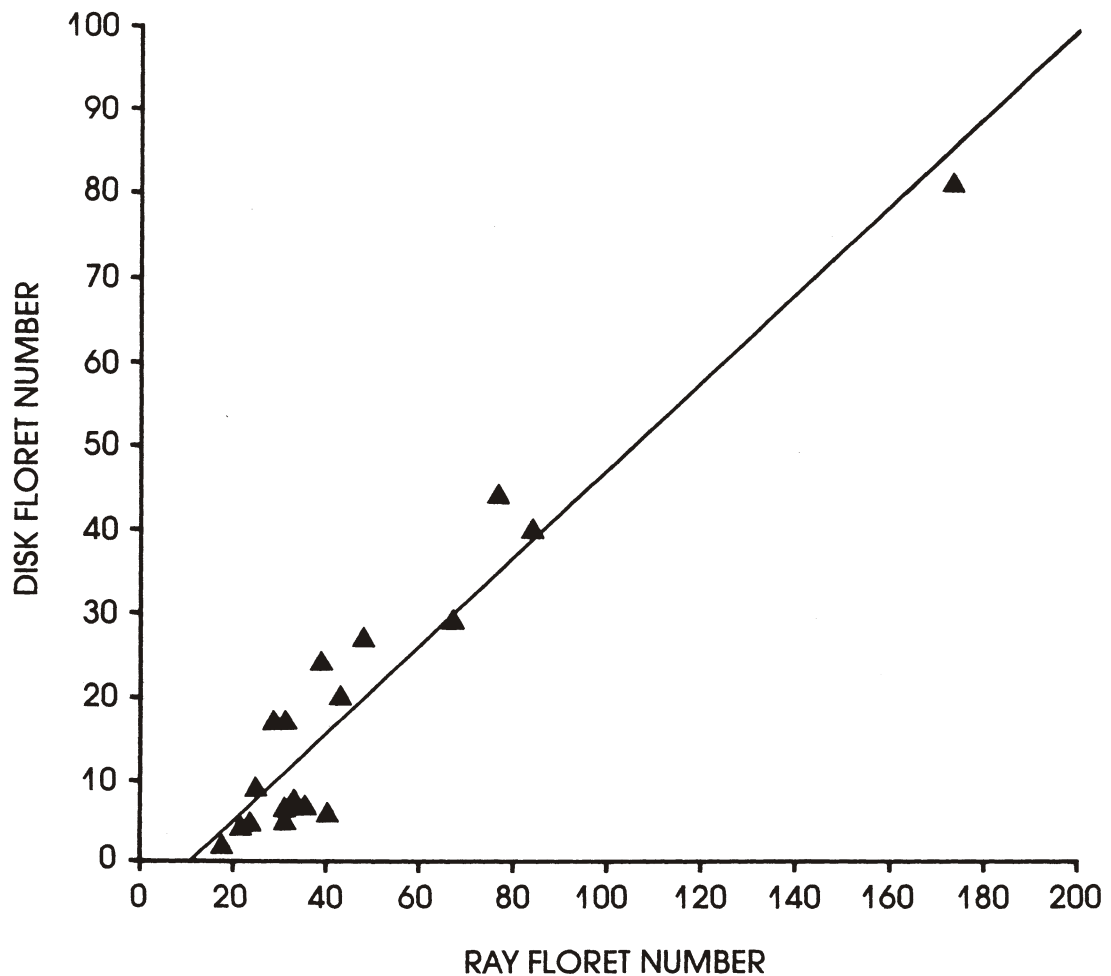


FIGURE 7. Correlation graph for ray floret number vs. disk floret number.

correlated, although the values are somewhat lower ($r = 0.85$, $r = 0.73$, respectively; $p \leq 0.01$; FIGURES 8, 9). It should be noted that in FIGURE 8 the outlying point on the graph (corresponding to *T. remyi*) greatly influences the position of the regression line. Analysis of the data indicates that this is actually a function of differences between sects. *Sandwicense* and *Tetramolopium* with regard to internal correlations. That is, within each of these sections the characters are strongly correlated but the regression lines have different slopes. When the two sections are compared on one graph the line appears to be skewed towards *T. remyi*.

The ray to disk floret ratio is not significantly correlated with either disk floret number or ray floret number. Interestingly, there is a significant negative correlation between the floret ratio and the ray floret lamina length ($r = -0.79$, $p \leq 0.01$; FIGURE 10). This same relationship was reported also for *Cotula* (Lloyd, 1972b). The floret ratio is actually a measure of the percentage of pistillate rays relative to staminate or perfect disk florets. Those species with large ratios have a larger percentage of pistillate ray florets, yet the heads have shorter, less conspicuous ligules.

It is noteworthy that the two subspecies of *Tetramolopium humile* have ratios differing by a factor of nearly two. This is a function of a factor difference of two between the disk floret numbers of the two taxa. Additionally, the capitulescence type is also different in the two subspecies. This suggests that there is a relationship between

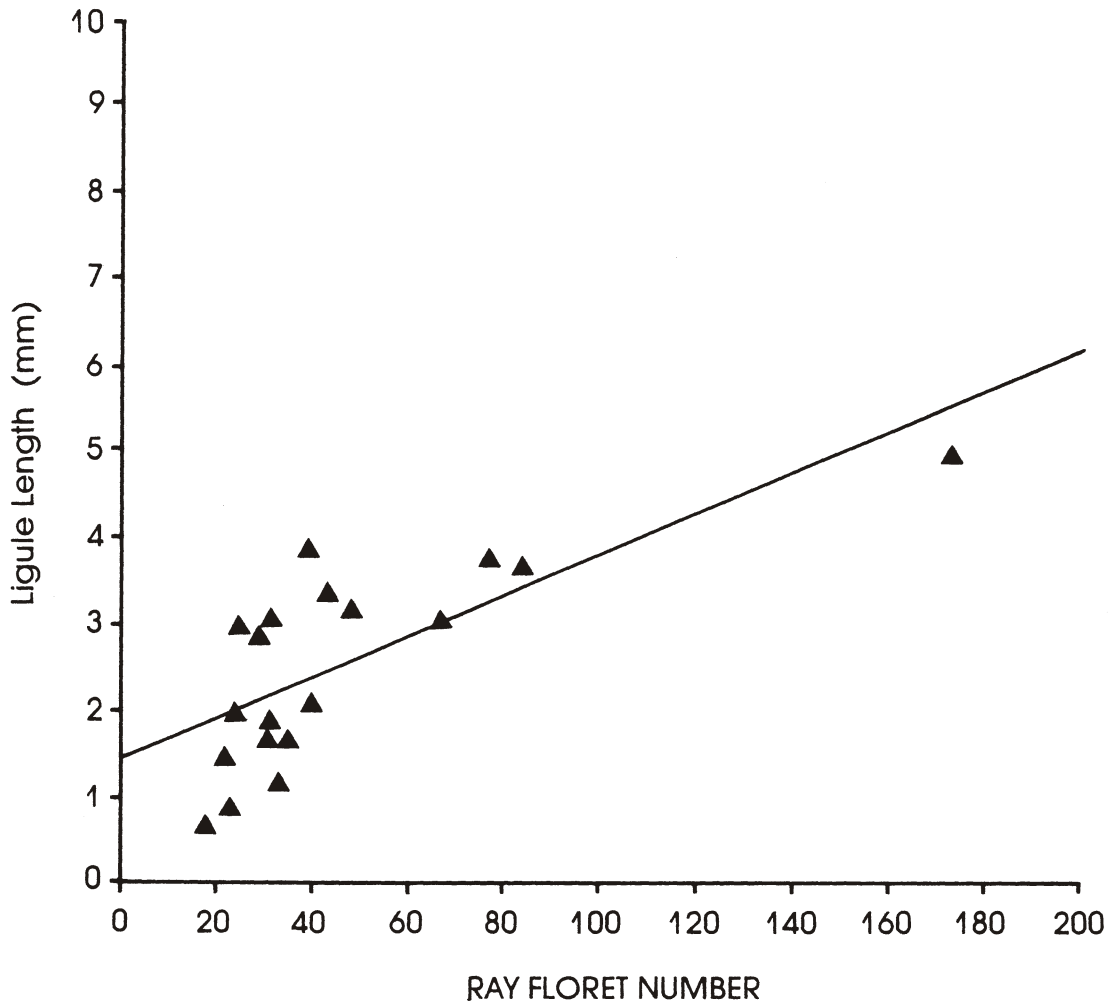


FIGURE 8. Correlation graph for ray floret number vs. ligule length.

the number of heads in a capitulescence and both the total disk floret number and the percentage of disk florets.

The taxonomic value of these characters is most evident at the sectional level. The character values provide one of the main bodies of evidence for sectional delimitation in *Tetramolopium* (TABLE 5). *Tetramolopium* sect. *Tetramolopium* is distinctive in being strictly monoecious with simple capitulescences and (mostly) yellow disk floret corollas. Additionally it has conspicuously radiate heads having large numbers of ray and disk florets and correspondingly large heads. The ray to disk floret ratio is small (about 2) meaning that about one-third of the florets are staminate disk florets. The species in the section are low, decumbent, or dwarf shrubs. Section *Sandwicense*, on the other hand, is gynomonocious with compound capitulescences and maroon (or pink) disk corollas. The heads are small, inconspicuously radiate with relatively low numbers of ray and disk florets. The ray to disk floret ratio is high (about 6), which means that the percentage of disk florets is 14%. All species are upright shrubs. As mentioned previously, sect. *Alpinum* in Hawaii occupies an anomalous taxonomic position with regard to the characters associated with sex expression. It is gynomonocious with maroon disk florets as is sect. *Sandwicense*, but it has intermediate charac-

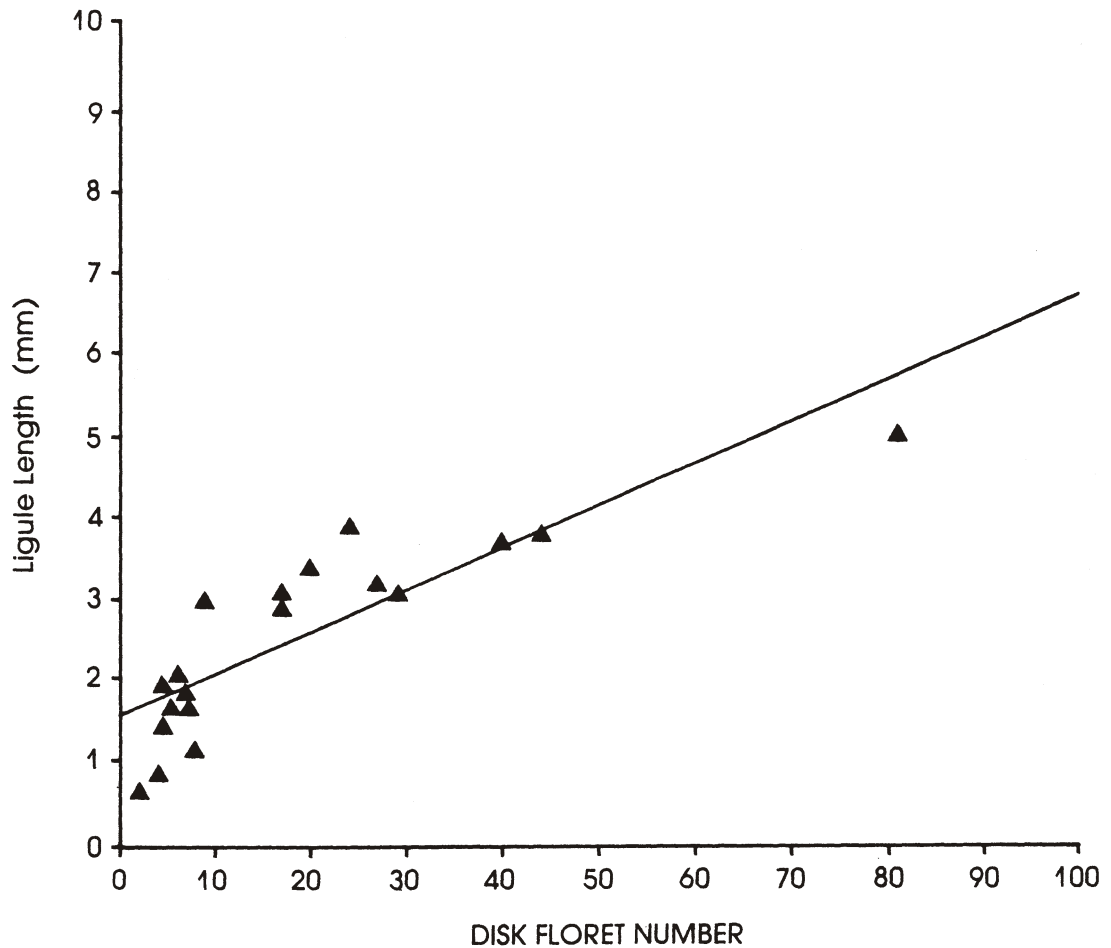


FIGURE 9. Correlation graph for disk floret number vs. ligule length.

ter state values between the other two sections with respect to the remaining characteristics excepting habit. It also has both capitulescence types. The caespitose dwarf shrub habit is unique, as are several other morphological characters that are not involved with the sex expression, i. e. disk corolla shape and achene shape.

The sex expression syndromes also correlate with habitat preference. The monoecious species inhabit xeric exposed habitats. With the exception of *Tetramolopium humile*, the gynomonocious species occur (or occurred) in dry forest communities.

COMPATIBILITY AND DICHOGAMY

The results of tests for apomixis, self-compatibility, and spontaneous selfing are presented in TABLE 6. No evidence of non-pseudogamous apomixis was detected in *Tetramolopium*. Seed set was zero in all pistillate ray florets from which pollen was excluded.

All taxa studied in the greenhouse were self-compatible and capable of self-pollination, as indicated by seed set in control (untreated) and geitonogamously pollinated heads. The heads in which geitonogamy was induced showed no difference in seed set from those that were outcrossed. Despite the existence of spontaneous selfing, the level of seed set was low in comparison to that obtained by hand-selfing. The mean percentage seed set of below 20% is contrasted to 40% or higher seed set in

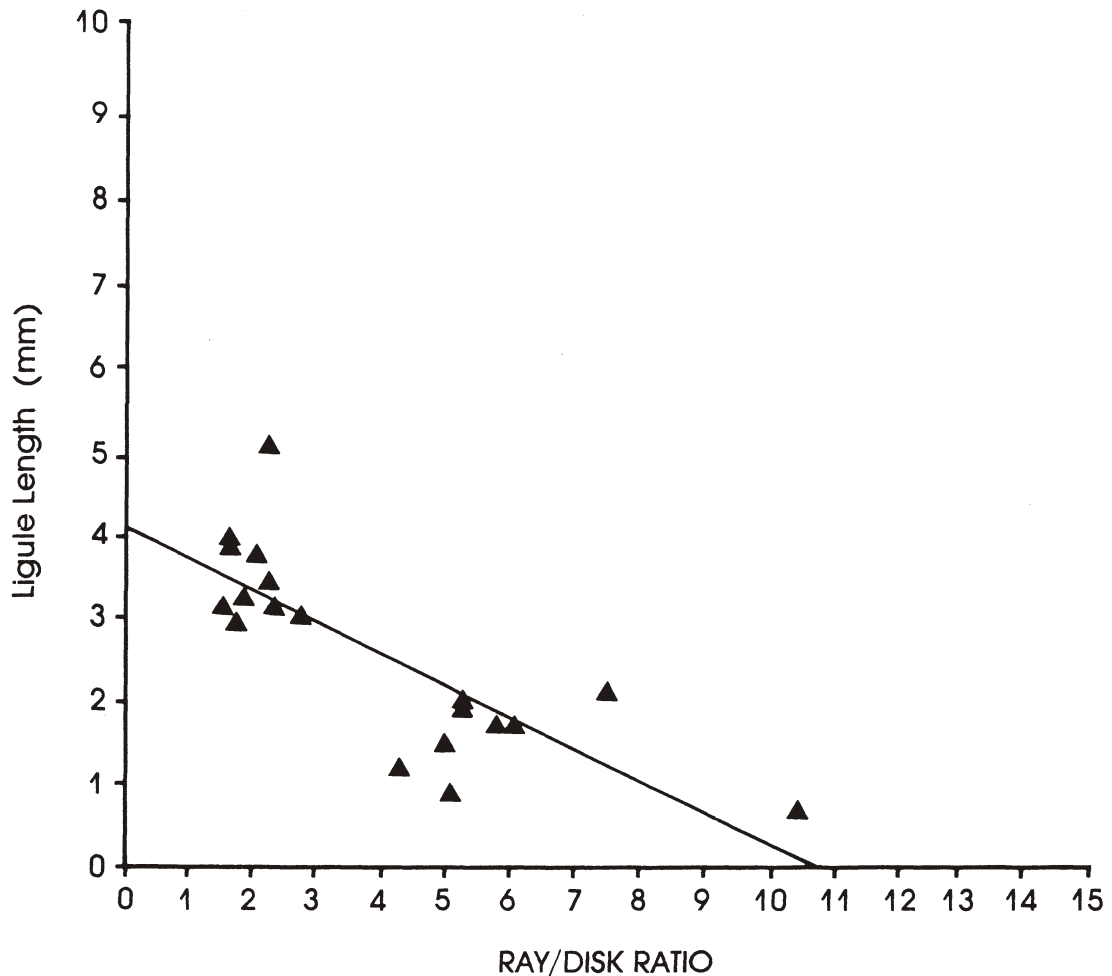


FIGURE 10. Correlation graph for ray/disk floret ratio vs. ligule length.

hand-selfed populations. There was a large amount of variability in seed set from hand-selfed populations. This may be due to low sample size and the difficulty involved in applying uniform amounts of pollen to the many florets in a head. The difference in seed set values between the two treatments is significant, however, and indicates that mechanical transfer of pollen is important for optimal seed set in *Tetramolopium* regardless of sex expression.

The hermaphrodite disk florets of sects. *Alpinum* and *Sandwicense* are protandrous, as is typical for the Compositae (Faegri and van der Pijl, 1979). The anthers dehisce introrsely and the pollen is then pushed out of the anther tube by the elongating style. The style branches do not separate and become receptive until one or two days after the pollen is presented. There is a centripetal maturation of disk florets. There is also some chance for self-pollination in the disk florets but it appears to be low.

The frequency for pollen transfer between florets of one head, resulting in geitonogamy, is influenced by the relative timing of the male (or hermaphrodite) disk anthesis and the female ray floret anthesis. The heads of *Tetramolopium* can be termed protogynous, although technically this is reserved for individual flowers. The stigmas of the pistillate ray florets become receptive before pollen is released by the disk florets.

TABLE 5. SECTIONAL COMPARISON OF CHARACTERS ASSOCIATED WITH SEX EXPRESSION

	Sect. <i>Tetramolopium</i>	Sect. <i>Alpinum</i>	Sect. <i>Sandwicense</i>
sex expression	monoecy	gynomonoecy	gynomonoecy
ray floret number*	70	24	29
disk floret number*	35	13	5
ray/disk floret ratio*	1.93	2.1	5.99
capitulescence type	simple	simple & compound	compound
disk corolla color	yellow (rarely maroon)	maroon	maroon
ray floret lamina length, mm.*	3.6	3.1	1.5
habit	prostrate, decumbent, or dwarf shrubs	caespitose shrubs	upright shrubs

*Average over all the taxa in each section.

The ray florets of sect. *Tetramolopium* are receptive (as judged by turgid and divaricate style branches) two or three days before disk floret anthesis. The ray florets of gynomonoecious species (*T. lepidotum* and *T. humile*) are receptive at most one day before disk anthesis.

The timing is very often nearly simultaneous. It is not known exactly how long the ray floret stigmas are receptive but it appears that both sex expression classes have considerable overlap between ray and disk anthesis.

DISCUSSION

The results indicate that the characters associated with the sex expression are highly correlated with each other. The seven characters listed in TABLE 4 thus constitute a syndrome directly related to the sex expression classes. Furthermore, the character sets are not mutually exclusive but rather constitute a continuum, with species of sects. *Tetramolopium* and *Sandwicense* representing extremes linked by a continuous range of intermediates (with sect. *Alpinum* occupying the midpoint).

Preliminary results also indicate that species vary in their degree of protogyny according to their particular mode of sex expression. It must be emphasized that only two gynomonoecious species were studied. Further studies are needed to verify these results and to determine the exact duration of stigma receptivity in the rays in relation to disk anthesis.

The presence in *Tetramolopium* of two different sexual systems which have different sex expression and associated character syndromes parallels in many respects the situation in *Cotula* (Lloyd, 1974a). Many of the same character trends noted for *Cotula* exist also in *Tetramolopium*. This is especially true with regard to the existence of character sets with extreme values linked by a continuum of intermediates. Additionally, in *Cotula* there are also different degrees of protogyny correlated with different syndromes. Lloyd (1974a) found that several monoecious species of *Cotula* are strongly protogynous in comparison with the gynomonoecious species.

These findings raise the fundamental question: What is the evolutionary significance and function of the different sex expression syndromes in *Tetramolopium* and in the Compositae generally? The traditional answer to this question is that the different sex expression syndromes function primarily as outcrossing mechanisms and regulators of genetic recombination (Bawa and Beach, 1981; Thomson and Barrett, 1981). This same explanation was invoked by Lloyd (1974a) for *Cotula*. According to his

TABLE 6. MEAN SEED SET IN TESTS FOR APOMIXIS, SELF-COMPATIBILITY, AND SPONTANEOUS SELFING

	control		geitonogamously selfed		disk removed
	mean	s.d.	mean	s.d.	
sect. <i>Alpinum</i>					
* <i>T. humile</i> subsp. <i>haleakalae</i>	15	10	49	9	0
* <i>T. humile</i> subsp. <i>humile</i>	19	11	41	13	0
sect. <i>Sandwicense</i>					
* <i>T. lepidotum</i>	15	11	38	31	0
sect. <i>Tetramolopium</i>					
<i>T. remyi</i>	17	11	74	16	0
<i>T. rockii</i>	5	5	49	32	0
<i>T. sylvae</i>	13	23	42	27	0
<i>T. polyphyllum</i>	15	11	43	20	0

* = gynomonocious; s.d. = standard deviation.

interpretation, the monoecious syndrome representative of *Tetramolopium* sect. *Tetramolopium* would be an outcrossing system. The combination of large heads with numerous florets, conspicuous ligules, and marked protogyny are adaptations that promote outcrossing. At the other extreme, the gynomonocious syndrome of sect. *Sandwicense* represents a selfing system. Here, the small heads with fewer florets, shorter inconspicuous ligules, and lessened protogyny promote selfing. Since the species are self-compatible, presumably there is a greater chance for geitonogamy between the ray and disk florets and also a chance for selfing in the hermaphrodite disk florets. Lloyd explained the negative correlation between the ray/disk floret ratio and ligule length as being indicative of the relative amounts of outcrossing among the species.

At first glance this breeding system explanation makes perfect sense and seems to provide a satisfactory answer to the question. Yet, it does not explain why gynomonocious species of *Tetramolopium* have a compound capitulescence which, through aggregation of numerous small heads, produces a large mass of florets that may be extremely attractive to pollinators. Nor does it explain the broad difference in habit and habitat among the sections. Both syndromes are also associated with production of abundant nectar, indicating that they both attract pollinators. Clearly, there are outcrossing characteristics in the gynomonocious species that are out of place with characters tending to promote selfing. The outcrossing explanation does not adequately explain situations in other Compositae genera either. Studies of the three species of *Blennosperma* by Ornduff (1963) indicate that monoecy may have little to do with promoting outcrossing as would be expected. Ornduff found that all three species were monoecious but differ in breeding systems. *Blennosperma nanum* and *B. bakeri* are self-incompatible and thus totally outcrossing. *Blennosperma chilense*, on the other hand, which was probably derived from the former two species, is self-compatible and largely autogamous. In this case sex expression appears not to be important for regulation of outcrossing; rather, compatibility mechanisms are operating in this respect.

Recently, other mechanisms have been proposed for the evolution and function of sexual systems that do not invoke outcrossing as the main selective force. Bawa and Beach (1981) propose that the sexual systems are fundamentally linked to the pollination biology of the plants and can be fully understood only in this context. Such

phenomena as the effects of foraging habits of pollinators may be important in this regard. The differences in capitulescence and flower color between the two sex expression classes in *Tetramolopium* could well be the result of differences in pollinators and their behavior patterns. This seems more likely given the different habitat preferences of the species in the two classes. Lloyd (1979) proposes that much of the adaptive significance of sex expression lies in the selection of relative pollen- and seed-packaging strategies, that is, selection for the optimal number of both polliniferous and seminiferous flowers. Gynomonoecy is thus a mechanism that selects for the optimum number of female flowers (see Lloyd, 1979, for further discussion). This explanation would account for the greater percentage of female florets in gynomonoeious species of *Tetramolopium*.

One intriguing aspect of the different sex expressions is the evolutionary pathway in *Tetramolopium*. All available evidence suggests that New Guinean species of *Tetramolopium* are strictly monoecious (Koster, 1966). Since the Hawaiian species were probably derived from the New Guinean taxa, the primitive species in Hawaii must have been monoecious. Gynomonoecy then has probably evolved autochthonously in Hawaii from a monoecious ancestor. This is the reverse of the situation in *Cotula*, where the primitive ancestor was postulated to be gynomonoeious. The gynomonoeious condition is known to be recessive (or possibly hypostatic) to monoecy in *Tetramolopium*. Further studies are needed to determine the genetics of sex expression control in *Tetramolopium*.

These preliminary studies have established that much of the morphological diversity in Hawaiian *Tetramolopium* is related to the different sexual systems. The studies to date on the sexual systems of *Tetramolopium* have just scratched the surface concerning the evolutionary development and function of the different patterns. Further research in *Tetramolopium* along these lines should include several different studies. First of all, extensive field observations of pollinators and their foraging behaviors are needed. Although the native insect flora of Hawaii has been disturbed, these studies would still provide important information. In this same vein, studies of the ultraviolet reflectance patterns in the two syndromes may reveal differences which would then suggest a difference in pollinators. Finally, the possible existence of cryptic self-compatibility (Weller and Ornduff, 1977) in the monoecious species of *Tetramolopium* should be investigated. Such a system could be promoting outcrossing in the same manner as the noncryptic self-incompatibility system in *Blennosperma*. Further research is needed to provide information about the function of these processes in *Tetramolopium* and in the Compositae in general.

NECTAR ANALYSIS

Nectar was collected in micropipettes. Nectar drops were then placed on strips of Whatman 1 chromatography paper in concentrated spots. Nectar from several florets in a head was pooled. The nectar was then analyzed for amino acid and sugar content (Baker and Baker, 1976). These analyses were performed by Irene Baker at the University of California at Berkeley.

The results of the sugar analyses of the nectar are presented in TABLE 7. The values represent relative proportions of each of three sugars: sucrose, fructose, and glucose, that were present in the nectar (after Baker and Baker, 1983). It is evident that the nectars are dominated by glucose and fructose, relatively little sucrose being present.

TABLE 7. SUGAR COMPOSITION OF NECTAR (PROPORTIONS)

	sucrose	glucose	fructose	<u>sucrose</u> glucose + fructose
<i>T. filiforme</i>	0.104	0.434	0.420	0.121
var. <i>polyphyllum</i>				
<i>T. consanguineum</i>	ND	0.626	0.374	0.021
subsp. <i>leptophyllum</i>				
var. <i>leptophyllum</i>				
<i>T. remyi</i>	0.96	0.547	0.360	0.106
<i>T. sylvae</i>	0.181	0.425	0.414	0.192
<i>T. lepidotum</i>	ND	0.455	0.545	0.072

ND = not detected.

Baker and Baker (1983) indicate that there is a general constancy in the relative proportions of sucrose and hexoses (fructose and glucose) within a species. They have formulated four categories of sucrose to hexose ratios in nectar: (1) hexose-dominant = sucrose/hexose ratio of less than 0.1, (2) hexose-rich = sucrose/hexose ratio between 0.1 and 0.499, (3) sucrose-rich = sucrose/hexose ratio between 0.5 and 0.99, and (4) sucrose-dominant = sucrose/hexose ratios of greater than 0.999. It has further been determined that certain plant families are constant with regard to a particular category and that correlations exist between sugar ratios of nectar and various pollination types. The sugar ratio values for *Tetramolopium* fall in the hexose-rich category. This is typical for the Compositae (Baker and Baker, 1983) and is indicative of insect pollination either by short-tongued butterflies, bees, or flies.

The nectar of *Tetramolopium* was also tested for the presence of amino acids. Baker and Baker (1976) demonstrated that amino acid patterns in nectar can be very useful in demonstrating affinities between taxa. Although the nectar samples collected for *Tetramolopium* did have amino acids, they are in extremely low concentrations. Only one sample (from *T. lepidotum*, Lowrey 421) had sufficiently high concentrations of amino acids to permit analysis. The amino acid complement of this sample was: glutamic acid, glutamine, glycine, isoleucine, leucine, lysine, phenylalanine, proline, serine, threonine, and valine. Certainly no conclusions concerning affinity can be made on the basis of this one sample, but the existence of amino acids in *Tetramolopium* has been demonstrated, albeit in low concentrations. Further studies involving larger samples of nectar are needed to determine the taxonomic potential of the amino acid patterns.

TAXONOMY

TAXONOMIC HISTORY

Tetramolopium was originally described by Nees von Esenbeck (1832), who failed to designate a type species. The genus included two species: *T. tenerimum* from the Hawaiian Islands and *T. rupestre* from the Ecuadorian Andes. *Tetramolopium rupestre* was later removed from the genus and placed in *Diplostephium* (Weddell, 1855–1861). Asa Gray (1861) relegated *Tetramolopium* to *Vittadinia* A. Rich., which at that time consisted of Australian and New Zealand species. He recognized six additional species but separated them into different sections within *Vittadinia*. Six of the species were placed in sect. *Tetramolopium*, while only one was included in sect. *Eurybiopsis*, on the basis of achene features. Bentham (1873) resurrected *Tetramolopium* as a

distinct genus but retained *T. humile* in *Vittadinia*. Pfeiffer (1871–1875) designated *T. tenerrimum* as the lectotype species for *Tetramolopium*.

In an unusual and arbitrary move, Drake del Castillo (1886–1892) transferred four species from *Tetramolopium*, including *T. tenerrimum*, to *Erigeron*. He further reduced two of these species to varietal status under *T. tenerrimum*. The accompanying illustrations bore no resemblance to any extant material of these two species, suggesting that the decisions were based upon inadequate specimens.

Hillebrand (1888) was the first botanist to conclude that all Hawaiian species of this alliance are closely related. He included the seven species of Gray (1861) under *Tetramolopium*, stating (p. 197) that “there would seem to be sufficient ground for maintaining the phylogenetic unity of all our species”. The first comprehensive revision of Hawaiian *Tetramolopium* after Hillebrand was that of Sherff (1934, 1935). Sherff recognized twelve species.

Mattfeld (1929) transferred eight species from New Guinea into *Tetramolopium*. These species had previously been placed in *Erigeron* or *Vittadinia*. Approximately 25 New Guinean species are recognized today (van Royen, 1981).

The only recent departure from the concepts of Hillebrand and Mattfeld for the genus was that of St. John (1974), who divided the species into two genera. In addition to describing a new species, he proposed a wholly new genus, *Luteidiscus*, to accommodate those species with yellow disk floret corollas; the species from both Hawaii and New Guinea with maroon disk corollas were kept in *Tetramolopium*. Not only is it (usually) unreasonable to base a genus on one character, but it is untenable to use such a variable character in the Compositae as floret color (Koster, 1976). St. John also did not uniformly apply his floret color criterion, as he kept *T. remyi* (a species with bright yellow disk florets) within *Tetramolopium*.

TAXONOMIC CONCEPTS

In the following treatment, one genus consisting of three sections is recognized. Both the New Guinean and Hawaiian species are considered at the sectional level. However, the taxonomic treatment below the sectional level deals only with Hawaiian taxa. The lack of sterility barriers among all Hawaiian taxa and the lack of wide morphological discontinuities among sections highlighted by the continuum of characters associated with the sex expression effectively establish Hawaiian *Tetramolopium* as a natural assemblage. Examination of New Guinean taxa leaves no doubt that these, too, form a cohesive assemblage and are related to the Hawaiian species. Two of the sections are wholly Hawaiian in distribution, while the third includes all the New Guinean taxa plus a single Hawaiian species, *T. humile*.

Sectional delimitation within *Tetramolopium* is based largely on three characteristics: (1) sex expression syndromes, (2) ecological preferences, and (3) habit and branching patterns. *Tetramolopium* sect. *Tetramolopium* occurs only in the Hawaiian Islands and includes those species that are monoecious, occur in xeric exposed habitats at low elevations, and are basally branched, prostrate, decumbent, or dwarf shrubs. Section *Sandwicense* encompasses those species that are gynomonocious, inhabit the dry forest understorey or submesic ridge top scrub, and are apically branched upright shrubs. Section *Alpinum* contains all the New Guinean taxa and a single Hawaiian

species, *T. humile*. The alpine habitat and the basally branched caespitose habit serve as obvious distinguishing features. Furthermore, disk corolla shape, achene features, and pappus structure strengthen the delimitation. The sex expression is somewhat anomalous in that the New Guinean species appear to be monoecious, while *T. humile* is obviously gynomonoecious, with both simple and compound capitulescences.

The eleven Hawaiian species recognized in this treatment are allopatric and each is distinct in at least three correlated morphological characters. Studies of plants grown under uniform conditions have provided valuable information for establishing which characters are environmentally or developmentally variable and thus not totally reliable taxonomically. One new species is described and three previously recognized species are reduced to either subspecific or varietal rank. The issue of bewildering morphological variability and blurred specific limits, due largely to hybridization, is not a problem in *Tetramolopium* as it is in so many other Hawaiian genera.

Two taxonomic ranks below the species level are utilized in this treatment. The subspecies level is used to denote morphologically distinguishable regional groups within species (Davis, 1978). The emphasis is placed on distinct morphological variation that is regional but discrete. The variety, in contrast, is used to denote distinctive local races within the range of either a subspecies or a species. The morphological variation exhibited by a variety is distinctive but not great and is limited to a very local population. Both taxonomic categories have been used to recognize morphological discontinuities within species, while conveying information about interrelationships of the infraspecific taxa.

TAXONOMIC TREATMENT

TETRAMOLOPIUM Nees, Gen. Sp. Aster. 202. 1832. LECTOTYPE (Pfeiffer, Nomencl. Bot.

2: 1376. 1874): *Tetramolopium tenerrimum* (Less.) Nees (*Aster tenerrimus* Less.).

Vittadinia sect. *Tetramolopium* A. Gray in Proc. Amer. Acad. Arts 5: 119. 1861.

Luteidiscus St. John in Bot. Jahrb. 94: 549. 1974. TYPE: *Luteidiscus calcisabulorum* St. John (= *Tetramolopium rockii* var. *calcisabulorum* (St. John) Lowrey).

Caespitose, decumbent (procumbent in New Guinean taxa), or erect shrubs, monoecious or gynomonoecious; stems sympodially branched, each terminated by a capitulescence, glabrous, glandular, or glandular-pubescent; leaves alternate, simple, entire or dentate, sessile (in all New Guinean taxa) or petiolate, deciduous but with decurrent and persistent bases often giving older stems a tuberculate appearance, sclerophyllous, succulent, or thin, spatulate, lanceolate, or linear-lanceolate, entire or dentate, glandular or glandular-pubescent; capitulescence terminal, of solitary heads or of 5-60 heads in loose to congested corymbose panicles; heads radiate, 2-15 mm. in diameter, pedunculate; peduncles glabrous or variously pubescent, bracteate, the bracts reduced upward; involucre cylindrical, campanulate, hemispheric, or turbinate; phyllaries 3-4-seriate, reduced outward, linear-lanceolate or lanceolate, obtuse, acute, or acuminate, narrowly or broadly scarious-hyaline-margined, the margin entire, denticulate, or lacerate; receptacle flat, naked, alveolate; ray florets 5-250, pistillate, ligulate, the ligule sometimes much reduced, the tube glabrous, the apex 2- or 3-toothed, the style branches linear-subulate, papillose; disk florets hermaphrodite or functionally staminate, 1-110, the corolla tubular or infundibular, 5-lobed, glabrous except for papillose abaxial faces of lobe apices, the style branches subulate or linear, with stigmatic lines on basal portions of branches, the style appendage subulate, densely papillate abaxially, the papillate portion half the length of style branches in hermaphrodite florets, extending the entire length in functionally staminate florets, the

stamens 5, the anthers obtuse or slightly cordate basally, the apical appendage lanceolate or linear-lanceolate; achenes laterally compressed, oblanceolate or obovoid (linear in functionally staminate disk florets, otherwise the ray and disk achenes similar), the faces 1-6-nerved or the nerves obsolete, glabrous, glandular, glandular-strigose, or appressed-hirsute; pappus similar in ray and disk florets, setaceous, white or variously colored, the bristles unequal, 1-2-seriate, shorter than disk corollas; $n = 9$.

DISTRIBUTION: New Guinea and the Hawaiian Islands. Alpine grassland, scree slopes, or open moist areas throughout the high mountains of New Guinea, mostly above 2,500 m. Xeric to submesic habitats from sea level to 3,300 m. on five of the six major islands of the Hawaiian archipelago (FIGURES 2, 3, 4).¹

KEY TO SPECIES OF HAWAIIAN TETRAMOLOPIUM

1. Caespitose, alpine or subalpine shrubs usually growing above 2,000 m.; involucre cylindrical; disk corollas tubular; achenes fusiform-cylindric, the facial nerves absent or, if present, only near base; pappus 5.5-7 (-8) mm. long, longer than involucre (sect. *Alpinum*). 1. *T. humile*
1. Prostrate, decumbent, or upright shrubs growing below 2,000 m.; involucre hemispheric, obconic, or campanulate; disk corollas infundibular; achenes obovoid or oblanceolate, the faces prominently 1-6-nerved; pappus 1.6-4 mm. long, equalling or shorter than involucre.
 2. Decumbent, prostrate, or low dwarf shrubs; capitulescence simple, occasionally subumbellate in *T. filiforme*; disk florets more than 15 per head, functionally staminate, the corolla yellow (except usually maroon in *T. filiforme*) (sect. *Tetramolopium*).
 3. Disk florets maroon, rarely yellow; low, upright, compact dwarf shrubs; leaves linear-filiform and entire or linear-oblanceolate and deeply dentate, never sclerophyllous or spatulate.
 3. *T. filiforme*
 3. Disk florets yellow; decumbent or prostrate shrubs, or if upright then not compact; leaves spatulate, spatulate-oblanceolate, or linear, if linear then sclerophyllous and with the margin strongly involute.
 4. Leaves mostly glabrous or only sparsely pubescent, obviously spatulate or spatulate-oblanceolate, never involute or sclerophyllous.
 5. Leaves succulent, short-petiolate, 3-7 mm. wide; branches stout; coastal bluffs of Maui and Molokai. 6. *T. sylvae*
 5. Leaves not succulent, on long narrow petioles, 1-3 mm. wide; branches thin and delicate; inland hills of Oahu. 7. *T. tenerrimum*
 4. Leaves densely pubescent and spatulate, or if glabrous then sclerophyllous and linear with the margins strongly involute.
 6. Leaves densely pubescent, glandular-pubescent or glandular-sericeous, spatulate, the blade 3-6 mm. wide, not involute; lithified calcareous sand dunes of western Molokai. 5. *T. rockii*
 6. Leaves mostly glabrous or minutely pubescent, strongly involute, the blade 0.3-1 mm. wide; dry ridges of Maui and Lanai.
 7. Disk florets 15-25; peduncles 1.5-3 cm. long. 2. *T. capillare*
 7. Disk florets 70-100; peduncles 3-16 cm. long. 4. *T. remyi*
 2. Upright shrubs; capitulescence compound, corymbose-paniculate; disk florets fewer than 15 per head, hermaphrodite, the corolla maroon or pinkish (sect. *Sandwicense*).
 8. Heads mostly 5-10 per capitulescence; ray floret lamina 1.5-2.5 mm. long.
 9. Leaves uniformly densely hispid, entire or shallowly dentate; capitulescence congested (except in subsp. *laxum*). 10. *T. arenarium*
 9. Leaves glandular-punctate, not densely hispid or hirsute, often coarsely dentate; capitulescence open. 8. *T. lepidotum*
 8. Heads mostly more than 10 per capitulescence, usually 15-60; ray floret lamina 0.5-1.5 mm. long.
 10. Disk florets 1-3 per head; ray floret lamina filiform; foliage densely pilose or hirsute.
 9. *T. conyzoides*
 10. Disk florets 4-12 per head; ray floret lamina not filiform; foliage resinous-glandular, never pilose or hirsute. 11. *T. consanguineum*

¹Note added in proof: *Tetramolopium sylvae*, herein described as a new species from Maui and Molokai, has recently been discovered growing on Mitiaro in the Cook Islands (W. R. Sykes, pers. comm.).

TETRAMOLOPIUM sect. ALPINUM Lowrey, sect. nov. TYPE: *Tetramolopium humile* (A. Gray) Hillebr.

Frutices alpini vel subalpini; capitula terminalia, plerumque solitaria raro composita, monoecia raro gynomonocia; achenia compressa, nervis facialibus nullis vel non nisi basim versus manifestis; pappus involucre superans.

DISTRIBUTION: New Guinea and Hawaiian Islands.

1. ***Tetramolopium humile*** (A. Gray) Hillebr. Fl. Hawaiian Isl. 198. 1888. *Vittadinia humilis* A. Gray in Proc. Amer. Acad. Arts 5: 118. 1861. TYPE: HAWAIIAN ISLANDS: HAWAII: 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: US!; ISOTYPES: GH!, MO!, NY!, PH!).

Tetramolopium humile var. *β* Hillebr. Fl. Hawaiian Isl. 199. 1888.

Tetramolopium humile f. *laxa* Skotts. in Acta Horti Gotob. 2: 273, nom. nud. 1926.

Tetramolopium humile var. *skottsbergii* Sherff in Bot. Gaz. 95: 104. 1934. LECTOTYPE (here designated, HOLOTYPE at B, destroyed): HAWAIIAN ISLANDS: HAWAII: Mauna Kea, 10,000 feet, June 1910, *J. F. Rock 8333* (GH!; ISOLECTOTYPES: BI, BISH!, FI, MICH!, NY!, UC!, US!).

Caespitose or somewhat low dwarf shrub, gynomonocious, 8–20 cm. high, the stems branching basally, densely glandular, somewhat resinous with pilose or hispidulose hairs; leaves petiolate, 1–2.5 cm. long, the blade 5–12 mm. long, 0.8–3 mm. wide, linear-oblongate or spatulate, obtuse, densely glandular-hispidulous, the margin entire; capitulescence simple or corymbose-paniculate, if compound having 5–7 heads; peduncles 2–3.5 cm. long, capitate-glandular, bracteate, the bracts linear-subulate; involucre cylindrical, 7–9 mm. high; phyllaries (22–) 24–45, linear or linear-lanceolate, acuminate, densely capitate-glandular (with scattered strigose hairs in subsp. *humile*), scarious-hyaline-margined, narrowly so in outer phyllaries, entire or fimbriate distally, the inner bracts often purple-tipped; ray florets 20–30 (13–36), uniseriate, white or tinged with lavender, the tube (4.1–) 4.5–5.5 mm. long, the lamina 2.9–3.3 mm. long, 0.7–0.9 mm. wide; disk florets tubular, 7–24 per head, the corollas pink to maroon (rarely yellow), 6.2–7.5 mm. long, the tube 3–4 mm. long, the anther appendage linear-lanceolate or lanceolate-oblong, 0.12–0.25 mm. long; achenes fusiform-cylindrical, 3.3–4 (–4.5) mm. long, 0.7–0.8 mm. wide, densely glandular and strigose, with some glands large and spherical, containing a resinous substance, the faces obscurely 1-nerved basally or nerves lacking, the pappus fulvous, stout, 5.5–7 (6–8) mm. long; *n* = 9.

KEY TO TAXA OF TETRAMOLOPIUM HUMILE

1. Capitulescence compound, the capitula corymbose-paniculate; leaves oblanceolate to spatulate; Hawaii.
 2. Foliage strongly hispid or hispid-hirsute with glandular hairs. 1a(i). subsp. *humile* var. *humile*
 2. Foliage minutely glandular only, appearing glabrous, not hispid or hispid-hirsute.
 - 1a(ii). subsp. *humile* var. *sublaeve*
1. Capitulescence simple, the capitula solitary; leaves linear-oblongate; Maui. . . . 1b. subsp. *haleakalae*

1a(i). ***Tetramolopium humile*** subsp. ***humile*** var. ***humile***.

FIGURE 11c, d.

Caespitose or somewhat lax dwarf shrub 10–20 cm. high; stems densely capitate-glandular, resinous, with scattered hispidulose hairs; leaves (1.1–) 1.5–2.5 cm. long, 1.5–3 cm. wide, linear-oblongate or spatulate, densely glandular and hispidulous, the margin entire, the blade 0.5–12 mm. long; capitulescence corymbose-paniculate, open, the heads 5–7; peduncles 2–3 cm. long, capitate-glandular, the bracts subulate; involucre cylindrical, 7–8 mm. high, the phyllaries 24–30 (22–32), capitate-glandular with scattered strigose-hispid hairs; receptacle 1.2–1.4 mm. diam.; ray florets uniseriate, (13–) 20–30, the tube (4.5–) 5–5.5 mm. long, the lamina 2.9–3.2 mm. long, 0.8–0.9 mm. wide; disk florets tubular, 7–10 (–13), the corolla 6.5–7.2 (6.2–7.5) mm. long, the tube (3.1–) 3.5–4 mm. long, the anther appendages linear-lanceolate, 0.15–0.25 mm. long; achenes 3.3–4 (–4.4) mm. long, obscurely 1-nerved basally.

DISTRIBUTION: Island of Hawaii, on the slopes of Mauna Kea, Mauna Loa, and Hualalai. (1,300–) 1,520–3,050 m. Crevices of pahoehoe lava flows or on cinder slopes. Flowering period: April to February.

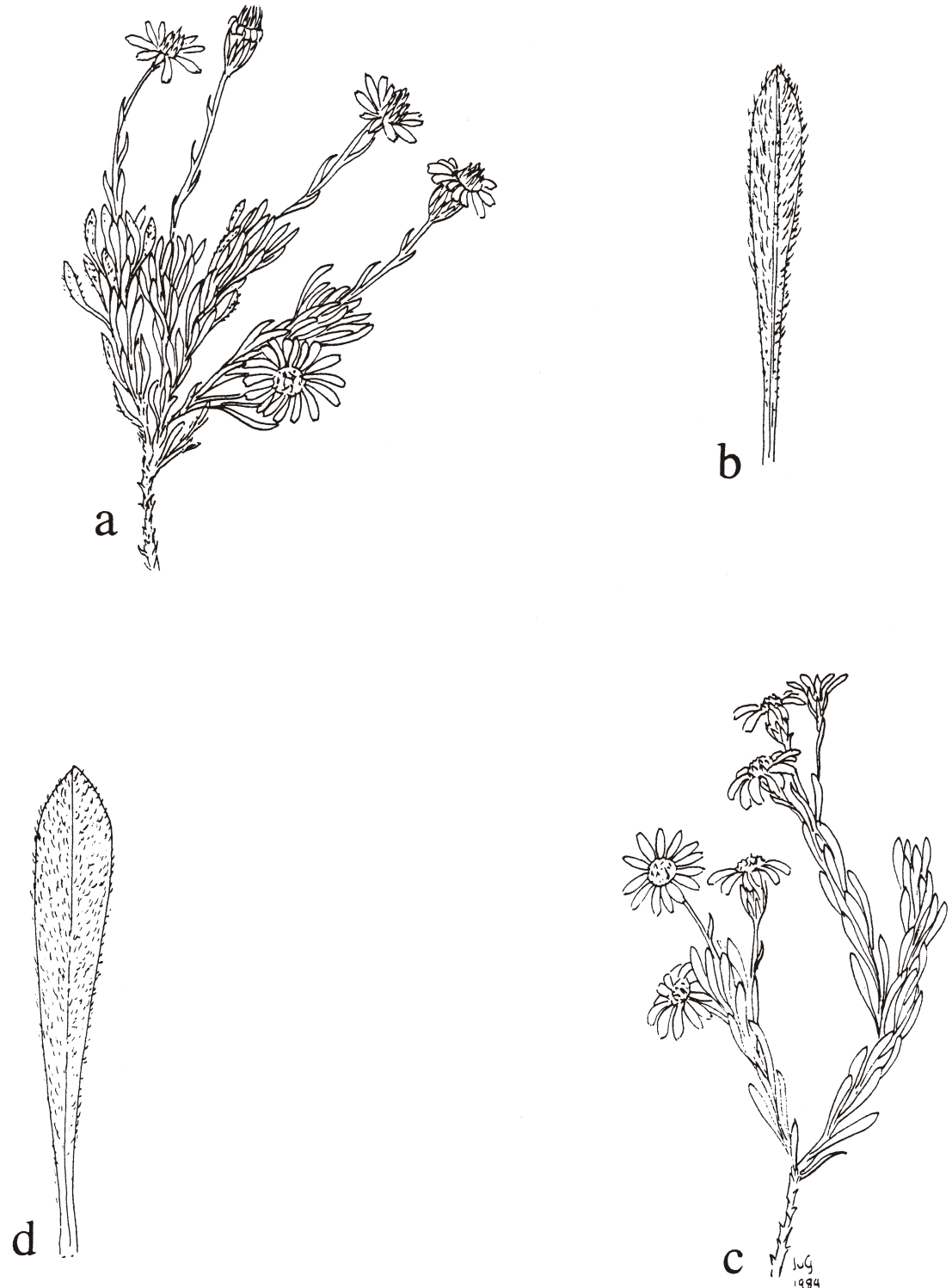


FIGURE 11. *Tetramolopium humile*. a, *T. humile* subsp. *haleakalae*, habit, life-size. b, *T. humile* subsp. *haleakalae*, leaf, $\times 4$. c, *T. humile* subsp. *humile* var. *humile*, habit, life-size. d, *T. humile* subsp. *humile* var. *humile*, leaf, $\times 4$.

REPRESENTATIVE SPECIMENS: HAWAII: Kona, Kealakekua Ranch, near Puu O Uo, 23 November 1958, *Christ s. n.* (BISH); end of Kilauea-Mauna Loa truck road, 14 September 1938, *Cranwell, Selling, and Skottsberg 3274* (GB, s); on 1859 lava flow at about 7,500 ft., 25 August 1949, *Degener et al. 19815* (NY); near summit of Hualalai, 9 July 1967, *Degener and Greenwell 31275* (B, GB); slopes of Hualalai behind Honohane, 16 June 1911, *Forbes 186* (BISH); Ahu-a-Umi, 16 September 1971, *Herbst 2146* (BISH, F, MICH, MO, NY); Mauna Kea north side, 22 August 1916, *Hitchcock 14278* (BISH, US); Hamakua Distr., Kaoke, slope of Mauna Kea, 100 m. north of Hale Pohaku Camp, 27 July 1978, *Lowrey 436* (BISH, CANB, HALEAKALA, K, LAM, MO, NY, OS, TEX); trail to Red Hill on Mauna Loa, 30 July 1978, *Lowrey 437* (BISH, CANB, HALEAKALA, K, LAM, MO, NY, OS, TEX).

1a(ii). ***Tetramolopium humile* subsp. *humile* var. *sublaeve*** Sherff in Bot. Gaz. 95: 501.

1934. TYPE: HAWAIIAN ISLANDS: HAWAII: 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: US!; ISOTYPE: GH!).

A glabrate variety of subsp. *humile*; stems and leaves minutely granular-glandular or sparsely pilose or hispid, appearing nearly glabrous without magnification.

DISTRIBUTION: Island of Hawaii. Previously known only from type collection, locality unknown. It has recently been recollected on the Pohakuloa Army Training Base east of the Saddle Road (Charles Lamoureux, pers. comm.). It apparently occurs at about 1,900 m. on sparsely vegetated lava outcrops. Flowering period: Unknown.

1b. ***Tetramolopium humile* subsp. *haleakalae*** Lowrey, subsp. nov. TYPE: HAWAIIAN ISLANDS: MAUI: Haleakala National Park, Lualailua Hills, cliff faces north of and below Haupaakea Peak, 2,700 m., 11 July 1978, *T. Lowrey 430* (HOLOTYPE: UC!; ISOTYPES: BISH!, CANB!, HALEAKALA!, K!, LAM!, MO!, NY!, OS!, TEX!).

FIGURE 11a, b.

Subspecies a subspecie typica capitulo solitario, foliis lineari-oblongatis, acheniis superficiebus enervibus, praesentia in insula Maui differt.

Caespitose dwarf shrubs 8–15 cm. high; stems densely pubescent with glandular and pilose hairs; leaves 1–1.5 cm. long, the blade 5–7 mm. long, 0.8–1.5 mm. wide, densely glandular-pilose, the pubescence slightly longer and softer than in subsp. *humile*; capitulescence simple; peduncles 3–3.5 cm. long, the pubescence with stalked or sessile capitate-glandular hairs; involucre 8–9 mm. high; phyllaries 35–45, scarious-hyaline-margined, with densely capitate-glandular hairs; ray florets 20–30 (18–36), the tube (4.1–) 4.5–5 mm. long, the lamina 3–3.3 mm. long, 0.7–0.9 mm. wide; disk florets 14–20 (13–24), the corolla tubular, 6.5–7 mm. long, the tube 3–3.5 mm. long, the anther appendage lanceolate-oblong, 0.12–0.2 mm. long; receptacle 2.5–3.5 mm. broad; achenes completely nerveless.

DISTRIBUTION: East Maui. Slopes and crater floor of Haleakala, 1,900–3,300 m. Crevices of pahoehoe lava flows, or on cinder fields. Flowering period: April to February.

REPRESENTATIVE SPECIMENS: MAUI: Haleakala, 16 May 1948, *Alexander and Kellogg 5343A* (MICH, NSW, NY, UC, US); Haleakala, Hawaii National Park, Highway 378 above Park Headquarters, 2 March 1962, *Carlson 3794* (F); near Koolau Gap within Haleakala Crater, 29 June 1927, *Degener 5003* (B, BM, DS, F, G-DEL, GH, MASS, NY, PH, S, UC, US); slopes of Haleakala above Ukulele, July 1910, *Forbes 182M* (A, B, BISH, F, MO, NY, US); Haleakala, Sliding Sands Trail, 8 July 1978, *Lowrey 424* (BISH, MO, UC); Haleakala Crater, trail to Paliku Cabin, 9 July 1978, *Lowrey 425* (BISH, HALEAKALA, K, LAM, NY, OS, UC, US); Haleakala, Halemauu Trail, 9 July 1978, *Lowrey 425* (BISH, CANB, HALEAKALA, MO, TEX, UC); Haleakala, southwest slope of White Hill, 11 July 1978, *Lowrey 426* (BISH, HALEAKALA, TEX, UC); Haleakala Crater, Kalahaku Overlook, 19 July 1978, *Lowrey 423* (BISH, HALEAKALA, K, LAM, OS, UC).

The necessity for the description of a new taxon within *Tetramolopium humile* comes as a surprise. The species is the most common one in the Hawaiian Islands and the most frequently collected.

The species is readily divisible into two quite distinct subspecies on morphological and geographical bases. This fact was recognized by Sherff (1934, 1935), who was the

first worker to delimit infraspecific taxa in the species. However, misinterpretation of the type material by him, probably due to wrong locality data on the specimen labels, generated hitherto unrecognized taxonomic confusion of the two entities.

The holotype of *Tetramolopium humile* was collected on the island of Hawaii by the U. S. Exploring Expedition. The specimen has polycephalous capitulescences together with oblanceolate to spatulate leaves and obscurely 1-nerved achene faces. Extensive field work and uniform growth studies have confirmed these characters to be diagnostic for all populations occurring on the island of Hawaii. Maui populations, on the other hand, uniformly possess monocephalous capitulescences, linear-oblanceolate leaves, and nerveless achene faces.

Sherff (1934, 1935) circumscribed *Tetramolopium humile* var. *skottsbergii* to include those plants on the island of Hawaii with polycephalous capitulescences, oblanceolate leaves, and obscurely 1-nerved achenes. He circumscribed var. *humile* to include plants from both Hawaii and Maui with monocephalous capitulescences and nerveless achenes. However, as previously stated, only the Maui plants have monocephalous capitulescences and nerveless achenes. The problem arose because the type material of *T. humile* collected by the U. S. Exploring Expedition is actually from Hawaii but is labelled as being from both Hawaii and Maui. The holotype and isotypes are clearly polycephalous and have obscurely nerved achenes, yet Sherff described them as being monocephalous and with nerveless achenes. Sherff thus described two different taxa (var. *humile* and var. *skottsbergii*) from material representing only one taxonomic entity. The Maui populations are hence unnamed and are here described as *T. humile* subsp. *haleakalae*. The new epithet commemorates the distributional range of the taxon on Haleakala Crater of East Maui. The two taxa have been recognized at the subspecific rather than the varietal level on the basis of substantial morphological differences and distinct geographic distributions.

In addition to the diagnostic characters already mentioned, subsp. *humile* is generally taller, laxer in habit, and has shorter, more hispid pubescence than subsp. *haleakalae*. However, populations of subsp. *humile* from Hualalai on Hawaii have the longer and softer pubescence of the Maui plants.

TETRAMOLOPIUM sect. TETRAMOLOPIUM.

Decumbent, prostrate, or dwarf shrubs; leaves spatulate or filiform, flat or involute; capitulescence simple, rarely subumbellate; involucre hemispheric or campanulate; ray floret ligules conspicuous; disk florets more than 15 per head, the corollas mostly yellow, maroon in *T. filiforme*.

DISTRIBUTION: Hawaiian Islands.

2. ***Tetramolopium capillare*** (Gaud.) St. John in Ann. Missouri Bot. Gard. 52: 432. 1965. *Senecio capillaris* Gaud. Bot. Voy. Uranie, 468. 1830. *Luteidiscus capillaris* St. John in Bot. Jahrb. 94: 555. 1974. TYPE: HAWAIIAN ISLANDS: "Iles Sandwich," *C. Gaudichaud s. n.* (HOLOTYPE: P, photocopy seen).

Tetramolopium bennettii Sherff in Bot. Gaz. 95: 498. 1934. TYPE: HAWAIIAN ISLANDS: MAUI: 1833-36. *Frederick Debell Bennett 18* (HOLOTYPE: B, destroyed; photograph of holotype: F!).

Slender, decumbent or sprawling shrub, monoecious; stems apically branched, 5-8 dm. long, densely glandular when young; leaves sessile, sclerophyllous, linear-filiform, strongly involute, (1-) 1.3-2.5 cm. long, 0.3-0.4 mm. wide, entire, acute, glabrous to sparsely glandular at base; capitulescence simple; peduncles 1-3.5 cm. long, glandular, bracteate, the bracts linear; involucre hemispheric, 3-4 mm. high, 7-10 mm. diam.; phyllaries 45-50, linear-lanceolate, acuminate, sparsely capitate-glandular, the margin

narrowly hyaline, capitate-glandular to lacerate; receptacle 2–2.5 mm. diam.; ray florets 30–50, the corolla white, the tube 1.3–2.3 mm. long, the lamina 3.5–4 (–4.3) mm. long, 0.6–8 mm. wide; disk florets 16–25, the corolla greenish yellow tinged with red, 3.6 mm. long, the tube 1.3 mm. long, the lobes 0.8–1 mm. long, the anther appendages deltoid, 0.04–0.05 mm. long; achenes 2–2.6 mm. long, 0.7–0.8 mm. broad, glandular-strigose, the faces 0–2-nerved, the pappus white, uniseriate, 1.9–2.1 mm. long.

DISTRIBUTION: Maui. Known only from the foothills of West Maui at 425 m. from Lahainaluna to Wailuku. Dry forest scrub among rocks. It is probably extinct. Flowering period: Unknown.

REPRESENTATIVE SPECIMENS: MAUI: Lahainaluna, *Forbes s. n.* (BISH); ridge east of Wainee, *Forbes 2760* (BISH); Lahainaluna, Kuia, *St. John 25604* (BISH).

Tetramolopium capillare was last collected in 1955 by Harold St. John from the Lahainaluna area of western Maui. I have made several unsuccessful attempts to locate the species. It is very likely extinct or at best extremely localized and on the verge of extinction.

The involute leaves, glandular pubescence, and intricate branching patterns indicate a close relationship to *Tetramolopium remyi*. The distribution of *T. capillare* also occurs very near to the range of *T. remyi* on Maui. Despite its probable close relationship with *T. remyi*, *T. capillare* is readily distinguished by its shorter peduncles, smaller heads with fewer florets, and the lax or sprawling habit.

3. ***Tetramolopium filiforme*** Sherff in Bot. Gaz. 95: 498. 1934. TYPE: HAWAIIAN ISLANDS: OAHU: Waianae Mountains, 1869, *W. Hillebrand s. n.* (HOLOTYPE: GH!; ISOTYPES: K!, MEL!).

Dwarf shrubs, somewhat caespitose, monoecious, 5–15 cm. high, basally and intricately branched; stems glabrous when mature except the ciliate leaf bases, minutely capitate-glandular when young; leaves clustered distally, sessile or petiolate, 1–2 cm. long, 0.4–1.2 mm. wide, filiform, linear or linear-lanceolate, entire or strongly dentate with linear lobes, glandular-punctate and sparsely strigose on margin and midrib; capitulescence simple or subumbellate, if compound with 2–4 heads; peduncles (1.9–) 2–4.7 cm. long, sparsely to densely capitate-glandular, the bracts linear; involucre 4–5 mm. high, 7–10 mm. wide; phyllaries 40–50 (32–59), lanceolate, acuminate, glabrous abaxially, the outer phyllaries with sparsely glandular margins, the inner phyllaries scarious-hyaline-margined, lacerate distally; receptacle 1.5–2.5 mm. broad; ray florets uniseriate, 35–52, white or pale lavender, the tube 1.6–2.1 mm. long, the lamina 3–4 mm. long, (0.5–) 0.7–1 mm. wide; disk florets 18–30, maroon or rarely yellow, the corolla infundibular, 3.1–4 (–4.3) mm. long, the tube 1.3–2.1 mm. long, the anther tips linear-lanceolate, 0.15–0.2 mm. long; achenes 2–2.7 mm. long, the fertile achenes 0.6–1 mm. wide, sparsely glandular-strigose to glabrous, the faces (0–) 1–3-nerved, the pappus white, 2.2–3.2 mm. long; $n = 9$.

KEY TO VARIETIES OF TETRAMOLOPIUM FILIFORME

1. Leaves linear or linear-filiform, the margin entire; xeric cliff faces below 770 m. on Ohikilolo Ridge, Waianae Mountains, Oahu. 3(i). var. *filiforme*
1. Leaves linear-oblongate, coarsely dentate; submesic mountain slopes above 770 m. on Ohikilolo Ridge. 3(ii). var. *polyphyllum*

3(i). ***Tetramolopium filiforme*** var. ***filiforme***.

FIGURE 12c, d.

Leaves 1–2 cm. long, 0.4–0.8 (–1.2) mm. wide, linear-lanceolate, linear, or filiform, entire, acute, the blade glandular-punctate, the margin and midrib sparsely strigose or glabrous; peduncles 2–4.7 cm. long; involucre 7–10 mm. diam.; phyllaries 40–50 (32–59), the receptacle 1.5–2.5 mm. diam.; ray florets 35–52, the lamina 3–4 mm. long, (0.5–) 0.7–1 mm. wide; disk florets 18–20, the corolla 3.1–4 (–4.3) mm. long, the tube 1.3–1.5 mm. long; achenes 2–2.5 mm. long, 0.6–0.8 mm. wide when fertile, sparsely glandular-strigose or occasionally glabrous, the faces (1–) 2–3-nerved, the pappus 2.2–3.2 mm. long.

DISTRIBUTION: Oahu. Ohikilolo ridge in the Waianae Mountains. Xeric ridge crest or rock crevices on north-facing cliffs. 500–700 m. Known from only one population. Flowering period: March to September.

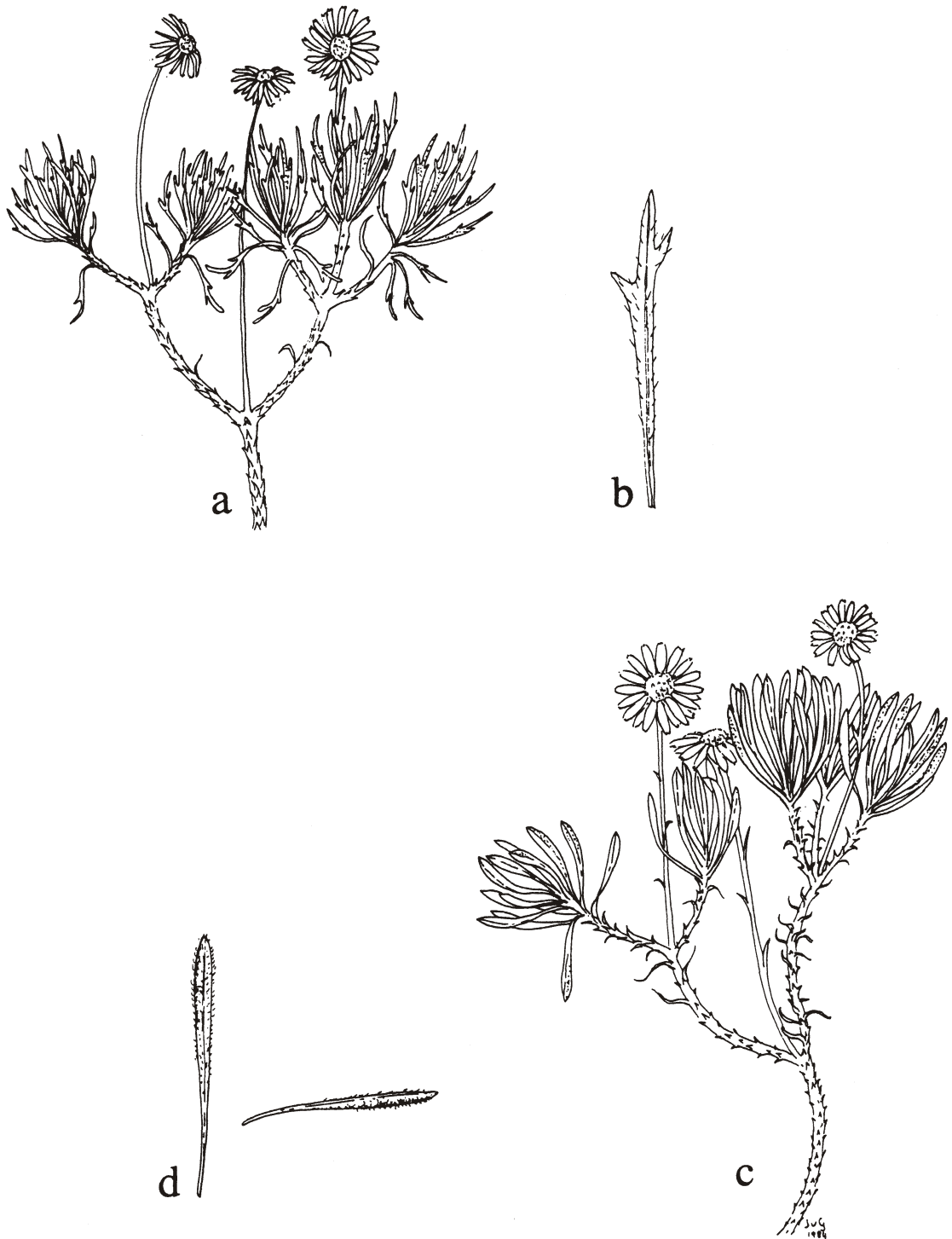


FIGURE 12. *Tetramolopium filiforme*. a, *T. filiforme* var. *polyphyllum*, habit, life-size. b, *T. filiforme* var. *polyphyllum*, leaf, $\times 2$. c, *T. filiforme* var. *filiforme*, habit, life-size. d, *T. filiforme* var. *filiforme*, leaves, $\times 2$.

REPRESENTATIVE SPECIMENS: OAHU: Waianae Mountains, on arid exposed crest of Ohikilolo Ridge, 25 May 1975, *Herbst and Obata 5333* (BISH, UC); valley of Makaha, Waianae Mountains, August 1869, *Hillebrand s. n.* (BM); Waianae District, Waianae Mountains, Ohikilolo Ridge, 4 July 1978, *Lowrey and Obata 419* (BISH, CANB, K, LAM, MO, OS, NY, UC, US); Waianae Distr., Waianae Mountains, Ohikilolo Ridge, 28 April 1979, *Lowrey, Perlman, and Witter 441* (BISH, MO, TEX, UC).

- 3(ii). **Tetramolopium filiforme** var. **polyphyllum** (Sherff) Lowrey, comb. et stat. nov.
Tetramolopium polyphyllum Sherff in Bot. Gaz. 95: 499. 1934. TYPE: HAWAIIAN ISLANDS: OAHU: 1868-71, *Heinrich Wawra s. n.* (HOLOTYPE: w!).

FIGURE 12a, b.

Leaves 1-2 (-2.3) cm. long, (0.8-) 0.9-1.2 mm. wide, linear to linear-lanceolate, the margin dentate, the lobes subopposite and linear, 0.5-0.7 mm. long, the pubescence sparsely glandular, the midrib and margin strigose; peduncles (1.9-) 2.2-3.8 cm. long; involucre 4-5 mm. high, 8-9 mm. diam.; phyllaries (32-) 34-42; receptacle 2-2.5 mm. diam.; ray florets 42-52, the lamina 3-3.4 mm. long, 0.7-1 mm. wide; disk florets 20-30, the corolla 3.3-3.8 mm. long, the tube 1.3-1.5 mm. long; achenes (2-) 2.2-2.7 mm. long, 0.8-1 mm. wide when fertile, glabrous or very sparsely strigose, the faces with 0-2 nerves, the pappus 2.3-2.9 mm. long.

DISTRIBUTION: Oahu. Waianae Mountains, known only from summit of Ohikilolo ridge. Submesic ridge tops of grassy slopes. 900-1,000 m. Flowering period: April to January.

Tetramolopium filiforme is exceptional in sect. *Tetramolopium* by virtue of its maroon disk floret corollas, occasionally compound capitulescence, and nonspatulate leaves. As discussed previously, these characters match those seen in sect. *Sandwicense* and may have resulted from an introgressive hybridization event with *T. lepidotum*. More studies are needed to clarify this situation.

REPRESENTATIVE SPECIMENS: OAHU: Makaha, Waianae Range, August 1869, *Hillebrand s. n.* (BISH); Waianae Distr., Waianae Mountains, volcanic cone beyond Puu Ohikilolo, *Lowrey and Obata 420* (BISH, CANB, K, MO, NY, OS, UC); Waianae Distr., Waianae Mountains, volcanic cone beyond Puu Ohikilolo, 28 April 1979, *Lowrey, Perlman, and Witter 442* (BISH, MO, US).

The recognition of *Tetramolopium filiforme* var. *filiforme* and *T. filiforme* var. *polyphyllum* by Sherff (1934) as distinct species was based on scanty herbarium material and ignorance of their distributions. The main morphological distinctions are based on leaf characters. The achenes also show minor differences. These character differences are certainly not of the same magnitude as those separating other species in the genus. Both taxa are confined to the same ridge in the Waianae Mountains on Oahu. The populations of the two varieties were probably contiguous in the past but have become separated recently due to heavy erosion. The few morphological differences between the taxa, their probable sympatric distribution in the recent past, and the possible influence of hybridization give support to their treatment as varieties.

4. **Tetramolopium remyi** (A. Gray) Hillebr. Fl. Hawaiian Isl. 197. 1888. *Vittadinia remyi* A. Gray in Proc. Amer. Acad. Arts 5: 119. 1861. *Erigeron remyi* Drake, Ill. Fl. Ins. Mar. Pacif. 65. pl. 31. 1888. TYPE: HAWAIIAN ISLANDS: MAUI: 1851-1855, *J. Remy 239* (HOLOTYPE: GH!).

FIGURE 13.

Decumbent or occasionally upright shrubs, monoecious, 1-4 dm. high; stem apically and intricately branched, often appearing dichotomously branched, capitate-glandular and scabrid on young portions; leaves linear, sclerophyllous, strongly involute in mature foliage, oblanceolate to spatulate in juvenile foliage, 1.5-3 (1.2-3.4) cm. long, 0.5-1 mm. wide, glandular-punctate and sparsely strigose, the margin entire and strigose; capitulescence simple; peduncle 4-12 (2.7-16) cm. long, capitate-



FIGURE 13. *Tetramolopium remyi*. a, habit, life-size. b, leaf, $\times 4$. c, side view of leaf, $\times 4$.

glandular with short, stout ornithorhynchous hairs, the bracts filiform; receptacle (2.7–) 3–5 mm. diam.; involucre broadly hemispheric, 5–7 mm. high, 9–15 mm. diam.; phyllaries (60–) 65–80, linear-lanceolate, acuminate, capitate-glandular abaxially and marginally, scarious-hyaline-margined, erose distally; ray florets 150–250, biseriate, the corolla white, the tube 2–3 mm. long, the lamina 4–6 mm. long, 0.4–0.7 mm. wide; disk florets 70–100, the corolla yellow, 3.5–4.5 mm. long, the tube 1.5–2 mm. long, the anther appendages short-deltoid, 0.04–0.05 mm. long; achenes 2–3 mm. long, the fertile ones 0.5–0.9 mm. wide, glandular-strigose (glands amber-colored), the faces 1–2-nerved, the pappus white, 2–3 mm. long; $n = 9$.

DISTRIBUTION: West Maui and Lanai. Dry exposed ridges and flats, 150–300 m. elevation. *Tetramolopium remyi* is probably extirpated on Maui, where it occurred in the foothills between Lahaina and Wailuku. The only known extant population is on Awalua ridge on northern Lanai. It has been collected there in the past on dry ridges between Awalua and Kahinahina. There is a possibility that other small populations may still be present in these areas. Flowering period: April to January.

REPRESENTATIVE SPECIMENS: LANAI: Mauka of Awalua, 29 January 1964, *Degener and Degener 28771* (B, F, G, L, MASS, MICH, NY, UC, W); Paomi, 1 January 1956, *Hobdy and Lehman 3* (BISH); Kahinahina, 24 June 1915, *Munro 263* (B, BISH, BM, DS, F, L, MO, NSW, NY, US, W, WELT); Kaohi, 16 October 1916, *Munro s. n.* (BISH); Awalua road, 3 miles makai from Awalua road signpost, 10 May 1979, *Lowrey 450* (UC).

MAUI: Mountain Road between Lahaina and Wailuku, August 1870, *Hillebrand s. n.* (BISH, BM, W); mountains of West Maui above Maalaea Bay, *Mann and Brigham 373* (BISH, BM, F, G, GH, K, MASS, MO, NY).

Tetramolopium remyi is a highly specialized species in sect. *Tetramolopium*. The taxon has the largest heads and consequently the greatest numbers of ray and disk florets of any *Tetramolopium*. These characters alone serve to distinguish it from all other taxa in the genus. The possession of involute leaves indicates a specialized adaptation to a xeric environment. This character is also shared with *T. capillare*, which is its closest relative.

There is not much morphological variability within the species. Specimens collected from Maui tend to be somewhat smaller in stature than Lanai plants. This tendency is not absolute and is probably only a reflection of varying precipitation patterns. There is also a developmental difference in leaf shape between the adult and juvenile leaves. The adult leaves are linear and involute while the juvenile leaves are spatulate and flat.

5. ***Tetramolopium rockii*** Sherff in Bot. Gaz. **95**: 500. 1934. *Luteidiscus rockii* St. John in Bot. Jahrb. **94**: 553. 1974. TYPE: HAWAIIAN ISLANDS: MOLOKAI: Moomomi, on beach, March 1910, *J. F. Rock 10299* (HOLOTYPE: GH!; ISOTYPES: BISH!, BO!, F!, MICH!, UC!).

Prostrate shrub, forming compact mats, monoecious, 5–10 cm. high, 8–40 cm. diam.; stems basally and intricately branched, glandular and hirtellous or strongly sericeous; leaves yellowish green or whitish, spatulate, mucronate, 1.5–3 cm. long, 3–7 mm. wide, densely glandular-pubescent or glandular-sericeous, the epidermis papillate-punctate, the margin entire, the blade 1–2 cm. long; capitulescence simple; peduncles 4–12 cm. long, glandular-pubescent or pilose, the bracts oblanceolate proximally, becoming subulate distally; involucre hemispheric, 4–8 mm. long, 1–1.8 cm. wide; phyllaries 50–65, lanceolate, acuminate, glandular-pubescent abaxially, the margin ciliate with stalked capitate glands; receptacle 3–5 mm. diam.; ray florets 60–100 (55–108), the corolla white, the tube 2–3.3 mm. long, the lamina 3–4.5 mm. long, 0.5–1 mm. wide; disk florets 30–55 (20–58), the corolla yellow, 4–5 mm. long, the tube 1.3–2.2 mm. long, the anther appendages linear-lanceolate, 0.1–0.15 mm. long; achenes glandular-strigose, moderately to strongly so, 2–2.5 mm. long, the fertile achenes 0.7–0.9 mm. wide, the carpodium ringed with hairs, the faces 1–3-nerved, the pappus white, 2.5–4 mm. long; $n = 9$.

KEY TO VARIETIES OF *TETRAMOLOPIUM ROCKII*

1. Foliage and peduncles densely glandular, yellowish green, not sericeous; leaves 1.5–2 cm. long.
5(i). var. *rockii*
1. Foliage and peduncles glandular and strongly sericeous, whitish; leaves 2–3 cm. long, slightly involute.
5(ii). var. *calcisabulorum*

5(i). *Tetramolopium rockii* var. *rockii*.

FIGURE 14a, b.

Plants forming compact mats 8–30 cm. diam.; stems glandular-pubescent and hirtellous when young; leaves yellowish green, 1.5–2.1 cm. long, (3–) 4–6 mm. wide, spatulate, mucronate, entire, densely glandular-pubescent, the margin and midrib strigose, the blade 1–1.5 cm. long; capitulescence simple; peduncles 5–10 (4–12) cm. long, minutely glandular-pubescent; involucre 5–8 mm. high, 1.1–1.8 cm. diam.; phyllaries 50–65, glandular-pubescent abaxially; ray florets 60–100 (55–108), the tube (2.1–) 2.5–3.3 mm. long, the lamina 3–4.5 mm. long, 0.5–0.8 (–0.9) mm. wide; disk florets 30–55 (20–58), the corolla 4.3–5 mm. long, the tube 1.6–2 (–2.2) mm. long, the anther appendage 1 mm. long; achenes glandular-strigose, moderately so, the faces 1–2-nerved, the pappus 3–4 mm. long.

DISTRIBUTION: Northwestern Molokai. Lithified calcareous sand dunes on the “desert strip” of West Molokai. Confined to those portions of the dunes nearest the ocean. Intergrading with var. *calcisabulorum*. Flowering period: March to January.

REPRESENTATIVE SPECIMENS: MOLOKAI: Moomomi Beach, 14 March 1969, *Bishop 36922* (BISH); Moomomi, 13 November 1974, *Herbst and Spence 5113* (M, UC); Kalani, 0.9 miles due west of Moomomi Beach, 1 July 1978, *Lowrey, Montgomery, and van der Akker 417* (BISH, CANB, K, LAM, MO, NY, OS, TEX, UC, US).

5(ii). *Tetramolopium rockii* var. *calcisabulorum* (St. John) Lowrey, comb. et stat. nov.

Luteidiscus calcisabulorum St. John in Bot. Jahrb. **94**: 549. 1974. TYPE:

HAWAIIAN ISLANDS: MOLOKAI: Moomomi, limestone sand mound, 22 Jan. 1973, *Noah Pekelo, Jr. 19* (HOLOTYPE: BISH!).

FIGURE 14c, d.

Plants forming compact mats 8–40 cm. diam.; stems glandular-sericeous when young; leaves whitish, 2–3 cm. long, 5–7 mm. wide, spatulate, glandular-sericeous, the blade 1.5–2 cm. long, slightly involute; peduncles 4–12 cm. long, densely glandular-pilose; involucre (4–) 5–6 mm. high, 10–14 mm. diam.; phyllaries 50–60, glandular-pilose abaxially; receptacle 3.2–4 mm. diam.; ray florets 60–90 (–93), the tube 2–3 mm. long, the lamina 3.2–4.5 mm. long, 0.6–1 mm. wide; disk florets 35–55 (32–58), the corolla 4–5 mm. long, the tube (1.3–) 1.5–1.8 mm. long, the anther appendages oblong, 0.1–0.12 mm. long; achenes densely strigose-glandular, the faces 1–3-nerved; pappus 2.5–4 mm. long.

DISTRIBUTION: Northwestern Molokai. Lithified calcareous sand dunes on the inland portions of the “desert strip”. Intergrading with var. *rockii* on the coastal dunes. Flowering period: March to January.

REPRESENTATIVE SPECIMENS: MOLOKAI: Southeast of Kalani (near Moomomi), 19 April 1928, *Degener 4998* (BM, CU, DS, F, GH, NY, W); in arid region southeast of Kalani, West Molokai, 25 April 1928, *Degener 4999* (BM, F, GH, NY); dirt road to Kaiehu Pt., west of Manalo Gulch, 1 km. south of Kapalauoa, 24 July 1978, *Lowrey and Aidem 435* (BISH, CANB, K, LAM, MO, NY, OS, TEX, UC); mauka of Kapalauoa, NW. of Manalo Gulch, 14 May 1976, *Lowrey and Aidem 456* (BISH, CANB, K, LAM, MO, NY, OS, TEX, US); Moomomi, 1 January 1973, *Pekelo 9* (BISH).

The inclusion of *Luteidiscus calcisabulorum* with *Tetramolopium rockii* is supported by the few morphological differences separating them, by greenhouse studies, and by field studies of their population structure. The two taxa are genetically distinct races consisting of the inland var. *calcisabulorum*, having sericeous pubescence with larger and slightly involute leaves, and the coastal var. *rockii*, having glandular pubescence with small, flat leaves. The two varieties are endemic to the same group of lithified sand dunes on Molokai.

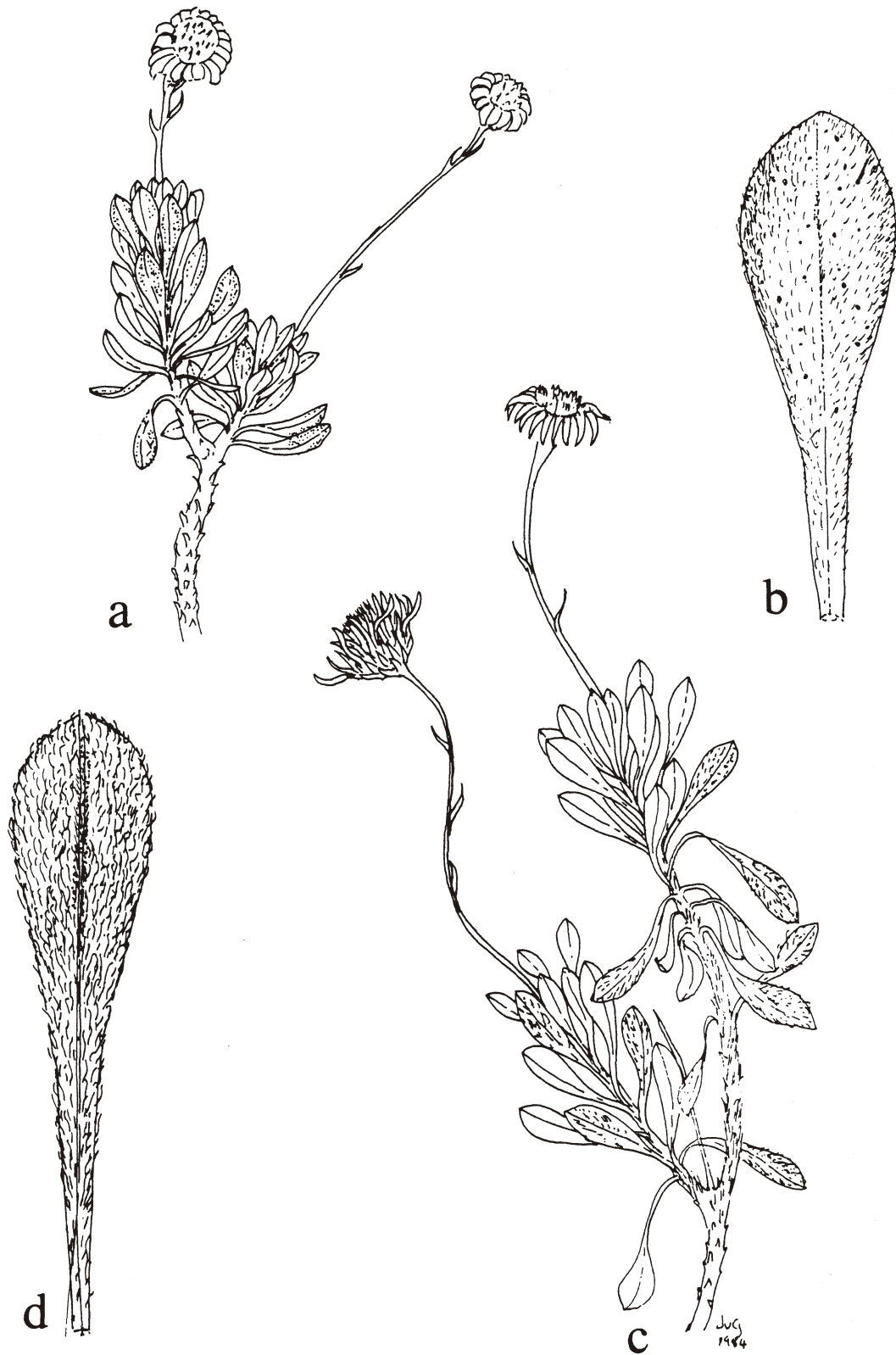
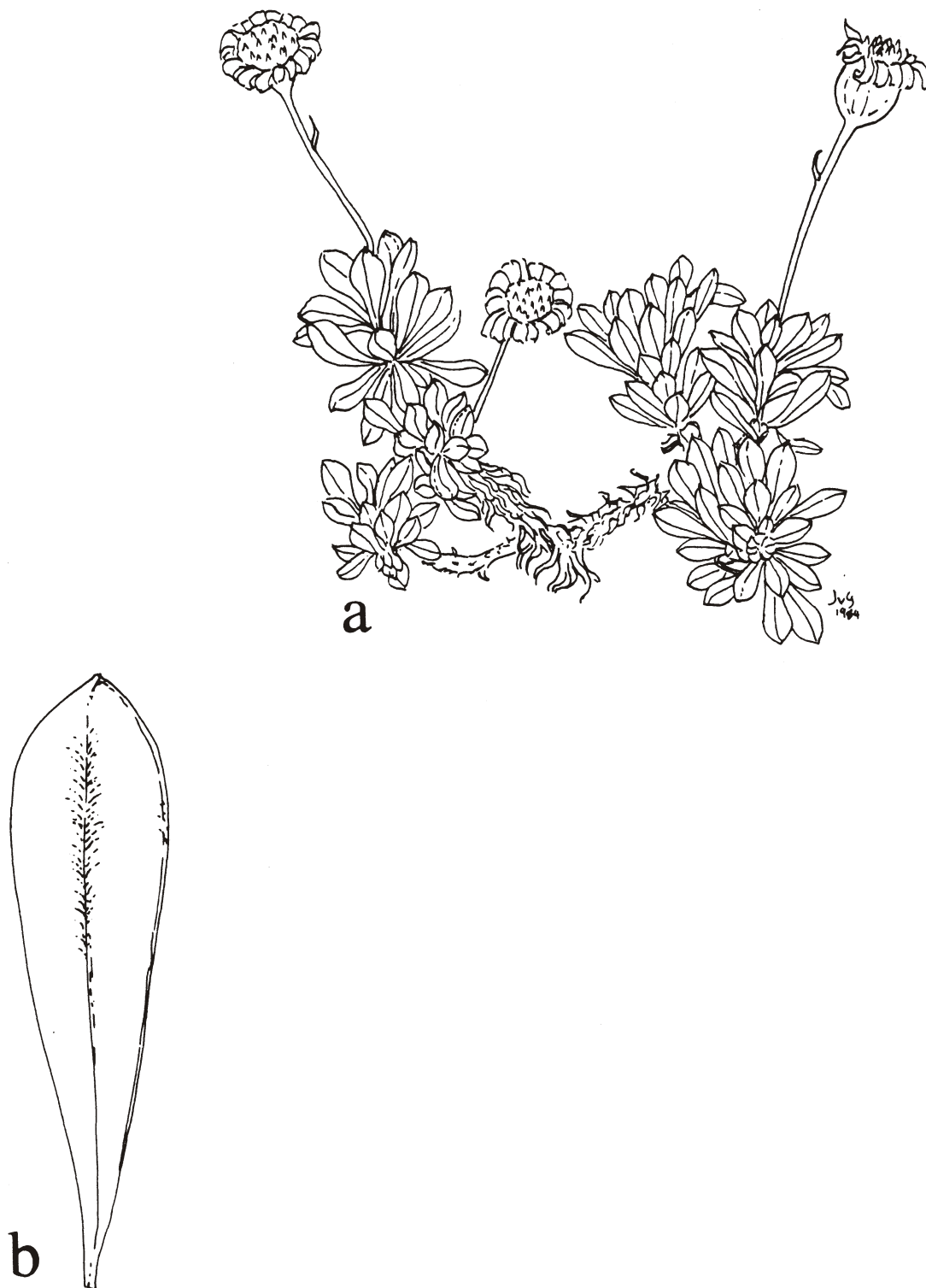


FIGURE 14. *Tetramolopium rockii*. a, *T. rockii* var. *rockii*, habit, life-size. b, *T. rockii* var. *rockii*, leaf, $\times 4$. c, *T. rockii* var. *calcisabulorum*, habit, life-size. d, *T. rockii* var. *calcisabulorum*, leaf, $\times 4$.

6. *Tetramolopium sylvae* Lowrey, sp. nov. TYPE: HAWAIIAN ISLANDS: MOLOKAI: Ahupuaa of Pelekunu, Kaneaimoa Pt., rocky seacliffs, 100 m. elev., 13 May 1979, *Lowrey and Perlman 454* (HOLOTYPE: UC!; ISOTYPES: BISH!, CANB!, K!, LAM!, MO!, NY!, OS!, TEX!, US!).

FIGURE 15.

FIGURE 15. *Tetramolopium sylvae*. a, habit, $\times 1.2$. b, leaf, $\times 4.8$.

Ab aliis speciebus habitatione in scopulo volcanico littorali differt; ab affinis *Tetramolopium tenerrimum* et *T. rockii* praeclare distinguitur foliis succidis glabris 3–7 mm. latis, quae in *T. tenerrimum* minus quam 3 mm. lata et in *T. rockii* dense pubescentia sunt.

Prostrate rosette shrub, monoecious, 4.5–6 cm. high with basal branching; stems glabrous; leaves 1.5–3 cm. long, 3–7 mm. wide, petiolate, spatulate, succulent, glabrous or slightly glandular-punctate or rarely sparsely strigose marginally, the margin entire or occasionally coarsely dentate when young, the teeth (when present) 0.4–0.6 mm. long; capitulescence simple; peduncles 2.5–4.5 (2.1–4.9) cm. long, glabrous or minutely glandular-pubescent, bracteate, the bracts subulate; involucre hemispheric, (4.5–) 5–6 mm. high, 0.9–1.3 cm. diam.; phyllaries lanceolate, sparsely glandular-punctate, the margin entire or slightly fimbriate, the apex lanceolate; receptacle 2.5–5 mm. diam.; ray florets 55–75 (–79), uniseriate, the corolla tube (1.5–) 1.2–1.6 (–2) mm. long, the lamina 2.5–3.5 (–3.9) mm. long, 0.5–1 mm. wide; disk florets 20–40, the corolla yellow, 3.5–4 mm. long, the tube 1.2–1.6 mm. long, the anther appendages lanceolate, 0.08–0.12 (–0.14) mm. long; achenes (1.6–) 1.9–2.6 mm. long, the fertile achenes 0.7–1 mm. wide, strigose distally to mostly glabrous, the faces 1–2-nerved, the pappus white, 2–2.8 mm. long, uniseriate; $n = 9$.

DISTRIBUTION: Molokai and Maui. Seacliffs on volcanic soils, 250–350 m. elevation. The species occurs along the coastal cliffs of northern Molokai and of northwestern Maui near Kahuku. Flowering period: March to January.

REPRESENTATIVE SPECIMENS: MAUI: 25 miles post Lahaina toward Kahakaloa near the Wailuku-Lahaina district boundaries, 12 July 1978, *Lowrey and Sylva 431* (BISH, CANB, K, LAM, MO, NY, OS, TEX, UC).

MOLOKAI: Molokai Distr., Palaau, Hoolehua Dump, 12 May 1979, *Lowrey 451* (BISH, CANB, HALEAKALA, K, LAM, MO, NY, OS, TEX, US).

Tetramolopium sylvae is an interesting new species that incorporates characteristics of both *T. rockii* and *T. tenerrimum*, while occupying a unique habitat. The prostrate-rosette habit of *T. sylvae* is similar to that of *T. rockii*. It has glabrous spatulate leaves like *T. tenerrimum*, although the petioles are much shorter. The species is unique in the genus with its seacliff habitat and glabrous, succulent leaves.

One population of *Tetramolopium sylvae* from Hoolehua, Molokai, has much longer branch internodes than is typical for the species, resembling *T. rockii* in this respect. This feature is not readily apparent in the field but is obvious in greenhouse plants. In addition it has large juvenile leaves that may be coarsely toothed. I have chosen not to recognize this formally as a distinct taxon on the basis of these few characters. It does deserve mention and further study of its population structure is needed.

Tetramolopium sylvae is named in honor of Rene Sylva, from Paia, Maui. Mr. Sylva is an avid amateur botanist and is also the guiding force behind the Maui Botanical Garden. He is responsible for the discovery of this new species on Maui.

7. ***Tetramolopium tenerrimum*** (Less.) Nees, Gen. Sp. Aster. 203. 1832. *Aster tenerrimus* Less. in *Linnaea* 6: 120. 1831. *Vittadinia tenerrima* A. Gray in Proc. Amer. Acad. Arts 5: 119. 1861. *Erigeron tenerrimus* Drake, Ill. Fl. Ins. Mar. Pacif. 67. pl. 32. 1888. TYPE: HAWAIIAN ISLANDS: OAHU: 1817, *A. von Chamisso s. n.* (HOLOTYPE: LE!; ISOTYPE: B, destroyed).

Decumbent, somewhat caespitose shrub, monoecious, 2.5–5 cm. high, branching basally and divaricately; stems glabrous; leaves 1–2 cm. long, 1–3 mm. wide, thin, oblanceolate or spatulate, glandular-punctate, the margin entire but strigose; capitulescence simple; peduncles (1.6–) 2–6 cm. long, glandular-scabrid, the bracts subulate; involucre campanulate, 3–5 mm. high, 4–6 mm. wide; phyllaries 25–30, linear-lanceolate, the outer phyllaries glandular-punctate, the inner ones glabrous, the mar-

gin fimbriate proximally, lacerate distally; receptacle 1.5–2 (–2.5) mm. diam.; ray florets 25–35, uniseriate, the corolla white, the tube 1.5–2.5 (–3) mm. long, the lamina 2.5–3.5 mm. long, 0.6–0.8 mm. wide; disk florets 15–20, the corolla yellow, (2.8–) 3–3.5 mm. long, the tube 1–1.5 mm. long; achenes 1.5–2.3 mm. long, the fertile achenes 0.5–0.7 mm. wide, glabrous or sparsely strigose, the faces 1-nerved, the pappus white, 2–3 mm. long.

DISTRIBUTION: Oahu. Locality and habitat data are poor. It probably occurred in the Koolau Mountains. Flowering period: Unknown.

REPRESENTATIVE SPECIMENS: OAHU: Pa bergen, 1852, *Anderson s. n.* (s); no locality, *Eschscholtz s. n.* (E); no locality, May 1825, *Macrae s. n.* (GH); in rupibus, *Parry s. n.* (BM).

Lessing described the species from Chamisso collections. Sherff designated a lectotype at B (later destroyed), while an adequate specimen existed in Chamisso's herbarium at LE. It seems advisable to reject Sherff's lectotypification and accept the LE specimen as the holotype. The species is most closely related to *Tetramolopium sylvae* and *T. rockii*.

TETRAMOLOPIUM sect. SANDWICENSE Lowrey, sect. nov. TYPE: *Tetramolopium lepidotum* (Less.) Sherff.

Frutices erecti lignosi; folia lineari-oblongata vel oblongata non spatulata; capitula gynomonoecia, corymboso-paniculata non solitaria; flosculi radii laminis redactis plerumque minus quam 2.5 mm. longis; flosculi disci minus quam 15, corollis purpureis vel subroseis.

DISTRIBUTION: Hawaiian Islands.

8. ***Tetramolopium lepidotum*** (Less.) Sherff in Bot. Gaz. 95: 500. 1934. *Erigeron lepidotus* Less. in Linnaea 6: 502. 1831. *Erigeron tenerrimus* var. *lepidotus* Drake, Ill. Fl. Ins. Mar. Pacif. 67. pl. 32. 1888. TYPE: HAWAIIAN ISLANDS: OAHU: 1816–1817, *A. von Chamisso s. n.* (HOLOTYPE: LE!; ISOTYPE: P!, B, destroyed).

Erigeron pauciflorus Hook. & Arn. Bot. Beechey Voy. 87. 1832. TYPE: HAWAIIAN ISLANDS: OAHU: *Captain Beechey s. n.* (HOLOTYPE: K!).

Vittadinia chamissonis A. Gray in Proc. Amer. Acad. Arts 5: 119. 1861. *Tetramolopium chamissonis* Hillebr. Fl. Hawaiian Isl. 199. 1888. TYPE: HAWAIIAN ISLANDS: OAHU: 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: US!; ISOTYPES: GH!, NY!).

Tetramolopium chamissonis var. *luxurians* Hillebr. Fl. Hawaiian Isl. 199. 1888. LECTOTYPE (here designated): HAWAIIAN ISLANDS: OAHU: Waianae, *W. Hillebrand s. n.* (MEL!). The holotype at B having been destroyed, the lectotype has been chosen from an isotype at MEL.

Upright shrub, gynomonoecious, 12–36 cm. high, branching apically; stems glandular-punctate to pustulose and pilose to hirsute when young; leaves petiolate or nearly sessile, filiform to oblanceolate-elliptic, 2.5–4.5 (1–5) cm. long, 1–7 mm. wide, glandular-punctate and/or pilose, petiolate or nearly sessile, strigose on margin and major veins, the margin entire or coarsely 2–8-toothed, the teeth 0.5–2 (–2.3) mm. long; capitulescence corymbose-paniculate, not extended beyond foliage, the heads (4–) 6–12; peduncles minutely glandular and pilose; involucre campanulate, (2.7–) 3–4.6 mm. high, 5.5–7.5 mm. wide; phyllaries 30–35 (26–37), lanceolate or linear-lanceolate, acute or acuminate, glandular and sparsely pilose (especially on outer phyllaries), the margin scarious, ciliate or lacerate distally; receptacle 1–2 mm. wide; ray florets 21–40 (–57), white to pinkish lavender, the tube (0.5–) 1–2 mm. long, the lamina (1–) 1.5–2 mm. long; disk florets 4–11, the corolla maroon to pale salmon, 2.5–3.7 mm. long, the tube 0.6–1.4 mm. long, the anther appendage linear-lanceolate to deltoid, 0.09–0.22 mm. long; achenes 1.6–2.5 mm. long, 0.5–0.8 mm. wide, strigose distally, glabrous proximally, the faces 1–2-nerved (rarely nerveless), the pappus white, 2–3.5 mm. long; $n = 9$.

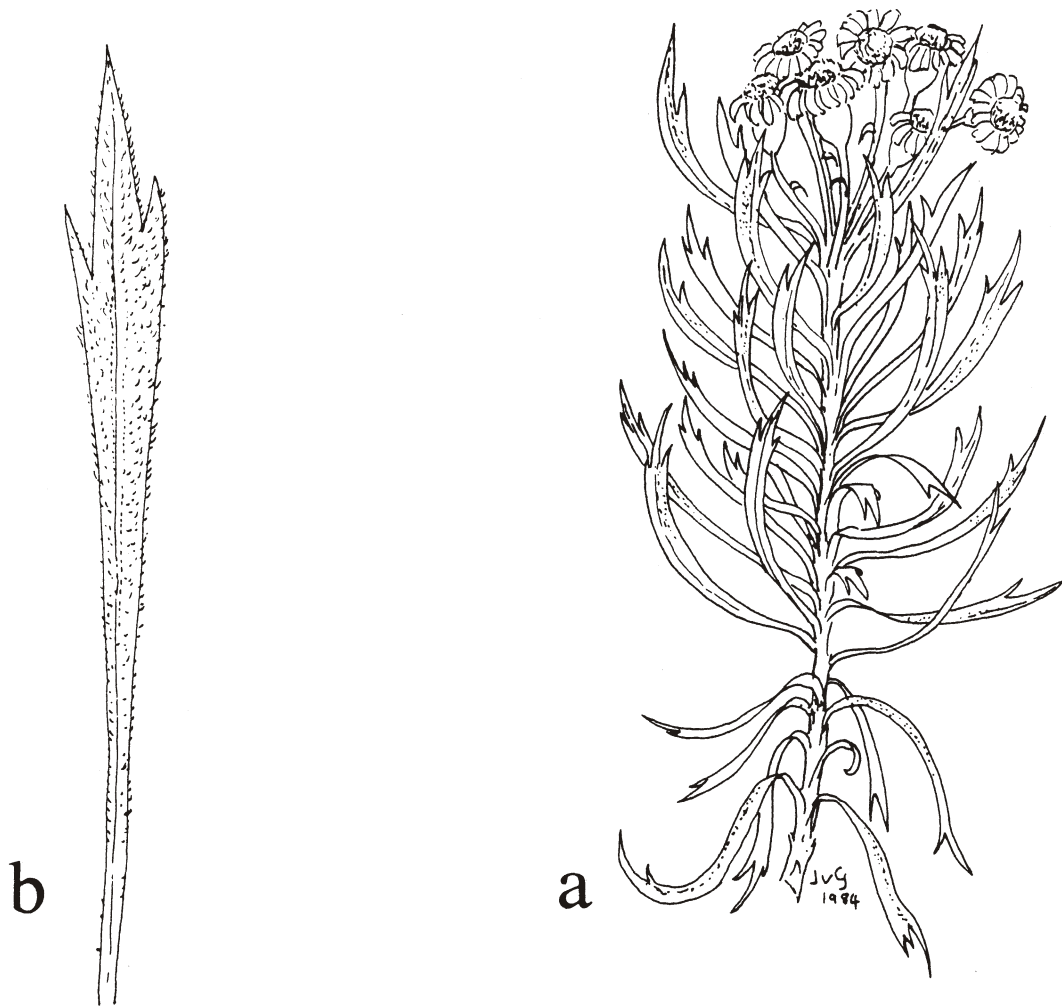


FIGURE 16. *Tetramolopium lepidotum* subsp. *lepidotum*. a, habit, $\times 1.25$. b, leaf, $\times 2.5$.

KEY TO SUBSPECIES OF *TETRAMOLOPIUM LEPIDOTUM*

1. Leaves linear-ob lanceolate, oblanceolate, or oblanceolate-elliptic, mostly 3–7 mm. wide; involucre 3–4 mm. high; disk floret corolla 2.5–3.5 mm. in length; Oahu and Lanai. 8a. subsp. *lepidotum*
1. Leaves linear to filiform, mostly 1–1.5 mm. wide; involucre 4.2–4.6 mm. long; disk floret corolla 3.5–3.7 mm. in length; Maui. 8b. subsp. *arbusculum*

8a. *Tetramolopium lepidotum* subsp. *lepidotum*.

FIGURE 16.

Stems glandular-punctate to pustulose and pilose to hirsute when young; leaves 2.5–4.5 (1–5) cm. long, (2–) 3–7 mm. wide, densely glandular-punctate and sparsely pilose, the margin entire or coarsely 2–8-toothed, the lobes 0.5–2.3 mm. long, the blade 2–3.5 (0.8–3.9) cm. long; capitulescence with (4–) 6–12 heads; pedicels glandular-pilose; involucre campanulate, (2.7–) 3–4 mm. high, 5.5–7 (5.3–7.5) mm. diam.; phyllaries 30–35 (26–37), lanceolate; receptacle 1–2 mm. diam.; ray florets 21–40 (–57), the corolla tube 1–1.7 (0.5–2) mm. long, the lamina (1–) 1.5–2.5 mm. long, 0.2–0.6 mm. wide; disk florets 4–11, the corolla 2.5–3.5 mm. long, the tube (0.6–) 0.8–1.3 mm. long, the anther appendage deltoid or linear, 0.9–0.12 (0.6–0.15) mm. long; achenes 1.6–2.2 (–2.5) mm. long, 0.5–0.8 mm. wide, the pappus 2–2.6 (–3.5) mm. long; $n = 9$.

DISTRIBUTION: West Oahu and Lanai. Waianae Mountains of Oahu and the southern portion of Lanai. Grassy ridge tops or flats and west-facing cliff faces. The Lanai populations are probably extirpated. Flowering period: May to December.

REPRESENTATIVE SPECIMENS: LANAI: No locality, September 1919, *Forbes 5091* (B, BISH, DS, F, GB, L, MICH, NY, UC, US, W, WELT); west end, 22 September 1916, *Hitchcock 13954* (BISH, US); Puu Ulaula, 20 May 1927, *Munro 26* (BISH); Miki, 8 February 1916, *Munro 507* (B, BISH, BM, BO, F, MO, NSW, NY, UC, US).

OAHU: Partly up Puu Kaala from Waianae Valley, 24 April 1932, *Degener and Park 5000* (BM, DS, F, GH, NY, PH); near summit of ridge on right side of head of Makua Valley, 26 June 1932, *Degener, Park, and Bush 5001* (B, F, GH, NY, PH); ridge above Kupehau, Honouliuli, 30 June 1935, *Fosberg 10989* (BISH); ridge below Mauna Kapu, Waianae Mountains, *Lowrey, Obata, and Carr 416* (LAM, UC); NE.-facing slope below summit trail leading to Puu Kaua, 29 April 1979, *Lowrey and Perlmann 443* (BISH, NY, TEX, UC, US); cliffs on east ridge of Puu Hapapa, 1 June 1979, *Lowrey and Palmer 460* (UC); east ridge of second gulch east of Puu Kaupakuhale, Mokuleia, Puu Kaala, Waianae Mountains, 23 October 1932, *St. John and Fosberg 12157* (BISH, US).

Lessing described the species from Chamisso's collections; Chamisso's herbarium is deposited at LE and an adequate specimen is present there. Sherff (1943) doubtfully designated a specimen at B as the holotype, at the same time stating that material at LE might be taken as the holotype. In view of this, his designation of the B specimen as holotype seems unwarranted.

Tetramolopium lepidotum subsp. *lepidotum* is extremely variable with regard to leaf morphology. Plants from Oahu all have dentate leaves with varying numbers of teeth (2–6) and varying lengths of these teeth. Plants grown from three different populations maintained their individual lobing characteristics. Specimens studied from Lanai indicate that populations there had both entire and dentate or even strictly entire leaves. There is also a wide range in leaf length and width among populations on both islands. These size characteristics are variable depending on their developmental stage and available moisture for plant growth.

In view of this leaf variability data the recognition of a var. *luxurians* by Hillebrand, based mainly on the size of leaves, is unwarranted. The capitulum characters also included in the description do not show sufficient morphologic discontinuities for varietal delimitation.

8b. *Tetramolopium lepidotum* subsp. *arbusculum* (A. Gray) Lowrey, comb. et stat. nov. *Vittadinia chamissonis* var. *arbuscula* A. Gray in Proc. Amer. Acad. Arts 5: 120. 1861. *Tetramolopium chamissonis* var. *arbusculum* Hillebr. Fl. Hawaiian Isl. 199, as var. *arbuscula*. 1888. *Tetramolopium arbusculum* Sherff in Bot. Gaz. 95: 502. 1934. TYPE: HAWAIIAN ISLANDS: MAUI: 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: US!; ISOTYPE: GH!).

Stems sparsely pilose when young; leaves 2.5–3 cm. long, 1–1.5 (–1.8) cm. wide, linear to nearly filiform, clustered distally on branches, glandular-punctate, strigose on margin, the margin usually entire, occasionally 1–3-toothed, the lobes about 1 mm. long; capitulescence with 8 or 9 heads; pedicels glandular and sparsely to densely pilose; involucre campanulate, 4.2–4.6 mm. high, 6–7 mm. wide; phyllaries 28–35, linear-lanceolate, sparsely pilose to glabrous, entire; receptacle 1.5–2 mm. diam.; ray florets 30–32, the corolla tube 2 mm. long, the lamina 1.6–1.8 mm. long, 0.4–0.5 mm. wide; disk florets 5 or 6, the corolla maroon, 3.5–3.7 mm. long, the tube 1.2–1.4 mm. long, the anther appendage linear-lanceolate, 0.18–0.22 mm. long; achenes 1.8–2.3 mm. long, 0.6–0.8 mm. wide, the faces 1-nerved, the pappus dirty-white, 2.9–3.3 mm. long.

DISTRIBUTION: Maui. Known only from type collection made “on the Great Crater of E. Maui”. It is presumed extinct. Flowering period: Unknown.

9. **Tetramolopium conyzoides** (A. Gray) Hillebr. Fl. Hawaiian Isl. 200. 1888. *Vittadinia conyzoides* A. Gray in Proc. Amer. Acad. Arts 5: 120. 1861. TYPE: HAWAIIAN ISLANDS: MAUI: On the sand hills of Maui, 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: US!; ISOTYPE: GH!).

Tetramolopium conyzoides var. *dentatum* Sherff in Bot. Gaz. 95: 502. 1934. *Vittadinia conyzoides* var. *dentata* Mann in Proc. Amer. Acad. Arts 7: 173. 1867. TYPE: HAWAIIAN ISLANDS: LANAI: *Mann and Brigham 361* (HOLOTYPE: GH!).

Upright shrub, gynomonoecious, branching apically, the height unknown; stems densely glandular-pilose when young; leaves 3–5 cm. long, 3–5 mm. wide, petiolate, oblanceolate, entire or sparsely dentate, the lobes 0.5–1 mm. long, yellowish glandular-punctate and pilose, the apex acute; capitulescence corymbose-paniculate, congested, the heads mostly greater than 40; peduncles densely glandular-villous; involucre 2.5–3.5 (–4) mm. high, 2.2–3 mm. wide; phyllaries 15–18, lanceolate, sparsely glandular-pilose to glabrous, entire; receptacle 0.5–1 mm. diam.; ray florets 15–25 (13–30), the corolla white, the tube 1–1.7 mm. long, the lamina filiform, 0.5–1 (–1.2) mm. long, 0.2–0.3 mm. wide; disk florets 1–3, the corolla maroon, 2.2–2.6 mm. long, the tube 0.7–0.9 mm. long, the anther appendage deltoid to lanceolate, 0.07–0.12 mm. long; achenes 1.3–1.6 mm. long, 0.5–0.6 mm. wide, sparsely strigose, the faces 1–2-nerved, rarely nerveless, the pappus buff-colored, 1.8–2.5 (–2.7) mm. long.

DISTRIBUTION: Hawaii, Maui, Molokai, and Lanai. Lowland dry forest areas. The species probably was a constituent of the dry forest understory. It is presumed extinct. Flowering period: Unknown.

REPRESENTATIVE SPECIMENS: HAWAII: Central plateau, *Hillebrand s. n.* (BISH).

LANAI: No locality, 1867, *Mann and Brigham 532* (BISH, BM, F, G-BOIS, G-DC, GH, MO, NY, P).

MAUI: Kula, *Hillebrand and Lydgate s. n.* (BISH).

MOLOKAI: Kumikaipo, 22 June 1919, *G. C. Munro 675* (B, BISH, BM, US).

Tetramolopium conyzoides is a distinct and unusual species in the genus. Its numerous small heads, few disk florets, and filiform ray floret laminae are strongly reminiscent of similar characters in *Conyza*, hence the specific epithet. This appears to be an example of morphological convergence. The species represents a highly derived taxon in sect. *Sandwicense*. It is most closely related to *T. consanguineum* subsp. *leptophyllum*, which also has numerous small heads and reduced ligules.

Mann (1867) accorded varietal status to one specimen from Lanai on the sole basis of its having large denticulate leaves. These characters have been shown to be affected by environmental and developmental conditions in two other members of sect. *Sandwicense*, and for this reason I have placed the variety in synonymy under the species.

10. **Tetramolopium arenarium** (A. Gray) Hillebr. Fl. Hawaiian Isl. 199. 1888. *Vittadinia arenaria* A. Gray in Proc. Amer. Acad. Arts 5: 120. 1861. LECTOTYPE (here designated): HAWAIIAN ISLANDS: HAWAII: 1840, *U. S. Exploring Expedition* (US!, mixed collection with isotype of *T. arenarium* subsp. *laxum*).

Upright shrubs, gynomonoecious, 0.8–1.3 m. high, apically branching; stems minutely glandular and strigose or hirsute when young; leaves 1.5–3.7 cm. long, 3–9 mm. wide, the blade 1.2–3.5 cm. long, short-petiolate, oblanceolate to oblong-lanceolate, dark brown or yellowish green when dried, glandular and hispid or pilose, entire or sparsely dentate; capitulescence corymbose-paniculate, congested or lax, the heads 5–11; peduncles straight or flexuous, glandular and pilose; involucre campanulate, 2.5–5 mm. high, 4–9 mm. diam.; phyllaries 20–34, lanceolate, glabrous or

glandular-pilose, entire or lacerate; receptacle 0.9–3 mm. diam.; ray florets 22–45, uniseriate, the corolla tube 1.5–2.2 mm. long, the lamina 1.3–2.2 mm. long; disk florets 4–9, the corolla maroon, 3.1–4.4 mm. long, the tube 1–2.2 mm. long, the anther appendages lanceolate or linear-lanceolate, 0.15–0.2 mm. long; achenes oblanceolate, 1.5–3 mm. long, 0.5–0.8 mm. wide, granuliferous-glandular, densely glandular-strigose, or nearly glabrous, the faces 1–4-nerved, the pappus white, 2.5–4 mm. long.

KEY TO TAXA OF *TETRAMOLOPIUM ARENARIUM*

1. Foliage turning dark upon drying; capitulescence compact, the pedicels not flexuous; achenes densely strigose.
 2. Involucre mostly 3.5–5 mm. high, 6–9 mm. diam.; disk florets 5–9; leaves entire.
 - 10a(i). subsp. *arenarium* var. *arenarium*
 2. Involucre 2.5–3 mm. high, 4–6 mm. diam.; disk florets 4 or 5; leaves dentate.
 - 10a(ii). subsp. *arenarium* var. *confertum*
1. Foliage not turning dark when dried, yellowish green; capitulescence open or lax, the pedicels flexuous; achenes granuliferous-glandular, not strigose. 10b. subsp. *laxum*

10a(i). *Tetramolopium arenarium* subsp. *arenarium* var. *arenarium*.

Stem minutely glandular and strigose or hirsute when young; leaves 2–3 (–3.5) cm. long, 3–9 mm. wide, oblong-oblanceolate to narrowly oblanceolate, dark brown when dried, glandular-hispid, entire, the blade 1.8–3.3 cm. long; capitulescence congested, the heads 6–10; pedicels straight, densely glandular and pilose; involucre (3–) 3.5–5 mm. high, 6–9 mm. diam.; phyllaries 26–30, oblong-lanceolate, glandular and sparsely pilose or nearly glabrous; receptacle (1.2–) 1.5–2 (–2.2) mm. diam.; ray florets 35–45, the corolla tube 1.5–2.2 mm. long, the lamina 1.8–2 (–2.5) mm. long, 0.4–0.6 mm. wide; disk florets 5–9, the corolla 3.3–3.5 mm. long, the tube 1.1–1.4 mm. long, the anther appendage linear-lanceolate, 0.15–0.2 mm. long; achenes oblanceolate, 1.8–2.2 mm. long, 0.6–0.8 mm. wide, densely glandular-strigose, the faces 2–4-nerved, the pappus white, 2.5–3 (–3.3) mm. long.

DISTRIBUTION: Maui and Hawaii. Known from Puu Hualalai and Waimea on Hawaii, and from Kula, East Maui. It was probably a component of the dry forest. Presumably extinct. Flowering period: Unknown.

REPRESENTATIVE SPECIMENS: HAWAII: Hualalai, *Mann and Brigham 519* (BISH, BM, G-BOIS, G-DC, GH, MASS, MO, NY, US); no locality, *Hillebrand s. n.* (w).

MAUI: Kula, *Hillebrand s. n.* (BISH, BM, MEL); no locality, *Wawra 2308* (w).

ISLAND UNKNOWN: "Sandwich Island," *Hillebrand s. n.* (GH, K); no locality, *Hillebrand 318* (us).

10a(ii). *Tetramolopium arenarium* subsp. *arenarium* var. *confertum* Sherff in Bot.

Gaz. 95: 502. 1934. TYPE: HAWAIIAN ISLANDS: HAWAII: Nohoanaoahae near Waimea, Dec. 1872, *Hillebrand and Lydgate s. n.* (HOLOTYPE: B, destroyed; photograph of holotype: F!; ISOTYPES: BISH!, fragments of BISH specimen at F!).

Leaves 1.5–3 cm. long, 3–5 mm. wide, oblanceolate, glandular and hispid or strigose, dark brown when dried, entire or 2-toothed, the lobes 0.5–1 mm. long, the blade 1.3–2.7 cm. long, the apex acuminate; capitulescence congested, the heads 9–11; pedicels densely glandular and pilose; involucre 2.5–3 mm. tall, 4–6 mm. wide; phyllaries 20–30, lanceolate, glabrous abaxially, the margin entire or lacerate, the apex acuminate; receptacle 0.9–1 mm. diam.; ray florets 22–26, the corolla tube 1.5–1.7 mm. long, the lamina 2–2.2 mm. long, 0.5–0.6 mm. wide; disk florets 4 or 5, the corolla 3.1–3.5 mm. long, the tube 1–1.3 mm. long, the anther appendage linear-lanceolate, 0.17–0.2 mm. long; achenes 1.5–2.1 mm. long, 0.5–0.7 mm. wide, densely glandular-strigose, the faces 1–2-nerved, the pappus 2.5–3 mm. long, white.

DISTRIBUTION: Known only from the type locality on the island of Hawaii. Dry forest community. Flowering period: Type material flowering in December.

- 10b. **Tetramolopium arenarium** subsp. **laxum** Lowrey, subsp. nov. TYPE: HAWAIIAN ISLANDS: MAUI: Sandhills of Maui, 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: GH!; ISOTYPE: US!, mixed collection with lectotype of *T. arenarium* subsp. *arenarium*).

Tetramolopium arenarium var. *dentatum* Hillebr. Fl. Hawaiian Isl. 200, as var. *dentata*. 1888. TYPE: HAWAIIAN ISLANDS: MAUI: Hamakua, no date, *J. M. Lydgate s. n.* (HOLOTYPE: B, destroyed; photograph of holotype at F!).

Subspecies a subspecie typica foliis flavovirentibus in siccitate non denigrantibus, capitulis laxe dispositis, pedicellis flexuosis, acheniis granuliferis non strigosis differt.

Leaves 2.1–3.7 cm. long, 3–7 mm. wide, oblanceolate, yellowish green when dried, granuliferous- or pustulose-glandular and pilose or hispid, entire or 1–3-dentate, the apex acute, the blade 1.9–3.5 cm. long; capitulescence lax, the heads 5–8; pedicels flexuous, glandular and pilose; involucre 4–5 mm. high, 6–9 mm. diam.; phyllaries 28–34, lanceolate, sparsely glandular-dotted or glabrous abaxially, the margin lacerate; receptacles 1.5–3 mm. diam.; ray florets 24–32, the corolla tube 1.6–2.1 mm. long, the lamina 1.3–1.6 mm. long, 0.4 mm. wide; disk florets 6–8, the corolla 3.5–4.2 (–4.4) mm. long, the tube 1.3–1.5 mm. long, the anther appendages lanceolate, 0.15 mm. long; achenes 2.3–3 mm. long, 0.5–0.8 mm. wide, granuliferous-glandular and sparsely or not strigose, the faces 1–2-nerved, the pappus dirty-white, 2.7–4 mm. long.

DISTRIBUTION: Maui. Known from Kula, East Maui, and “the sandhills of Maui”.

Flowering period: Unknown.

The holotype of *Tetramolopium arenarium* subsp. *arenarium* consists of two different collections, one from Maui and the other from Hawaii. The lectotype has been chosen from the Hawaii collection. The protologue describes the taxon as having a contracted capitulescence, which only the plants from the Hawaii collection exhibit.

The specimens from Maui are so distinctive that they are recognized as *Tetramolopium arenarium* subsp. *laxum*. The epithet refers to the lax or open capitulescence. The yellowish green color of the dried foliage, the flexuous pedicels, and the glabrous or granuliferous glandular achenes are the major diagnostic characters for the taxon. The basis for the interesting and unusual color differences of the foliage in the two taxa is not known. The dark color of subsp. *arenarium* may be due to anthocyanin pigments.

11. **Tetramolopium consanguineum** (A. Gray) Hillebr. Fl. Hawaiian Isl. 199. 1888.

Vittadinia consanguinea A. Gray in Proc. Amer. Acad. Arts 5: 120. 1861. *Eriogon tenerrimus* var. *consanguineus* Drake, Ill. Fl. Ins. Mar. Pacif. 67. pl. 32. 1888. TYPE: HAWAIIAN ISLANDS: KAUAI: 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: US!; ISOTYPE: GH!, mixed collection with isotype of *T. consanguineum* subsp. *leptophyllum*).

Upright shrub, gynomonocious, 0.5–2 m. high, branching basally; young stems minutely capitate-glandular with scattered pilose hairs; leaves 1.3–6.5 cm. long, 1.5–4.5 mm. wide, linear-oblanceolate, short-petiolate or nearly sessile, glandular-punctate, strigose on margin and midrib, entire or distally 1–2-dentate, the lobes 0.3–1 mm. long, the apex acute or acuminate; capitulescence corymbose-paniculate, congested, the heads 10–40; peduncles glandular-pubescent and pilose or hispid; involucre turbinate or obconic, 2–3 mm. high, 3–6 mm. diam.; phyllaries 20–35, lanceolate, purplish distally, glabrous or sparsely glandular abaxially, the margin strongly denticulate, the apex obtuse to acute; receptacles 0.5–2 mm. wide; ray florets 20–40, uniseriate, the corolla white or pink, the tube 1.1–1.5 mm. long, the lamina 0.8–1.7 mm. long, 0.3–0.6 mm. wide; disk florets 3–12, the corolla maroon or purplish brown, 2.3–3 mm. long, the tube 0.6–1.1 mm. long, the anther appendage short and deltoid or lanceolate and longer, 0.05–0.15 mm. long, the style branches lanceolate or linear; achenes oblanceolate, 1.5–2.2 mm. long, 0.5–0.8 mm. wide, glandular or glandular-strigose, the faces 2–6-nerved, the pappus brownish, brittle, 1.6–2.5 mm. long; $n = 9$.

KEY TO TAXA OF TETRAMOLOPIUM CONSANGUINEUM

1. Leaves 1.3–1.6 cm. long; heads mostly fewer than 15 per capitulescence; ray floret lamina 1.4–1.7 mm. long. 11a. subsp. *consanguineum*
1. Leaves 3–6 cm. long; heads more than 15 per capitulescence; ray floret lamina 0.8–1.4 mm. long.
2. Ray floret lamina 1.1–1.4 mm. long; disk florets mostly 5–12 per head. 11b(i). subsp. *leptophyllum* var. *leptophyllum*
2. Ray floret lamina 0.8–1 mm. long; disk florets 3–5 per head. 11b(ii). subsp. *leptophyllum* var. *kauense*

11a. *Tetramolopium consanguineum* subsp. *consanguineum*.

Leaves 1.3–1.6 cm. long, 0.2–0.3 mm. wide, linear-oblongate, entire; capitulescence with 9–13 heads; pedicels capitate-glandular and pilose; involucre obconic, 3 mm. high, 4–6 mm. diam.; phyllaries 28–30, linear-lanceolate, obtuse, sparsely glandular or glabrous, ciliate or denticulate-margined; receptacle (1.4–) 1.7–2 mm. diam.; ray florets 20–24, the corolla tube 1.3–1.5 mm. long, the lamina (1.1–) 1.4–1.7 mm. long, 0.4–0.5 mm. wide; disk florets 5–7, the corolla 2.3–2.6 mm. long, the tube 0.6–0.8 mm. long, the anther appendage lanceolate, 0.08–0.15 mm. long, the style branches lanceolate; achenes 1.6–2 mm. long, 0.6–0.8 mm. wide, glandular distally, the faces 4–6-nerved, the median nerve prominent, the pappus brownish white, (1.7–) 2.4–2.5 mm. long.

DISTRIBUTION: Kauai? Known only from the type collection. The label lists the locality as “Mtns. of Kauai”. Presumably extinct. Flowering period: Unknown.

The exact locality of *Tetramolopium consanguineum* subsp. *consanguineum* is not known. If the label data are correct this taxon is the only representative of the genus on Kauai. However, there is good reason to believe that the label information may be erroneous. The other members of the species are endemic to the island of Hawaii. A disjunct distribution of this magnitude is unusual in the Hawaiian flora. Short of rediscovering the taxon, the question as to its true locality will remain a mystery.

11b. *Tetramolopium consanguineum* subsp. *leptophyllum* (Sherff) Lowrey, stat. nov.

Tetramolopium consanguineum var. *leptophyllum* Sherff in Bot. Gaz. **95**: 502. 1934. TYPE: HAWAIIAN ISLANDS: HAWAII: Waimea, 1840, *U. S. Exploring Expedition s. n.* (HOLOTYPE: NY!; ISOTYPE: GH!, mixed collection with isotype of *T. consanguineum* subsp. *consanguineum*).

11b(i). *Tetramolopium consanguineum* subsp. *leptophyllum* var. *leptophyllum*.

FIGURE 17a, b, c.

Stems minutely capitate-glandular; leaves (2.5–) 3–6.5 cm. long, 1.5–4.5 mm. wide, linear-oblongate, glandular-punctate and resinous with a sweet aromatic odor, strigose on margin; capitulescence with 20–40 heads; pedicels capitate-glandular and moderately hispid; involucre turbinate, 2–3 mm. high, (2.5–) 3–5 mm. diam.; phyllaries 20–35, lanceolate-ovate, obtuse, glabrous abaxially, the margin prominently denticulate; receptacle 1–2 mm. diam.; ray florets (22–) 30–40, the corolla tube 1.2–1.5 mm. long, the lamina 1.1–1.4 mm. long, 0.4–0.6 mm. wide; disk florets (4–) 5–12, the corolla salmon-pink to maroon, 2.5–2.9 mm. long, the tube 0.8–1 mm. long, the anther appendages deltoid, 0.05–0.08 mm. long, the style branches linear-lanceolate; achenes 1.8–2.2 mm. long, 0.6–0.7 mm. wide, glandular-strigose distally, the faces 3–5-nerved, the pappus brown, 1.7–2.2 mm. long; $n = 9$.

DISTRIBUTION: Island of Hawaii. Known only from the central plateau of Hawaii. In the understorey of *Metrosideros* dry forest communities. Flowering period: April to February.

REPRESENTATIVE SPECIMENS: HAWAII: Near Judd Trail between Na Puukulua and 1859 lava flow, 21 August 1949, *Degener et al.* 34836 (B, BISH, F, MO, NY, PH, W); Pohakuloa Army Training Area, New Bobcat Trail, 27 May 1979, *Lowrey* 459 (BISH, CANB, K, LAM, MO, NY, OS, TEX, UC, US); Pohakuloa Military Training Area, 8 January 1977, *Stemmermann* 1474 (BISH).

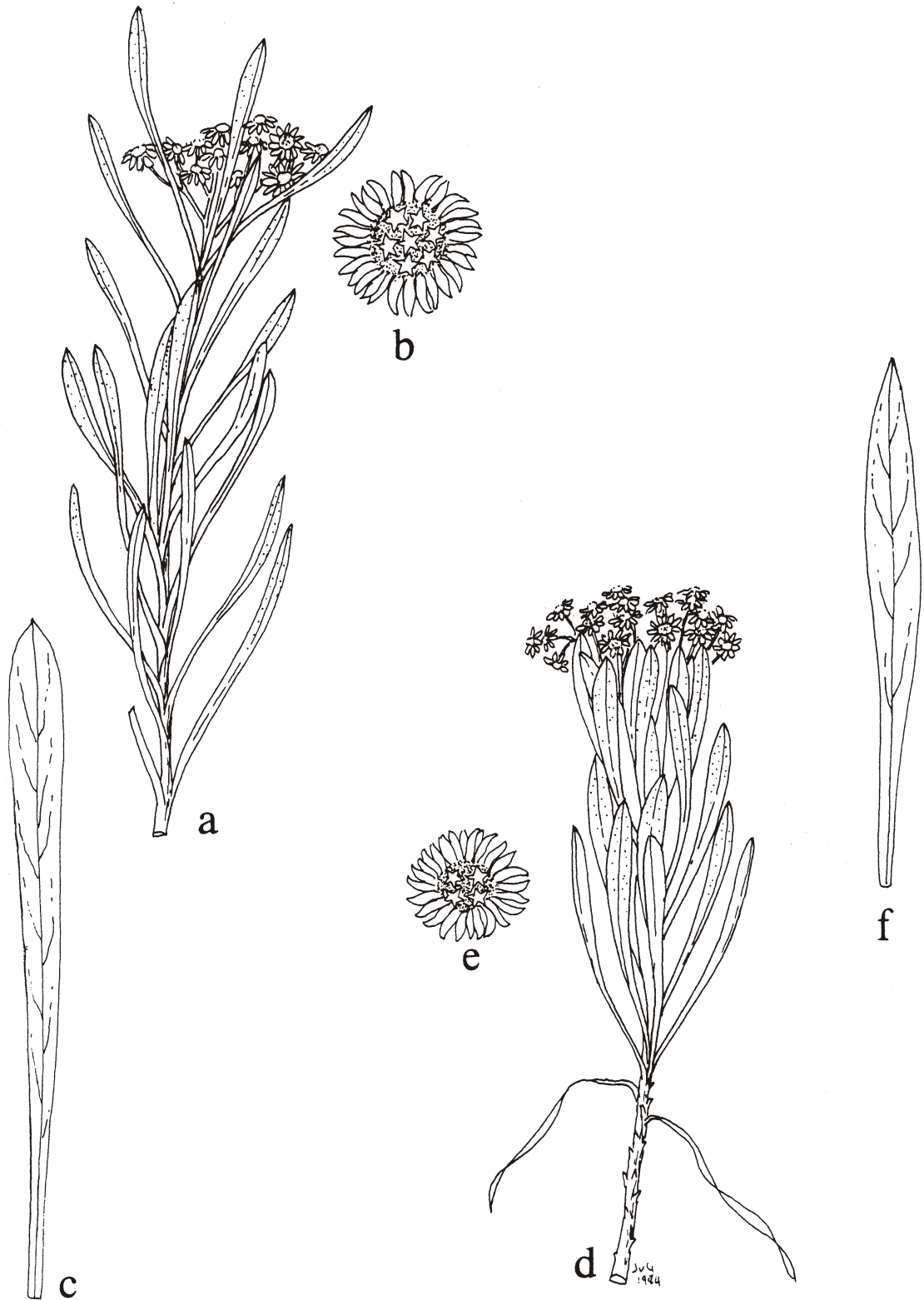


FIGURE 17. *Tetramolopium consanguineum*. a, *T. consanguineum* subsp. *leptophyllum* var. *leptophyllum*, habit, $\times 0.9$. b, *T. consanguineum* subsp. *leptophyllum* var. *leptophyllum*, head showing actual number of disc florets, $\times 5.4$. c, *T. consanguineum* subsp. *leptophyllum* var. *leptophyllum*, leaf, $\times 1.8$. d, *T. consanguineum* subsp. *leptophyllum* var. *kauense*, habit, $\times 0.9$. e, *T. consanguineum* subsp. *leptophyllum* var. *kauense*, head showing actual number of disc florets, $\times 5.4$. f, *T. consanguineum* subsp. *leptophyllum* var. *kauense*, leaf, $\times 1.8$.

11b(ii). *Tetramolopium consanguineum* subsp. *leptophyllum* var. *kauense* Lowrey, var. nov. TYPE: HAWAIIAN ISLANDS: HAWAII: Kau District, Kipuka Kamiloaina, 3–4 miles south of Highway 11, 6 June 1980, T. Lowrey, L. Stemmermann, and H. St. John 462 (HOLOTYPE: UC!; ISOTYPES: BISH!, K!, LAM!, MO!, NY!, OS!, TEX!, US!).

FIGURE 17d, e, f.

Varietas a *Tetramolopio consanguineo* subsp. *leptophyllo* var. *leptophyllo* flosculorum radii laminis brevioribus (0.8–1 mm. longis) et flosculis discii paucioribus (3–5) in quoque capitulo differt.

Stems 0.8–1.3 m. high, glabrous or resinous-glandular; leaves short-petiolate to sessile, 3–4.2 cm. long, 2–3 mm. wide, entire or rarely 1–2-dentate, the teeth 0.4–0.7 mm. long, the apex acute, the pubescence as in var. *leptophyllum*; capitulescence with 20–35 heads; peduncles glandular-pubescent; involucre 2.2–2.5 mm. long, 3–4 mm. diam.; phyllaries 20–25, lanceolate, glabrous abaxially, the margin proximally entire, distally denticulate; receptacle 0.5–1 mm. wide; ray florets 20–25, the corolla white, the tube 1.2–1.5 mm. long, the lamina 0.8–1 mm. long, 0.3–0.4 mm. wide; disk florets 3–5, the corolla purplish or pinkish brown, 2.5–3 mm. long, the tube 0.9–1.1 mm. long, the anther appendages deltoid, 0.07–0.09 mm. long, the style branches linear; achenes 1.5–1.7 mm. long, 0.5–0.6 mm. wide, glandular-strigose, the faces 2-nerved, the pappus brown, 1.6–2 mm. long.

DISTRIBUTION: Island of Hawaii. Known only from the locality of the type collection. Crevices of pahoehoe lava and a'a lava at edge of *Metrosideros* dry forest community. Flowering period: April to February.

REPRESENTATIVE SPECIMENS: HAWAII: Near Kipuka Kamiloaina, Kau District, 2 February 1968, Degener et al. 34836 (B, GB, MASS).

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