Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 81 July, 1979 No. 827

REVISION OF LIPOCHAETA (COMPOSITAE:HELIANTHEAE) OF THE HAWAIIAN ISLANDS

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Understanding patterns of speciation and phylogeny in plants involves gathering comparative data from available populations. These data, from such sources as morphology, cytology, and flavonoid chemistry, when considered together, can help indicate degrees of relationship among the taxa being investigated. Along these lines, to maximize the efficacy of such evolutionary studies, groups of plants are selected that appear to reflect a diversity of evolutionary trends. These tendencies are often more obvious in groups that (a) are isolated from extant presumptive relatives, and (b) are in regions with broad ranges of habitat diversity, yet in relatively small geographical areas. These criteria are especially fulfilled in taxa of oceanic islands. *Lipochaeta* DC. of the Hawaiian Islands was selected as a system for asking evolutionary questions.

Although the initial focus on *Lipochaeta* was evolutionary, it soon became evident that broad revisionary work needed to be done. This need was somewhat surprising, because the genus was revised recently by Sherff (1935). It was necessary, however, to develop a new revision of these Hawaiian plants before meaningful statements could be made regarding evolutionary relationships.

The following treatment is the result of four years of study including four months of field work in the Hawaiian Islands. Especially important to this investigation, and what we may hope has resulted in a more predictive system of classification, has been the observation and documentation of populational variation of most of the taxa in their natural habitats. In addition, over 2,400

herbarium specimens have been examined, including collections of the earliest botanical expeditions to the islands.

TAXONOMIC HISTORY

Robert Brown (1817) described the genus *Lipotriche,* based on plants collected by a Dr. Smith "on the banks of the Congo," Africa, without including any recognized species. In 1831, Lessing described the first two species of *Lipotriche;* one from Mexico, *L. gymnolomoides,* and the other from Hawaii, *L. australis.* At this point there were really three species of *Lipotriche;* the invalid species of Brown from Africa and the two from Mexico and Hawaii of Lessing. De Candolle (1836) validated the species based on the African collection of Smith, calling it *Lipotriche brownei.* He also moved *L. gymnolomoides* to *Perymenium,* and transferred Lessing's *Lipotriche australis* to a new genus, *Lipochaeta,* along with nine additional species from Mexico and Hawaii. Because the type species of *Lipochaeta* was based on *Verbesina lobata* Gaud. (1829), Lessing's name, *L. australis* is superfluous and must be replaced by *Lipochaeta lobata* (Gaud.) DC.

In de Candolle's treatment (1836) he included ten species: five were from the Americas (mainly Mexico), and the other five from the Hawaiian Islands. Nuttall (1841), recognizing that the American taxa differed from those of Hawaii, transferred the five Hawaiian taxa, plus three new species from Hawaii, out of *Lipochaeta* and into two new genera: *Microchaeta* with seven species, and *Schizophyllum* with one species [this latter generic name being a later homonym of *Schizophyllum* Fries (1831) and therefore re-named *Aphanopappus* by Endlicher (1842)]. Gray (1861), believing that all of de Candolle's American species of *Lipochaeta* belonged in *Zexmenia,* treated just those taxa from the Hawaiian Islands as belonging to *Lipochaeta.* He also placed the two genera of Nuttall in synonymy with *Lipochaeta.* In addition, he described four new species and transferred *Macraea laricifolia* Hook. f. of the Galapogos Islands to *Lipochaeta.* Bentham and Hooker (1873) accepted Gray's treatment, and also recognized two sections within *Lipochaeta: Microchaeta* and *Aphanopappus,* which were differentiated by features of the pappus. Harling (1962), re-elevated *L. laricifolia* to generic status as *Macraea laricifolia* Hook. f. This decision is accepted here and by Cronquist (1971).

Sherff (1933) described numerous new taxa of *Lipochaeta* and in 1935 revised the genus. In these and subsequent works by Sherff (1939, 1941, 1951, 1954, and 1960), Degener and Sherff (1940), Degener and Clay (1949), St. John (1959, 1972, and 1976b) more than 65 taxa have been described in some 33 species.

In the present treatment, *Lipochaeta* is recognized as endemic to the Hawaiian Islands and has two sections: Section *Lipochaeta* with nine taxa in six species and Section *Aphanopappus* which includes 18 taxa in 17 species.

GENERIC RELATIONSHIPS

Lipochaeta has traditionally (Gray, 1861; Bentham & Hooker, 1873; Sherff, 1935) been considered intermediate between *Wedelia* Jacq. and *Zexmenia* La Llave & Lexarza. In fact, de Candolle's (1836) original description included four species now recognized as belonging to *Zexmenia,* one species of *Wedelia,* and five *Lipochaetas.* Other workers (Gray, 1852; Bentham & Hooker, 1873; Jones, 1905) have recognized under various names, a "Wedelioid" section of *Zexmenia.* Becker (1972) has concluded that the species of this section represent a separate genus[1] very close to *Wedelia.* These "Wedelioid" taxa are characterized by involucral bracts in two series of approximately equal length, achenes with a neck or slight constriction, fragile awns, and variously developed wings along the angles of the achenes. These features are also typical of most species of *Wedelia* and *Lipochaeta.*

In a recent revision of the subtribal limits within the Heliantheae (Stuessy, 1977), a closer relationship between *Lipochaeta* and *Wedelia* has been indicated by the inclusion of both genera in the subtribe Ecliptinae. *Zexmenia,* on the other hand, has been placed in the subtribe Verbesininae near *Perymenium* and *Oyedaea,* a positioning with which I concur.

Further evidence suggesting a connection between *Lipochaeta* and *Wedelia* comes from cytological data. *Lipochaeta* is known as $x = 15$ (Solbrig, et al., 1972; Gardner, 1977a); *Wedelia* as $x = 11$, 12, and 15 (Solbrig, et al., 1972). The species complex to which

[1]Due to nomenclatural requirements (Becker, 1972; McVaugh, 1975), this genus must bear the name *Zexmenia,* and the species of the traditional grouping become known as *Lasianthaea* DC.

Lipochaeta is most similar morphologically (those features listed above) is the $x = 15$ group of *Wedelia*.

MORPHOLOGICAL AND TAXONOMIC CRITERIA

In the past, considerable emphasis has been placed on variations in leaf morphology as a basis for delimitation of taxa of *Lipochaeta*. In the present study, field observations of populational variation have indicated that caution is necessary in recognizing taxa, especially at the species level, on differences in leaf morphology. Two examples will illustrate the dubious utility of some of these features. (**1**) Sherff (1935) lists as the major distinction between *Lipochaeta rockii* var. *rockii* and var. *subovata*, leaves 3–5 parted in the former and coarsely dentate or incisely lobulate for the latter. Single specimens have been seen in the field (*Gardner 406*) with both kinds of leaves, and virtually every population of *L. rockii* observed showed a range of variation from almost entire to deeply five lobed. (**2**) The major difference between *L. profusa* and *L. alata* (Sherff, 1935) is that the former has sessile leaves with connate-perfoliate bases, while the latter has winged petioles, but no connate bases. After examining numerous specimens, both in the field and from pressed material, I found a morphological range from petiolate to connate-perfoliate leaf bases at least within a single population and occasionally on the same plant. From limited observations on plants grown in the greenhouse, it appears that the amount of leaf material produced at a node increases with the age of the specimen, i.e., first formed leaves are nearly petiolate, and later formed leaves become sessile with connate-perfoliate bases. This variability does not mean that leaf characteristics are totally useless for recognizing taxa; clearly, the thick, succulent leaves of *L. integrifolia* distinguish it from all other species of the genus, just as the ternately compound leaves of *L. tenuifolia* make it distinct. Although these and other vegetative features can be used to delimit some taxa (see key), most of the useful taxonomic characters in *Lipochaeta* are floral.

FLORAL FEATURES

Involucre. The number and series of involucral bracts is relatively constant throughout *Lipochaeta*. The phyllaries are produced in two series with four or five bracts in each whorl. However,

differences in length, width, and shape of the phyllaries have been useful for differentiating between closely related taxa.

Chaff. The chaff is relatively uniform throughout the genus. Slight differences in texture exist, but these are difficult to describe in a meaningful way, and also tend to vary within taxa. Certain collections of *Lipochaeta succulenta* are atypical within the genus in having a slightly three-lobed (typically unlobed) chaff. However, this lobing does not appear to be correlated with any other consistent variation, and therefore is not regarded as taxonomically significant.

Ray Florets. The number of rays varies from four to as many as 16. This variation in number is useful in interpreting relationships among several taxa in Section *Aphanopappus* (e.g., *Lipochaeta fauriei, L. kamolensis, L. micrantha, L. remyi, L. subcordata, L. venosa,* and *L. waimeaensis*) that produce only four to six rays. Length and width of the ligule and length of the tube are also useful markers. The number of lobes per ligule, however, may vary from none to three on the same specimen, and thus is not considered useful in differentiating taxa.

Disc Florets. Approximately one-third of the species of *Lipochaeta* have four-lobed disc corollas and four anthers. The others are five-merous, as is typical of the Compositae (Gardner, 1977b). Without additional data from cytology and leaf flavonoid chemistry, the significance of this morphological difference cannot be appreciated, as indicated by Sherff's 1935 revision. It is now apparent, however, that the tetramerous Lipochaetas are tetraploid and synthesize flavones and flavonols, while the pentamerous taxa are diploid and produce only flavonols. This combination of characters is significant for sectional assignment. Section *Lipochaeta* is distinguished morphologically by tetramerous florets, and Section *Aphanopappus* hy pentamerous florets. Characters useful at the specific and subspecific levels are length of corollas, corolla lobes, and anthers.

Fruits. Diagnostic features of mature ray and disc achenes that are significant at the specific and varietal levels include fruit length and width and presence or absence of a corona and/or wings. These characters, however, are not useful for delimitation at the sectional level. Bentham and Hooker (1873), in recognizing two sections of

Lipochaeta, relied primarily on pappus features. Their section *Microchaeta* (=*Lipochaeta*) has prominent aristae, and section *Aphanopappus* has a rudimentary pappus or none. Sherff (1935) recognized these same sections and added a third, *Macraea* to accommodate *Lipochaeta laricifolia* (Hook. f.) A. Gray, of the Galapagos Islands; Harling (1962), has since re-elevated *L. laricifolia* to generic status as *Macraea laricifolia* Hook. f., this latter section being characterized by a corona. These sectional characters do not seem workable for two important reasons. First, variation in the pappus of some taxa (e.g., *L. connata* and *L. heterophylla*) ranges from a distinct corona as long as 2 mm to a few uneven scales. Numerous overlapping conditions, therefore, occur in this feature within the genus. Second, in early stages of fruit development, all Lipochaetas produce short (to 3 mm) pappus awns, and as the fruits mature the awns become increasingly less tightly attached. Specimens containing ripe fruits, therefore, often lack awns whether observed in the field or in the herbarium, and cannot be referred successfully to any of the sections. Thus, pappus variation is not used as a basis for assigning taxa at the sectional level in this treatment.

HYBRIDIZATION

Natural hybridization in *Lipochaeta* is uncommon. Although no hybrids have been detected during the present field studies, two examples can be mentioned that indicate its probable but infrequent occurrence. First, Degener and Sherff (1935) described × *L. procumbens* as a hybrid between *L. lobata* (a tetraploid) and *L. integrifolia* (a diploid). Pollen stainability (in lactophenol-aniline blue) in this plant is 2 per cent, no full achenes are present, and it has a leaf morphology intermediate between the two putative parents. In addition, it has been determined that the plant has an additive leaf flavonoid profile. In view of these data, it is probable that a sterile triploid has been formed. These plants were collected near Kaena Point, Oahu (*Degener, et al. 4187*), an area of sympatry for the parental taxa. Another possible hybrid is *L. intermedia* Degener and Sherff (placed in synonymy with *L. subcordata* in this treatment). Known from a single collection, *Meebold 4254,* this taxon was found on Hawaii in an area where both *L. subcordata* and *L. lavarum* occur. It is intermediate between the two species. The

specimen does, however, have a pollen stainability of 90 per cent, and several full achenes.

LEAF FLAVONOID CHEMISTRY

The usefulness of flavonoid chemistry in determining degrees of relationship among plant taxa is well established (Turner & Alston, 1959; Alston & Turner, 1962; Levin, 1967; Crawford, 1974; Gardner, 1974; Giannasi, 1975). In the hope of gaining insight concerning the systematics of *Lipochaeta,* a chemical study was initiated.

Specimens of 16 of the 23 species of *Lipochaeta* were surveyed for flavonoid content. Population samples from throughout the morphological and geographical range of each taxon were examined (indicated by asterisks in the representative specimens). Voucher specimens for all personal collections are deposited in OS.

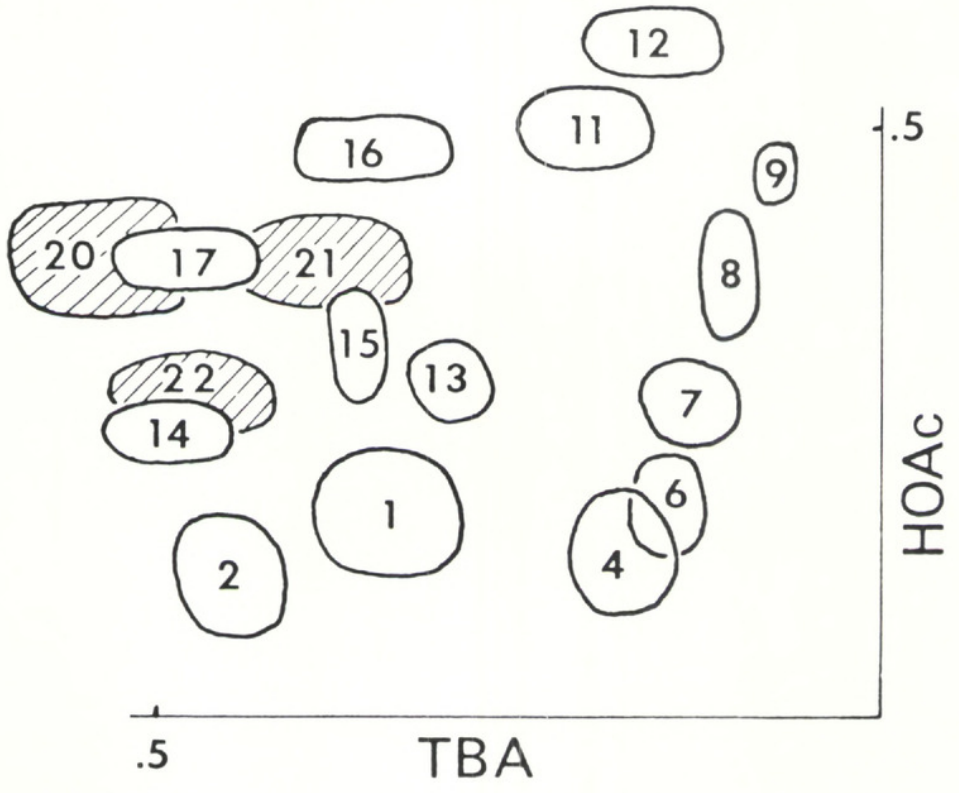


Figure 1. **Drawing of two dimensional paper chromatogram of *Lipochaeta* leaf extracts.** Hatching shows compounds of Section *Aphanopappus,* all others are characteristic of Section *Lipochaeta.*

Materials and Methods

The methods of Mabry et al. (1970) were followed for paper chromatography and spectral analyses except that fused sodium acetate was used. Extraction and isolation of compounds was achieved following the procedures of Bacon (1975). A single collection of each taxon was subjected to the bulk extraction methods, while all additional collections were surveyed using two dimensional paper chromatography. If the resultant chromatogram was judged to differ from those obtained with the mass samples the unique compounds were identified. If, however, the profiles were considered to be identical, no additional identification was done.

Intact leaves were taken from herbarium specimen packets and soaked for 24 hours in 85 per cent aqueous methanol. After extraction, the leaves were air dried and returned to the packets. The extract was concentrated under vacuum and checked for flavonoid content using thin layer chromatography (glass plates coated with PH-101 microcrystalline cellulose). Because of insufficiency of material, no compounds were identified, but rather the TLC profiles were compared with known paper profiles.

Results

Leaf flavonoid chemistry is useful for making sectional assignments in *Lipochaeta*. The species of Section *Lipochaeta* (tetraploid and four-merous) synthesize both flavones and flavonols, whereas the taxa of Section *Aphanopappus* (diploid and five-merous) produce only flavonols (Figure 1, Table 1). Considerable infrasectional similarity is also indicated. Although the utility of recognizing species, based on chemical constituents, in either section is weak, some patterns (primarily absence of compounds) are species-specific in the tetraploids (e.g., *L. succulenta, L. degeneri*).

PHYLOGENY

Phylogenetic relationships among the taxa are depicted in Figure 2; taxa below the dashed line are diploid, those above are tetraploid. Although the diploids are at least partially ancestral to the tetraploids, once formed the two sections have evolved independently.

Many of the taxa, e.g., *Lipochaeta ovata,* are known only from single collections, and it is estimated that at least one third of those

Table 1. **Major leaf flavonoid constituents of *Lipochaeta*.**

In the ratios, the first figure is the number of populations sampled and the second is the number of collections examined. Compounds in all samples tested are indicated by +; those absent from some populations are indicated by −. Compounds 1–7 are luteolin glycosides, 13–15 are apigenin glycosides, and 16–22 are quercetin glycosides.

		Compound	Flavones												Flavonols				
	Ratio	Number	1	2	4	6	7	8	9	11	12	13	14	15	16	17	20	21	22
Sect. *Lipochaeta*																			
L. rockii	(9:22)		+	+	+	+	+		−	−	−	−	−	−	+	+			
L. connata var. *acris*	(6:6)		+		+	+	+	+	−			+			+				
L. connata var. *connata*	(4:6)		+		+		−		−		−		+		+	+			
L. lobata var. *lobata*	(3:5)		+		+	+	+		−	+			+		+	+			
L. heterophylla	(6:11)		+	−	+	+	+	−	−		−	−	−		−	−			
L. succulenta	(5:6)		+		+	+							−						
L. degeneri	(1:1)		+							+	+								
Sect. *Aphanopappus*																			
L. tenuifolia	(1:1)																	+	
L. populifolia	(1:1)																+	+	
L. lavarum	(9:9)																	+	
L. integrifolia	(9:15)																	+	+
L. waimeaensis	(1:1)																	+	
L. micrantha var. *exigua*	(1:1)																	+	
L. kamolensis	(1:1)																+	+	+
L. subcordata	(1:1)																	+	
L. remyi	(1:1)																	+	
L. tenuis	(1:1)																	+	

species are extinct. It is believed that some of the extinctions are recent, e.g. *L. degeneri* was collected on Molokai in 1910 (*Rock 10288*), 1912 (*Forbes 59-Mo*) and 1928 (*Degener 4198*). A thorough search of the type locality in 1974 was unsuccessful in re-discovering the taxon.

Lipochaeta ovata, a diploid, is believed to be the most primitive species of the genus. It is similar to the close relative *Wedelia,* especially *W. biflora,* in habit (upright shrub, petiolate leaves to 7.5 cm long, 3.5 cm wide) and in characters of the mature achenes (smooth external surface, thickened pericarp, and lacking a pappus).

The diploids can be separated into two major groups (Figure 2). Group A is characterized by large headed taxa with mostly more than 30 disc florets per head. The habit of these taxa varies from coarse and upright (*Lipochaeta lavarum, L. populifolia, L. perdita, L. ovata*) to more delicate and decumbent (*L. dubia, L. tenuifolia, L. tenuis*) to succulent and prostrate (*L. integrifolia*). *Lipochaeta tenuifolia* has ternately compound leaves, which is atypical for the genus; some other species have leaves deeply dissected, but not truly compound.

Group B (Figure 2) is characterized by generally fewer ray and disc florets and smaller heads than group A. All are suffruiticose except *Lipochaeta remyi,* an herb. The remaining taxa show variations in growth habit similar to group A; upright (*L. bryanii, L. deltoidea, L. fauriei, L. subcordata, L. venosa*) or decumbent (*L. kamolensis, L. micrantha, L. waimeaensis*). *Lipochaeta deltoidea* has characters that tie it to each of the other subgroups and is therefore considered as the ancestral type for group B.

Lipochaeta deltoidea shows also a resemblance to *L. connata* var. *acris* (a tetraploid) through the vegetative features listed above. In addition, *L. deltoidea* has tuberculate achenes and purple paleae. These features are common throughout the tetraploids. *Lipochaeta connata* var. *acris* is a taxon from which all of the tetraploid species can be derived, except for *L. degeneri.* This species, unknown cytologically, is included in Section *Lipochaeta* based on floral morphology and leaf flavonoid chemistry, but its connection to the remaining tetraploids is obscure.

Many of the islands are characterized by certain tetraploid species that are unique to that island e.g.; Kauai, *Lipochaeta connata;* Oahu, *L. lobata;* Molokai, *L. rockii;* Lanai, *L. heterophylla.* One

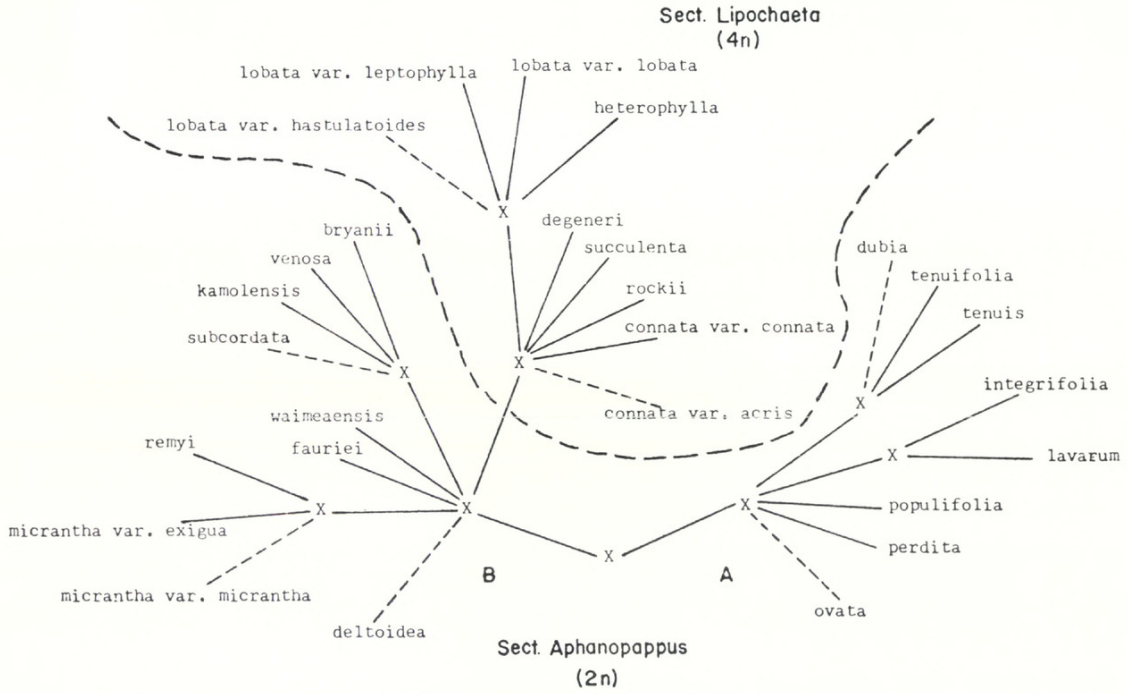


Figure 2. **Phylogenetic relationships among *Lipochaeta* taxa.**

taxon, however, *L. succulenta,* which may be dispersed by water, has been found on all of the major islands except Lanai.

TAXONOMIC TREATMENT

Lipochaeta DC.

Lipochaeta DC. Prodr. **5:** 610. 1836. Type species: *Lipochaeta lobata* (Gaud.) DC.

Microchaeta Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841. *nom. superfl.* Type species: *Lipochaeta lobata* (Gaud.) DC.

Schizophyllum Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 452. 1841. *nom. illegit.* non Fries. 1831. Type species: *Schizophyllum micranthum* Nutt. (=*Lipochaeta micrantha* (Nutt.) A. Gray).

Aphanoppaus Endl. Gen. Plantarum Suppl. **2:** 43. 1842. *nom. nov.,* based on *Schizophyllum micranthum* Nutt.

Plants suffruticose perennial or rarely annual; stems upright to 2 m tall, or arcuate-spreading or decumbent to prostrate and rooting along lower surface. Leaves opposite, simple or rarely ternately compound, petiolate, often with alate-margined petioles or sessile with connate-perfoliate bases, margin entire to pinnate-pinnatifid, on both surfaces glabrous to hispidulose. Heads solitary or in cymose clusters, terminal on stems and branches, pedunculate. Phyllaries in 2 equal or subequal series, 4 or 5 per series, green to tan and sometimes purple near base and along midrib. Ray florets carpellate, fertile; ligule yellow, divergent or reflexed, at apex entire to 3-dentate. Disc florets hermaphrodite, generally all fertile; corollas yellow, four- or five-merous. Achenes tuberculate or smooth, sometimes winged, with outer wall of mature achenes becoming thick, approximately doubling external size of fruit; pappus often of scales or forming a corona and also of deciduous awns, ray achenes 3-angled, disc achenes 2 or 4 angled. Paleae rigid, erect or arching over developing florets, sometimes purple near tip or along midrib.

KEY TO THE TAXA

a. Majority of disc florets in a single head with 4-lobed corollas (Section *Lipochaeta*). (b)

b. Leaves to 2 cm long and 0.5 cm wide; ray florets 6 or fewer. 2. *L. degeneri*

b. Leaves more than 2 cm long, more than 0.5 cm wide; ray florets more than 6. (c)

c. Leaves and stems fleshy in the field, stems often flattened on mounted specimens; ray ligules reflexed, to 6 mm long; mature achenes nearly smooth. ..... 1. *L. succulenta*

c. Leaves subcoriaceous to herbaceous and stems suffruticose, rigid on mounted specimens; ray ligules divergent, more than 6 mm long; mature achenes tuberculate. (d)

d. Leaves entire, if rarely divided then outer phyllaries broadly ovate, broadly acute to rounded at apex and leaves petiolate; leaf vestiture strigulose to nearly glabrous. (e)

e. Outer phyllaries broadly acute to rounded at apex, if attenuate, then leaves lanceolate-linear; heads solitary or in 3 headed cymes. (f)

f. Leaves ovate; phyllaries broadly acute to rounded. (g)

g. Leaves sessile or short petiolate, bases not extending across node. ..... 5a. *L. lobata* var. *lobata*

g. Leaves sessile, bases connate-perfoliate. ..... 5b. *L. lobata* var. *hastulatoides*

f. Leaves lanceolate-linear; phyllaries attenuate. ..... 5c. *L. lobata* var. *leptophylla*

e. Outer phyllaries acute to attenuate, if attenuate, then leaves ovate; heads in compound cymose clusters. (h)

h. Leaf bases connate-perfoliate. ... 6a. *L. connata* var. *connata*

h. Leaf bases narrowed to an alate margined petiole ..... 6b. *L. connata* var. *acris*

d. Leaves divided or parted, if not divided than outer phyllaries acute and/or leaves sessile; leaf vestiture strigose to appressed hispidulose. (i)

i. Heads in compound cymose clusters; outer phyllaries narrowly ovate; leaves petiolate or sessile. ..... 3. *L. rockii*

i. Heads in 3 headed cymes; outer phyllaries broadly ovate; leaves sessile. ..... 4. *L. heterophylla*

a. Majority of disc florets in a single head with 5-lobed corollas (Section *Aphanopappus*). (k)

k. Plants annual, herbaceous. ..... 10. *L. remyi*

k. Plants perennial, suffruticose. (l)

l. Stems decumbent or prostrate. (m)

m. Leaves appearing as six per node (ternately compound with sessile leaflets), leaflets pinnatifid, ultimate segments less than 3 mm wide. ..... 7. *L. tenuifolia*

m. Leaves 2 per node, simple (some species with divided leaves, but not compound), ultimate segments more than 3 mm wide. (n)

n. Leaves thick and succulent; mature achenes nearly smooth. ..... 23. *L. integrifolia*

n. Leaves herbaceous; mature achenes tuberculate. (o)

o. Leaves linear to narrowly elliptic, nearly entire, less than 1 cm wide. ..... 12. *L. waimeaensis*

o. Leaves ovate to deltoid or divided, more than 1 cm wide. (p)

p. Ray florets 4 or 5, ligules less than 6.5 mm long. (q)

q. Ray ligules more than 2.5 mm long. ..... 15a. *L. micrantha* var. *micrantha*

q. Ray ligules to 2.5 mm long. 15b. *L. micrantha* var. *exigua*

p. Ray florets 6–12, ligules more than 6.5 mm long. (r)

r. Leaves pinnatifid to pinnate-pinnatifid; ray florets 6. ..... 19. *L. kamolensis*

r. Leaves entire or with 2 or 4 basal lobes, ray florets more than 6. (s)

s. Leaves deltoid, usually with 2 or 4 basal lobes. ..... 8. *L. dubia*

s. Leaves ovate, not lobed basally. ..... 9. *L. tenuis*

l. Stems arcuate spreading or upright. (t)

t. Achenes nearly smooth. (u)

u. Heads in compound cymose clusters; outer phyllaries less than 2.5 mm long. ..... 11. *L. ovata*

u. Heads solitary or in 3 headed cymes; outer phyllaries more than 2.5 mm long. ..... 21. *L. lavarum*

t. Achenes tuberculate. (v)

v. Ray ligules less than 7 mm long. (w)

w. Disc corollas more than 3.8 mm long; petioles narrowly alate margined. ..... 14. *L. fauriei*

w. Disc corollas less than 3.5 mm long, and/or petioles not alate margined. (x)

x. Heads in compound cymose clusters; achenes with scales along upper, outer rim. ..... 16. *L. subcordata*

x. Heads solitary or in 3 headed cymes; achenes with hairs along upper, outer rim or naked, but without scales. (y)

y. Outer phyllaries obtuse at apex; ray ligules less than 5 mm long. ..... 17. *L. venosa*

y. Outer phyllaries attenuate at apex; ray ligules more than 5.5 mm long. ..... 13. *L. deltoidea*

v. Ray ligules more than 7 mm long. (z)

z. Ray florets 5 or fewer. ..... 20. *L. bryanii*

z. Ray florets more than 5. (aa)

aa. Leaves less than 4.5 cm long and less than 2.8 cm wide; disc corollas more than 3.5 mm long. ..... 22. *L. perdita*

aa. Leaves more than 4.5 cm long and more than 2.8 cm wide; disc corollas less than 3.5 mm long. ..... 18. *L. populifolia*

LIPOCHAETA SECTION LIPOCHAETA

Lipochaeta DC. section *Microchaeta* (Nutt.) Bentham and Hooker, Gen. Plantarum **2:** 372. 1873. *Microchaeta* Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841. *nom. superfl.* TYPE SPECIES: *Lipochaeta lobata* (Gaud.) DC.

Leaves with narrowly alate-margined petioles or broadly connate-perfoliate at the base. Majority of disc florets four-merous. Chromosome number, $n = 26$. Species numbers 1–6.

1. **Lipochaeta succulenta** (Hook. & Arn.) DC. Prodr. **5:** 611. 1836.

Verbesina succulenta Hook. & Arn. Bot. Beechey's Voyage. **87.** 1832. TYPE: Hawaii: Oneeheow [Niihau]: 1826–27, *G. T. Lay & A. Collie s.n.* (Holotype, K!). *Microchaeta succulenta* (Hook. & Arn.) Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841.

Lipochaeta lanceolata Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841. TYPE: Hawaii: Oahu: near the sea, *Nuttall s.n.* (Holotype, BM!).

Lipochaeta australis Lessing var. *decurrens* A. Gray, Proc. Amer. Acad. Arts **5:** 129. 1861. TYPE: Hawaii: Kauai: 1838–42, *U. S. Exploring Expedition s.n.* (Lectotype chosen, US!). *Lipochaeta connata* (Gaud.) DC. var. *decurrens* (A. Gray) Hillebrand, Flora Hawaiian Islands. 206. 1888.

Lipochaeta connata (Gaud.) DC. var. *littoralis* Hillebrand, Flora Hawaiian Islands. 206. 1888. TYPE: Hawaii: Molokai: *W. Hillebrand s.n.* (Holotype, apparently destroyed, not at B).

Lipochaeta variolosa Léveillé, Repert. Spec. Nov. Regni Veg. **10:** 122. 1911. TYPE: Hawaii: Kauai: Wainiha, Jan 1910, *A. U. Faurie 1008* (Lectotype chosen, P!; isotypes, BISH!, G[2]!).

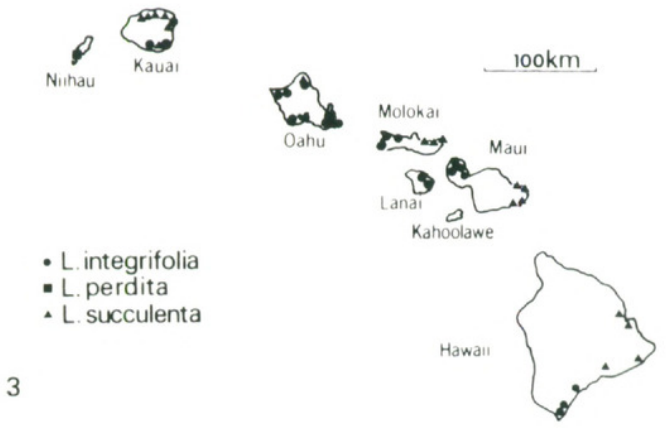
Lipochaeta succulenta (Hook. & Arn.) DC. var. *angustata* Sherff, Bot. Gaz. (Crawfordsville) **95:** 87. 1933. TYPE: Hawaii: Kauai: 1909, *C. N. Forbes s.n.* (Holotype, F!; isotypes, BISH!, F!).

Lipochaeta succulenta (Hook. & Arn.) DC. var. *barclayi* Sherff, Bot. Gaz. (Crawfordsville) **95:** 87. 1933. TYPE: Hawaii: Atooi [Kauai]: in loam soil, hills, Jul 1837, *G. Barclay 1327* (Holotype, BM; photo of holotype, F!).

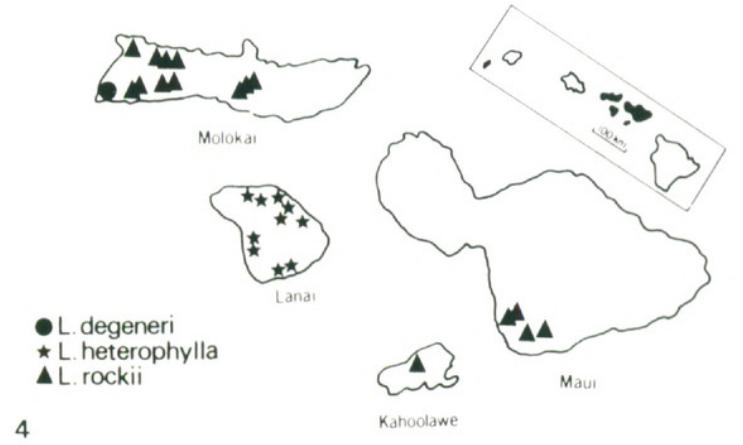
Suffruticose; stems decumbent, rooting along lower surface, to 1.5 m long. Leaves with narrowly alate margined petiloes 2–10 mm long; blades linear to elliptic-ovate, 6–12.5 (–14) cm long, (1–) 2–4 (–6.5) cm wide, entire to serrate, glabrous to strigulose.[1] Heads in simple or compound cymes. Outer phyllaries ovate, 3.2–5 mm long, 1.5–3.8 mm wide, acute, occasionally purple near apex, sparsely strigulose. Ray florets 9–15; ligules oval to oblong, (3.8–) 4.5–6 mm long, (1.3–) 2.3–3.3 mm wide; tube 1.2–1.5 (–1.8) mm long. Disc florets 25–40 (–50); corollas 3.1–3.7 mm long, lobes 0.9–1.2 mm long; anthers 1.3–1.5 mm long. Achenes nearly smooth, those of ray 2.3–2.7 mm long, 1.2–1.7 mm wide, with wings to 0.5 mm, those of disc 2.2–2.9 mm long, 1.1–1.4 mm wide, with wings to 0.6 mm; pappus of fused scales forming an uneven corona and with awns to 0.6 mm long. Paleae occasionally purple near apex.

Known from all of the major islands except Lanai (Figure 3); generally near sea level to 100 m in coastal areas, but occasionally

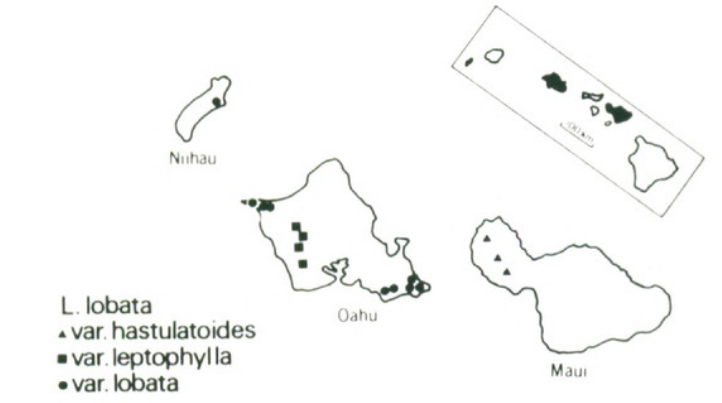
[1]Length and width of leaves at second node below the peduncles.



3



4



5

Figures 3–5. **Documented distributions of *Lipochaeta*.** 3. *L. integrifolia*, *L. perdita*, and *L. succulenta*. 4. *L. degeneri*, *L. heterophylla*, and *L. rockii*. 5. *L. lobata* var. *hastulatoides*, var. *leptophylla*, and var. *lobata*.

further inland and at higher elevations (200 m). Flowering throughout the year. Extant.[1]

Lipochaeta succulenta is similar to *L. connata* var. *acris* in several gross morphological features, but can be distinguished from the latter by the much shorter ray ligules; shorter and broader, smooth fruits; fleshy leaves; and ovate phyllaries. The achenes of this taxon have a very thick outer layer of cork which may facilitate flotation and thus serve in dispersal.

Sherff (1935) recognized four varieties of *Lipochaeta succulenta,* based almost entirely on variations in leaf shape and size. Variety *trifida* was distinguished by "commonly" trilobed leaves. Closer examination, especially of floral features, has shown it to be a large leaved variant of *L. rockii.* The extremes of the type specimens of the other three varieties recognized by Sherff (1935) intergrade to a large degree, and this character is most obvious when population samples are analyzed. In addition, observations of plants grown in the greenhouse indicate that differences in water availability and light levels can make considerable differences in leaf size and shape.

Representative specimens. HAWAII. **Hawaii:** Hilo Bay, *Brumaglin 4300* (F, NY), *Degener 4029* (GH, NY, US); S side of Hilo Bay, *Degener 18077* (NY); between Keaukaha and Leleiwii Pt, Puno,*Degener & Picco 31642* (MO, W); Hawaii National Park, *Fagerlind & Mitchell 1116* (BISH, NY); Hilo, *Hitchcock 14155* (BISH, US); Kalapaua, *Rock 13007* (BISH). **Kauai:** Hanalei, Makahoa Pt, *Degener 20507* (BISH, NY); Waiahuakua, *Degener & Ordonez 12612* (A, BISH, F, G, GH, MO, US); Haena-Kalalau Trail, *Gardner 284, 285** (OS); Anini Beach, *Gardner 289** (OS); S side of Moloaa Bay, *Gardner 354* (OS); N of Ka Lae Amana Pt, Moloaa Bay, *Gardner 356, 356A* (OS); Pakala Pt, *Gardner 357** (OS); S of light house, Kilauea Pt, *Gardner 358* (OS); Hanakapiai, *St. John, et al. 10870* (US). **Maui:** Keanae, *Degener & Degener 23645* (G, NY, W); near Kaapahu Bay, *Degener & Degener 25237* (BISH, F, G, K, MO, NY, W); Nahiku, *Degener & Degener 27564* (BISH, F); Kaapahu Bay, *Degener & Degener 27567* (BISH, F, NY); Hana, N side of Kauiki Head, *Degener et al. 12422* (A, BISH, F, MO, NY, US); *Degener & Murashize 19797* (BISH, NY, US); beach at Kipahula, *Forbes 274-M* (BISH, F); Kaapahu, *Forbes 1774-M* (BISH, US); Kahanu Gardens of Pacific Tropical Botanical Gardens, *Gardner 381** (OS); Kaapahu Bay, *Gardner 383*, 384** (OS). **Molokai:** Wailau Valley, *Degener & Nitta 4028* (BISH, CAS, DS, F, K), *4211* (F, G, GB, GH, K, MO, NY, UC, US, W); Manawai, *Forbes 396-Mo* (BISH, F, K, UC); Wailau Valley, *Forbes 522-Mo* (BISH, F); Pelekunu Valley, *Forbes 577-Mo* (BISH, F); W of Wailau Valley, *Fosberg 9657* (BISH); Wailau Valley, *Fosberg 9663* (BISH, DS, F, GH); Manawai,

[1]Because of the inclusion of nearly all of the taxa of *Lipochaeta* on the endangered species list for Hawaii (Fosberg & Herbst, 1975), comments will be made on the presumptive current status of each taxon.

Kahanami Ridge, *Fosberg 13393* (BISH, F); mouth of Halawa Valley, *Fosberg 13407* (F, GH, US); Kalaupapa, *Gardner 313* (OS). **Niihau:** no locality, *Remy 287* (GH, NY). **Oahu:** Kahuku, *Pearsall 100* (BISH).

2. **Lipochaeta degeneri** Sherff, Bot. Gaz. (Crawfordsville) **95:** 84. 1933. TYPE: Hawaii: Molokai: hot, arid boulder-covered plain near sea, SW point of island, 16 May 1928, *O. Degener 4198* (Holotype, F!; isotypes, A!, F!, G!, GH!, K!, MO!, US!, W[2]!).

Suffruticose, stems upright, to 30 cm tall. Leaves sessile, spatulate, 1.7–2 cm long, 0.3–0.4 cm wide, entire, sparsely strigulose. Heads solitary or in 2's or 3's. Outer phyllaries ovate, 3–3.8 mm long, 1.3–2.1 mm wide, acute, often purple near apex, strigulose. Ray florets about 6; ligules oblong, 3.6–4 mm long, 2–2.4 mm wide; tube 1–1.2 mm long. Disc florets about 15; corollas 2.7–3.3 mm long, lobes 0.6–0.7 mm long; anthers 1.2–1.5 mm long. Achenes tuberculate, those of ray 2.3–2.4 mm long, 1.1–1.5 mm wide, with wings to 0.4 mm, those of disc 2.7–3.2 mm long, 0.8–1.8 mm wide, with wings to 0.3 mm; pappus of scales to 0.2 mm long, fused at the base and with deciduous awns to 1 mm long. Paleae with a purple midrib and often purple near apex. Chromosome number unknown.

Known from three collections near the southwest point of Molokai (Figure 4), near sea level. Habitat information scarce except for "hot, arid, boulder-covered plain" (*Degener 4198*). Flowering May-Jun. Probably extinct.

Lipochaeata degeneri superficially resembles an upright *L. integrifolia*. Closer examination, however, shows that the leaves of the former are not succulent, the heads are few-flowered, and the achenes are winged and tuberculate. Its position within this section is unclear.

Representative specimens. HAWAII. **Molokai:** Ka Lae O Ka Laau, *Forbes 59-Mo* (F, US); *Rock 10288* (GH, NY, US, W); *Rock 14011* (UC).

3. **Lipochaeta rockii** Sherff, Bot. Gaz. (Crawfordsville) **95:** 100. 1933. TYPE: Hawaii: Molokai: Mapulou, 22 Mar 1910, *J. F. Rock 6156* (Holotype, GH!; isotypes, BISH!, F[3]!).

Lipochaeta forbesii Sherff, Bot. Gaz. (Crawfordsville) **95:** 83. 1933. TYPE: Hawaii: Maui: Nuu, S slope of Haleakala, 9 Mar 1920, *C. N. Forbes 1916-M* (Holotype, F!; isotypes, K!, NY!, UC!, US!).

Lipochaeta heterophylla A. Gray var. *malvacea* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 96. 1933. TYPE: Hawaii: Molokai: arid, rocky

plain near Kolo, 5 Apr 1928, *O. Degener 4199* (Lectotype chosen, F!; isotypes, BISH! CAS!, F[4]!, G[2-frag.]!, GB!, MO[2]!, NY!, UC!, US!, W[2]!).

Lipochaeta kahoolawensis Sherff, Bot. Gaz. (Crawfordsville) **95:** 98. 1933. TYPE: Hawaii: Kahoolawe: 1851–1855, *J. Remy 269* (Holotype, P!).

Lipochaeta lobata (Gaud.) DC. var. *maunaloensis* Sherff, Bot. Gaz. (Crawfordsville) **95:** 93. 1933. TYPE: Hawaii: Molokai: Mauna Loa, Jun 1912, *C. N. Forbes 7-Mo* (Holotype, F!; isotype, BISH!).

Lipochaeta rockii Sherff var. *dissecta* Sherff, Bot. Gaz. (Crawfordsville) **95:** 101. 1933. TYPE: Hawaii: Maui: 1838–42, *U.S. Exploring Expedition s.n.* (Holotype, US!).

Lipochaeta rockii Sherff var. *subovata* Sherff, Bot. Gaz. (Crawfordsville) **95:** 101. 1933. TYPE: Hawaii: Molokai: 1851–1855, *J. Remy 270* (Holotype, P!).

Lipochaeta succulenta (Hook. & Arn.) DC. var. *trifida* Sherff, Bot. Gaz. (Crawfordsville) **95:** 87. 1933. TYPE: Hawaii: Molokai: Manawai, Aug 1912, *C. N. Forbes 397-Mo* (Lectotype chosen, F!; isotypes, BISH!, F[2]!, UC!).

Lipochaeta forbesii Sherff var. *sherffii* Degener & Clay, Flora Hawaiiensis, Fam. 344:Lip:Forb. 1949. TYPE: Hawaii: Maui: between Kepuni and Palaha Gulches, 25 Dec 1948, *O. Degener 19292* (Holotype, BISH!; isotypes, A!, B!, F[3]!, G!, GB!, NY[2]!, US!).

Lipochaeta lobata (Gaud.) DC. var. *makenensis* Degener & Sherff *In:* Sherff, Brittonia **12:** 174. 1960. TYPE: Hawaii: Maui: Makena, arid lava flow. 40 ft, 1 Apr 1959, *O. Degener, I. Degener, & W. Fleming 25133* (Holotype, F!; isotypes, BISH!, F[2]!, G!, UC!, W[2]!).

Lipochaeta scabra St. John, Pacific Sci. **30:** 40. 1976. TYPE: Hawaii: Hawaii: *D. Nelson s.n.* (Holotype, BM!).

Suffruticose, stems arcuate-spreading to upright, 0.5–1 m tall. Leaves with narrowly alate margined petioles 9–25 mm long or sessile with connate-perfoliate bases; blades ovate 4–7.3 (–10) cm long, 2.5–5 (–7.2) cm wide, nearly entire to deeply 3–5 divided, terminal segment lanceolate to obovate, entire to pinnatifid, appressed hispidulose on both surfaces. Heads in simple or compound cymes. Outer phyllaries ovate, (2.5–) 3–5.3 mm long, 1.5–2.5 mm wide, acute, appressed hispidulose. Ray florets 7–12; ligules oblong, (5–) 7–10 (–11.5) mm long, 2.3–4.3 mm wide, tube 1.3–2 mm long. Disc florets 20–45 (–55); corollas 2.8–3.5 (–4) mm long, lobes 0.7–1 (–1.2) mm long; anthers 1.3–1.7 mm long. Achenes tuberculate, those of ray 2.2–3.1 mm long, 1.1–2 mm wide, with wings to 0.5 mm, those of disc 2.1–3 mm long, 1–2 mm wide, with wings to 0.5 mm. Pappus of fused scales forming an uneven corona and with awns to 1.5 mm long. Paleae purple near apex.

Known from several localities from central to western Molokai, south-central Maui, and Kahoolawe 30–500 m (Figure 4). Often

found in areas disturbed by erosion or along the margins of and out into "aa" lava flows. Flowering Dec-Jul. Extant, except possibly those from Kahoolawe.

With respect to leaf morphology, *L. rockii* is the most variable species in the genus. Most populations have plants that vary from nearly entire to deeply dissected five-lobed leaves. Occasionally an individual plant even shows this spectrum of variation (*Gardner 406*). The leaf bases also are variable, ranging from petiolate to sessile, and if sessile, then the bases are connate-perfoliate. Generally one finds that the plants in a particular population are either petiolate or they are sessile, but not plants of both types. This geographical separation of morphological types, suggests that with time perhaps additional differences will be accumulated such that distinct varieties might be recognized.

Lipochaeta scabra St. John is placed in synonymy here as it fits within the range of variation of *L. rockii* in all aspects. This early collection of David Nelson does represent a new record for *L. rockii,* previously known only from Molokai and Maui. As stated by St. John (1976b), this population is probably extinct.

Representative specimens. HAWAII. **Maui:** Makena, *Degener & Degener 30313* (A, BISH, G, NY, W); Hwy 31 to Makena, *Gardner 330** (OS); E of Ulupalakua, *Gardner 334** (OS); Hwy 31, 1.1 mi N of Makena, *Gardner 374* (OS); Hwy 31, 5.5 mi SE of Ulupalakua Ranch Office, *Gardner 378* (OS); Mahawao, *Hillebrand & Lydgate 135* (BISH). **Molokai:** Kakaaukuu Gulch, *Degener 22204* (BISH, F, G, MO, NY, UC, US, W); Waiele, *Degener 22207* (BISH, DS, F, G, K, MO, NY, UC, US, W); between airport and Homelani Cemetery, *Degener 22209* (BISH, F, G, K, MO, NY, US, W); Hwy 46, 5 mi W of Jct Hwy 46 and airport road, *Gardner 299A-F*, 399 A & B, 400 A & B* (OS); Kolo Rd, *Gardner 300-D** (OS); Moomomi Beach, *Gardner 301*, 303A* & B** (OS); S of Moomomi Beach, *Gardner 304A-C*, 305** (OS); road up Makakupoia, *Gardner 306*, 307*, 308** (OS); Rd to Kolo Wharf, *Gardner 402, 403, 404, 405* (OS); E of Kaunakakai, *Gardner 406, 407, 408, 409* (OS).

4. **Lipochaeta heterophylla** A. Gray, Proc. Amer. Acad. Arts **5:** 130. 1861. TYPE: Hawaii: Maui: W. Maui, 1838–42, *U.S. Exploring Expedition s.n.* (Holotype, US!).

Lipochaeta lobata (Gaud.) DC. var. *heterophylla* (A. Gray) Hillebrand, Flora Hawaiian Islands. 209. 1888. TYPE: Hawaii: Lanai: 1870, *W. Hillebrand s.n.* (Holotype, B; isotypes, BISH [frag]!, GH!, US!).

Lipochaeta pedunculariis del Castillo, Florae Insularum Maris Pacifici. **72.** *t. 35.* 1888. TYPE: Hawaii: Lanai: 1851–1855, *J. Remy 267* (Holotype, P!).

Lipochaeta heterophylla A. Gray var. *molokaiensis* Sherff, Bot. Gaz. (Crawfordsville) **95:**96. 1933. TYPE: Hawaii: Molokai: W. end, 1910, *J. F. Rock 10287* (Holotype, F!; isotypes, BISH[2]!, GH!, UC!).

Suffruticose, stems arcuate-spreading, 0.5–1 m tall. Leaves sessile, with connate-perfoliate bases; blade narrowly to broadly elliptic, 4.5–6.5 (–9.5) cm long, 2–3.5 (–4.5) cm wide, scarcely serrate, occasionally with 2 basal lobes, on both surfaces appressed hispidulose. Heads in simple cymes. Outer phyllaries ovate 4–6.5 (–10) mm long, 2.5–4 (–4.5) mm wide, broadly acute, appressed hispidulose. Ray florets 8–12; ligules oblong, 8–12 mm long, 2–3.5 (–5) mm wide, tube (1.5–) 2–2.8 (–3.3) mm long. Disc florets (35–) 45–60; corollas (3.4–) 3.6–4.2 mm long, lobes 0.6–1 mm long; anthers (1.5–) 1.7–2 mm long. Achenes tuberculate, those of ray (2.2–) 2.6–3 mm long, 1.3–1.7 mm wide, with wings to 0.5 mm, those of disc (2.5–) 2.7–3.5 (–3.8) mm long, 1.1–1.5 mm wide, with wings to 0.6 mm. Pappus of fused scales forming an uneven corona and with awns to 1.3 mm long. Paleae often purple near apex.

Known from western Maui, Molokai, and numerous localities on Lanai (Figure 4), near sea level to 400 m. On dry open hillsides and along margins of lava flows. Flowering throughout the year. Extant on Lanai, probably extinct on Maui & Molokai.

Based on habit, Sherff (1935) recognized three varieties of this species: one being weak, scarcely erect (var. *heterophylla*), the second, robust, branches stronger (var. *molokaiensis*), and the third intermediate in these features (var. *malvacea*). Between the former two these differences intergrade frequently and make varietal delimitation unwarranted. Comparisons of floral characters show the latter taxon to be indistinguishable from *L. rockii*. *Lipochaeta heterophylla* is most closely related to *L. lobata* from which the former can be distinguished by broadly connate-perfoliate leaf bases.

Representative specimens. HAWAII: **Lanai:** Keomuku, *Degener 21995* (CAS, G, GB, NY, UC); Keomuku Hwy, *Gardner 314*, 315** (OS); near Poaiwa, *Gardner 316A* & B** (OS); Lapaiki Rd, *Gardner 318*, 319** (OS); Awalua Rd, *Gardner 320A & B** (OS); Naupaka Rd, *Gardner 321** (OS); Manele Bay, *Gardner 327A* & B** (OS); Hwy 44, 12 mi NE of Lanai City, *Gardner 386* (OS); Kuahua Gulch, *Degener & Degener 28741* (A, BISH, DS, F, G, MO, NY, UC, W); Point across Puu Pehe, Manele, *Hobdy 57* (BISH).

5. **Lipochaeta lobata** (Gaud.) DC. Prodr. **5:** 611. 1836.

Suffruticose, stems arcuate-spreading to decumbent, 0.5–1.5 m tall. Leaves with narrowly alate margined petioles 2–5 mm long or sessile with narrowly connate-perfoliate bases; blades lanceolate-linear to ovate, 4–9.7 cm long, 1–5.6 cm wide, scarcely serrate to

serrate, occasionally with 2 or 4 basal lobes or with undulate margin, on both surfaces sparsely strigulose. Heads solitary or in 2's or 3's. Outer phyllaries oblong to lanceolate, 4.7–8.2 mm long, 1.7–4.7 mm wide, rounded to long attenuate, sparsely strigulose. Ray florets 8–15; ligules oblong, 7.5–11 mm long, 2.1–4.5 mm wide, tube 1.5–2.2 mm long. Disc florets 20–65; corollas 3.6–4.4 mm long, lobes 0.7–1 mm long; anthers 1.5–2 mm long. Achenes tuberculate, those of ray 2.5–3.2 mm long, 1.1–1.5 mm wide, with wings to 0.4 mm, those of disc 2.8–3.7 mm long, 1–1.3 mm wide, with wings to 0.5 mm. Pappus of fused scales forming an uneven corona and with awns to 1.5 mm long. Paleae purple near apex.

Known from numerous localities on Oahu, and from western Maui and Niihau (Figure 5), near sea level to 900 m. Flowering Oct.-July. All varieties probably extant.

Lipochaeta lobata, as recognized here, consists of three varieties. Variety *lobata* is the most common of the three, being found in the southeast and northwest corners of Oahu, in low coastal dune areas to a few hundred meters elevation, on shrubby, open hillsides. *Lipochaeta niihauensis* St. John, known only from the type specimen, also belongs in this variety.

Variety *leptophylla* is apparently restricted to the Waianae Range of western Oahu, (although certain collections of var. *lobata* from eastern Oahu approach var. *leptophylla*) where it occurs at several hundred meters elevation. It is distinguished by the generally lanceolate leaves, long, narrow phyllaries with attenuate to acuminate-aristate apices, and more numerous disc florets.

Variety *hastulatoides* occurs at middle elevations in the mountains of western Maui. Through this variety a connection between *Lipochaeta heterophylla* and *L. lobata* can be seen. Variety *hastulatoides* can be distinguished from var. *lobata* by the narrowly connate-perfoliate leaf bases, and ovate to oval blades and from var. *leptophylla* by the same characters plus the broad phyllaries.

5a. **Lipochaeta lobata** (Gaud.) DC. var. **lobata**

Lipochaeta lobata (Gaud.) DC. Prodr. **5:** 611. 1836. *Verbesina lobata* Gaud. *In:* L.C.D. de Freycinet (ed.), Voyage Autour de Monde, Botanique **4:** 464. 1829. TYPE: "In insulus Sandwicensibus," *C. Gaudichaud s.n.* (Holotype, P!; isotype, C!). *Lipotriche australis* Less. Linnaea **6:** 510. 1831. *nom.*

superfl., based on type of *Verbesina lobata* Gaud. *Microchaeta lobata* Gaud.) Nutt. Trans. Amer. Philos. Soc. **7**(n.s.): 451. 1841. *Lipochaeta australis* Less. var. *lobata* (Gaud.) A. Gray, Proc. Amer. Acad. Arts **5:** 129. 1861.

Verbesina hastulata Hook. & Arn. Bot. Beechey's Voyage **87.** 1832. TYPE: Hawaii: Oahu: 1826–27, *G. T. Lay & A. Collie s.n.* (Holotype, K!). *Lipochaeta hastulata* (Hook. & Arn.) DC. Prodr. **5:** 611. 1836. *Microchaeta lobata* (Gaud.) Nutt. var. *hastulata* (Hook. & Arn.) Nutt. Trans. Amer. Philos. Soc. **7**(n.s.): 451. 1841. *Lipochaeta lobata* (Gaud.) DC. var. *hastulata* (Hook. & Arn.) Sherff, Bot. Gaz. (Crawfordsville) **95:** 91. 1933.

Lipochaeta calycosa A. Gray, Proc. Amer. Acad. Arts. **5:** 130. 1861. TYPE: Hawaii: Oahu: 1838–42, *U.S. Exploring Expedition s.n.* (Holotype, GH!; isotype, US!).

Lipochaeta australis Less. var. *denticulata* Wawra, Beiträge zur flora der Hawi'schen Inseln **56**(n.s. 31): 77. 1873. TYPE: Hawaii: Oahu: 1868–71, *H. Wawra 2294* (Holotype, W!). *Lipochaeta lobata* (Gaud.) DC. var. *denticulata* (Wawra) Sherff, Bot. Gaz. (Crawfordsville) **95:** 92. 1933.

Lipochaeta aprevalliana del Castillo, Florae Insularum Maris Pacifici **71.** *t. 34.* 1888. TYPE: Hawaii: Oahu: 1851–1855, *J. Remy 272* (Holotype, P, apparently lost. The illustration is taken to be the holotype.). *Lipochaeta lobata* (Gaud.) DC. var. *aprevalliana* (del Castillo) Sherff, Bot. Gaz. (Crawfordsville) **95:** 92. 1933.

Lipochaeta lobata (Gaud.) DC. var. *albescens* Sherff, Bot. Gaz. (Crawfordsville) **95:** 92. 1933. TYPE: Hawaii: Oahu: Diamond Head, 28 Mar 1895, *A. A. Heller 2021* (Holotype, F!; isotypes, A!, GH!, K!, MO!, NY!, UC!, US!).

Lipochaeta niihauensis St. John, Pacific Sci. **13:** 188. 1959. TYPE: Hawaii: Niihau: Kii, among rocks on basalt knoll, 100 ft, 2 Apr 1949, *H. St. John 23664* (Holotype, BISH!).

Lipochaeta trilobata St. John, Pacific Sci. **30:** 42. 1976. TYPE: Hawaii: Hawaii: Mountain slope above Kealakekua, 1779, *D. Nelson s.n.* (Holotype, BM; photo of holotype, OS!).

Leaf blades ovate, 4–5.6 (–9.7) cm long, (1.5–) 2.2–5.6 cm wide, occasionally with 2 or 5 basal lobes or with undulate margin. Outer phyllaries oblong, (4–) 4.7–5.8 (–6.5) mm long; 2.3–4.7 mm wide, broadly acute to rounded. Ray florets 7.5–10 mm long. Disc florets 20–25.

Common around Kaena Pt and from Koko Head to Makapuu Pt on Oahu and at Kii on Niihau (Figure 5), near sea level to 100 m. Flowering Dec-Jul. Extant.

Lipochaeta trilobata St. John is placed in synonymy here as it falls within the range of variation of *L. lobata* var. *lobata*. St. John's type, collected by David Nelson, extends considerably the distribu-

tion of this variety, although it is doubtful that the population from which this collection was taken is extant.

Representative specimens. HAWAII. **Oahu:** Kaena Pt, *Degener 4177b* (BISH, DS, F, G, GB, GH, K, MO, NY, UC, US, W); S side of Manakuli Valley, *Degener, et al. 20836* (F, K, NY, US, W); Diamond Head Crater, *Fosberg 13884* (BISH, DS, F, GH); near Makapuu Pt, *Gardner 278** (OS); Kaena Pt, *Gardner 279A* & B*, 280*, 281*, 346, 347* (OS); 0.2 mi from Diamond Head Rd on rd into crater, *Gardner 341* (OS); Hwy 72, 0.8 mi N of Hawaii-Kai Golf Course, *Gardner 350* (OS); Hwy 72, 0.7 mi N of Hawaii-Kai Golf Course, *Gardner 351* (OS).

5b. **Lipochaeta lobata** (Gaud.) DC. var. **hastulatoides** Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 93. 1933. TYPE: Hawaii: Maui: Pohakea Gulch, southernmost part of western Maui, 11 Jul 1927, *O. Degener 4305* (Lectotype chosen, F!; isotypes, F!, G!, GH!, K!, NY[2]!).

Leaf bases scarcely connate-perfoliate, blades ovate to oval, 3–6 cm long, 2–2.6 cm wide. Outer phyllaries ovate, 4.6–5.5 mm long, 3.1–4 mm wide, broadly acute to rounded. Ray florets 8.7–10.5 mm long. Disc florets 35–40. Chromosome number, unknown.

Known only from the mountains of Western Maui (Figure 5) to 700 m. Flowering Dec-Mar. Probably extant.

Representative specimens. HAWAII. **Maui:** Mauka of McGregor, *Degener 22034* (BISH, G, GB, NY, UC, US, W); Hanaula Rd, 1972, *Hobdy s.n.* (US); Lahainaluna, Kuia Ridge, *Pearsall 26* (BISH).

5c. **Lipochaeta lobata** (Gaud.) DC. var. **leptophylla** Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville), **95:** 92. 1933. TYPE: Hawaii: Oahu: Kolekole Pass, Waianae Mountains, 1–2 Feb 1915, *C. N. Forbes 2024-O* (Holotype, F!; isotypes, BISH! F[2]!, K!, NY!, UC!).

Lipochaeta lobata (Gaud.) DC. var. *grossedentata* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville), **95:** 92. 1933. TYPE: Hawaii: Oahu: N of middle ridge between Puu Pane and Puu Kanaohanui, 10 Jun 1932, *O. Degener, K. K. Park, & W. Bush 4299* (Lectotype chosen, F!; isotypes, F!, K!).

Leaf blades lanceolate to lanceolate-linear, 5.7–7 cm long, 1–1.5 (–2.4) cm wide. Outer phyllaries ovate to lanceolate, 5–8.2 mm long, 1–3 mm wide, long attenuate to acuminate-aristate. Ray florets 10–11 mm long. Disc florets (20–) 30–60. Chromosome number, unknown.

Known from the Waianae Range of Western Oahu (Figure 5), to 600 m. Flowering Oct-Jun. Probably extant.

Representative specimens. HAWAII. **Oahu:** NE of Puu Hapapa summit, *Degener & Hatheway 20976* (BISH); NE slope of Puu Hapapa, *Degener, et al. 12287* (A, F, G, GH, MO, NY, US).

6. **Lipochaeta connata** (Gaud.) DC. Prodr. **5:** 611. 1836.

Suffruticose, stems upright, 1–2 m tall. Leaves with alate margined petioles 6–30 mm long or sessile with connate-perfoliate bases; blades ovate to broadly elliptic, 8–19 cm long, 4–9.5 cm wide, on both surfaces strigulose. Heads in compound cymes. Outer phyllaries lanceolate to ovate, 3.5–6.5 mm long, 1.3–2.8 mm wide, attenuate to acute, usually purple near apex, strigulose. Ray florets 8–16; ligules oblong, 5–13 mm long, 2.3–4.8 mm wide, tube 1–2.4 mm long. Disc florets 20–45; corollas 3–5 mm long, lobes 0.8–1.3 mm long; anthers 1.4–1.8 mm long. Achenes tuberculate, those of ray 2.1–3 mm long, 1.1–1.7 mm wide, with wings to 0.5 mm, those of disc 2.5–3.3 mm long, 1–1.7 mm wide, with wings to 0.5 mm. Pappus of fused scales forming a corona or variously reduced and with awns to 1.6 mm long. Paleae usually purple near apex.

Known from several localities in the mountains and valleys of central, western, and northern Kauai, and from a few collections on western Maui (Figure 6), 50–710 m. Over a broad range of habitats from dry, open slopes to the margins of forested areas. Flowering throughout the year. Extant.

Lipochaeta connata represents a continuum of variation with respect to leaf morphology. Variety *acris* has narrowly alate margined petioles, with long narrow phyllaries, narrow ligules, generally more disc florets and longer lobes of the disc corollas. Variety *connata* has sessile leaves with connate-perfoliate leaf bases and shows considerable variation with respect to the amount of leaf material produced at the nodes, with leaf bases ranging from 5–50 mm wide at point of attachment to the stem. From observations on plants grown in the greenhouse, it has been shown that there is a gradual increase in the amount of leaf material produced at a node as the plant matures.

Most of the collections in this complex show various stages in the development of a corona on the achenes. Particularly striking are plants of var. *acris* in the Polihale Ridge-Hikimoe Valley region and also in the Hanakapiai area along the Kalalau Trail. In these specimens a well developed corona (in excess of 1 mm long) can be seen. From this extreme a reduction series has been observed, finally

resulting in a few uneven scales around apex of the achene in var. *connata*.

6a. **Lipochaeta connata** (Gaud.) DC. var. **connata**

Lipochaeta connata (Gaud.) DC. Prodr. **5**: 611. 1836. *Verbesina connata* Gaud. *In:* L.C.D. de Freycinet (ed.), Voyage Autour de Monde, Botanique **4**: 464. 1829. TYPE: "In insulis Sandwicensibus," *C. Gaudichaud s.n.* (Holotype, P!). *Microchaeta connata* (Gaud.) Nutt. Amer. Philos. Soc. **7**(n.s.): 452. 1841.

Lipochaeta alata Sherff, Bot. Gaz. (Crawfordsville) **95**: 81. 1933. TYPE: Hawaii: Kauai: along Hanapepe River, near the Falls, 12 Jul 1895, *A. A. Heller 2563* (Holotype, F!; isotype, UC!).

Lipochaeta alata Sherff var. *acrior* Sherff, Bot. Gaz. (Crawfordsville) **95**: 82. 1933. TYPE: Hawaii: Kauai: 1840, *U.S. Exploring Expedition, s.n.* (Holotype, US!; isotype, GH!).

Lipochaeta alta Sherff var. *pulcrior* Sherff, nom. nud.

Lipochaeta profusa Sherff, Bot. Gaz. (Crawfordsville) **95**: 95. 1933. TYPE: Hawaii: [No island] Jan 1885, *Sinclair s.n.* (Holotype, K!).

Lipochaeta profusa Sherff var. *robustior* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95**: 96. 1933. TYPE: Hawaii: Kauai: 2 mi from Kekaha, in lowlands, 18 Jul 1932, *O. Swezey 4185* (Holotype, F!; isotype, K!).

Leaves sessile, with connate-perfoliate bases. Outer phyllaries ovate, with acute apices. Disc florets 20–30; corolla lobes 0.8–1 mm long.

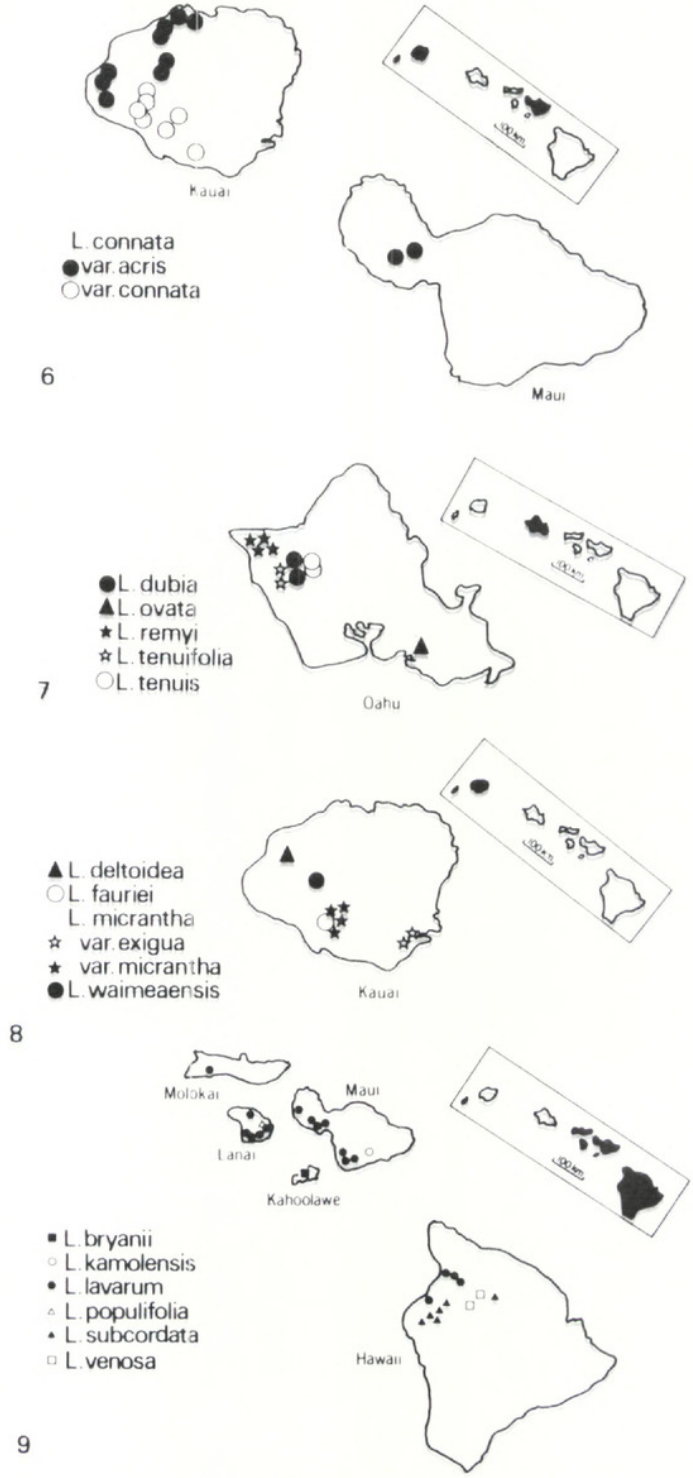
Common in the foothills of western Kauai (Figure 6), 70 to 400 m. Flowering Sep-Jul. Extant.

Representative specimens. HAWAII: **Kauai:** Waipao Valley, *Degener 20514* (BISH, GB, GH, NY); Waimea, *Faurie 1006, 1007* (A, G); Lawai Valley, *Gardner 294** (OS); N of Waimea, *Gardner 296** (OS); Hwy 55, N of Kekaha, *Gardner 359, 360A & B* (OS); Waimea Canyon Rim, 3 mi S of Jct Hwy 55, *Gardner 369* (OS); Kukui Trail, Waimea Canyon, *Gardner 370* (OS); Hanapepe River, near falls, *Heller 2563A* (F, G); by Waimea Canyon Rim Lookout, *Hobdy 39* (BISH); Olokele Canyon, *Skottsberg 1041* (BISH, GB).

6b. **Lipochaeta connata** (Gaud.) DC. var. **acris** (Sherff) Gardner, comb. et stat. nov.

Lipochaeta acris Sherff, Bot. Gaz. (Crawfordsville) **95**: 83. 1933. TYPE: Hawaii: Kauai: Waimea, 2000–3000 ft. *Mann & Brigham 540* (Holotype, F!; isotypes, BISH!, G!, GH[2]!, MO!, NY!).

Lipochaeta lobata (Gaud.) DC. var. *incisor* St. John, Pacific Sci. **13**: 185. 1959. TYPE: Hawaii: Niihau: Kaaliwai, in thicket, 750 ft, 1–1.5 m tall, 29 Mar 1949, *H. St. John 23572* (Holotype, not located; isotype, BISH!).



Figures 6–9. **Documented distributions of *Lipochaeta*.** 6. *L. connata* var. *acris* and var. *connata*. 7. *L. dubia*, *L. ovata*, *L. remyi*, *L. tenuifolia*, and *L. tenuis*. 8. *L. deltoidea*, *L. fauriei*, *L. micrantha* var. *exigua*, and var. *micrantha*, and *L. waimeaensis*. 9. *L. bryanii*, *L. kamolensis*, *L. lavarum*, *L. populiflolia*, *L. subcordata*, and *L. venosa*.

Leaves with alate margined petioles 6–30 mm long. Outer phyllaries lanceolate to ovate, with attenuate apices. Disc florets 25–45; corolla lobes 1–1.3 mm long.

Found along the northern and western valleys of Kauai, south central Kauai, Niihau, and western Maui (Figure 6), 20–400 m. Flowering throughout the year. Extant.

Representative specimens. HAWAII. **Kauai:** Kokee Stream between YMCA Camp & Waipoo Falls, *Degener 21489* (BISH, F, C, K, NY, UC, US, W); 100 ft E of Kalalau lookout (Kilohana), *Degener & Hatheway 20505* (BISH, NY); Haena-Kalalau Trail, *Gardner 286, 287*, 288* (OS); Waikapalae Wet Cave, *Gardner 291** (OS); Maniniholo Dry Cave, *Gardner 292** (OS); Polihale Ridge, *Gardner 364** (OS); Hikimoe Valley, *Gardner 365, 366** (OS); Waikapalae Wet Cave, *Gardner 371* (OS); Halemanu Stream near brink of Waimea Canyon, *Greenwell 21539* (F); Kaaweiki, *Hobdy 94* (US); Hanakapiai Valley *Hobdy 221* (US); **Maui:** Waliluku, Black Gorge, *Degener & Degener 23736* (BISH, NY, US, W); Olowalu Valley, *Forbes 2431-M* (NY); Olowalu Valley, ridge above Wailuku Poi, *Forbes 2451-M* (BISH, F); Black Gorge, *Gardner 376** (OS); W Maui, no date, *U.S. Exploring Expedition s.n.* (US); no locality, 1868–1871, *Wawra 2094* (W).

LIPOCHAETA SECTION **APHANOPAPPUS** (Endl.) Bentham and Hooker

Lipochaeta DC. section *Aphanopappus* (Endl.) Bentham and Hooker, Gen. Plantarum **2:** 372. 1873. *Aphanopappus* Endl. Gen. Plantarum Suppl. **2:** 43. 1842. *nom. nov.*, based on *Schizophyllum micranthum* Nutt.

Schizophyllum Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 452. 1841. *nom. illegit.* non Fries. 1831. TYPE SPECIES: *Schizophyllum micranthum* Nutt. = *Lipochaeta micrantha* (Nutt.) A. Gray.

Leaves petiolate (rarely alate margined). Majority of disc florets five-merous. Chromosome number, n = 15. Species numbers 7–23.

7. **Lipochaeta tenuifolia** A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. TYPE: Hawaii: Oahu: 1838–42, *U.S. Exploring Expedition s.n.* (Lectotype chosen, GH!; frag of holotype, BISH!).

Suffruticose, stems decumbent and rooting along lower surface, stem length unknown. Leaves sessile, ternately compound, leaflets 3–8.5 cm long, 1–3 cm wide, deeply dissected, ultimate divisions usually cut clear to midrib, sparsely strigulose. Heads solitary or 2. Outer phyllaries lanceolate, 5–7.5 mm long, 1–1.8 mm wide, attenuate, strigulose. Ray florets 8–10; ligules oblong, 8–11.5 mm long, 2.7–3.9 mm wide, tube 0.7–1 mm long. Disc florets 20–30;

corollas 2.7–3 mm long, lobes 0.7–0.9 mm long; anthers 1.3–1.5 mm long. Achenes tuberculate, those of ray 1.8–2.6 mm long, 1.2–1.5 mm wide, with wings to 0.3 mm, those of disc 1.8–2.4 mm long, 1.1–1.5 mm wide, with wings to 0.2 mm. Pappus of deciduous awns to 1 mm long. Paleae tan throughout.

Known from the central portion of the Waianae range, Oahu (Figure 7), 700–900 m. Flowering May. Extant.

Lipochaeta tenuifolia is most similar to *L. dubia* and *L. tenuis* from which the former can be distinguished by ternately compound, finely dissected leaves. *Lipochaeta tenuifolia* is the only member of the genus that has truly compound leaves. From studies of plants grown in the greenhouse, it has been shown, however, that if branches are cut back the leaves that develop first are not compound, but rather range from nearly entire to dissected.

Representative specimens. HAWAII. **Oahu:** Upper Makua Valley, *Degener, et al. 4174* (BISH, CAS, DS, F, G, GB, GH, K, MO, NY, UC, US, W); Makaha, *Gagne 640* (US); Makaha, Waianae, no date, *Hillebrand & Lydgate s.n.* (BISH); Kaala Mts, *Mann & Brigham 534* (BISH, F, G, GH, MO, NY, US).

8. **Lipochaeta dubia** Degener & Sherff *In:* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 580. 1939. TYPE: Hawaii: Oahu: NE slope of Puu Hapapa, among lantana and grasses, 7 May 1939, *O. Degener, E. Ordonez, & J. Foster 12331* (Holotype, F!; isotypes, A[2]!, F[2]!, GB! GH! MO!, NY! US!).

Lipochaeta minuscula Degener & Sherff *In:* Sherff, Bot. Leafl. No. **9:** 9. 1954. TYPE: Hawaii: Oahu: ridge N of Kolekole Pass, 15 Jun 1947, *M. Kerr 21660* (Lectotype chosen, BISH!).

Suffruticose, stems decumbent and probably rooting along lower surface, length unknown. Leaves with petioles 8–12 mm long, overall shape deltoid, but most leaves with 2 or 4 basal lobes and a long spatulate terminal segment; blades 2.4–4.4 cm long, 1–2.1 cm wide, entire to serrate, strigulose above, densely so below. Heads solitary or occasionally 2. Outer phyllaries lanceolate, 4.5–5.1 mm long, 1.2–2.1 mm wide, attenuate, strigulose. Ray florets 8–10; ligules oblong, 8.3–12 mm long, 3.5–4.3 mm wide, tube 1–1.2 mm long. Disc florets 30–45; corollas 3.2–3.4 mm long, lobes 0.8 mm long; anthers 1.5–1.7 mm long. Achenes tuberculate, those of ray 2.2–2.5 mm long, 1.7–1.9 mm wide, with wings to 0.3 mm, those of disc 2.3–2.6 mm long, 1.2–1.4 mm wide, with wings to 0.2 mm.

Pappus of deciduous awns to 1.4 mm long. Paleae often purple near apex. Chromosome number unknown.

Known from the central portion of the Waianae Range, Oahu (Figure 7). 700–900 m. Apparently on open slopes with lantana and grasses. Flowering Apr-Jun. Probably extant.

Lipochaeta dubia is most similar to *L. tenuis* with respect to floral features but can be distinguished by the basally lobed leaves of the former. *Lipochaeta minuscula* was collected in the same general vicinity as *L. dubia* and except for having leaves which are slightly smaller than most specimens of *L. dubia,* it is indistinguishable.

Representative specimens. HAWAII. **Oahu:** NE slope of Puu Hapapa, *Degener, et al. 12285* (A, F, G, MO, NY, UC, US), *12287* (F, G, NY, UC, US), *12290* (F, G, GH, NY, UC).

9. **Lipochaeta tenuis** Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfrodsville) **95:** 102. 1933. TYPE: Hawaii: Oahu: in the rain forest, Waianae Valley, up toward Puu Kaala, on lateral spur leading to summit ridge between Kaala and Kalena, 24 Apr 1932, *O. Degener, K. K. Park, & W. Bush 4258* (Lectotype chosen, F!; isotypes, F!, K!, MO!, NY!).

Lipochaeta tenuis Degener & Sherff var. *sellingii* Degerer & Sherff *In:* Flora Hawaiiensis, Fam. 344:Lip: Ten. 1940. TYPE: Hawaii: Oahu: NE slope of Puu Hapapa, in sunny stream-bed near contour trail, 3 Sep 1938, *O. Degener, O. H. Selling & E. Ordonez 12253* (Holotype, GB; isotypes, BISH!, F!, G!, MO!, NY!).

Suffruticose, stems decumbent, probably rooting along lower surface, stem length unknown. Leaves with petioles 8–17 mm long, ovate, 2.2–3.9 cm long, 1–1.9 cm wide, serrate, on both surfaces strigulose, most densely so below. Heads solitary or in 2's or 3's. Outer phyllaries lanceolate, 5–6.8 mm long, 1.1–2.2 mm wide, attenuate, strigulose. Ray florets 8–12; ligules oblong, 8.8–11.5 mm long, 3–4.5 mm wide, tube 1.1–1.4 mm long. Disc florets 40–60; corollas 3.2–3.5 mm long, lobe 0.7–1 mm long; anthers 1.3–1.4 mm long. Achenes tuberculate, those of ray 2.5–3 mm long, 1.5–2 mm wide, with wings to 0.3 mm, those of disc 2.5 mm long, 1.5 mm wide, with wings to 0.3 mm. Pappus of deciduous awns to 1.4 mm long. Paleae often purple at apex. Chromosome number unknown.

Known from the central portion of the Waianae range, Oahu (Figure 7), 700–900 m. Flowering Apr.-Sep. Probably extant.

Lipochaeta tenuis is most similar to *L. dubia.* The former is

distinguished by unlobed leaves. The two varieties of *L. tenuis* of Degener and Sherff (1940) are identical except for minor differences in size of plant which are not here accorded formal recognition.

Representative specimens. HAWAII. **Oahu:** 0.75 mi S of Kolekole Pass, *Cranwell, et al. 3336* (GB); NE slope of Puu Hapapa, *Degener, et al. 12288* (A, BISH, F, G, GH, MO, NY, US), *12291* (BISH, F, GH, MO, NY, US), *12332* (BISH, F, G, K).

10. **Lipochaeta remyi** A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. TYPE: Hawaii: Oahu: 1851–1855, *J. Remy 260* (Holotype, GH!; frag of holotype, BISH!).

Annual herb, stems upright, 50–60 cm tall. Leaves with petioles (6–) 20–40 mm long, overall shape ovate, (1.3–) 3.4–7 cm long, (1–) 2.6–5 cm wide, dissected, ranging from cleft with scarcely noticable basal lobes to lobes which are cut clear to the midrib, on both surfaces strigulose. Heads solitary or in 2's or 3's. Outer phyllaries lanceolate, 3.5–5.3 (–7) mm long, 1.2–1.8 (–2.2) mm wide, attenuate, often purple near base, strigulose. Ray florets 5–8; ligules oval, 3–5 mm long, 1.7–3.5 (–4.2) mm wide, tube 0.6–1 mm long. Disc florets 20–30 (–35); corollas 2.5–2.9 mm long, lobes 0.3–0.5 mm long; anthers 1.2–1.4 mm long. Achenes tuberculate, those of ray 1.9–2.3 mm long, 1.1–1.6 mm wide, with wings to 0.3 mm, those of disc 1.9–2.4 mm long, 1–1.4 mm wide, with wings to 0.3 mm. Pappus of deciduous awns to 1.3 mm long. Paleae often purple near apex.

Known from numerous localities in the Waianae Range of northwestern Oahu (Figure 7), 30–200 m. Moist, often spring-fed hillsides, in the forest understory. Flowering Dec.-Jun. Extant.

Lipochaeta remyi is most closely related to *L. micrantha* of Kauai, from which the former can be distinguished by the annual, herbaceous growth habit and more numerous disc florets.

Representative specimens. HAWAII. **Oahu:** Kealia Trail, Kawaihapai, *Carlson 3828* (F); Kawaihapai, *Degener 18078* (GH, MO, NY, US); CCC Trail, Kawaihapai, *Degener, et al. 11032* (BISH, CAS, F, G, GH, MO, NY, US); Kawaihapai, *Forbes, et al. 1840-O* (BISH, F, NY, W); Kealia, Waianae Mts, *Fosberg & Fosberg 12859* (BISH, DS, F, GB, GH, UC); Kealia, *Gagne 647* (US); Kealia Trail, S of Dillingham Airstrip, *Gardner 349** (OS); Kealia, Waianae Mts, *Hosaka 1328* (BISH); Kaala Mts, *Mann & Brigham 533* (BISH, GH, MO, NY, US); Kaena Pt, *Pearsall 84* (BISH).

11. **Lipochaeta ovata** R. C. Gardner, sp. nov. Figure 10.

TYPUS: Hawaii: Oahu: Honolulu, 1852, *N. J. Anderson s.n.* (Holotype, GB!, photo of holotype, OS!).

Plantae suffruticosae; caules apparenter erecti, altitudines ignotae. Folia petiolis usque ad 21 mm longis, ovata usque elliptica, 7.5 cm longa, 3.3 cm lata, vix serrata, strigulosa apprime subtus et secus venas. Capitula cymis disposita. Phyllaria externa ovata, 2.3 mm longa, 2.8 mm lata, obtusa, strigulosa. Flosculi radii 7 vel 8; ligulae oblongae, 7 mm longae, 2.8 latae; tubi 1.2 mm longi. Flosculi disci circa 30; corollae 4.3 mm longae, lobis 0.8 mm longis; antherae 2.1 mm longae. Achenia laevia; achenia radii 2.2 mm longa, 1.7 mm lata, sine alis; achenia disci 2.4 mm longa, 1.6 mm lata, sine alis. Pappus ex aristis deciduis usque ad 0.4 mm longis compositis. Paleae penitus brunneolae. Chromosomatum numerus ignotus.

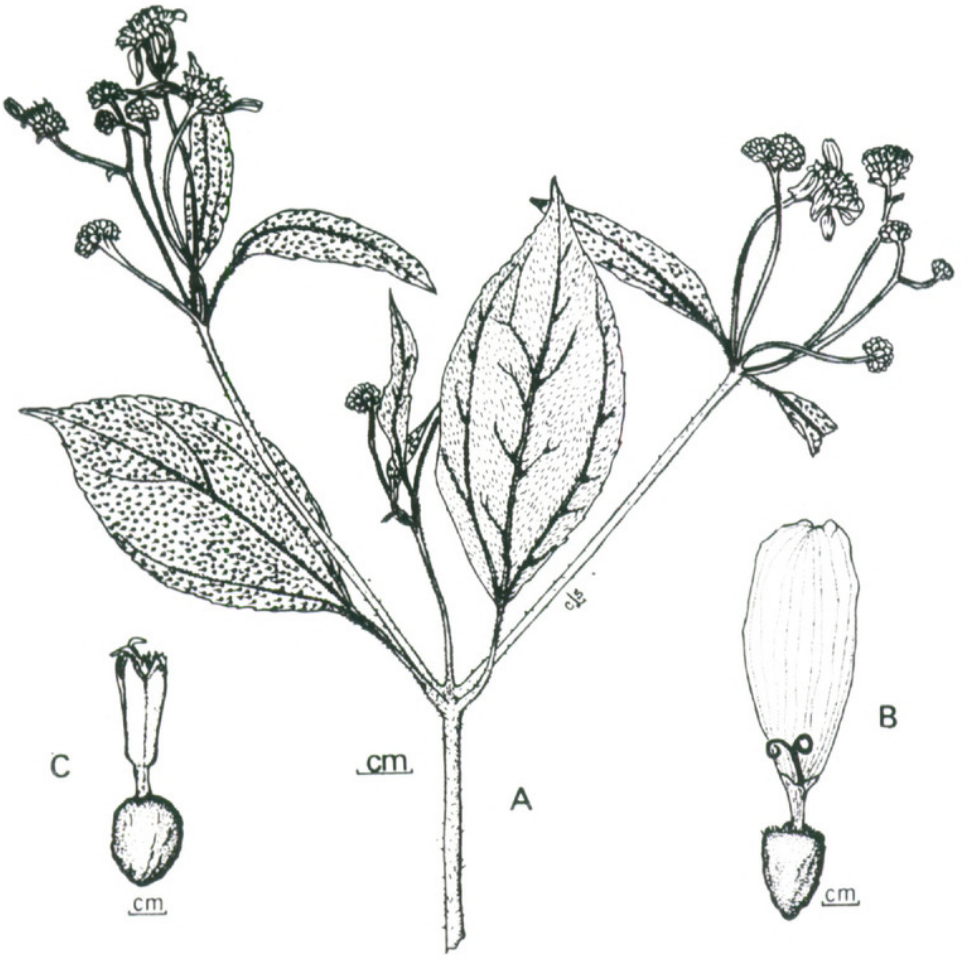


Figure 10. **Holotype of *Lipochaeta ovata*.** A, habit; B, ray floret and achene; C, disc floret and achene.

Known only from the type specimen, collected at Honolulu, Oahu (Figure 7). Habitat and flowering period unknown. Probably extinct.

Lipochaeta ovata is one of the least specialized members of this section. It is distinguished by its large leaves, compound cymose inflorescences, upright habit, and smooth achenes.

12. **Lipochaeta waimeaensis** St. John, Pacific Sci. **26:** 293. 1972. TYPE: Hawaii: Kauai: Waimea Canyon, upper slope of W side, 1200 ft, 17 Apr 1967, *R. W. Hobdy 101* (Holotype, BISH!).

Suffruticose, stems decumbent and rooting along lower surface, to 2 m long. Leaves with petioles 5–8 mm long, linear to narrowly elliptic, 4.7–5 cm long, 0.5–0.8 cm wide scarcely serrate, strigulose along major veins above, evenly strigulose below. Heads solitary or in 2's or 3's. Outer phyllaries lanceolate, 3–4 mm long, 1.5–2 mm wide, attenuate, often with the lower quarter purple, strigulose. Ray florets 4 or 5; ligules nearly oval, 3.2–3.5 mm long, 2.8–2.9 mm wide, tube 0.6–0.8 mm long. Disc florets 20–25; corollas 2.3–2.8 mm long, lobes 0.8–0.9 mm long; anthers 1.2–1.4 mm long. Achenes tuberculate, those of ray 2.2–2.5 mm long, 1.7–2.3 mm wide, with wings to 0.2 mm, those of disc 2.2–2.4 mm long, 1.2–1.6 mm wide, with wings to 0.1 mm. Pappus of scales fused at the base and with deciduous awns to 1 mm long. Paleae often purple near apex.

Known only from the type locality on the upper slope, west side of Waimea Canyon, Kauai (Figure 8), 350–400 m. Flowering Feb.-Apr. Extant.

Lipochaeta waimeaensis is most similar to *L. deltoidea* from which the former can be distinguished by fewer and smaller ray and disc florets and linear or narrowly elliptic leaves.

Representative specimens. HAWAII. **Kauai:** Waimea Canyon Rim, 3 mi S of Jct with Hwy 55, *Gardner 368** (OS); Waimea Heights Rd, *Hobdy 170* (US).

13. **Lipochaeta deltoidea** St. John, Pacific Sci. **26:** 291. 1972. TYPE: Hawaii: Kauai: lower Hikimoe Valley, 1800 ft, 18 Apr 1969, *R. W. Hobdy 102* (Lectotype chosen, BISH!; isotype BISH!).

Suffruticose, stems upright, to 40 cm tall. Leaves with petioles to 11 mm long, narrowly deltoid, 8.4 cm long, 4 cm wide, biserrate, on both surfaces strigulose. Heads in 2's or 3's. Outer phyllaries lanceolate, 4.8 mm long, 1.5 mm wide, attenuate, strigulose. Ray

florets about 7; ligules oblong, 5.9 mm long, 3.4 mm wide, tube 1 mm long. Disc florets about 35; corollas 3.3 mm long, lobes 1.3 mm long; anthers 1.5 mm long. Achenes tuberculate, those of ray 2.5 mm long, 2 mm wide, with wings to 0.4 mm, those of disc 2.5 mm long, 1.5 mm wide, with wings to 0.2 mm. Pappus of numerous deciduous awns to 1.3 mm long. Paleae often purple near apex. Chromosome number unknown.

Known only from type locality, ca. 600 m, Hikimoe Valley, Kauai (Figure 8). Flowering Apr. Extant.

Lipochaeta deltoidea is an unspecialized member of the genus, and as mentioned previously, has characters in common with most of the taxa of group B (Figure 2). Because of this similarity, a form similar to *L. deltoidea* is considered to be ancestral to the Lipochaetas of this group.

14. **Lipochaeta fauriei** Léveillé, Repert. Spec. Nov. Regni Veg. **10:** 122. TYPE: Hawaii: Kauai: Holokele [Olokele?], Mar 1910, *A. U. Faurie 1012* (Holotype, not located; isotype, P!).

Suffruticose, stems apparently upright, height unknown. Leaves with alate margined petioles to 6 mm long; blades lanceolate, 7 cm long, 3 cm wide, serrate, sparsely strigulose. Heads in 2's or 3's. Outer phyllaries ovate, 4.5 mm long, 2.3 mm wide, acute, purple near base, strigulose. Ray florets about 6; ligules oblong, 4.2 mm long, 2.3 mm wide, tube 1.3 mm long. Disc florets about 30; corollas 3.9 mm long, lobes 0.8 mm long; anthers 1.8 mm long. Achenes unknown. Pappus unknown. Paleae tan throughout. Chromosome number unknown.

Known only from type collections gathered at Holokele, this taken to mean Olokele Canyon (Figure 8), south central Kauai. Habitat unknown. Flowering Mar. Probably extinct.

Lipochaeta fauriei is most similar to *L. deltoidea* from which the former can be distinguished by ovate phyllaries, smaller ray ligules and larger disc corollas.

15. **Lipochaeta micrantha** (Nutt.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861.

Suffruticose, stems decumbent and rooting along lower surface, to 2 m long. Leaves with petioles 8–22 mm long, overall shape deltoid, 2.1–9.7 cm long, 1.2–7.8 cm wide, entire to variously

dissected, sparsely strigulose. Heads in 2's or 3's. Outer phyllaries ovate to lanceolate, 3.2–5.5 mm long, 1–3 mm wide, attenuate, often purple near base and along midrib, sparsely strigulose. Ray florets 4 or 5; ligules oval to oblong, 2.3–5.8 mm long, 1.4–3.5 mm wide, tube 0.7–1.4 mm long. Disc florets 5–9; corollas 2.7–3.1 mm long, lobes 0.4–0.7 mm long; anthers 1.2–1.5 mm long. Achenes tuberculate, those of ray 2.1–2.9 mm long, 1.5–1.8 mm wide, occasionally with wings to 0.2 mm, those of disc 2.2–2.6 mm long, 1–1.3 mm wide, without wings. Pappus of scales forming an uneven corona and with deciduous awns to 1.4 mm long. Paleae often purple near apex.

Two varieties are recognized here within *Lipochaeta micrantha.*

15a. **Lipochaeta micrantha** (Nutt.) A. Gray var. **micrantha**

Lipochaeta micrantha (Nutt.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. *Schizophyllum micranthum* Nutt. Trans. Amer. Philos. Soc. **7** (n.s.): 452. 1841. TYPE: Hawaii: Atooi [Kauai]: In shady woods near Kolao [Koloa], *T. Nuttall s.n.* (Holotype, BM!). *Aphanopappus nuttallii* Walpers, Repertorium Botanices Systematicae **2:** 620. 1843. *nom. superfl.*, based on type of *Schizophyllum micranthus* Nutt. *Aphanopappus micranthus* (Nutt.) Heller, Minnesota Bot. Stud. **1:** 915. 1897.

Leaves 2.1–9.7 cm long, 1.2–7.8 cm wide, dissected, ranging from incised or cleft to pinnate-pinnatifid. Ray ligules oval to ovate, 2.7–5.8 mm long, 1.7–3.5 mm wide, tube 0.9–1.4 mm long. Ray achenes 2.3–2.9 mm long, 1.6–1.8 mm wide, with wings to 0.5 mm. Disc achenes 2.5–2.6 mm long, 1.3 mm wide, without wings. Chromosome number, unknown.

Variety *micrantha* is known from several localities in Olokele and Hanapepe Valleys (Figure 8), south central Kauai, apparently in forest understory, and along canyon sides. Flowering June-Oct. Extant (John Fay, pers. comm.).

Representative specimens. HAWAII. **Kauai:** Olokele Canyon, *Degener & Wiebke 2143* (F, G, GB, GH, MO, NY, UC, US, W); Olokele Canyon, *Degener & Wiebke 2144* (F, GH, NY); Hanapepe Valley, *Forbes 304-K* (BISH, F); Hanapepe River, near falls, *Heller 2439* (F, GH, K, MO, NY, UC, US); Olokele Gulch, *Hitchcock 15239, 15244* (US); Hanapepe, *Mann & Brigham 536* (BISH, F, G, GH, MO, NY); no locality, Oct 1916, *Rock s.n.* (BISH); Olokele Canyon, *Skottsberg 1035* (BISH, GB); Koloa, no date, *U.S. Exploring Expedition s.n.* (NY); Olokele Canyon, Jul 1927, *Winne s.n.* (BISH).

15b. **Lipochaeta micrantha** (Nutt.) A. Gray var. **exigua** (Degener & Sherff) Gardner, comb. et stat. nov.

Lipochaeta exigua Degener & Sherff *In:* Sherff, Amer. J. Bot. **28:** 30. 1941. TYPE: Hawaii: Kauai: Grassy shrubby summit ridge, 0.71 mi SW of Ho-

kunui, Nawiliwili, 8 Jan 1940, *O. Degener & E. Ordonez 12610* (Lectotype chosen, F!; isotypes, B!, F[2]!, G!, GH!, MO[2]!, NY[3], UC[3]!, US[2]!).

Leaves to 3.1 cm long, 2.2 cm wide, many with 2 or 4 basal lobes, these occasionally cut clear to midrib, terminal segment elliptic. Ray ligules oblong, 2.3 mm long, 1.4 mm wide, tube 0.7 mm long. Ray achenes 2.1 mm long, 1.5 mm wide, without wings. Disc achenes 2.2 mm long, 1 mm wide, with wings to 0.2 mm.

Variety *exigua* is known from a few localities in the Haupu range of southeastern Kauai (Figure 8), 300–400 m, in grass and shrub areas. Flowering Jan.-July. Extant (John Fay, pers. comm.).

16. **Lipochaeta subcordata** A. Gray, Proc. Amer. Acad. Arts **5:** 130. 1861. TYPE: Hawaii: Hawaii: 1840, *U.S. Exploring Expedition s.n.* (Holotype, US, not located).

Lipochaeta flexuosa del Castillo, Florae insularum Maris Pacifici, **72.** *t. 35.* 1886. TYPE: Hawaii: Hawaii: 1851–1855, *J. Remy 265* (Holotype, P!).

Lipochaeta intermedia Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 102. 1933. TYPE: Hawaii: Hawaii: Huehue, Kona District, among lava, May 1932, *Meebold 4254* (Holotype, F!; frag of holotype, G!).

Suffruticose, stems upright to 3 m tall. Leaves with petioles 12–25 mm long, deltoid, (3.2–) 5–10 cm long, (2.4–) 3–4.8 cm wide, occasionally with 2 basal lobes, terminal segment cleft to biserrate, sparsely strigulose above, densely so below. Heads in compound cymes. Outer phyllaries ovate, 3.2–6 mm long, 1.5–2.3 mm wide, narrowly acuminate, often purple along midrib, strigulose. Ray florets 5–7; ligules oblong, (3–) 4–6.3 mm long, 2–3.8 mm wide, tube 0.7–1 mm long. Disc florets 11–20; corollas 2.5–3.4 mm long, lobes 0.5–0.9 mm long; anthers 1.1–1.5 mm long. Achenes tuberculate, often spotted with purple, and with a fringe of scales on upper outer rim, those of ray 1.9–2.5 mm long, 1.5–2 mm wide, with wings to 0.3 mm, those of disc 2.1–2.8 mm long, 1.1–1.7 mm wide, with wings to 0.2 mm. Pappus of scales forming an uneven corona and with deciduous awns to 1.5 mm long. Paleae often purple near apex.

Known from several localities on Hawaii, but mainly in the North Kona District (Figure 9), 600–1500 m. Flowering throughout the year. Extant.

Lipochaeta subcordata is most similar to *L. venosa* from which the former can be distinguished by the much larger, usually unlobed

leaves, greater number of flower heads, and fewer disc florets. The taxa included in synonymy are minor variants, *L. flexuosa* having slightly more divided leaves and *L. intermedia* having slightly smaller leaves than typical. *Lipochaeta intermedia* is intermediate between *L. subcordata* and *L. lavarum* in vegetative features and is possibly of hybrid origin, however, pollen stainability (in lacto-phenol-analine blue) is 90 per cent and several full achenes are on the specimens.

Representative specimens. HAWAII. **Hawaii:** between Puuwaawaa & Huehue, *Degener 4214* (F, G, GB, GH, K, MO, NY, US, UC, W); Huehue, *Degener 21816* (BISH, CAS, G, GB, MO, NY, UC, US); 1801 lava flow, *Degener & Degener 27562* (BISH, F, G, K, MO, NY, UC, W); northern edge of 1859 lava flow, *Degener, et al. 19810* (BISH, F, G, GH, K, MO, NY, UC, US); Kohala Rd, near 1859 lava flow, *Fosberg 10169A* (BISH, DS, GH); N Kona District, Hwy 19, *Gardner 410** (OS); Kau, 1868, *Hillebrand s.n.* (GH, K); lava flows of Puuwaawaa, 9 Dec 1955, *Rock s.n.* (BISH); Puuokeanui Crater, *Rock 10049* (BISH, F, K, NY, UC, US).

17. **Lipochaeta venosa** Sherff, Bot. Gaz. (Crawfordsville) **95:** 100. 1933. TYPE: Hawaii: Hawaii: Waimea, at Nohonaohae Crater, Jun 1910, *J. F. Rock 8349* (Holotype, F!, isotypes. BISH[2]!, GH!, UC!).

Suffruticose, stems apparently arcuate-spreading, length unknown. Leaves with petioles 8–10 mm long, overall shape deltoid, 2.1–2.8 cm long, 1.5–1.9 cm wide, dissected, usually with 2 basal lobes, terminal segment incised or cleft, sparsely strigulose above, more densely so below. Heads solitary or 2. Outer phyllaries ovate, 5–5.5 mm long, 2.5–3.5 mm wide, obtuse, strigulose. Ray florets about 5; ligules oval, 3–4.8 mm long, 2–2.8 mm wide, tube 0.7–0.9 mm long. Disc florets 20–30; corollas 3–3.3 mm long, lobes 0.5–0.8 mm long; anthers 1.4–1.5 mm long. Achenes tuberculate, often spotted with purple, those of ray 2–2.4 mm long, 1.5–1.8 mm wide, with wings to 0.2 mm, those of disc 2–2.4 mm long, 1.4–1.5 mm wide, without wings. Pappus of deciduous awns to 0.7 mm long. Paleae often purple near apex. Chromosome number, unknown.

Known from two localities in the South Kohala District of northwestern Hawaii (Figure 9), 1000 m. Flowering May-June. Probably extant.

Lipochaeta venosa is most similar to *L. subcordata* from which the former can be distinguished by the much smaller, lobed leaves, fewer flower heads, and more disc florets.

Representative specimens. HAWAII. **Hawaii:** S. Kohala, Waimea, Puu Holoholoku, *Hosaka 2114* (BISH, K).

18. **Lipochaeta populifolia** (Sherff) Gardner, stat. nov.

Lipochaeta subcordata A. Gray var. *populifolia* Sherff, Bot. Gaz. (Crawfordsville) **95:** 91. 1933. TYPE: Hawaii: Lanai: Maunalei Valley, 18 Jun 1918, *G. C. Munro 670* (Holotype, F!; isotype, US!).

Suffruticose, stems upright, height unknown. Leaves with petioles to 28 mm long, deltoid, 7.5 cm long, 6 cm wide, biserrate, on both surfaces strigulose. Heads in 2's or 3's. Outer phyllaries ovate, to 5.5 mm long, 1.8 mm wide, obtuse, sparsely strigulose. Ray florets 7 or 8; ligules oblong, 9.3 mm long, 4 mm wide, tube 1.3 mm long. Disc florets about 45; corollas 3.3 mm long, lobes 1 mm long; anthers 1.5 mm long. Achenes tuberculate and with a fringe of scales on upper outer rim, those of ray 2.8 mm long, 2.5 mm wide, with wings to 0.3 mm, those of disc 2.8 mm long, 2.2 mm wide, without wings. Pappus of deciduous awns to 1.9 mm long. Paleae tan throughout. Chromosome number, unknown.

Known only from type specimens collected in Maunalei Valley, east central Lanai (Figure 9), ca. 100 m. Habitat unknown. Flowering June. Probably extinct.

Lipochaeta populifolia is a fairly unspecialized member of this section. Sherff (1935) described it as a variety of *L. subcordata,* without giving any explanation of why it belonged there. I cannot see a connection between the two unless it might be that both have rather large leaves. The two taxa are quite distinct in most other characters.

19. **Lipochaeta kamolensis** Degener & Sherff *In:* Sherff, Amer. J. Bot. **38:** 54. 1951. TYPE: Hawaii: Maui. Very rare, among lantana and grass on side of Kamole Gulch, southernmost central eastern Maui, 21 Dec 1948, *O. Degener, H. F. Clay & R. Bertram 19288* (Lectotype chosen, GH!; isotypes, BISH!, G[2]!, MO[2]!, NY!, UC!, US[2]!).

Suffruticose, stems decumbent and rooting along lower surface, to 3 m long. Leaves with petioles 13–17 mm long, overall shape deltoid, 4.3–6.5 cm long, 1.2–4.4 cm wide, basal lobes widely flaring, the lobes pinnatifid, remainder of leaf pinnatifid to pinnate-pinnatifid, on both surfaces strigulose, especially along veins. Heads solitary or 2. Outer phyllaries lanceolate, 6–6.8 mm long, 1.7–2.5

mm wide, attenuate, strigulose. Ray florets 6; ligules oblong, 8.5–9 mm long, 3.7–4 mm wide, tube 1.2–1.4 mm long. Disc florets about 15; corollas 3.3–3.4 mm long, lobes 0.5–0.7 mm long; anthers 1.4 mm long. Achenes tuberculate, those of ray 2.2 mm long, 1.9 mm wide, without wings, those of disc 2.1 mm long, 1.4 mm wide, without wings. Pappus of fused scales and with deciduous awns to 0.9 mm long. Paleae tan throughout.

Known only from Kamole Gulch, Maui (Figure 9), 240 m. Flowering Dec.-Feb. Extant.

The closest extant relative to *L. kamolensis* is probably *L. subcordata,* however, the former has diverged considerably from this taxon in the deeply dissected, pinnatifid to pinnate-pinnatifid leaves.

Representative specimens. HAWAII. **Maui:** Hwy 31, 11.8 mi SE of Ulupalakua Ranch Office, *Gardner 385** (OS).

20. **Lipochaeta bryanii** Sherff, Bot. Gaz. (Crawfordsville) **95:** 97. 1933. TYPE: Hawaii: Kahoolawe: on slope, amid pili grass, 300 m, 16 Feb 1931, *Bryan 736* (Holotype, BISH, not located; isotype, BISH!).

Suffruticose, stems upright, 30–50 cm tall. Leaves with petioles to 10 mm long, generally oblong, but often with 2 basal lobes, to 3.5 cm long, 1.4 cm wide, scarcely serrate, on both surfaces strigulose. Heads in compound cymose clusters. Outer phyllaries ovate, to 4 mm long, 2.5 mm wide, obtuse, sparsely strigulose. Ray florets 4 or 5; ligules oblong, 8.8 mm long, 3.3 mm wide, tube 0.8 mm long. Disc florets about 25; corollas 3.1 mm long, lobe to 0.5 mm long; anthers 1.5 mm long. Achenes tuberculate, those of ray 2.2 mm long, 2.2 mm wide, without wings, those of disc 2.3 mm long, 1.7 mm wide, without wings. Pappus of scales forming an uneven corona and with awns to 1 mm long. Paleae tan throughout. Chromosome number unknown.

Known only from the type specimens collected on Kahoolawe (Figure 9), 300 m. Habitat unknown except "amid pili grass." Flowering Feb. Probably extinct.

Lipochaeta bryanii is most similar to *L. subcordata* from which the former can be distinguished by much smaller leaves, broader phyllaries, more numerous disc florets, and tan phyllaries.

21. **Lipochaeta lavarum** (Gaud.) DC. Prodr. **5:** 611. 1836.

Verbesina lavarum Gaud. *In:* L.C.D. de Freycinet (ed.), Voyage Autour de Monde, Botanique **4:** 464. 1829. TYPE: "In insulis Sandwicensibus," *C. Gaudichaud s.n.* (Holotype, P!; isotypes, G[2]!). *Microchaeta lavarum* Nutt. Trans. Amer. Philos. Soc. 7(n.s.): 451. 1841.

Lipochaeta lavarum (Gaud.) DC. var. *hillebrandiana* Sherff, Bot. Gaz. (Crawfordsville) **95:** 89. 1933. TYPE: Hawaii: Maui: Lahaina, on rocks near sea, *Hillebrand s.n.* (Holotype, B, photo of holotype, F!).

Lipochaeta lavarum (Gaud.) DC. var. *longifolia* Sherff, Bot. Gaz. (Crawfordsville) **95:** 90. 1933. TYPE: Hawaii: Lanai: Maunalei Valley, 9 Mar 1915, *G. C. Munroe 202* (Holotype, BISH!; isotype, BISH!).

Lipochaeta lavarum (Gaud.) DC. var. *ovata* Sherff, Bot. Gaz. (Crawfordsville) **95:** 88. 1933. TYPE: Hawaii: Maui: Kahikinui, below crater, Nov 1910, *J. F. Rock 8674* (Holotype, GH!; isotypes, BISH[2]!, CAS!, F!, K!, NY!, UC!).

Lipochaeta lavarum (Gaud.) DC. var. *salicifolia* Sherff, Bot. Gaz. (Crawfordsville) **95:** 88. 1933. TYPE: Hawaii: Maui: near Lahaina, *E. Bishop s.n.* (Holotype, B, photo of holotype, F!).

Lipochaeta lavarum (Gaud.) DC. var. *skottsbergii* Sherff, Bot. Gaz. (Crawfordsville) **95:** 89. 1933. TYPE: Hawaii: Maui: 1833–36, *Bennett 43* (Holotype, B, photo of holotype, F!).

Lipochaeta lavarum (Gaud.) DC. var. *conferta* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 582. 1939. TYPE: Hawaii: Lanai: *H. Mann & W. T. Brigham 358* (Holotype, F!; isotypes, BISH[2]!, GH!, MO!, NY!, US!).

Lipochaeta lavarum (Gaud.) DC. var. *lanaiensis* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 582. 1939. TYPE: Hawaii: Lanai: Maunalei Gulch, Sep 1917, *C. N. Forbes 507-L* (Lectotype chosen, F!; isotypes, BISH!, F[2]!).

Lipochaeta lavarum (Gaud.) DC. var. *maneleana* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 583. 1939. TYPE: Hawaii: Lanai: on slopes above Manele, Jun 1913, *C. N. Forbes 288-L* (Lectotype chosen, F!; isotypes, BISH!, F!, NY[2]!, US!, W!).

Lipochaeta lavarum (Gaud.) DC. var. *stearnsii* Degener & Sherff *In:* Sherff, Field Mus. Nat. Hist., Bot. Ser. **17:** 581. 1939: TYPE: Hawaii: Lanai: Kapoho Canyon, 800 ft, June 1936, *H. Sterns 11050* (Holotype, F!; isotypes, F!, G!, GH!, MO!).

Suffruticose, stems upright, to 2 m tall. Leaves with narrowly alate margined petioles, 5–15 mm long; blades ranging from linear lanceolate to elliptic to subovate, (2.3–) 3–6.5 (–8) cm long, (0.6–) 0.8–1.5 cm wide, entire to serrate, strigulose above, densely so below. Heads solitary or in 2's or 3's. Outer phyllaries ovate to oblong, (3–) 3.8–6.5 mm long, 2–2.6 mm wide, acute to rounded at apex, strigulose. Ray florets 8–10; ligules oblong, (9–) 10–15 mm long, 4–6.2 mm wide, tube 1–2 mm long. Disc florets 40–60; corollas 3.2–4.1 mm long, lobes 0.8–1 mm long; anthers 1.6–2 mm long.

Achenes nearly smooth, often with a fringe of scales along upper outer rim, those of ray 2.2–2.8 (–3.2) mm long, 3 mm wide, with wings to 0.5 mm, those of disc 2.2–3 mm long, 1.6–2.3 mm wide, with wings to 0.2 mm. Pappus of scales forming an uneven corona and with awns to 1.5 mm long. Paleae tan throughout.

Known from numerous localities along the western and southern side of eastern Maui, around most of the southern half of Lanai and northwestern Hawaii (Figure 9), 20–520 m. Usually in dry, exposed areas often along margins of old "aa" or "pahoehoe" lava flows. Flowering throughout year. Extant.

Lipochaeta lavarum is a specialized member of this section. It is distinguished by the upright habit, relatively long and narrow leaves, long ligules and numerous disc florets. Sherff (1935, 1939) and Degener and Sherff (1939) recognized ten varieties based almost entirely on differences in leaf size. A comparison of the specimens reveals that considerable variation can be seen at the population level. Sherff (1935) in attempting to justifiy *Lipochaeta lavarum* var. *ovata* states (p. 57) "Indeed the cited cotype sheet has, besides two sprays of the ovate-leaved form, one spray with numerous smaller and narrower leaves hardly atypic for *L. lavarum.*" If one considers only the extremes, differences can be recognized, but all are tied together through a continuum of overlapping variation, which makes any attempt to recognize distinct varieties impracticable.

Representative specimens. HAWAII. **Hawaii:** between Kawaihae & Waimea, *Christensen & Christensen 27912* (F); mauka of Kawaihae, *Degener 4188* (BISH, CAS, DS, F, G, GH, MO, NY, UC, W); near Kona Village Resort, *Gardner 338** (OS); S of Waimea, *Gardner 339** (OS); no locality, *Remy 277* (GH). **Lanai:** S Lanai, *Degener 21986* (BISH, CAS, G, GB, K, MO, NY, UC, US, W); mauka of Hulopoe Bay, *Degener & Degener 28391* (BISH, F, G, GH, MO, NY, UC, W); lower Naio Gulch, *Degener, et al. 24161* (BISH, DS, G, K, MO, NY, US, W); Awehi Rd, *Gardner 317* (OS); Naupaka Rd, *Gardner 322* (OS); Puu Makani Rd, *Gardner 323** (OS); Kaunolu Rd, *Gardner 325*, 326* (OS); Malawea Rd, *Gardner 394* (OS); Anapuka Rd, *Gardner 395* (OS); Maunalei Rd, *Gardner 396** (OS); **Maui:** near McGregor, *Degener 4027* (DS, F, G, GB, GH, MO, NY, UC, US, W); Kanaio, *Degener 21975* (BISH, CAS, G, GB, K, MO, NY, UC, US); Papawai Pt, *Degener, et al. 25134* (BISH, F, G, K, MO, NY, UC, US, W); Lahaina *Forbes 2270-M* (A, BISH, F); E of Olowalu Store, *Gardner 331** (OS); E of Ulupalakua, *Gardner 335** (OS); Hwy 30, 0.6 mi E of road tunnel, *Gardner 372* (OS); Hwy 31, 4.8 mi SE of Ulupalakua Ranch Office, *Gardner 379** (OS); Mts of W Maui above Maalaea Bay, *Mann & Brigham 374* (F, NY); Ulupalakua. 27 Feb 1962, *Uehara s.n.* (BISH, US). **Molokai:** no locality, *Rock 10286* (BISH, F, GH).

22. **Lipochaeta perdita** Sherff, Bot. Gaz. (Crawfordsville) **95:** 99. 1933. TYPE: Hawaii: no island: no locality, 1788–1789, *D. Nelson s.n.* (Holotype, BM!).

Lipochaeta kawaihoaensis St. John, Pacific Sci. **13:** 181. 1959. TYPE: Hawaii: Niihau: Kawaihoa Pt., 300 ft, in dry tuff, head of steep gully, 31 Mar 1949, *H. St. John 23611* (Holotype, not located; isotype, BISH!).

Suffruticose, stems upright, to 1 m tall. Leaves with petioles 4–18 mm long, ovate to deltoid-ovate, 1.2–4 cm long, 0.7–2.8 cm wide, serrate, on both surfaces hispidulose. Heads solitary or in 3's. Outer phyllaries broadly or narrowly elliptic or lanceolate, 4–8 mm long, 3 mm wide, subacute, appressed hispidulose. Ray florets 6–9; ligules elliptic, 7–9 mm long, 4 mm wide, tube 1 mm long. Disc florets 80; corollas 4 mm long, lobes 0.8 mm long; anthers 1.8 mm long. Achenes tuberculate, often with brown spots, and with a fringe of scales on upper outer rim, those of ray 2.7–3.1 mm long, 1.9–2.7 mm wide, wings to 0.5 mm, those of disc 2.5 mm long, 1.7–2 mm wide, wings to 0.5 mm. Pappus of deciduous awns to 2.3 mm long. Paleae tan throughout. Chromosome number, unknown.

The only precise locality for this taxon is the collection of *St. John 23611,* near Kawaihoa Pt, Niihau, 100 m, in dry tuff (Figure 3). Flowering Mar. Probably extant.

These two names are put into synonymy with some reservation. David Nelson, who collected the type of *Lipochaeta perdita,* supposedly only went ashore on the island of Hawaii (St. John, 1976a). If that is the case, there is a wide disjunction in the distribution of *L. perdita,* however, St. John (1976) also states that Kauai was on the itinerary of Nelson's voyage. If Nelson did collect on Kauai, even if only briefly, the chances of finding this taxon there would not be so surprising. Another reason for questioning the reliability of this taxonomic decision is that the Nelson collection is in very poor condition. The ray florets and disc achenes are completely lacking, yet on the basis of the characters that can be measured, the two specimens are strikingly similar. St. John's conclusion that *L. kawaihoaensis* is most closely related to *L. lobata* is not acceptable. The latter taxon is known to be a tetraploid whereas the collection from Kawaihoa Pt, although unknown cytologically, is 5-merous and presumably a diploid.

23. **Lipochaeta integrifolia** (Nutt.) A. Gray, Proc. Amer. Acad. Arts **5:** 130. 1861.

Microchaeta integrifolia Nutt. Trans. Amer. Philos. Soc. **7**(n.s.): 451. 1841. TYPE: Hawaii: Atooi [Kauai]: *T. Nuttall s.n.* (Holotype, BM!).

Lipochaeta integrifolia (Nutt.) A. Gray var. *argentea* Sherff, Bot. Gaz. (Crawfordsville) **95:** 84. 1933. TYPE: Hawaii: Maui: on sandy isthmus, *H. Mann & W. T. Brigham 371* (Holotype, F!; isotypes, BISH!, F!, G!, GH[2]!, MO!, NY!).

Lipochaeta integrifolia (Nutt.) A. Gray var. *gracilis* Sherff, Bot. Gaz. (Crawfordsville) **95:** 85. 1933. TYPE: Hawaii: [No island] Sep-Oct 1836, *C. Gaudichaud 217* (Holotype, GH!; isotype, P!).

Lipochaeta integrifolia (Nutt.) A. Gray var. *major* Sherff, Bot. Gaz. (Crawfordsville) **95:** 85. 1933. TYPE: Hawaii: Oahu: old lava flow back of Diamond Head, 8 Apr 1895, *A. A. Heller 2092* (Holotype, GH!; isotypes A!, BISH!, F!, G!, K[2]!, MO!, NY!, UC!, US!).

Lipochaeta integrifolia (Nutt.) A. Gray var. *megacephala* Degener & Sherff *In:* Sherff, Bot. Gaz. (Crawfordsville) **95:** 86. 1933. TYPE: Hawaii: Oahu: Kaena Pt, in sand, 5 m, 14 Dec 1930, *E. Christophersen 1400* (Holotype, F!; isotype, BISH!).

Suffruticose, stems prostrate and rooting along lower surface, to 2 m long. Leaves with alate margined petioles 2–10 mm long; blades ranging from oblong to spatulate, (0.4–) 0.8–3 cm long, (0.2–) 0.4–1.2 cm wide, entire to scarcely serrate, on both surfaces densely strigulose. Heads solitary or in 2's or 3's. Outer phyllaries ovate to oblong, 3–3.6 mm long, 1.6–2.3 mm wide, rounded at apex, strigulose. Ray florets 8–10; ligules oval to oblong, 3.3–5.1 mm long, 2.5–4.3 mm wide, tube 0.7–1.2 mm long. Disc florets 30–50; corollas (2.4–) 2.7–3.6 mm long, lobes 0.6–0.9 mm long; anthers (1.2–) 1.4–1.6 mm long. Achenes nearly smooth, those of ray 2–2.5 mm long, 1.9–2.7 mm wide, without wings, those of disc 2.4–3 mm long, 1.7–2.7 mm wide, without wings. Pappus of deciduous awns to 1.2 mm long. Paleae tan throughout.

Known from several localities on all of the major islands (Figure 3), generally found near sea level to 20 or 30 m, but on Molokai it occurs along the pali near Hoolehua at 170 m. In exposed, windswept areas, usually prostrate over rocks and other vegetation and forming dense mats. Flowering throughout the year. Extant.

Lipochaeta integrifolia is a specialized member of this section. It is distinguished by thick succulent leaves and a mat forming habit. Sherff (1935) and Degener and Sherff (1935) recognized five

varieties based on leaf and capitulum size. When one examines multiple collections made from a single population (e.g. *Gardner 298A-C*), a continuum of variation is seen in both leaf and head size. It is true that Oahu specimens tend to be a bit larger than those from Maui or Lanai, but because of intergradation, these size differences cannot be recognized formally.

Representative specimens. HAWAII. **Hawaii:** first aa lava flow NE of South Pt, *Degener 31583* (BISH); Punaluu, *Degener & Degener 30836* (A, BISH, G, K, NY, UC, W), *Gardner 336* (OS); South Pt, *Gardner 337 A & B* (OS), *Greenwell 19561* (BISH, F, NY); 1–2 mi S of South Pt light house, *Greenwell 20684* (BISH, G, US); Punaluu, *St. John, et al. 11317* (US); Kaalualu Bay, *Whistler W7* (BISH). **Kaohikaipu:** Waimanolo Bay, *Fosberg 14051* (BISH, F). **Kapapa:** Kanehoe Bay, *Fosberg & Egler 14028* (BISH, GH). **Kauai:** Kipu Kai, *Alexander & Kellogg 5332* (BISH, K, NY, UC, US), makai of Puu Keke, *Degener, et al. 27167* (BISH, F, G, NY, US, W); near Puu Keke, *Gardner 293** (OS); Kipu Kai, *Gardner 297A* & B** (OS); Ka Lae Amana Pt, Moloaa Bay, *Gardner 355* (OS). **Kure:** central plain, *Caum 14* (NY, US); no locality, *Lamoureux 1911* (A); E end, *Long 2243* (BISH, US). **Lanai:** Poaiwa, *Degener & Degener 28374* (A, BISH, DS, F, G, MO, NY), *Gardner 388* (OS); Limestone Pt, 31 Mar 1914, *Munro s.n.* (BISH), *Munro 143* (BISH),Munro 257 (BISH), *Munro 414* (BISH). **Laysan:** no locality, Apr 1903, *Bryan s.n.* (BISH, F). **Maui:** between Waihee Golf Course and Maunlani Cemetery, *Carlquist 2124* (BISH); Puu Ohai, SW of Honokahua Valley, *Cranwell, et al. 2735* (BISH, GB); Wailuku, *Degener 4203* (F, K, US); Honokohua, *Degener 12417* (A, F, MO, NY); between Wailuku & Waiehu, *Degener 19572* (BISH, F, G, NY); Kahakuloa, *Degener 21969* (BISH, CAS, G, GB, NY, UC, US); NE of Kaanapali, *Gardner 332** (OS); Hwy 34, 15.4 mi NW of jct Hwys 33 and 34, *Gardner 333** (OS); Hwy 30, 14 mi NE of Lahaina, *Gardner 373* (OS); between Kahului and Wailua, *Melville & Melville 1098* (K); **Mokulua:** N peak, *Long 1674* (US), *1676* (BISH, US), *Long 1745* (US). **Molokai:** Hoolehua Dump, W of Hoolehua, *Carlquist 2236* (BISH); near Moomomi, *Degener 4216* (F, GH); near Waiakanapo, *Degener 4216B* (F, G, GH, NY, UC); beach near Ka Lae Ka Ilio Ilio, *Forbes 615-Mo* (F); Moomomi sand dunes, *Fosberg & Fosberg 13439* (BISH, US); Hoolehua Dump, *Gardner 298A-C** (OS), *Gardner 401** (OS); Moomomi Beach, *Gardner 302* (OS); N of Laau Pt, *Gardner 309** (OS); Ilio Pt, *Gardner 311* (OS). **Oahu:** Makapuu Pt, 8 Apr 1923, *Degener s.n.* (F, GH, MO, NY); Makapuu Peninsula, Pyramid Rock, *Fosberg 10575* (BISH, F, GH); divide at head of Kalama Valley, *Fosberg 13615* (BISH, F, GH, US); Hanauma Bay, *Gardner 275A*, 275 POP** (OS); near Koko Head Shooting Range, *Gardner 276** (OS); Kaena Pt, N shore road, *Gardner 282*, 283*, 348** (OS); Blowhole, *Gardner 277A & B* (OS); Blowhole, Koko Crater, *St. John 10402* (BISH, K); Hanauma Bay Beach Park, *Van Royen 10195* (A, BISH, K, US). **Popoia:** no locality, *Forbes 2194-O* (F near Kailua, *Fosberg 10556* (BISH, F).

DOUBTFUL AND EXCLUDED NAMES

Lipochaeta amazonica Poeppig & Endlicher, Nov. Gen. et Sp. **3:** 49. *t. 256.* 1845. TYPE: "Crescit in insulis arenosis fluminis Ama-

zonum inter Ega et Rio Negro," no date, collector unknown (Holotype, ?). The type has not been located, but the illustration is taken to be of the holotype = *Zexmenia.*

Lipochaeta asymetrica Léveillé, Feddes Repert. Spec. Nov. Veg. **10:** 122. 1911. TYPE: Hawaii: Oahu: Kaliki, Oct 1909, *A. U. Faurie 960* (Holotype, location not known) = *Bidens asymmetrica (Lé*veillé) Sherff, Bot. Gaz. (Crawfordsville) **81:** 49. 1926. *fide* Sherff (1926).

Lipochaeta costaricensis Benth. Genera Plantarum **2:** 373. 1873. *nom. nud.*

Lipochaeta fasciculata DC. Prodr. **5:** 610. 1836. TYPE: Mexico: 1832. *J. L. Berlandier 2134* (Holotype, G-DC; photo of Holotype, F!) = *Zexmenia fasciculata* (DC.) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald **306.** 1856. *fide* Jones (1905).

Lipochaeta goyazensis Gardner, London J. Bot. **7:** 406. 1848. TYPE: Brazil: near Villa de Arrayas, Mar-May 1840, *G. Gardner 3847* (Holotype, K; isotype, G; photo of isotype, F!) = *Zexmenia goyazensis* (Gardner) Benth. & Hook. Genera Plantarum **2:** 373. 1873. *fide* Jones (1905).

Lipochaeta hastata Kellogg, Proc. Calif. Acad. Sci. **2:** 106. 1836. TYPE: Cerros Island, *J. A. Veatch s.n.* (Holotype, UC) = *Verbesina hastata* Kellogg ex. Curran, Bull. Calif. Acad. Sci. **1:** 140. 1885. *fide* Sherff (1935).

Lipochaeta lantanifolia Schauer, Linnaea **19:** 729. 1847. TYPE: Mexico: "circa Zimapan," *Aschenborn 210* (Holotype, B?) = *Zexmenia lantanifolia* (Schauer) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald 306. 1856. *fide* Jones (1905).

Lipochaeta laricifolia (Hook. f.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861. = *Macraea laricifolia* Hook. f. Proc. Linn. Soc. London **1:** 278. 1845. TYPE: Ecuador: Galapagos Islands, Charles Island, *C. Darwin s.n.* (Lectotype, CGE; syntype, [*Macrae s.n.*] G!, K!).

Lipochaeta lifuana Hochreutiner, Bull. New York Bot. Gard. **6:** 297. 1910. TYPE: Loyalty Islands, Lifu, *E. Vieillard 799* (Holotype, NY!; isotype, G!, NY[2]!, P!) = *Wedelia uniflora* (Forst.) Moore, J. Linn. Soc. Bot. **45:** 347. 1921. *fide* Moore (1921).

Lipochaeta longipes Benth. Genera Plantarum **2:** 373. 1873. *nom. nud.*

Lipochaeta DC. section *Macraea* Sherff, Bot. Gaz. (Crawfordsville) **95:** 77. 1935. TYPE SPECIES: *Lipochaeta laricifolia* (Hook. f.) A. Gray, Proc. Amer. Acad. Arts **5:** 131. 1861.

Lipochaeta macrocephala Hook. & Arn. Bot. Beechey's Voy. 436. 1841. TYPE: Mexico: Guerrero: Acapulco, *Hinds 1841* (Holotype, K) = *Zexmenia macrocephala* (Hook. & Arn.) Hemsley, Biologia Centrali-Americana, Bot. **2:** 137. 1881. *fide* Jones (1905).

Lipochaeta monocephala DC. Prodr. **5:** 610. 1836. TYPE: "Caribaeis: in horto Paris, culta" (Holotype, G-DC; photo of holotype, F!) = *Zexmenia monocephala* (DC.) Heynhold, Nomenclature ed. **1:** 863. 1840. *fide* Jones (1905).

Lipochaeta scaberrima Benth., J. Bot. (Hooker), **2:** 43. 1840. TYPE: British Guiana: Mount Roraima, 1839, *Schomburgk s.n.* (Holotype, K!; isotype, W; photo of isotype, F!) = *Oyedaea scaberrima* (Benth.) Blake, Contr. U.S. Natl. Herb. **20:** 414. 1921. *fide* Blake (1921).

Lipochaeta serrata (La Llave & Lexarza) DC. Prodr. **5:** 611. 1836. = *Zexmenia serrata* La Llave & Lexarza, Nov. Veg. Description. fasc. **1:** 13. 1824. TYPE: Mexico: San Jose del Corral, *La Llave s.n.* (Holotype: G-DC). *fide* Jones (1905).

Lipochaeta strigosa DC. Prodr. **5:** 610. 1836. TYPE: Mexico: "Oaxacana australi circa Tehuantepec," *Andrieux 313* (Holotype, G-DC; photo of holotype, F!) = *Zexmenia strigosa* (DC.) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald 306. 1856. *fide* Jones (1905).

Lipochaeta tagetiflora G. Don, *In:* Sweets Hort. Brit. ed. 3. 360. 1856. TYPE: cultivated from Mexico in 1828 (Holotype, ? not located at BM [R. Ross, in litt.] = *Zexmenia tagetiflora* D. Don, *In:* Sweets Hort. Brit. ed. 2. 309. 1830.

Lipochaeta texana Torrey & Gray, Flora North Amer. **2:** 357. 1842. TYPE: Texas: *Riddell s.n.* (Holotype, NY!) = *Zexmenia hispida* A. Gray, Synoptical Flora North Amer. **1:** 286. 1884. *fide* Jones (1905).

Lipochaeta umbellata DC. Prodr. **5:** 610. 1836. TYPE: Mexico: Cuernavaca, *J. L. Berlandier 1065* (Holotype, G-DC; photo of

holotype, F!) = *Zexmenia ceanothifolia* (Wild.) Sch.-Bip. *In:* Seemann, Bot. Voy. Herald 306. 1856.

Lipochaeta umbellata DC. var. *conferta* DC. Prodr. **5:** 610. 1836. TYPE: Mexico: Morelos: Cuernavaca, *J. L. Berlandier 1053* (Holotype, G-DC; photo of holotype, F!) = *Zexmenia ceanothifolia* (Wild.) Sch.-Bip. var. *conferta* (DC.) A. Gray ex Jones, Proc. Amer. Acad. Arts **41:** 155. 1905. *fide* Jones (1905).

ACKNOWLEDGMENTS

This research could not have been completed without the assistance of numerous people. I acknowledge especially the willingness to help, the encouragement, and direction offered by Dr. Tod F. Stuessy, my major professor. He served as principal investigator under the terms of the grant funded by the National Science Foundation. I also thank Dr. Sherwin Carlquist of the Rancho Santa Ana Botanical Garden for advice concerning the logistics of the field work and for reviewing the grant proposal.

Several people assisted me during the field work by acting as guides or by allowing access to their private land. Especially helpful were: Dr. John J. Fay, formerly of the Pacific Tropical Botanical Garden, Kauai; Mr. Noah Pekelo, of the Hawaii Department of Natural Resources; Mr. Akah Hodges, of Molokai Ranch, Molokai; the Hawaiian Homelands Commission, Molokai; and Mr. Robert Cushnie, of the Lanai Company, Lanai. Drs. Derryl Herbst, Lyon Arboretum, and John J. Fay provided me with living and pressed material for some of the taxa I did not locate while in the field.

I wish to thank the curators of the herbaria from which specimens were borrowed (A, B, BISH, CAS, DS, F, G, GB, GH, K, MO, NY, PH, UC, US, W). Without the support and field assistance of my wife, Pat, and without the ideas and suggestions of my fellow graduate students this research would have been much more difficult.

Appreciation is expressed to Drs. Jere N. Brunken, and Tod F. Stuessy for their comments on and criticisms of the manuscript, and to Carol Stuessy for preparing Figure 10.

Financial support for chemical supplies from Sigma Xi Grants-in-Aid of Research and for the field work from National Science Foundation grant GB-41175 is gratefully acknowledged.

LITERATURE CITED

ALSTON, R. E., & B. L. TURNER. 1962. New techniques in analysis of complex natural hybridization. Proc. Natl. Acad. U.S.A. **48:** 130–137.

BACON, J. D. 1975. The genus *Nerisyrenia* (Cruciferae): A chemosystematic and cytotaxonomic study. Ph.D. Dissertation: Univ. Texas, Austin.

BECKER, K. M 1972. Proposal to conserve the generic name 9216. *Zexmenia* A. Gray (1852) non La Llave and Lexarza (1824) Asteraceae. Taxon **21:** 712–715.

BROWN, R. 1817. Some observations on the natural family of plants called Compositae. Trans. Linn. Soc. London **12:** 76–142.

BENTHAM, G., & J. D. HOOKER. 1873. Genera Plantarum **2:** 370–374.

DE CANDOLLE, A. P. 1836. Prodromus Systematis Naturalis Regni Vegetabilis **5:** 610–611.

CRAWFORD, D. J. 1974. A morphological and chemical study of *Populus acuminata* Rydberg. Brittonia **26:** 74–89.

CRONQUIST, A. 1971. *In,* I. L. Wiggins and D. M. Porter, Flora of the Galápagos Islands. Stanford University Press.

DEGENER, O., & H. F. CLAY. 1949. Family 344. Flora Hawaiiensis. Patten Co., Honolulu.

_____, & E. E. SHERFF. 1940. Family 344. Flora Hawaiiensis. Patten Co., Honolulu.

ENDLICHER, S. L. 1842. Genera Plantarum, Suppl. **2:** 43.

FOSBERG, F. R., & D. HERBST. 1975. Rare and endangered species of Hawaiian vascular plants. Allertonia **1:** 1–72.

GARDNER, R. C. 1974. Systematics of *Cirsium* (Compositae) in Wyoming. Madroño **22:** 239–265.

_____. 1976. Patterns of adaptive radiation in *Lipochaeta* DC. (Compositae) of the Hawaiian Islands. Syst. Bot. **1:** 383–391.

_____. 1977a. Chromosome numbers and their systematic implications in *Lipochaeta* (Compositae:Heliantheae). Amer. J. Bot. **64:** 810–813.

_____. 1977b. Observations on tetramerous disc corollas in the Compositae. Rhodora **79:** 139–146.

GAUDICHAUD, M. C. 1826–1830. Botanique. *In,* L. C. D. de Freycinet (ed), Voyage Autour du Monde, **4.** Paris.

GIANNASI, D. E. 1975. The flavonoid systematics of the genus *Dahlia* (Compositae). Mem. New York Bot. Gard. **26**(2): 1–125.

GRAY, A. 1852. Plantae Wrightianae **1:** 113.

_____. 1861. Characters of some Compositae in the United States South Pacific Exploring Expedition under Captain Wilkes, with observations by Asa Gray. Proc. Amer. Acad. Arts **5:** 114–146.

HARLING, G. 1962. On some Compositae endemic to the Galapagos Islands. Acta Horti Berg. **20:** 63–120.

HILLEBRAND, W. 1888. Flora of the Hawaiian Islands. Facsimile edition of 1888 ed. Hafner Publ. Co. New York and London. 1965.

JONES, W. W. 1905. A revision of the genus *Zexmenia.* Proc. Amer. Acad. Arts **41:** 143–167.

LESSING, C. F. 1831. Synanthereae Rich. *In*, A. de Chamisso & D. de Schlechtendal (eds.), De plantis in expeditione Romanzoffiana. Linnaea **6:** 83–170, 209–258 (addenda), 501–526 (continuatio).

LEVIN, D. A. 1967. Hybridization between annual species of *Phlox;* population structure. Amer. J. Bot. **54:** 1122–1130.

MABRY, T. J., K. R. MARKHAM, & M. B. THOMAS. 1970. The systematic identification of flavonoids. Springer-Verlag, New York.

MCVAUGH, R. 1975. Reports on proposals for conservation. Taxon **24:** 245.

NUTTALL, T. 1841. Descriptions of new species and genera of plants in the natural order of the Compositae, collected in a tour across the continent to the Pacific, a residence in Oregon, and a visit to the Sandwich Islands and Upper California, during the years 1834 and 1835. Trans. Amer. Philos. Soc. **7**(n.s.): 283–454.

SHERFF, E. E. 1933. New and otherwise noteworthy Compositae IX. Bot. Gaz. (Crawfordsville) **95:** 80–103.

———. 1935. Revision of *Tetramolopium, Lipochaeta, Dubautia,* and *Railliardia.* Bernice P. Bishop Mus. Bull. No. **135:** 1–136.

———. 1939. Some new and otherwise noteworthy Labiatae and Compositae. Field Mus. Nat. Hist., Bot. Ser. **17:** 577–612.

———. 1941. New or otherwise noteworthy plants from the Hawaiian Islands. Amer. J. Bot. **28:** 18–31.

———. 1951. Miscellaneous notes on new or otherwise noteworthy dicotyledonous plants. Amer. J. Bot. **38:** 54–73.

———. 1954. I. Further notes upon the flora of the Hawaiian Islands. Bot. Leafl. No. **9:** 2–10.

———. 1960. Some dicotyledonous plants recently collected in the Hawaiian Islands. Brittonia **12:** 170–175.

SOLBRIG, O. T., D. W. KYHOS, M. POWELL, & P. H. RAVEN. 1972. Chromosome numbers in Compositae VIII: Heliantheae. Amer. J. Bot. **59:** 869–878.

ST. JOHN, H. 1959. Botanical novelties on the Island of Niihau, Hawaiian Islands, Hawaiian plant studies 25. Pacific Sci. **13:** 156–190.

———. 1972. Plantae Hobdyanae Kauaienses. Hawaiian plant studies 31. Pacific Sci. **26:** 275–295.

———. 1976a. Biography of David Nelson, and an account of his botanizing in Hawaii. Pacific Sci. **30:** 1–5.

———. 1976b. New species of Hawaiian plants collected by David Nelson in 1779: Hawaiian Plant Studies 52. Pacific Sci. **30:** 7–44.

STUESSY, T. F. 1977. A revised subtribal classification of the Heliantheae. *In:* J. B. Harborne, V. H. Heywood, and B. L. Turner (eds.), The Biology and Chemistry of the Compositae. Academic Press, New York.

TURNER, B. L., & R. E. ALSTON. 1959. Segregation and recombination of chemical constituents in a hybrid swarm of *Baptisia laevicaulis* × *B. viridis* and their taxonomic implications. Amer. J. Bot. **46:** 678–686.

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LIST OF TAXA OF LIPOCHAETA

1. *L. succulenta* (Hook. & Arn.) DC.
2. *L. degeneri* Sherff
3. *L. rockii* Sherff
4. *L. heterophylla* A. Gray
5. *L. lobata* (Gaud.) DC.
   - 5a. *L. lobata* var. *lobata*
   - 5b. *L. lobata* var. *hastulatoides* Degener & Sherff
   - 5c. *L. lobata* var. *leptophylla* Degener & Sherff
6. *L. connata* (Gaud.) DC.
   - 6a. *L. connata* var. *connata*
   - 6b. *L. connata* var. *acris*
7. *L. tenuifolia* A. Gray
8. *L. dubia* Degener & Sherff
9. *L. tenuis* Degener & Sherff
10. *L. remyi* A. Gray
11. *L. ovata* Gardner
12. *L. waimeaensis* St. John
13. *L. deltoidea* St. John
14. *L. fauriei* Leveille
15. *L. micrantha* (Nutt.) A. Gray
    - 15a. *L. micrantha* var. *micrantha*
    - 15b. *L. micrantha* var. *exigua* (Degener & Sherff) Gardner
16. *L. subcordata* A. Gray
17. *L. venosa* Sherff
18. *L. populifolia* (Sherff) Gardner
19. *L. kamolensis* Degener & Sherff
20. *L. bryanii* Sherff
21. *L. lavarum* (Gaud.) DC.
22. *L. perdita* Sherff
23. *L. integrifolia* (Nutt.) A. Gray

INDEX TO EXSICCATAE

Numbers in parentheses represent the taxa recognized in this study (see preceding list).

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Bennett 43(21).
Bishop s.n.(21).
Bryan s.n.(23), 317(5a), 736(20).
Bush 9301(23).
Bush & Topping 3746(5a).
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Carlson 3828(10).
Caum 14(23).

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Christopherson s.n., 1368, 1400(23).
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Fosberg & Daker 9138(23).

Fosberg & Egler 14208(23).
Fosberg & Fosberg 12859(10), 13150(5a), 13439(23).
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