Pacific Science (1980), vol. 34, no. 1


# Infrageneric Relationships and the Origin of the Hawaiian Endemic Genus *Lipochaeta* (Compositae)[1]

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ABSTRACT: Infrageneric relationships of *Lipochaeta* were assessed by way of a controlled crossing program that produced 14 intrasectional and 5 intersectional hybrid combinations involving the two sections *Aphanopappus* and *Lipochaeta*. Results from uniform culture and hybridization studies confirm that specific differences involving many traits such as leaf shape, the number of disk floret lobes, and achene morphology have a genetic basis. Fertility data based on pollen stainability and achene set of some of the hybrids revealed that members of the same section are highly interfertile, whereas the two sections are extremely well isolated from each other reproductively. Cytogenetic evidence suggests that this isolation is due primarily to a difference in the ploidy level of the two sections and that section *Lipochaeta*, with $n = 26$, has an allopolyploid origin from a 15-paired taxon similar to a diploid *Lipochaeta* and an unknown 11-paired taxon in the extra-Hawaiian genus *Wedelia*. Chromosome counts for three diploid species and one tetraploid variety are reported for the first time.

A MEMBER OF THE FAMILY Compositae, tribe Heliantheae, *Lipochaeta* is considered endemic to the Hawaiian Islands (Gardner 1979). The genus is comprised of several self-compatible perennials and an annual species; these collectively occupy a wide array of habitats, ranging from the low coastal zone into dry or mesic uplands and steep slopes.

The lack of systematic information on the genus is reflected in the different names that have been applied to it and in the changes in its taxonomic delimitation (R. Brown 1817, Gaudichaud 1826–1830, De Candolle 1836, Nuttall 1841, Endlicher 1842, Gray 1861, Bentham and Hooker 1873, Sherff 1935, Harling 1962, Gardner 1976, 1977, 1979). Gardner points out that discontinuities in the variation of floral characters, leaf flavonoid constituents, and chromosome numbers coincide and allow the easy recognition of two natural sections in the genus *Lipochaeta*. According to him, section *Lipochaeta* is comprised of nine taxa in six species and includes only those species that have 26 pairs of chromosomes and can synthesize both flavones and flavonols. In this section the disk florets of all species have mostly four-lobed corollas. On the other hand, section *Aphanopappus* is comprised of 18 taxa in 17 species, each of which have 15 pairs of chromosomes and five-lobed disk corollas; these can synthesize flavonols but not flavones (Gardner 1976).

The relationship of section *Aphanopappus* to section *Lipochaeta* and the origin of the latter is of great interest, and relevant hypotheses have been advanced and discussed in the literature (Gardner 1976, 1977, Carr 1978). The present work reports the results of artificial infrasectional and intersectional crosses in the genus *Lipochaeta* and discusses the significance of these results to hypotheses about infrageneric relationships and the origin of section *Lipochaeta*.

[1] Supported by the African-American Institute AFGRAD program. This paper is part of a dissertation submitted to the Graduate Division of the University of Hawaii in partial fulfillment of the requirements for the Ph.D. degree in the botanical sciences. Manuscript accepted 15 December 1979.

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TABLE 1

CHROMOSOME NUMBERS AND ORIGIN OF *Lipochaeta* CULTURES

| TAXON | GAMETIC CHROMOSOME NUMBER | ORIGIN AND COLLECTOR |
|---|---|---|
| *Lipochaeta* section *Lipochaeta* | | |
| *L. connata* (Gaud.) DC. var. *connata* | 26 | Kauai: 4 mi north of Kekaha on Kokee road, *G. Carr* 908 |
| *L. heterophylla* A. Gray | 26 | Lanai: near Shipwreck Bay, *R.* 187* |
| *L. lobata* (Gaud.) DC. var. *lobata* | 26 | Molokai: east Ohia Ridge, 800 ft, *R.* 114 |
| | 26 | Oahu: Diamond Head, 450 ft, *G. Carr* 851 |
| | 26 | Oahu: Makapuu, sea level, *R.* 171 |
| | 26 | Oahu: Makapuu, sea level, *R.* 179 |
| | 26 | Oahu: Kaena Point, sea level, *R.* 193 |
| *L. lobata* (Gaud.) DC. var. *hastulatoides* Deg. & Sherff | 26 + B | Maui: west Maui, above McGregor Point, *R. Sylva s. n.* 1976 (Maui Zoo and Botanical Garden, *R.* 198) |
| *L. lobata* (Gaud.) DC. var. *leptophylla* Deg. & Sherff | 26 | Oahu: Niu Valley, *R.* 314 |
| *L. rockii* Sherff | 26 | Maui: Lualailua Hills, east of Ulupalakua, Piilani Hwy., *G. Carr* 963 |
| | 26 | Molokai: Makakupaia Ridge, *R.* 119 |
| *L. succulenta* (Hook. & Arn.) DC. | 26 | Kauai: Hanakapiai Beach, end of Kalalau Trail, *R.* 150 |
| | 26 | Maui: east Maui, between Nahieku and Keanae, *R. Sylva s. n.* 1977 (Maui Zoo and Botanical Garden, *R.* 195) |
| *Lipochaeta* section *Aphanopappus* | | |
| *L. dubia* Deg. & Sherff | 15 | Oahu: near Kolekole Pass, Waianae Mts., *R.* 175 |
| *L. tenuis* Deg. & Sherff | 15 | Oahu: near Kolekole Pass, Waianae Mts., *R.* 176 |
| *L. integrifolia* A. Gray | 15 | Kauai: near Haula Beach, *R.* 148 |
| | 15 | Oahu: near Makapuu, *R.* 172 |
| | 15 | Hawaii: South Point, *R.* 301 |
| | 15 | Oahu: Kaena Point, *R.* 194 |
| *L. lavarum* (Gaud.) DC. | 15 | Maui: east of Ulupalakua, *L. Stemmermann* 1225 |
| | 15 | Lanai: Manele Bay, *R.* 188 |
| | 15 | Maui: west Maui, La Perouse Bay, *R. Sylva s.n.* (Maui Zoo and Botanical Garden, *R.* 200) |
| | 15 | Maui: east of Ulupalakua, *R. Sylva s.n.* (Maui Zoo and Botanical Garden, *R.* 201) |
| *L. micrantha* (Nutt.) A. Gray var. *exigua* (Deg. & Sherff) Gardner | 15 | Kauai: Mt. Haupu, *S. Perlman* 75943 (Pacific Tropical Botanical Garden, *L. Stemmermann s.n.*) |
| *L. remyi* A. Gray | 15 + B | Oahu: Manini Gulch near Kaena Point, *R.* 183 |
| *L. subcordata* A. Gray | 15 | Hawaii: Kona, Hwy. 190, *R.* 186 |
| *L. venosa* Sherff | 15 | Hawaii: Pohakuloa training area, about 4200 ft, *L. Stemmermann* 3456 |
| *L. waimeaensis* St. John | 15 | Kauai: rim of Waimea Canyon, 1200 ft, *G. Carr s.n.* 21 June 1978 |

NOTE: Taxonomy after Gardner (1979).
*All collection numbers prefixed by *R.* are those of the author.

## MATERIALS AND METHODS

The plants used for this investigation were most frequently secured from the field as cuttings that were rooted and grown in the University of Hawaii greenhouse facilities. For rooting, the cuttings were put under a clock-regulated misting device in 4-inch pots containing horticultural perlite. To induce rooting, Rootone-F (Amchem Products, Inc.) was applied to the cut ends of the shoots. In some instances, field-collected achenes or achenes or cuttings secured from botanical gardens were used for propagation (Table 1). Achenes were put on moistened filter paper in petri dishes for one to several days, after which the embryos were excised and put on moist filter paper in petri dishes to germinate. The seedlings were transferred to a 1:1 mixture of perlite and potting soil, and then put under a clock-regulated mister in a greenhouse until the seedlings attained a height of 8–10 cm, whereupon they were transferred to larger pots and taken out of

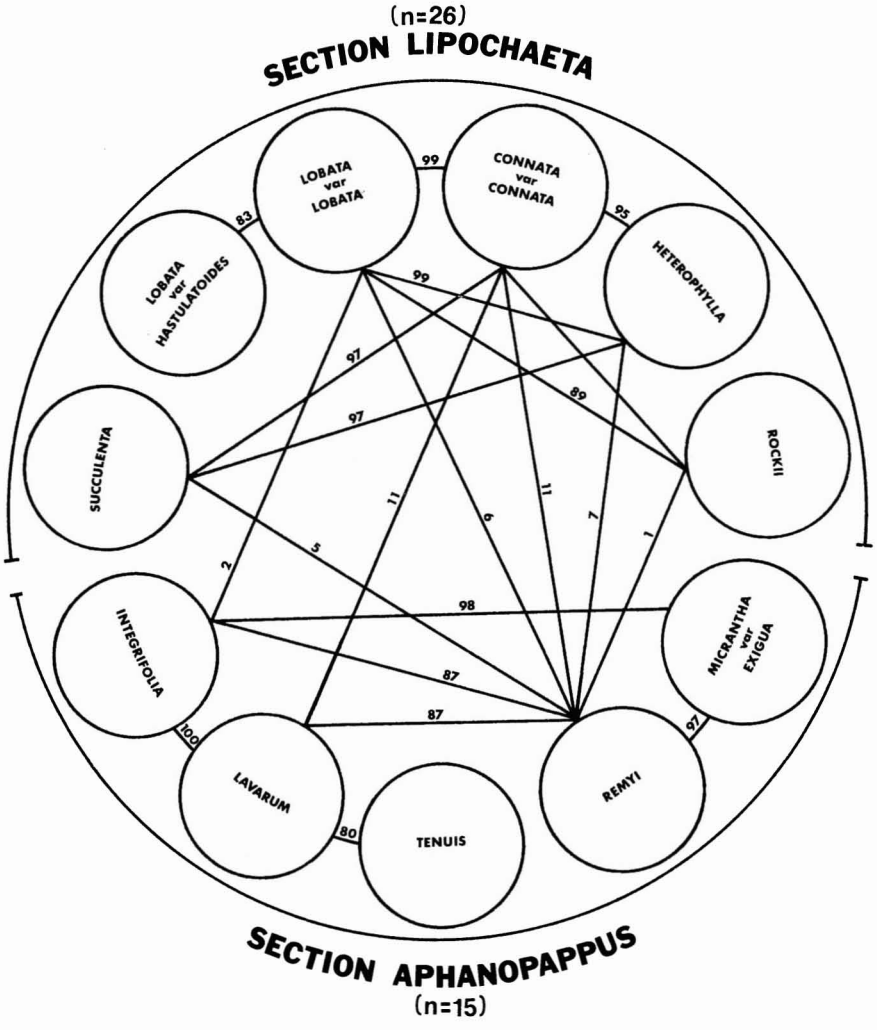
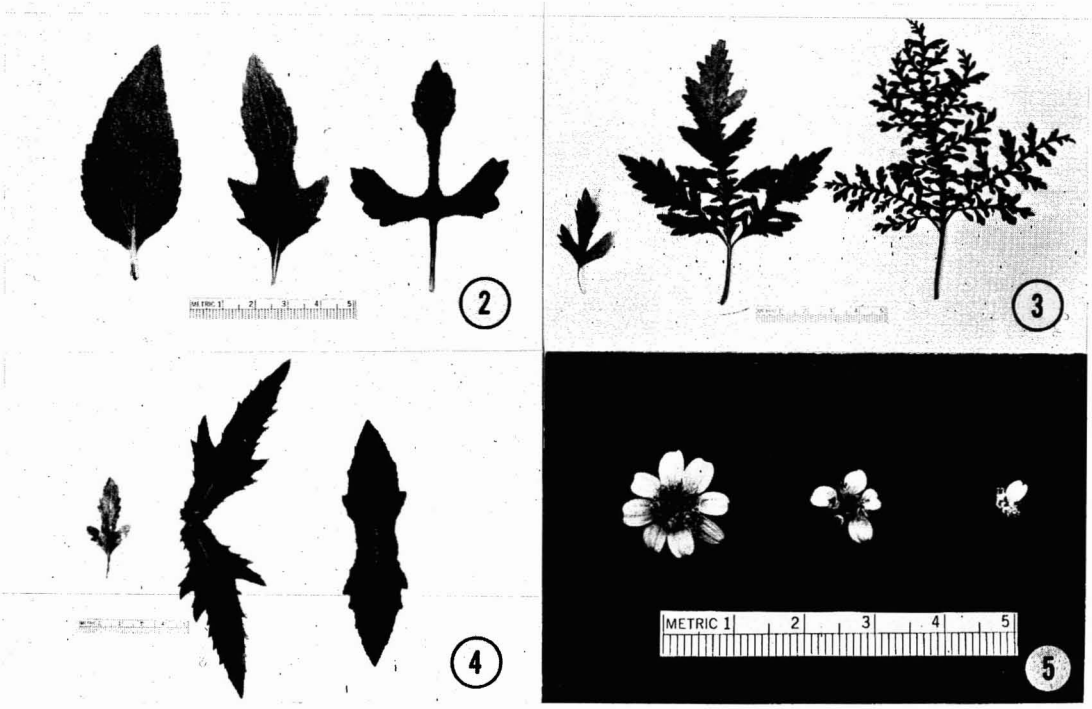



FIGURE 1. Summary of infrageneric relationships in *Lipochaeta*. Numbers on lines connecting taxa represent mean pollen stainabilities (%) of the hybrids.

the mist. The plants were grown under normal greenhouse conditions. Artificial crosses were made by rubbing heads of the desired combination together once a day for as many days as florets continued to open. Since the plants are self-compatible, the production of hybrids was promoted by starting pollination while only ray florets were open. Hybrid plants were selected for continued culture on the basis of morphological intermediacy. These were later verified as hybrids by observations of meiosis and pollen stainability. In one instance, meiotic material from a putative natural hybrid was also analyzed. Meiotic preparations were made according to the acetocarmine squash technique (Beeks 1955). Floral buds of appropriate size for meiotic analysis were usually collected before noon and fixed in a modified Carnoy's solution of 6 parts chloroform, 3 parts absolute ethanol, and 1 part glacial acetic acid. The buds were kept in the fixing solution at room temperature for 2 or 3 days and then stored at about −15°C until analyzed. All microscopical observations were made with phase-contrast optics. Pollen grains were stained with cotton blue in lactophenol at least 24 hr prior to assessment of stainability. No fewer than 300 grains provided the basis for each estimation of pollen viability. Herbarium vouchers of hybrids and species are deposited at the herbarium of the University of Hawaii (HAW).

## RESULTS

Intrasectional as well as intersectional $F_1$ hybrids were readily obtained. A total of 21 hybrid combinations (Figure 1) including 30 progenies and 201 individuals were grown to flowering maturity. Because all achenes were




FIGURES 2–5. Leaf and floral morphology in infrasectional and intersectional hybrids of *Lipochaeta*. *2*, left—*L. lobata* var. *lobata*, center—$F_1$, right—*L. rockii*; *3*, left—*L. remyi*, center—$F_1$, right—*L. micrantha* var. *exigua*; *4*, left—*L. remyi*, center—$F_1$, right—*L. heterophylla*; *5*, left—*L. remyi*, center—$F_1$, right—*L. micrantha* var. *exigua*.

not germinated due to space limitation and because the numbers of selfs were not recorded, no attempt was made to quantify crossability. Nevertheless, it seemed about equally easy to produce intersectional and infrasectional hybrids. In all cases, observation of meiosis and pollen stainability verified the hybrid origin of plants selected on the basis of morphological intermediacy. This intermediacy of $F_1$ hybrids was very apparent when considering features such as overall habit; foliar characters, including leaf size, shape, and texture (Figures 2–4); and floral characters (Figure 5). Intrasectional hybrids possess disk florets that are characteristic of the section, i.e., either mostly pentamerous (*Aphanopappus*) or tetramerous (*Lipochaeta*), whereas the heads of intersectional hybrids contain about equal numbers of each type of disk floret. Morphological observations of species seen during this study suggest that in addition to features already reported, section *Lipochaeta* characteristically has round stems whereas those of section *Aphanopappus* are normally angulate. Chromosome numbers of plants determined during this study (Table 1) confirm earlier reports. In addition, chromosome numbers of four taxa (*L. lobata* var. *leptophylla*, $n = 26$; *L. dubia*, *L. tenuis*, *L. venosa*, all $n = 15$) are reported here for the first time.

*Cytogenetics of Intrasectional Diploid Hybrids*

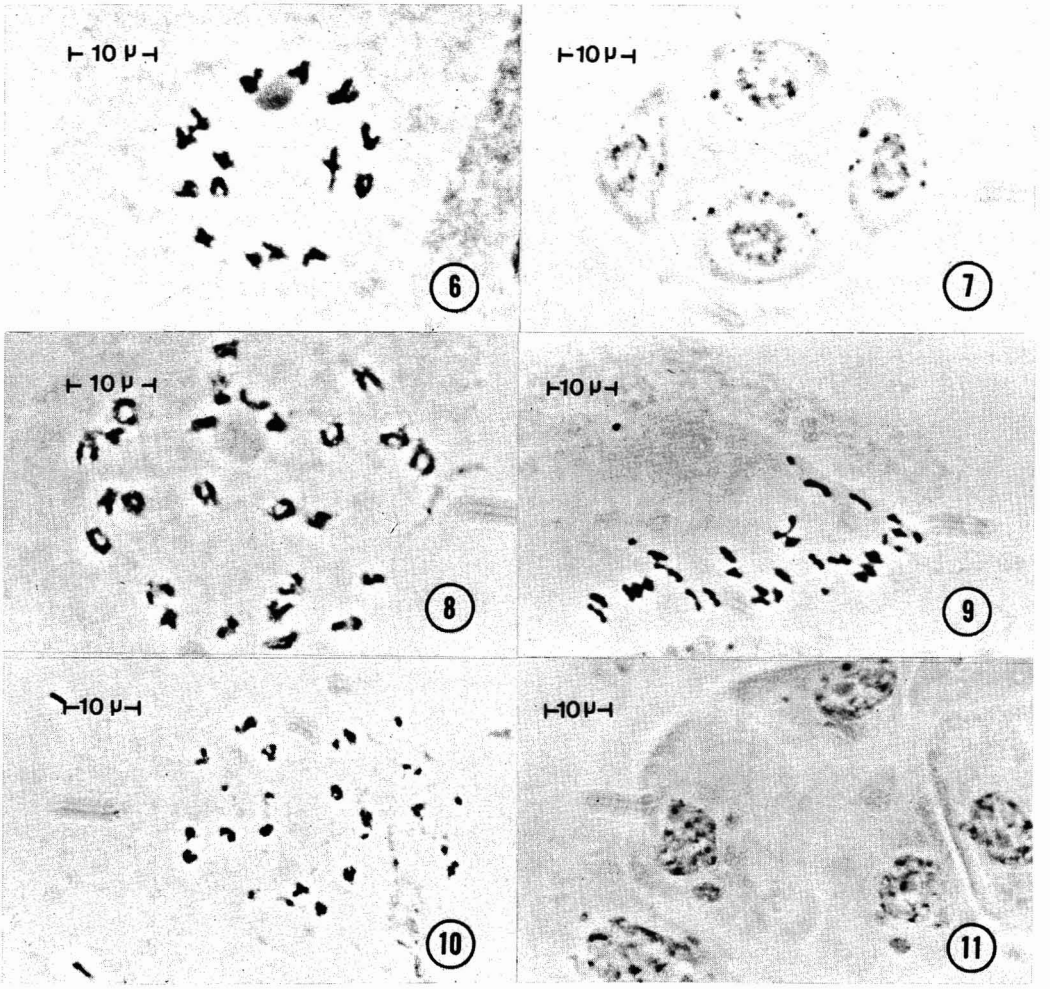
Six different intrasectional diploid hybrids were produced (Figure 1). Of these, 85 individuals in 10 progenies were grown to flowering maturity; 16 of these plants were studied meiotically and 19 were checked for pollen stainability (Table 2). For each combination, 71–198 microsporocytes were clear enough to be analyzed at meiosis. The most common chromosomal configuration seen at diakinesis and metaphase I was 15 bivalents (Figure 6). This configuration was observed in a total of 751 microsporocytes (Table 2). In 13 cells from hybrids of three combinations, $14_{II}$ and $2_I$ were observed (Table 2). Two combinations also displayed the maximum number of four unpaired chromosomes in a total of four cells (Table 2). An association of four chromosomes apparently involving nucleolar organizing chromosomes in one cell of the hybrid *L. integrifolia* × *L. lavarum* was considered the result of stickiness rather than chiasma formation. Anaphase I and subsequent stages appeared normal except for the exclusion of chromosomal material from telophase I nuclei in one cell of the hybrid *L. remyi* × *L. lavarum* and occasional laggards at telophase I and II. Normal tetrads (Figure 7) are consistently formed in intrasectional hybrids. The mean pollen stainability is high, ranging from 80

TABLE 2

SUMMARY OF MEIOTIC CHROMOSOME ASSOCIATIONS AND POLLEN STAINABILITIES OF DIPLOID INFRASECTIONAL $F_1$ HYBRIDS OF *Lipochaeta* SECTION *Aphanopappus*

| HYBRID COMBINATION | NUMBER OF PLANTS STUDIED* | NUMBER OF MICROSPOROCYTES RESOLVED | MEIOTIC CONFIGURATION, NUMBER OF CELLS WITH | | | POLLEN STAINABILITY (%) | | |
|---|---|---|---|---|---|---|---|---|
| | | | $15_{II}$ | $14_{II} + 2_I$ | $13_{II} + 4_I$ | MIN. | MAX. | $\bar{x}$ |
| *L. tenuis* × *L. lavarum* | 1 (1) | 111 | 110 | 1 | 0 | 80 | 80 | 80 |
| *L. remyi* × *L. integrifolia* | 3 (4) | 156 | 156 | 0 | 0 | 82 | 97 | 87 |
| *L. remyi* × *L. lavarum* | 6 (7) | 198 | 192 | 5 | 1 | 66 | 97 | 87 |
| *L. remyi* × *L. micrantha* var. *exigua* | 2 (2) | 71 | 71 | 0 | 0 | 95 | 99 | 97 |
| *L. micrantha* var. *exigua* × *L. integrifolia* | 3 (3) | 128 | 128 | 0 | 0 | 96 | 99 | 98 |
| *L. integrifolia* × *L. lavarum* | 1 (2) | 104 | 94 | 7 | 3 | 99 | 100 | 100 |

*The first number indicates the number of individuals analyzed cytologically; the number in parentheses indicates the number of individuals checked for pollen stainability.




FIGURES 6–11. Meiosis in infrasectional and intersectional hybrids of *Lipochaeta*. *6*, diakinesis in infrasectional diploid hybrid *L. micrantha* var. *exigua* × *L. integrifolia*, note $15_{II}$; *7*, tetrad in infrasectional hybrid *L. remyi* × *L. lavarum*; *8*, diakinesis in infrasectional tetraploid hybrid *L. lobata* var. *lobata* × *L. rockii*, note $26_{II}$; *9*, metaphase I in intervarietal tetraploid hybrid *L. lobata* var. *lobata* × *L. lobata hastulatoides*, note $26_{II}$ and six univalent B chromosomes; *10*, diakinesis in intersectional hybrid *L. connata* var. *connata* × *L. remyi*, note $15_{II} + 11_{I}$; *11*, polyad in intersectional hybrid *L. succulenta* × *L. remyi*.

to 100 percent (Table 2). The production of viable fruits by the two diploid hybrids checked (Table 3) further documents the fertile nature of the hybrids in this category.

### *Intrasectional Tetraploid Hybrids*

At the tetraploid level, eight hybrid combinations were produced (Figure 1), of which 70 individuals in 10 progenies were grown to flowering maturity. Of these, 21 were analyzed meiotically and 23 were analyzed for pollen stainability. Cytological analyses at diakinesis and metaphase I in intrasectional tetraploid hybrids revealed 26 bivalents in 860 microsporocytes (Figure 8), $25_{II} + 2_{I}$ in 14 cells, and $24_{II} + 4_{I}$ in one cell (Table 4). An association of four chromosomes was found at the nucleolus in one cell each of the hybrids *Lipochaeta succulenta* ×

TABLE 3

FERTILITY DATA BASED ON ACHENE SET OF INFRASECTIONAL AND INTERSECTIONAL $F_1$ HYBRIDS IN *Lipochaeta*

| HYBRID COMBINATION | NUMBER OF INDIVIDUALS SELFED | NUMBER OF HEADS POLLINATED | NUMBER OF GOOD ACHENES | NUMBER OF GOOD ACHENES PER HEAD |
|---|---|---|---|---|
| Tetraploids | | | | |
| *L. lobata* var. *lobata* × *L. rockii* | 3 | 10 | 41 | 4.1 |
| *L. connata* var. *connata* × *L. rockii* | 1 | 10 | 10 | 1.0 |
| Diploids | | | | |
| *L. remyi* × *L. lavarum* | 2 | 26 | 133 | 5.1 |
| *L. remyi* × *L. micrantha* var. *exigua* | 1 | 5 | 8 | 1.6 |
| Triploids | | | | |
| *L. remyi* × *L. lobata* var. *lobata* | 1 | 15 | 0 | 0 |
| *L. connata* var. *connata* × *L. remyi* | 3 | 24 | 0 | 0 |

NOTE: The trends apparent here are substantiated by many more unquantified observations in each major category, especially the triploids.

TABLE 4

SUMMARY OF MEIOTIC CHROMOSOME ASSOCIATIONS AND POLLEN STAINABILITIES OF TETRAPLOID INFRASECTIONAL $F_1$ HYBRIDS OF *Lipochaeta* SECTION *Lipochaeta*

| HYBRID COMBINATION | NUMBER OF PLANTS STUDIED* | NUMBER OF MICROSPOROCYTES RESOLVED | MEIOTIC CONFIGURATION, NUMBER OF CELLS WITH | | | POLLEN STAINABILITY (%) | | |
|---|---|---|---|---|---|---|---|---|
| | | | $26_{II}$ | $25_{II} + 2_I$ | $24_{II} + 4_I$ | MIN. | MAX. | $\bar{x}$ |
| *L. connata* var. *connata* × *L. rockii* | 1 (1) | 121 | 121 | 0 | 0 | 80 | 80 | 80 |
| *L. lobata* var. *hastulatoides* × *L. lobata* var. *lobata* | 4 (3) | 66 | 66 | 0 | 0 | 77 | 89 | 83 |
| *L. lobata* var. *lobata* × *L. rockii* | 3 (6) | 272 | 261 | 10 | 1 | 67 | 97 | 89 |
| *L. heterophylla* × *L. connata* var. *connata* | 5 (4) | 85 | 84 | 1 | 0 | 91 | 98 | 95 |
| *L. succulenta* × *L. heterophylla* | 3 (2) | 196 | 195 | 0 | 0 | 95 | 99 | 97 |
| *L. succulenta* × *L. connata* var. *connata* | 1 (1) | 39 | 38 | 1 | 0 | 97 | 97 | 97 |
| *L. lobata* var. *lobata* × *L. connata* var. *connata* | 2 (2) | 68 | 66 | 1 | 0 | 97 | 100 | 99 |
| *L. lobata* var. *lobata* × *L. heterophylla* | 2 (4) | 30 | 29 | 1 | 0 | 98 | 100 | 99 |

*The first number indicates the number of individuals analyzed cytologically; the number in parentheses indicates the number of individuals checked for pollen stainability.

*L. heterophylla* and *L. lobata* var. *lobata* × *L. connata* var. *connata*. As in the case of the diploid hybrid mentioned earlier, this association is interpreted as the result of stickiness of nucleolar organizing arms of chromosomes rather than chiasma formation. Later stages of meiosis were basically normal with occasional lagging chromosomal material at telophase I and II. Up to seven B chromosomes (compare six in Figure 9) were found in the combination *L. lobata* var. *lobata* × *L. lobata* var. *hastulatoides* and these are probably responsible for a slight decrease in the pollen stainability of this hybrid. The mean pollen stainability for tetraploid hybrids ranged from 80 to 99 percent (Table 4). The fertility of hybrids in this category was also indicated by the production of viable achenes in the two hybrid combinations checked (Table 3).

*Intersectional Triploid Hybrids*

Forty-six intersectional triploid hybrid individuals of seven hybrid combinations were grown to flowering maturity (Figure 1). Of these, 9 individuals were analyzed meiotically and 17 were checked for pollen stainability (Table 5, Figure 10). In addition to these artificial hybrids, material of one field-collected hybrid combination was analyzed. Although many microsporocytes exhibited some degree of stickiness, the apparent maximum chromosome association of 15 bivalents and 11 univalents was seen in 107 resolvable cells at diakinesis and metaphase I (Table 5). The same meiotic configuration was observed in microsporocytes of the field-collected natural hybrid, indicating that it is indeed an intersectional hybrid. The subsequent stages were greatly disturbed due to the presence of laggard chromosomes, and their uneven distribution resulted in polyad formation (Figure 11). Not one normal tetrad was formed among the hundreds of cells studied. The average mean pollen stainability was low, ranging from 1 to 11 percent (Table 5), and in spite of many selfing attempts, no filled achenes were recovered from triploid hybrids (Table 3).

## DISCUSSION

The lack of internal reproductive barriers between species of the same section, as indicated by the hybridization program (Figure 1), suggests that geographical and ecological barriers are important in maintaining species of the genus *Lipochaeta*. A similar circumstance was reported by Gillett and Lim (1970) in *Bidens*, which exhibits great morphological and ecological diversity without genetic barriers. These authors attributed the absence of fertile natural hybrids to the lack of habitat juxtaposition of the parent species. This explanation appears to apply equally well to the situation in the genus *Lipochaeta*. In fact, only one instance of natural hybridization has been reported, and this involves species from the different sections of the genus that are isolated by the sterility of the triploid $F_1$. Thus, under the present circumstances, natural hybridization between species is at most very rare. However, if future conditions permit contact between species of the same section, the lack of internal barriers could allow free gene flow and recombination that could lead to further speciation.

Gardner (1977) proposes three alternatives

TABLE 5

SUMMARY OF MEIOTIC CHROMOSOME ASSOCIATIONS AND POLLEN STAINABILITIES OF TRIPLOID INTERSECTIONAL $F_1$ HYBRIDS OF *Lipochaeta*

| HYBRID COMBINATION | NUMBER OF PLANTS STUDIED* | NUMBER OF MICRO-SPOROCYTES RESOLVED | MEIOTIC CONFIGURATION, NUMBER OF CELLS WITH | POLLEN STAINABILITY (%) | | |
|---|---|---|---|---|---|---|
| | | | $15_{II} + 11_I$ | MIN. | MAX. | $\bar{x}$ |
| *L. remyi* × *L. rockii* | 1 (2) | 16 | 16 | 1 | 1 | 1 |
| *L. lobata* var. *lobata* × *L. integrifolia* | 1 (1) | 19 | 19 | 2 | 2 | 2 |
| *L. succulenta* × *L. remyi* | 0 (2) | 0 | 0 | 4 | 7 | 6 |
| *L. remyi* × *L. lobata* var. *lobata* | 2 (4) | 8 | 8 | 3 | 10 | 6 |
| *L. heterophylla* × *L. remyi* | 3 (2) | 47 | 47 | 2 | 11 | 7 |
| *L. connata* var. *connata* × *L. remyi* | 2 (4) | 17 | 17 | 3 | 13 | 9 |
| *L. connata* var. *connata* × *L. lavarum* | 0 (2) | 0 | 0 | 8 | 14 | 11 |

*The first number indicates the number of individuals analyzed cytologically; the number in parentheses indicates the number of individuals checked for pollen stainability.

to account for the two cytotypes, i.e., the diploid and tetraploid sections of *Lipochaeta*. The first hypothesis states that the two cytotypes have no common ancestor. Gardner rejects this explanation based on the occurrence of a natural hybrid between *L. lobata* var. *lobata* and *L. integrifolia*. The production of intersectional hybrids in this study and the production of intergeneric hybrids between *Wedelia biflora* and the two sections of *Lipochaeta* (Rabakonandrianina 1979) clearly demonstrates the common origin of the two sections of *Lipochaeta*.

The second alternative Gardner (1977) proposes is that the 26-paired cytotype arose through chromosomal doubling of a 15-paired ancestor, followed by aneuploid reduction. Gardner (1976) argues in favor of such an autopolyploid origin of section *Lipochaeta* on the basis of the presence of B chromosomes in species of this section, which he interprets as fragments resulting from aneuploid reduction. However, this argument is weakened by reports of B chromosomes in *Wedelia*, e.g., *W. brasiliensis* (Turner and Irwin 1960) and *W. trilobata* (Powell and King 1969), and in diploid species of *Lipochaeta* (Table 1 and Gardner 1977). The lack of quadrivalent formation in tetraploid species and in triploid hybrids does not support the hypothesis of an autotetraploid origin of section *Lipochaeta*, especially in view of the common occurrence of quadrivalents of artificially induced autotetraploids of *L. remyi* (Rabakonandrianina 1979). However, one cannot exclude the possibility of the autotetraploid origin of section *Lipochaeta* on this basis alone, because selection for preferential bivalent pairing in autotetraploids has been demonstrated in some cases (Gilles and Randolph 1951).

Gardner's third alternative suggests that the 26-paired cytotype of *Lipochaeta* arose as an allopolyploid hybrid between a 15-paired *Lipochaeta* or a 15-paired *Lipochaeta*-like ancestor and an unknown 11-paired taxon. Carr (1978) favors the latter position. Carr's argument is based on the absence of intermediate numbers between $n = 30$ and $n = 26$ in *Lipochaeta* and on the occurrence of the overlapping array of chromosome numbers in *Wedelia*. The cytogenetic evidence presented herein strongly suggests an allopolyploid hybrid origin of the 26-paired section, i.e., it supports the third hypothesis of Gardner (1977). The consistent occurrence of $15_{II}$ and $11_{I}$ in all nine hybrids of seven combinations involving diploid and tetraploid parents indicates that a subgenome of the tetraploids ($n = 26$) is equivalent to the genome of the diploids ($n = 15$). The meiotic configuration of the intersectional hybrid in *Lipochaeta* is a typical *Drosera* scheme configuration that is often observed in triploid hybrids involving allotetraploid and diploid species (W. V. Brown 1972).

A situation somewhat similar to that of *Lipochaeta* is found in *Picradeniopsis* (Stuessy, Irving, and Ellison 1973). *Picradeniopsis oppositifolia* and *P. woodhousei* are allopatric species, consistently distinct in morphological, chemical, and cytological aspects. *Picradeniopsis oppositifolia* is a tetraploid ($n = 24$) whereas *P. woodhousei* is a diploid ($n = 12$). Intermediate natural hybrids were found in areas where the two species overlap, and their cytogenetic analyses revealed $12_{II} \times 12_{I}$ with an average pollen stainability of 1–11 percent. Stuessy et al. (1973) conclude that these were $F_1$ hybrids and that *P. oppositifolia* arose through allopolyploidy involving *P. woodhousei* and an unknown diploid, the morphological and chemical characters of which could be tentatively reconstructed by extrapolation.

Other examples have been reported, e.g., *Viola* (Stebbins et al. 1963) and *Coreopsis* (Crawford 1970), where the hybrid origin of a species could be ascertained with chemical studies. The similarity of the case of *Coreopsis* to that of *Lipochaeta* bears further discussion. The populations of the *C. mutica* complex of central Mexico comprise two taxa: *C. mutica* var. *leptomera*, a tetraploid with $2n = 56$, and *C. mutica* var. *mutica*, an octoploid with $2n \approx 112$. The difference in ploidy level between the two entities is associated with consistent morphological distinctions and a striking qualitative difference in leaf flavonoid chemistry. The tetraploid *C.*

*mutica* var. *leptomera* always has three-lobed leaves and relatively small heads and produces only flavones. The octoploid var. *mutica* possesses both simple and three-lobed leaves and large heads and always synthesizes flavonols and anthoclors in addition to flavones. Because of their isolation from the remaining members of the complex, a direct autopolyploid origin of the octoploid var. *mutica* from the tetraploid var. *leptomera* was envisaged until experimental hybridization of var. *leptomera* and var. *microcephala*, a distant tetraploid member of the complex with distinct morphology and chemistry, yielded $F_1$ hybrids virtually identical to var. *mutica* in morphology and chemistry. The only drawback is that *C. mutica* var. *leptomera* and var. *microcephala* are presently widely separated geographically.

As in *Picradeniopsis* and *Coreopsis*, cytological data and additional sources of evidence support the view of an allopolyploid origin of the tetraploid section in *Lipochaeta*. The additional sources of evidence include the qualitative morphological features such as stem cross section and lobing of disk corollas and the striking qualitative differences in leaf flavonoid chemistry that distinguish the two sections. It seems unlikely that these pronounced and consistent differences would be found in plants of recent autotetraploid origin within the Hawaiian Islands as suggested by Gardner (1976).

The crossability of each section of *Lipochaeta* with each of two diverse elements of the extra-Hawaiian genus *Wedelia* (*W. biflora*, $n = 15$, and *W. trilobata*, $n = 28$; Rabakonandrianina 1979) strongly infers the origin of both sections of *Lipochaeta* from the latter genus. Moreover, the pollen stainability of these hybrids indicates a stronger relationship between *Wedelia* and each section of *Lipochaeta* than between the two sections of *Lipochaeta*. These facts and the observation of $15_{II}$ and $11_I$ in hybrids between the two sections of *Lipochaeta* and in hybrids between section *Lipochaeta* and *Wedelia biflora* (Rabakonandrianina 1979) argue more strongly for an allopolyploid origin of section *Lipochaeta* than for an origin through autotetraploidy followed by aneuploid reduction to $n = 26$. In view of evidence presented here and elsewhere (Rabakonandrianina 1979), the statement by Gardner (1976:386) that "the two chromosomal complexes in *Lipochaeta* are much more similar to each other than to any other species group of *Wedelia*" appears unfounded. Indeed, it seems that each genome of *Lipochaeta* has a match within the genus *Wedelia* and that section *Lipochaeta* probably arose through extra-Hawaiian allopolyploidy involving a *Lipochaeta*-like 15-paired species and an unknown 11-paired species of *Wedelia*. All the cytotypes necessary for this hypothesis are known to occur in *Wedelia* (Carr 1978) and the only remaining task necessary to provide conclusive documentation is to determine the 11-paired genome involved through hybridization studies.

ACKNOWLEDGMENT

The author expresses her thanks to Gerald D. Carr for his advice and assistance in this research.

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