
CONTRASTING PATTERNS AND PROCESSES OF EVOLUTIONARY CHANGE IN THE TARWEED–SILVERSWORD LINEAGE: REVISITING CLAUSEN, KECK, AND HIESEY’S FINDINGS¹ *Bruce G. Baldwin*²

ABSTRACT

Jens C. Clausen, David D. Keck, and William M. Hiesey’s biosystematic research on continental tarweeds (Madiinae; Compositae) provided diverse examples of evolutionary change for Clausen’s synthesis, *Stages in the Evolution of Plant Species*. Subsequent anatomical work by Sherwin Carlquist demonstrated that the tarweed lineage also includes a spectacular example of adaptive radiation, the Hawaiian silversword alliance. Molecular phylogenetic data and evidence from genetic and hybridization studies have allowed additional perspectives on Clausen et al.’s and Carlquist’s hypotheses of tarweed–silversword evolution. In Californian *Layia*, Clausen et al.’s evidence for gradual allopatric diversification for the $n = 7$ taxa accords with patterns of molecular divergence and decay of interfertility across lineages inferred from a rate-constant rDNA tree. In contrast, recent evidence on patterns and timing of diversification in an $n = 8$ *Layia* clade indicates multiple examples of accelerated phenotypic evolution, unresolved by Clausen et al., that evidently reflect rapid “budding off” of morphologically distinct lineages in ecologically novel settings. In rDNA trees of Californian *Holocarpha*, lineages representing different cryptic biological species, documented by Clausen, appear to predate the origin of a morphologically and ecologically distinctive taxon (*H. macradenia* (DC.) Greene) that retains interfertility with relatives of ancestral phenotype; at fine-scale levels of divergence, a disconnect is evident between evolution of intrinsic, post-mating reproductive barriers and phenotypic evolution in *Holocarpha*. Clausen’s evidence for strong intersterility barriers between the mostly annual, continental species of the “Madia” lineage contrasts with Gerald D. Carr and Donald W. Kyhos’s subsequent finding of partial to full interfertility between the phenotypically disparate, insular species of the Hawaiian silversword alliance, a monophyletic group that descended from continental ancestors in the “Madia” lineage. Molecular phylogenetic data indicating major ecological changes associated with diversification, a brief timeframe for diversification, and a shift to woodiness in the ancestry of the silversword alliance uphold Carlquist’s hypothesis of adaptive radiation of the group and help explain the lack of substantial, internal barriers to gene flow across lineages therein. Results of recent investigations have shown that highly dynamic evolutionary change in Madiinae, both in phenotypic characters and in modes and patterns of diversification, extends to even finer-scale evolutionary levels than indicated by Clausen et al.’s elegant studies. In general, current evidence on diversification in Madiinae appears to be consistent with Clausen et al.’s views concerning the importance of ecological factors in incipient evolutionary divergence. Phylogeny of Madiinae is no longer the intractable problem perceived by Clausen; relatively little is known about the biological basis for the extreme evolutionary propensities of tarweeds.

Key words: Adaptive radiation, cryptic diversity, diversification, edaphic endemism, *Holocarpha*, *Layia*, *Madia*, Madiinae, peripheral isolates, reproductive isolation, speciation.

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Contrasting modes of diversification (speciation) have been suggested to explain evolutionary change within different lineages of subtribe Madiinae (Compositae), a monophyletic plant group of 119 species commonly known as tarweeds (see Baldwin, 2003a). The name “tarweed” belies the great morphological and ecological breadth of plant life encompassed by Madiinae, especially by the Hawaiian silversword alliance, a famous example of adaptive radiation (see Baldwin, 2003b, c). The Californian or continental tarweeds, in general, are less diverse ecologically than the silversword alliance but contain about three-fold more recognized species and have been under evolutionary investigation far longer than have the Hawaiian taxa. A recent book, *Tarweeds & Silverswords: Evolution of the Madiinae (Asteraceae)*, includes extensive reviews on natural history, morphological and taxonomic diversity, chromosome evolution, hybridization, glandular structures, leaf and wood anatomy, secondary chemistry, molecular evolution, conservation genetics, evolutionary relationships, and processes of diversification in Californian and Hawaiian Madiinae (Carlquist et al., 2003).

The first evolutionary studies of tarweeds began at the Carnegie Institution of Washington at Stanford, California, with pioneering biosystematic investigations by Harvey Monroe Hall and E. B. Babcock on *Hemizonia* DC. (Babcock & Hall, 1924) and by Hall and his two junior colleagues David D. Keck and William M. Hiesey on various lineages of Madiinae (Hall, 1932). Hall recruited Danish plant evolutionist Jens Clausen to join the research team at the Carnegie Institution in 1931; Clausen assumed the position of principal researcher four months later, following Hall’s untimely death in 1932, and pursued decades of tarweed research there as leader of the renowned Clausen, Keck, and Hiesey team (see French, 1989).

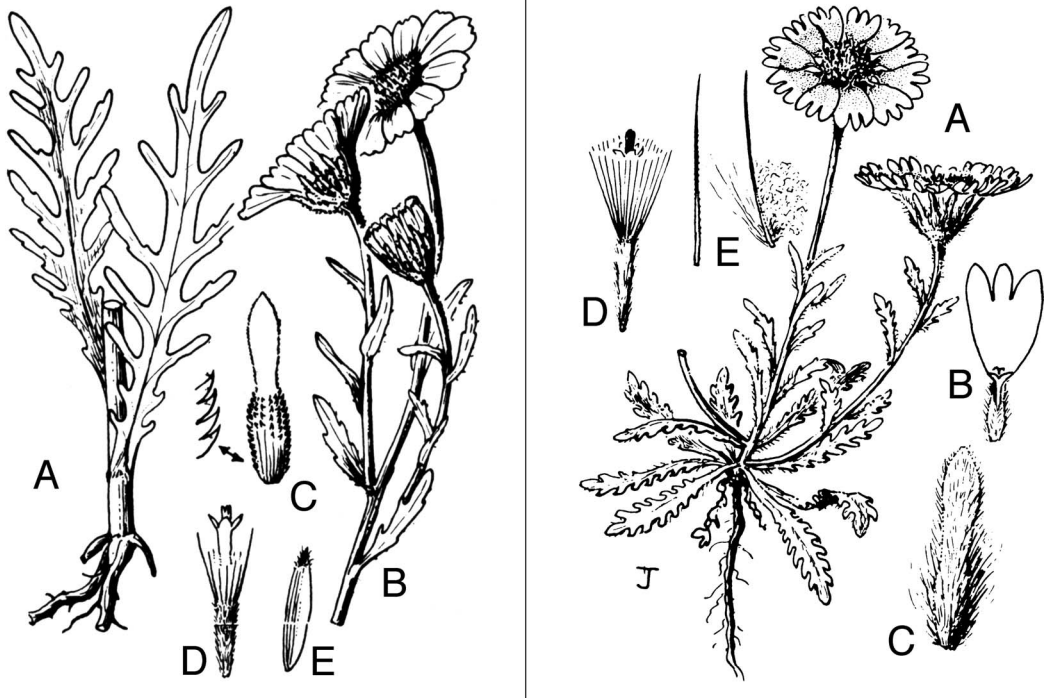
Clausen, Keck, and Hiesey are best known for their reciprocal transplant studies along Hall’s (1932) west-east ecological transect of California (e.g., Clausen et al., 1940, 1948), which helped establish the importance of local adaptation in explaining variation in widespread plant species. Less widely appreciated are Clausen, Keck, and Hiesey’s broader interests in understanding how diversity arises in plants and their extensive experimental studies on Californian tarweeds. In his synthesis, *Stages in the Evolution of Plant Species*, Clausen (1951) showed that plant groups recognized by taxonomists as species represent a wide diversity of evolutionary entities that can differ greatly in relative levels of morphological, ecological, and genetic divergence and can arise by distinct processes. Californian tarweeds constitute about half of the evolutionary examples

presented by Clausen in his 1951 book, which has been a major inspiration for generations of Madiinae researchers.

Here, I revisit some of Clausen, Keck, and Hiesey’s hypotheses of evolutionary change in Madiinae and evolutionary hypotheses of subsequent tarweed researchers who, at least in part, based their studies on previous work by one or more members of the Carnegie team. Addition of a molecular phylogenetic framework has proven useful for re-evaluating previously suggested modes of diversification in various groups of Madiinae, bearing in mind the limitations of phylogenetic data for inferring such evolutionary processes (see Losos & Glor, 2003). In light of data from those recent and ongoing studies, I suggest that the contrasts in processes of tarweed evolution so well documented by Clausen, Keck, and Hiesey in comparisons across genera are far more extensive than earlier appreciated. In addition, new molecular perspectives demonstrate that phylogenetic structure in Madiinae extends to finer-scale levels than previously suggested, in part probably reflecting divergence of ecologically distinct lineages that conform, at least in some measure, to Clausen et al.’s (1939, 1940, 1948) ecotype concept.

EVOLUTIONARY CONTRASTS BETWEEN MAJOR LINEAGES OF *LAYIA*

Gradual allopatric divergence in the n = 7 Layia lineage. A widely studied hypothesis of diversification in the California tarweeds considered by Clausen, Keck, and Hiesey concerns the group of taxa in *Layia* Hook. & Arn. ex DC. with seven pairs of chromosomes. Members of *Layia* are spring ephemerals that sometimes have white-tipped ray corollas and are commonly called “tidy-tips” (Figs. 1, 2; see Baldwin, 2003b, c). Clausen et al. (1941) investigated the evolution of *Layia* extensively, in part by examining crossability and interfertility among all members of the genus. Their crossing diagram for *Layia* (Fig. 3) illustrates the intrinsic potential for gene flow estimated from seed set and extent of chromosome pairing in F₁ hybrids. Clausen et al. (1941) regarded taxa with seven pairs of chromosomes, on the left side of the figure, as constituting one of two “major blocks of species” in *Layia*, which in turn was subdivided into three, informal “complexes,” each united by morphological characteristics and moderate levels of interfertility: (1) *L. chrysanthemoides* (DC.) A. Gray and *L. fremontii* (Torr. & A. Gray ex A. Gray) A. Gray, (2) *L. jonesii* A. Gray, *L. leucopappa* D. D. Keck, and *L. munzii* D. D. Keck, and (3) *L. platyglossa* (Fisch. & C. A. Mey.) A. Gray. Stebbins (1949: 232) regarded the interfertile taxa in



Figures 1 and 2. Widely sympatric, \pm intersterile members of *Layia* with seven pairs of chromosomes. Figure 1 (left). *Layia chrysanthemoides*. —A. Base of plant. —B. Capitulescence. —C. Involucral bract (abaxial view). —D. Disk floret. —E. Receptacular bract. Figure 2 (right). *Layia platyglossa*. —A. Habit. —B. Ray floret and enfolding involucral bract (adaxial view). —C. Involucral bract (abaxial view). —D. Disk floret. —E. Pappus elements (two forms).

each of the first two complexes as “species in the state of becoming.”

Stebbins (1966) showcased Clausen, Keck, and Hiesey’s (1941) biosystematic data on the members of *Layia* with $n = 7$ as exemplary of gradual, allopatric divergence (see also Stebbins, 1982). Stebbins (1966) noted that taxa of *Layia* with moderate interfertility are invariably allopatric; in contrast, taxa that are sympatric are moderately to highly intersterile, with reduced chromosome pairing at meiotic metaphase I in F_1 hybrids (Fig. 4). Under the assumption that degree of interfertility reflects recency of common ancestry (a risky premise; see Donoghue, 1985), the patterns shown in Figure 4 are consistent with the hypothesis that sympatric taxa underwent earlier divergence from a common ancestor compared to allopatric taxa or populations in each of the three subgroups, and that sympatry is secondary, following a period of lineage divergence in geographic isolation. Warwick and Gottlieb (1985) re-examined the hypothesis of gradual, allopatric divergence among the $n = 7$ members of *Layia* from the perspective of allozymes. Their results mirrored the findings of Clausen, Keck, and Hiesey (1941) and the scenario

outlined by Stebbins (1966) by showing highly reduced genetic similarities in pairwise comparisons among the three subgroups relative to genetic identities within each group.

A molecular phylogenetic perspective on diversification of the $n = 7$ members of *Layia* based on nuclear ribosomal DNA (rDNA) internal transcribed spacer (ITS) sequences (Fig. 5; Baldwin, 2003a, unpublished) reinforces the evolutionary conclusions of Clausen et al. (1941), Stebbins (1966), and Warwick and Gottlieb (1985). Monophyly of the $n = 7$ group is well supported, as are each of the three subgroups (“complexes”) proposed by Clausen et al. (1941). The tree topology and branch-lengths correspond well to Clausen et al.’s (1941) model of gradual, allopatric diversification, with sympatric taxa being deeply divergent relative to allopatric members of each subgroup and in comparison to lineages in the ($n = 8$) sister-group to the $n = 7$ lineage. The results provide no evidence of accelerated loss of interfertility within any part of the $n = 7$ group, wherein internal barriers to gene flow may well reflect byproducts of gradual evolutionary divergence. Not shown in Figure 5 is the finding (Baldwin, un-

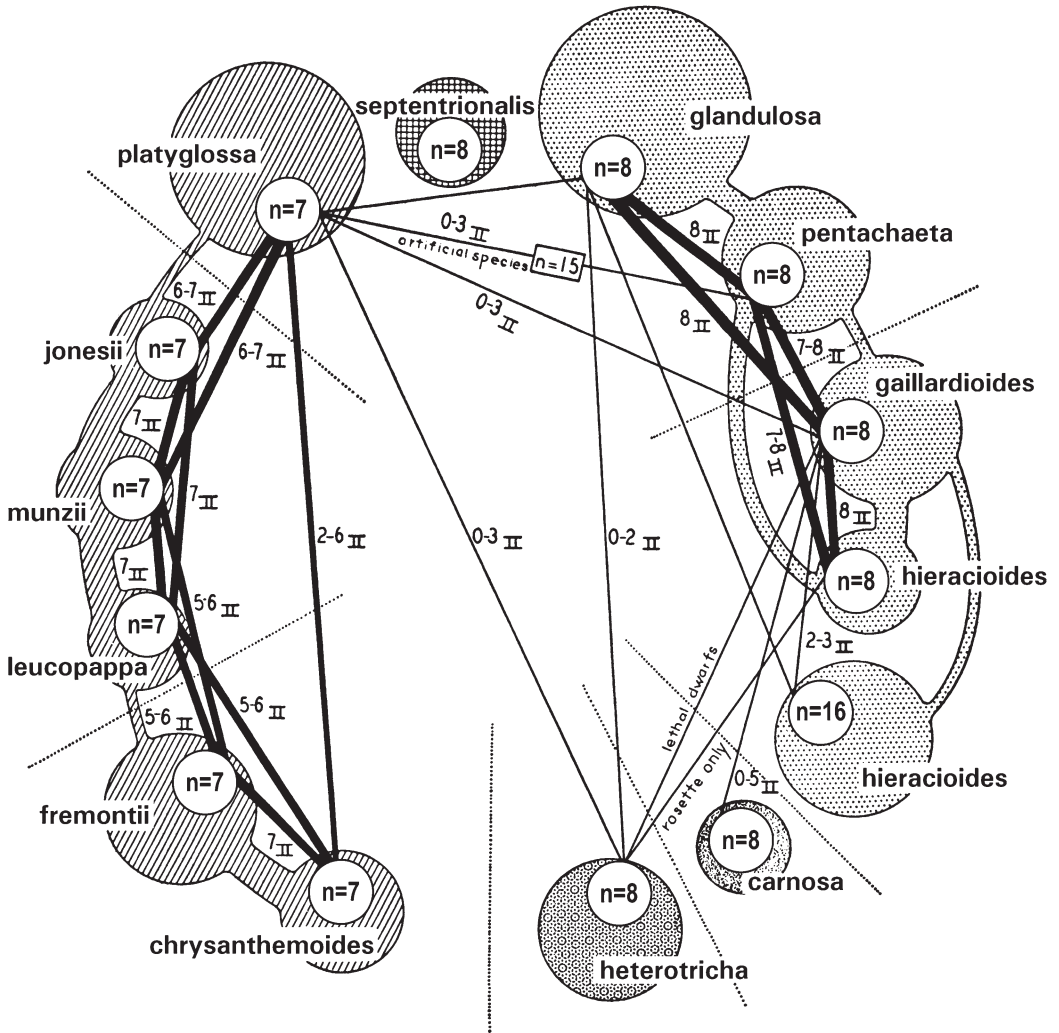


Figure 3. Crossing diagram of *Layia*, adapted from Clausen, Keck, and Hiesey (1941). Circles represent different species; size of circles roughly illustrates relative abundance of each species. Width of shaded connections between species indicates estimated intrinsic potential for gene flow based on seed set in F₁ hybrids. Width of lines connecting species indicates degree of chromosome pairing at meiotic metaphase I in F₁ hybrids; number(s) of meiotic chromosome pairs in F₁ hybrids or vegetative condition of non-flowering hybrids are presented along lines. Dotted lines between species or groups of species indicate major discontinuities in morphological variation. Used by permission of the publisher, Carnegie Institution of Washington.

published) that rDNA sequences from different, often widely separated populations of each species were resolved within a common, monophyletic lineage, as expected under Clausen et al.'s (1941) evolutionary model.

The $n = 7$ lineage of *Layia* evidently conforms to Clausen's view of the "most normal pattern of speciation," with "a more or less simultaneous and gradual separation in morphologic, ecologic, genetic, and cytologic characteristics" (Clausen, 1951: 90). Groups that exhibit approximately rate-constant di-

vergence of characteristics across lineages present minimal problems for systematists; even application of phenetic criteria should provide accurate reconstructions of relationships under such conditions (see Felsenstein, 2004). These attributes are putatively reflected by congruence between Clausen et al.'s (1941) phylogenetic hypotheses for the $n = 7$ *Layia* group (based on essentially phenetic considerations of morphological similarity, chromosome-number similarity, and levels of meiotic chromosome pairing and interfertility) and clades resolved from molecular

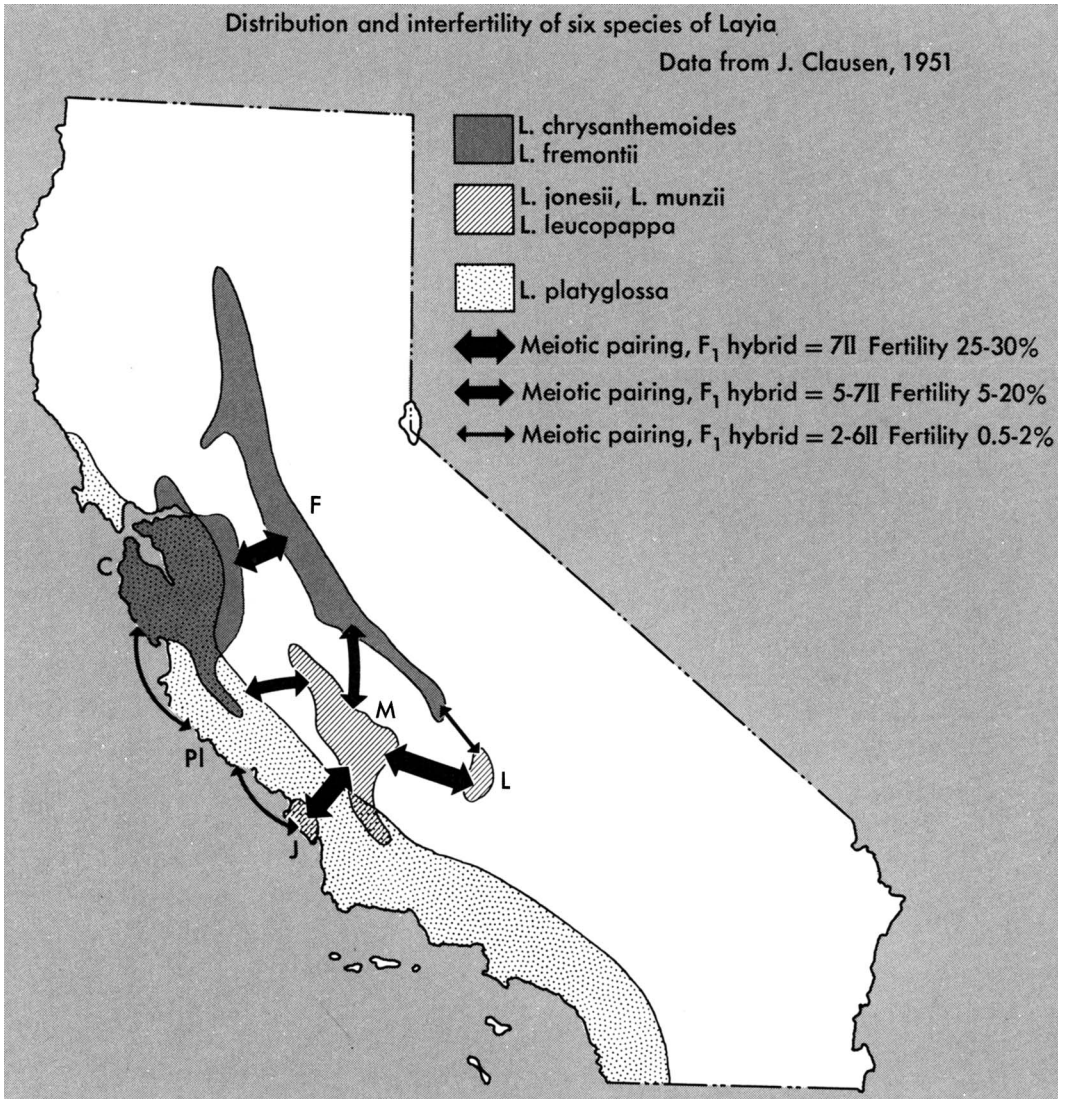


Figure 4. Distributions and interfertilities of species of *Layia* with seven pairs of chromosomes. Letters alongside species distributions correspond to the first letter(s) in species epithet of those taxa (C = *L. chrysanthemoides*; F = *L. fremontii*; J = *L. jonesii*; L = *L. leucopappa*; M = *L. munzii*; PI = *L. platyglossa*). Note moderate to high interfertility of most allopatric species and low interfertility of widely sympatric species. Reprinted from Stebbins (1966), by permission of Pearson Education, Upper Saddle River, New Jersey.

phylogenetic analyses. As noted above, the three $n = 7$ "species complexes" proposed by Clausen et al. (1941) correspond precisely to clades 1–3 in Figure 5; in addition, Clausen (1951: 129–130) indicated that "*Layia platyglossa* is almost a species complex in itself...It is genetically sharply separated from *chrysanthemoides* and *Fremontii* and...is more closely related...to...*leucopappa*, *Munzii*, and *Jonesii*", in complete conformity with the rDNA tree topology (Figure 5).

Accelerated phenotypic divergence in $n = 8$ Layia lineages. In contrast to evidence for gradual, allopatric divergence in the $n = 7$ *Layia* lineage, experimental and molecular data from the congeneric $n = 8$ sister-lineage have revealed multiple examples of taxa that likely arose rapidly in peripheral or otherwise isolated, ecologically distinct settings. Phylogenetic and phenotypic patterns and timing of diversification resolved in two $n = 8$ sublineages are similar, at least in part, to expected outcomes of

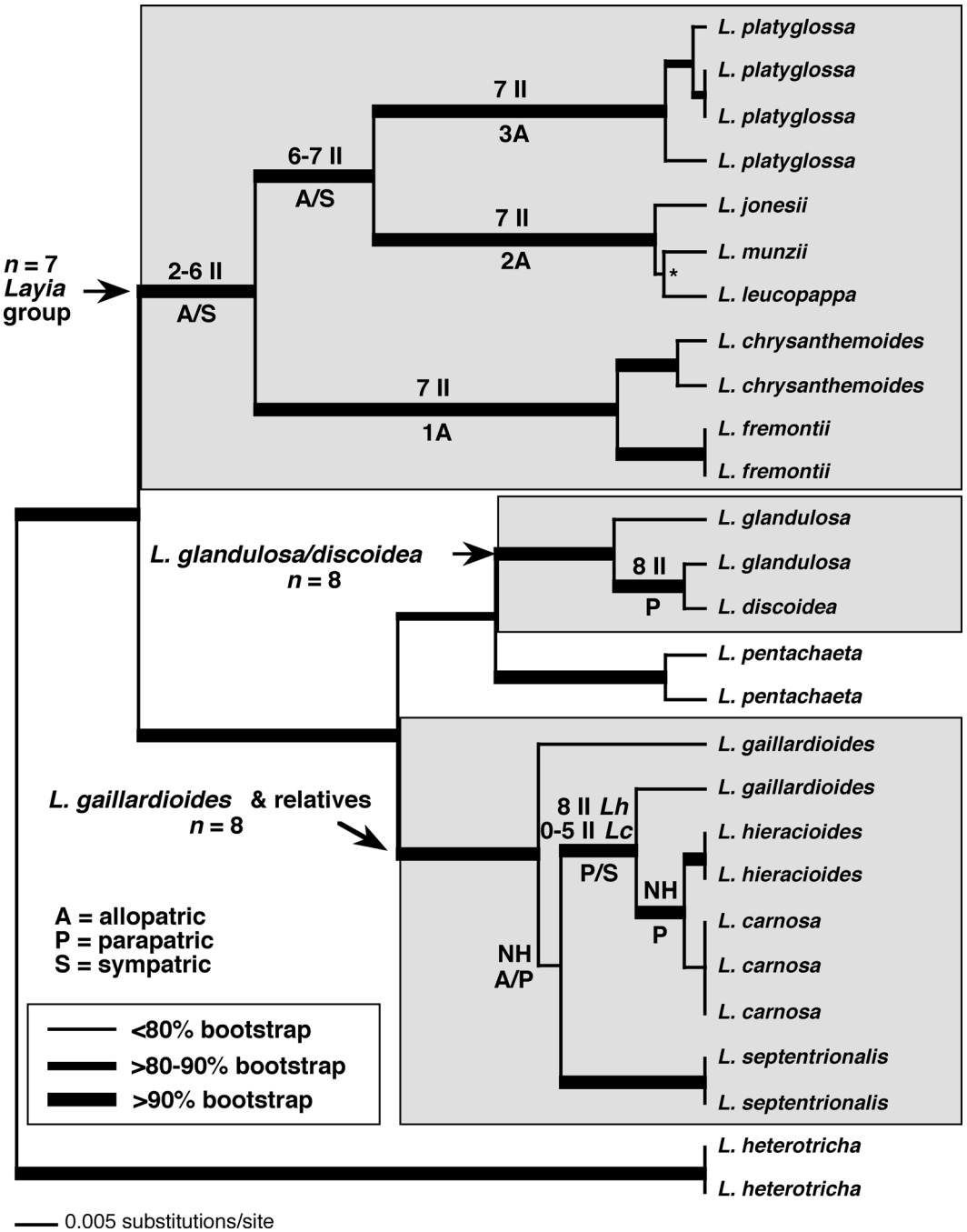
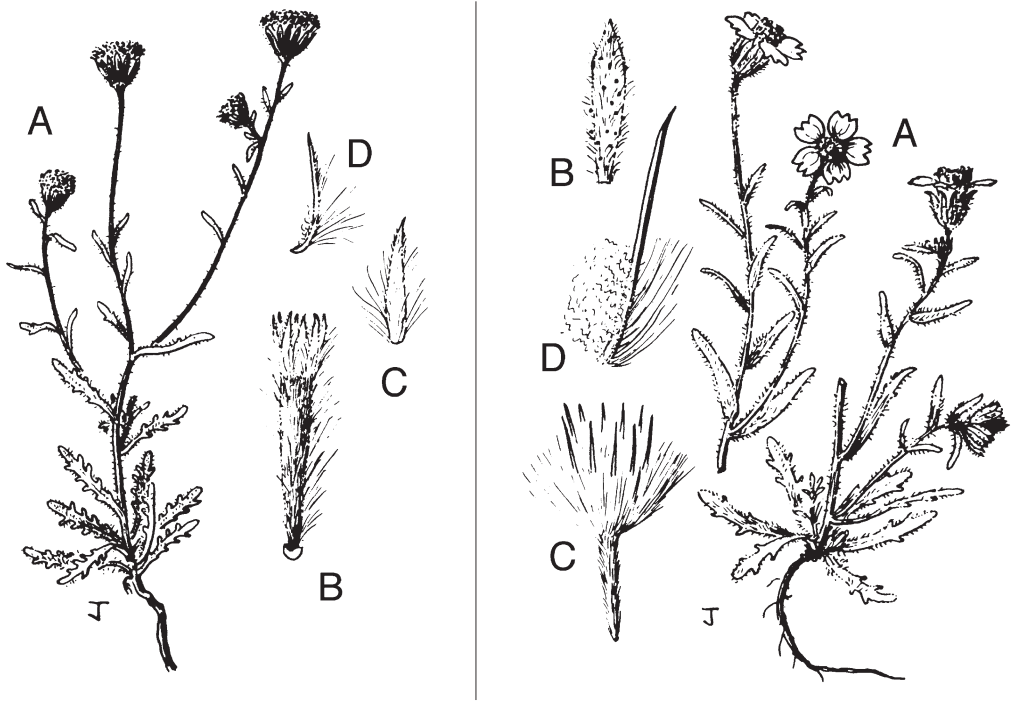


Figure 5. Phylogenetic hypothesis for *Layia* based on nuclear 18S–26S rDNA internal transcribed spacer sequences (Baldwin, 2003a, unpublished); one of two maximally parsimonious trees (* = clade unresolved in strict consensus tree). Branch lengths correspond to relative time since divergence, under maximum-likelihood optimization; rate constancy of ITS evolution across lineages could not be rejected using Felsenstein’s (1988) likelihood-ratio test. In the $n = 7$ group, clades 1A, 2A, and 3A represent Clausen et al.’s (1941) three “complexes” of allopatric species, discussed in the text. Numbers of meiotic chromosome pairs in F_1 hybrids between taxa in a clade are indicated above branches (Lh = hybrid with diploid *L. hieracioides*; Lc = hybrid with *L. carnosa*; NH = no hybrids reported), based on Clausen et al.’s (1941) crossing data for *Layia* (see Fig. 3). The tree was rooted using *Arnica mollis* Hook., *Hulsea algida* A. Gray, *Raillardella pringlei* Greene, and *Adenothamnus validus* (Brandege) D. D. Keck as the outgroup. Terminal taxa of the same name represent geographically disjunct populations. See Appendix 1 for authorship of species names not mentioned in text.



Figures 6 and 7. Ecologically distinct, interfertile members of *Layia* with eight pairs of chromosomes. Figure 6 (left). *Layia discoidea*. —A. Habit. —B. Fruit with pappus. —C. Pappus element (abaxial view). —D. Pappus element (lateral view). Figure 7 (right). *Layia glandulosa*. —A. Habit (bisected). —B. Involucral bract. —C. Fruit with pappus. —D. Pappus element (lateral view).

peripatric speciation (Mayr, 1982), quantum evolution (Simpson, 1944), or quantum speciation (Grant, 1963, 1971; Lewis, 1966), as discussed below.

Evolutionary divergence on a local geographic scale in general has been widely suggested to be of major importance in plant evolution (e.g., Ehrlich & Raven, 1969; Levin, 1993), although convincing phylogenetic evidence for a putatively common pattern of local diversification, i.e., “budding off” of distinctive, new lineages from within a relatively uniform set of related lineages, is usually lacking in studies of suspected “progenitor–derivative” species pairs (see Gottlieb, 2004). Expected paraphyly of a widespread “progenitor” species relative to a “derivative” isolate in some models of local diversification may fail to be resolved in phylogenetic analyses because of insufficiently high rates of evolution in the characters under study, extinction or inadequate sampling of populations (see Neigel & Avise, 1986), or gene flow among lineages within the paraphyletic progenitor taxon (e.g., for genes under strong selection; see Rieseberg & Burke, 2001). Based on various theoretical considerations, Rieseberg & Brouillet (1994) suggested that paraphyly of plant species may be common. Gottlieb (2004) listed 31

examples of species pairs in plants that represent putative examples of lineages wherein one species descended from ancestors in another; he discussed evidence for budding-off of three annual, diploid species of angiosperms, including an $n = 8$ member of *Layia*, *L. discoidea* D. D. Keck.

The best-studied hypothesis of rapid evolution among the $n = 8$ *Layia* taxa concerns the origin of *L. discoidea* (Fig. 6), which is morphologically so unusual that it was not initially recognized to be a tarweed—and was about to be described in a monotypic genus (“Roxira,” for co-discoverers Roxana S. Ferris and Ira L. Wiggins)—until Clausen et al. (1941) observed some similarities with tarweeds and subsequently found that the plant was completely interfertile with *L. glandulosa* (Hook.) Hook. & Arn. (Fig. 7). Despite being fully interfertile, *L. glandulosa* and *L. discoidea* differ greatly in morphology and ecology. For example, like most tarweeds, *L. glandulosa* has ray florets and involucral bracts; *L. discoidea* lacks both ray florets and true involucral bracts, with marginal receptacular bracts constituting a false involucre. The two taxa also differ substantially in features of the pappus. *Layia glandulosa* occurs mostly in coarse, sandy soils, including sand dunes,

in semi-arid and montane regions of California and the western deserts; *L. glandulosa* has the widest distribution of any obligate outcrosser in Madiinae (see Baldwin, 2003b, c). *Layia discoidea* is confined to serpentine barrens in a small region of the Inner South Coast Ranges of California (San Benito and western Fresno counties). Serpentine erodes to clay (structurally unlike the sandy habitats of *L. glandulosa*), has a high magnesium/calcium ratio unfavorable for most plants, is low in some essential plant nutrients, and contains concentrations of heavy metals that can be toxic to angiosperms (see Kruckeberg, 2002). Approximately 9% of minimal-rank vascular plant taxa (species, subspecies, and varieties) endemic to the California Floristic Province are confined to serpentines (Kruckeberg, 1992) and have been interpreted either as products of recent, *in situ* evolution (neoendemics) or as evolutionary relicts (paleoendemics) that became secondarily restricted to serpentine habitats, possibly by competition or interference with other taxa, in association with late Cenozoic climatic changes (see Raven & Axelrod, 1978).

On the basis of morphological and ecological considerations, Clausen (1951: 82) concluded that *Layia discoidea* was "probably an edaphic race (of *L. glandulosa*) adapted to the serpentine soil, and possibly an ancient relict." Clausen et al. (1947: 121) were unable to resolve the relationship between the two taxa: "There is no way of determining which race was first, the rare, inconspicuous one from the serpentine (*L. discoidea*), or the common, showy one from sandy habitats (*L. glandulosa*)."

In the 1980s, Gottlieb and colleagues revisited the origin and age of *Layia discoidea*. Gottlieb et al. (1985) found that genetic similarity between *L. discoidea* and *L. glandulosa*, based on allozymes, was almost as high as values typical of conspecific plant populations. They concluded that the serpentine endemic *L. discoidea* represents an example of a peripheral isolate that diverged relatively rapidly and recently in an ecologically marginal setting from an ancestor referable to the geographically widespread *L. glandulosa*. Ford and Gottlieb (1989, 1990) corroborated Clausen et al.'s (1947) conclusion that only two major genes are responsible for presence or absence of ray florets and associated involucre bracts in *L. glandulosa* and *L. discoidea* and showed that morphological differences between the two taxa are controlled by "a complex admixture of genes with large and small, qualitative and quantitative effects" (Ford & Gottlieb, 1990: 44).

In the ITS trees for *Layia* (Fig. 5), resolution of a clade comprising *L. discoidea* and *L. glandulosa* corroborates Clausen et al.'s (1947) hypothesis that

the two phenotypically dissimilar taxa constitute a natural group. Strong support for the nested placement of *L. discoidea* within *L. glandulosa* corroborates Gottlieb et al.'s (1985) hypothesis that *L. discoidea* descended from a lineage of *L. glandulosa*. Gottlieb et al.'s (1985) additional conclusion that *L. discoidea* represents an example of relatively recent evolution is also evident from the ITS tree; the branch separating *L. discoidea* from the most closely related lineage of *L. glandulosa* in the rate-constant ITS tree is comparable or shorter in length to branches of conspecific sequences in other members of *Layia*, e.g., *L. pentachaeta* A. Gray, the sister-species to *L. glandulosa* and *L. discoidea*.

A more extensive phylogenetic analysis of relationships within the *Layia glandulosa*/*L. discoidea* lineage based on expanded sampling of populations and sequences, with combined ITS and ETS (external transcribed spacer) data, yielded a nearly noise-free tree that reinforces support for recent descent of *L. discoidea* from a sublineage of *L. glandulosa* (Baldwin, 2005). Sequences of the five populations of *L. discoidea* sampled are identical; sequences of *L. glandulosa* are heterogeneous and are resolved as a grade of lineages that are geographically distinct and, to some extent, morphologically divergent. For example, the sister-group to all other lineages in the *L. glandulosa*/*L. discoidea* clade is a morphologically and ecologically discrete group endemic to coastal sand dunes. Phenotypic disparity among the lineages of *L. glandulosa* is minimal, however, compared to morphological and ecological differences between *L. discoidea* and relatives in *L. glandulosa*. Fine-scale patterns resolved in the ETS+ITS tree are consistent with Ford and Gottlieb's (1990) conclusion that yellow-rayed populations of *L. glandulosa*, sometimes treated as *L. glandulosa* subsp. *lutea* D. D. Keck, are the closest relatives of *L. discoidea*, which lacks ray florets but has one or more modifier gene(s) for yellow ray-corolla color; most populations of *L. glandulosa* have white ray corollas and all but one of the sampled white-rayed populations are resolved, based on the molecular data, as more distantly related to *L. discoidea* than are the sampled yellow-rayed populations.

As noted by Gottlieb (2004), the evolutionary origin of *Layia discoidea* did not involve the major genotypic effects predicted under quantum speciation (Grant, 1981); complete interfertility with *L. glandulosa* and the highly contrasting edaphic settings of the two taxa implicate ecological selection without radical genetic reorganization in divergence of *L. discoidea*, in keeping with some recent, general views on accelerated evolution in peripheral populations (e.g., Barton & Charlesworth, 1984; Coyne, 1994). Mayr's (1982: 5)

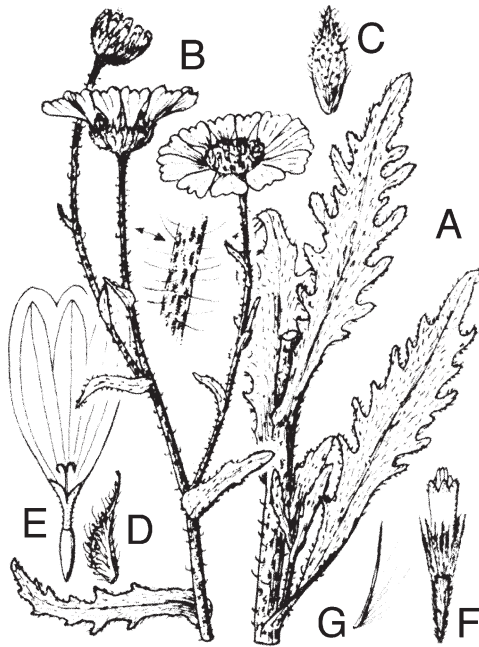


Figure 8. *Layia gaillardoides* ($n = 8$). —A. Stem segment. —B. Capitulescence, with peduncle detail. —C. Involucral bract (abaxial view). —D. Involucral bract (lateral view). —E. Ray floret (adaxial view). —F. Disk floret. —G. Pappus element (lateral view).

refinement of his earlier ideas on rapid divergence of peripheral isolates or founders (“peripatric speciation”) allowed for the possibility of “rapid change... due more to greatly increased selection pressures... than to the genetic consequences of inbreeding,” in closer accord with the proposed evolutionary scenario for *L. discoidea*. Proximity of potential habitats of *L. glandulosa* and *L. discoidea* even leaves open the possibility that divergence of *L. discoidea* may have occurred in the presence of potential for gene flow with *L. glandulosa*, although adjacency of populations of the two taxa has not been documented and no evidence of hybridization is apparent from the rDNA sequences.

A less widely studied example of rapid evolutionary change among the $n = 8$ *Layia* taxa concerns *L. gaillardoides* (Hook. & Arn.) DC. (Fig. 8) and close relatives. Clausen (1951: 16) regarded the extensive interpopulational variation in ray corolla color, vegetative morphology, and flowering time within *L. gaillardoides* as “very spectacular.” In part based on common-garden studies, he concluded that some variation among populations of *L. gaillardoides*, e.g., in leaf margins (Fig. 9), is heritable and follows a west–east geographic pattern “correlated with ecological differences between the outer and inner Coast Range” (Clausen, 1951: 14–15). Phylogenetic analysis of rDNA sequences of *Layia* corroborates

Clausen’s (1951) suggestion that west–east interpopulational differences in *L. gaillardoides* reflect genetic divergence, though at a deeper evolutionary level than he proposed. Four major, allopatric evolutionary lineages within *L. gaillardoides* are well supported by rDNA data and three of the four lineages replace one another from west to east through the Coast Ranges (Baldwin, unpublished).

The four semi-cryptic, allopatric lineages of *Layia gaillardoides* do not constitute a clade in rDNA trees; the morphologically and ecologically distinct *L. carnosa* (Nutt.) Torr. & A. Gray, *L. hieracioides* (DC.) Hook. & Arn., and *L. septentrionalis* D. D. Keck are nested among lineages of *L. gaillardoides* and appear to represent examples of accelerated phenotypic divergence from *L. gaillardoides*-like ancestors (Baldwin, unpublished; Fig. 5 includes representatives of three of the four major lineages of *L. gaillardoides*). *Layia carnosa* (Fig. 10), a rare endemic of outer coastal foredunes, occupies a marginal ecological setting where *L. gaillardoides* does not occur. A hypothesis that *L. carnosa* arose as a peripheral isolate at the coastal-most limits of a widespread progenitor is consistent with distributions of the two closest relatives of “beach layia”: (1) a lineage of *L. gaillardoides* that occurs along windward slopes of the North Coast Ranges and San Francisco Bay Area and (2) *L. hieracioides* (Fig. 11),

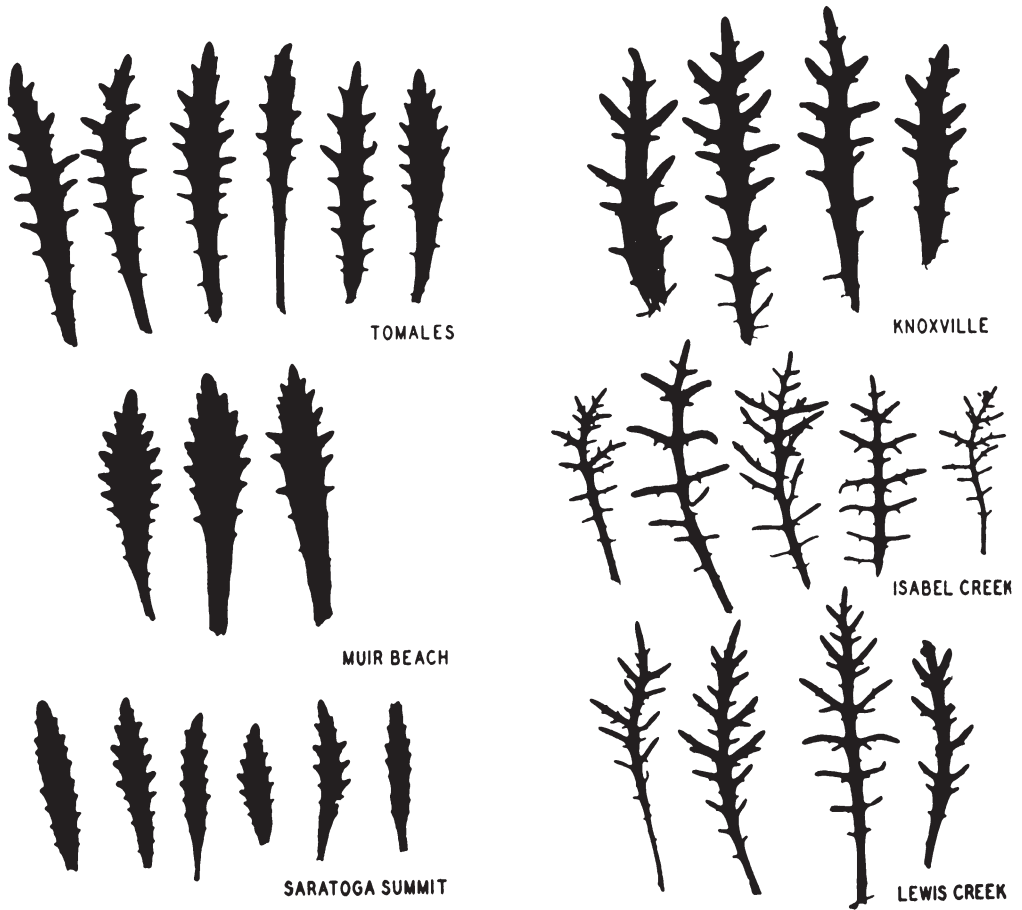
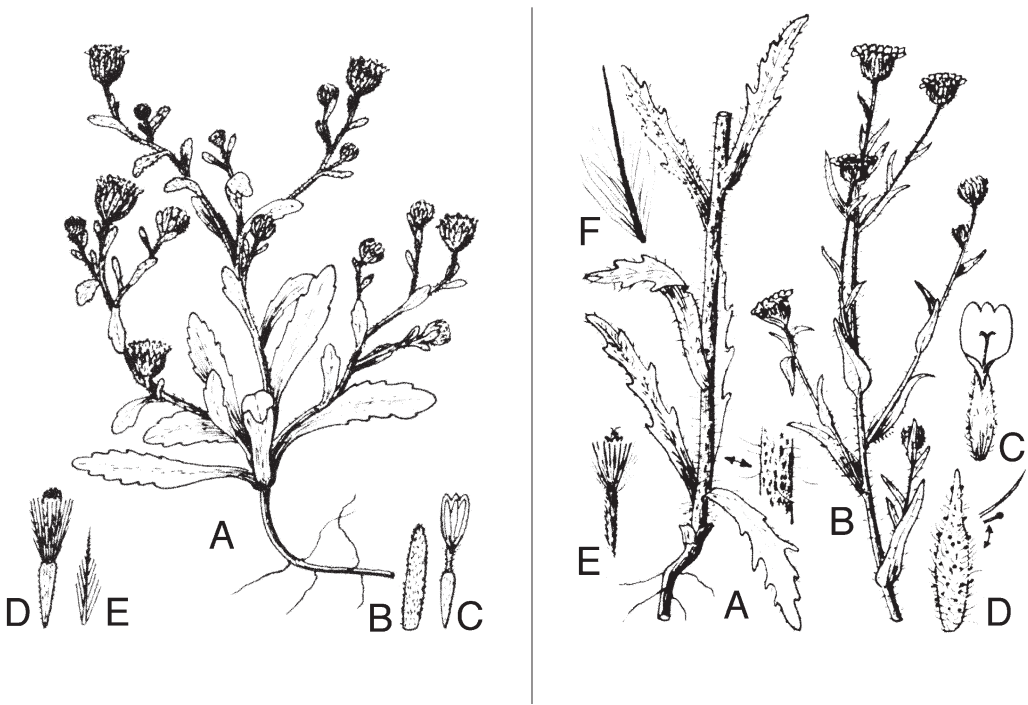


Figure 9. Basal-leaf variation within and among six populations of *Layia gaillardiioides*. Each leaf represents a different individual grown under common-garden conditions at Stanford. Three populations from the outer Coast Ranges of California are represented at left; three populations from the inner Coast Ranges of California are represented at right (top-to-bottom equates to north-to-south distribution of populations). Note deeper leaf-lobing in populations from the drier, hotter interior of the state. Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell Univ. Press.

which occurs widely in the South Coast Ranges, in part on sandy soils and even coastal backdunes. Self-compatibility in *L. carnosa* and *L. hieracioides* (Clausen, 1951)—otherwise unknown in *Layia*—is associated with some conspicuous morphological differences from other members of the *L. gaillardiioides* clade (e.g., reduced sizes of ray corollas and heads). The putative shift toward a more highly inbreeding mating system in the self-compatible taxa can be reasonably suspected to have promoted evolutionary change, as suggested by Gottlieb (1973) for origin of the self-compatible *Stephanomeria malheurensis* Gottlieb (Cichorieae; Compositae), a well-studied example of local, rapid phenotypic divergence from self-incompatible ancestors (see Gottlieb, 2004). *Layia septentrionalis*, the other taxon nested among lineages of *L. gaillardiioides* in the

rDNA trees (Fig. 5), is an obligately outcrossing, narrowly distributed plant of poor, sandy or serpentine soils that occurs in interior regions of the North Coast Ranges, where populations of one major lineage of *L. gaillardiioides* occur sporadically; the two taxa have not been reported to occur together.

Parallels between patterns of evolutionary change in the *L. gaillardiioides* assemblage and the *L. glandulosa*/*L. discoidea* lineage, discussed above, do not extend to patterns of interfertility. In contrast to complete interfertility between members of *L. glandulosa* and *L. discoidea*, members of *L. gaillardiioides* are largely to completely intersterile with members of *L. carnosa* and *L. septentrionalis* and are largely interfertile with diploid members of *L. hieracioides* (Fig. 3; Clausen, 1951; Baldwin, unpublished). Consideration of the observed interfertility patterns



Figures 10 and 11. Self-compatible taxa in *Layia* with eight pairs of chromosomes. Figure 10 (left). *Layia carnosa*. —A. Habit. —B. Involucrel bract (abaxial view). —C. Ray floret (adaxial view). —D. Disk floret. —E. Pappus element. Figure 11 (right). *Layia hieracioides*. —A. Proximal stem, leaves, and roots. —B. Capitulescence. —C. Ray floret and enfolding involucrel bract (adaxial view). —D. Involucrel bract (abaxial view). —E. Disk floret. —F. Pappus element.

in a phylogenetic context leads me to conclude that *L. carnosa* and *L. septentrionalis* underwent accelerated evolution of intrinsic, post-mating reproductive barriers, as expected with quantum speciation (Grant, 1971), although no evidence of chromosome repatterning has been detected in *Layia* (Clausen, 1951), unlike in such well-studied, plant examples of quantum speciation as *Clarkia lingulata* Harlan Lewis & M. Lewis (Lewis & Roberts, 1956; see Gottlieb, 2004) and *Stephanomeria malheurensis* (Gottlieb, 1973, 2004). Clausen (1951: 130) concluded that *L. carnosa* and *L. septentrionalis* each represents a “monotypic species complex,” largely based on intersterility or lack of crossability with other layias. In addition, Clausen et al. (1941) regarded *L. carnosa* as highly divergent morphologically from other species or groups of species in *Layia* (Fig. 3). The major morphological discontinuity between *L. carnosa* and other members of *Layia* perceived by Clausen, Keck, and Hiesey now appears to reflect accelerated morphological evolution in *L. carnosa*, as documented in the origin of *L. discoidea* (Ford & Gottlieb, 1990), rather than a distant evolutionary relationship with other members of the same genus.

The $n = 8$ *Layia* clade encompassing *L. glandulosa*/*L. discoidea* and the paraphyletic *L. gaillardoides* and relatives stands out in *Layia* as an exceptional example of how levels of interfertility or morphological divergence can be misleading about phylogeny, unlike in the $n = 7$ *Layia* clade, where an evidently different mode of evolutionary divergence led to congruent patterns of interfertility, morphological similarity, and relationship. Whether such stark contrasts between the $n = 7$ and $n = 8$ sister lineages in patterns of evolutionary change are attributable to intrinsic or extrinsic factors in the history of the two groups remains unknown. The principal conclusion that has emerged from molecular phylogenetic research reviewed here is that evolutionary processes in *Layia* have been more dynamic than was evident based on Clausen et al.’s (1941) biosystematic data alone. Evidence for multiple instances of accelerated phenotypic divergence in *Layia* underscores the potential importance of peripherally isolated populations in plant evolution (see Rieseberg & Brouillet, 1994; Gottlieb, 2004). For systematists, the possibility that diversification is often marked by major changes in rates of phenotypic evolution and rates of decay of

interfertility across lineages, as inferred for the principal $n = 8$ *Layia* clade, makes risky a reliance on phenetic considerations for estimating relationships or circumscribing taxa, as noted earlier (e.g., Donoghue, 1985).

CRYPTIC BIOLOGICAL SPECIES AND RAPID PHENOTYPIC EVOLUTION IN *Holocarpa*

As noted by Clausen (1951: 94): "There is one genus of the tarweeds of California which differs strikingly from the pattern of speciation in *Layia* of the same subtribe of the Compositae in that it has very strong barriers of sterility even between neighboring populations of one species. These populations are so similar in external appearance that they cannot be distinguished. This genus is *Holocarpa*." *Holocarpa* Greene also differs greatly from *Layia* in ecology. For example, members of *Layia* escape summer drought by flowering and fruiting during the wet spring months; most members of *Holocarpa* tolerate summer drought and flower in summer and fall (see Baldwin, 2003b, c).

Clausen (1951) emphasized that reproductive isolation in plants can be achieved by different means. He provided examples of "groups having predominantly ecological barriers" (e.g., physiological/habitat differences), "predominantly morphological differentiation" (e.g., in floral features associated with pollination), and "predominantly genetic barriers" (Clausen, 1951: 90–107) in opposition to "more typical species" wherein "the pattern of development... from ecological races is through small steps involving the genetic and chromosome systems and the morphological characters" (Clausen, 1951: 107). Clausen's (1951) main example of diversification dominated by the evolution of genetic barriers to gene flow across lineages was *Holocarpa*, a tarweed genus with four taxonomic species (recognized on the basis of morphological characteristics and chromosome numbers) and an indefinite number of unrecognized, cryptic biological species.

Clausen, Keck, and Hiesey's experimental studies in *Holocarpa* revealed that interpopulational crosses within each of two widespread, taxonomic species, *H. heermannii* (Greene) D. D. Keck and *H. virgata* (A. Gray) D. D. Keck, were either unsuccessful or yielded inviable or sterile hybrids (Fig. 12; Clausen, 1951). Chromosomal studies revealed karyotypic differences between intersterile, often morphologically indistinguishable plants from different populations (Fig. 13; Clausen, 1951). Clausen (1951: 99) concluded that chromosome evolution via structural rearrangements had resulted in each population of *H. heermannii* and *H. virgata* becoming "a breeding unit by itself and

genetically sharply separated from its neighbors." Hybrids between members of *H. virgata* (Fig. 14) and a rare species, *H. macradenia* (DC.) Greene (Fig. 15), exhibited modest fertility, in contrast to intersterility between members of different "conspecific" populations of *H. virgata*. Palmer (1982) conducted additional cytogenetic and morphological studies in *Holocarpa* that extended Clausen's (1951) characterization of patterns of interfertility and chromosomal evolution in the genus.

An ongoing molecular phylogenetic study of *Holocarpa* (Baldwin, unpublished) has revealed evidence of a disconnection between evolutionary divergence in conspicuous morphological and ecological characteristics and the origin of intrinsic, post-mating reproductive barriers in the group. Well-supported rDNA trees based on ITS and ETS sequences have confirmed that each of the three widespread species recognized by Clausen, Keck, and Hiesey, i.e., *H. heermannii*, *H. obconica* (J. C. Clausen & D. D. Keck) D. D. Keck, and *H. virgata*, descended from distinct ancestors; the rare *H. macradenia* descended from an ancestor within (paraphyletic) *H. virgata* (Fig. 16). Detailed comparisons of the relative timing of evolutionary changes in *Holocarpa* are now possible because of minimal noise in the molecular dataset, phylogenetic structure both among and within recognized species, and inability to reject rate constancy of molecular evolution across lineages using Felsenstein's (1988) likelihood-ratio test.

Based on branch-length comparisons across the rate-constant rDNA trees, divergence of the highly distinctive *Holocarpa macradenia* from an ancestor within *H. virgata* was more recent than evolutionary divergence of some cryptic, intersterile lineages within *H. virgata* (Fig. 16; Baldwin, unpublished). Recent origin of *H. macradenia* is consistent with modest interfertility between *H. macradenia* and some populations of *H. virgata*, in contrast to strong intersterility barriers between most studied populations of *H. virgata* (Clausen, 1951; Palmer, 1982). In short, extensive morphological and ecological evolution of *H. macradenia* was not accompanied by development of intersterility with closely-related members of *H. virgata*; conversely, evolution of intersterility between "conspecific" lineages within *H. virgata* (and *H. heermannii*) was accompanied by relatively minor or insubstantial phenotypic divergence, despite longer evolutionary timeframes for such divergence to have occurred compared to the relatively rapid rise of *H. macradenia*.

Based on available data, *Holocarpa macradenia* appears to represent yet another example among continental tarweeds of a peripheral isolate that underwent rapid morphological and ecological di-

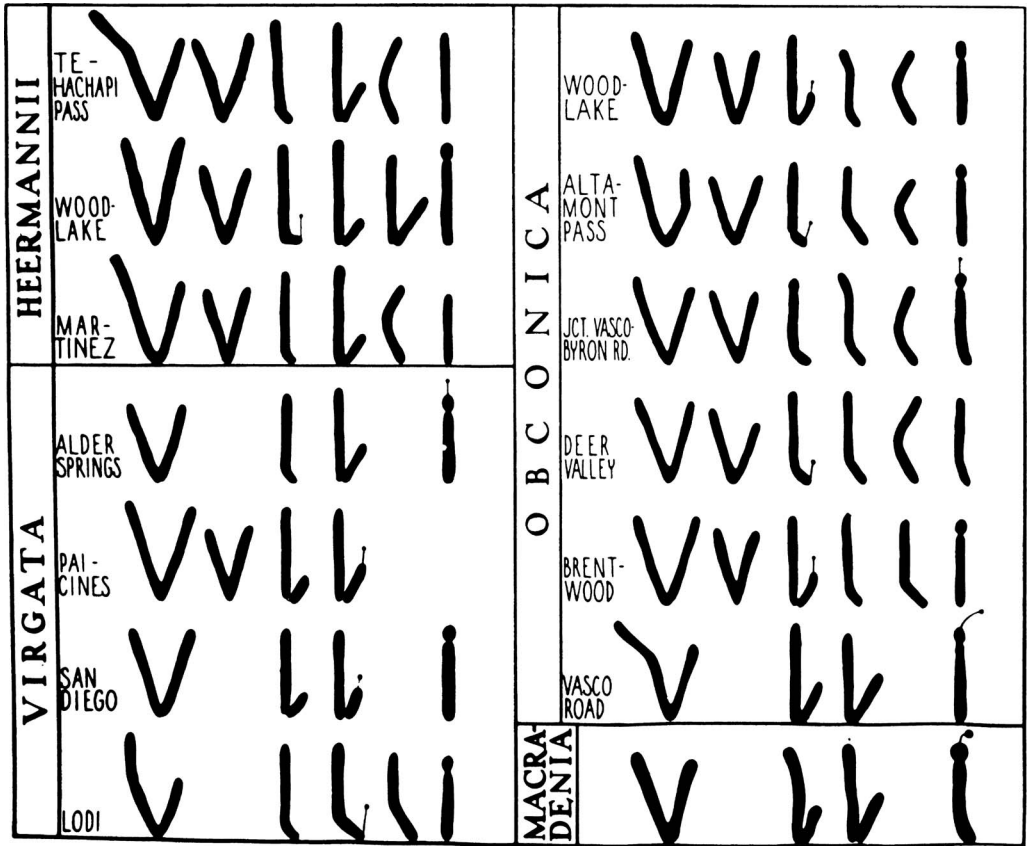


Figure 13. Illustrations of somatic chromosome sets from root-tip preparations for representatives of different populations and species of *Holocarpa* (one chromosome of each pair is shown). Note extensive chromosomal variation among populations of *H. heermannii* and *H. virgata*. Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell Univ. Press.

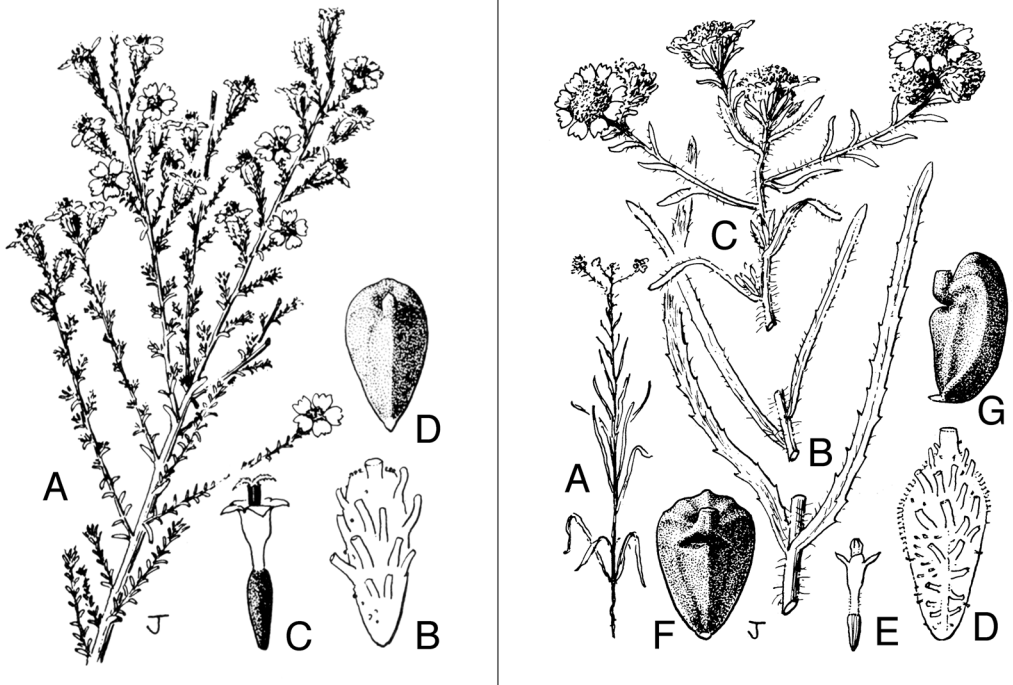
H. macradenia may represent merely “a juvenile form” of the distal-leaf condition in other taxa of *Holocarpa*. Molecular phylogenetic data are most consistent with Palmer’s (1987) evolutionary scenario; the actual time of divergence of *H. macradenia* is still under investigation.

As in the origin of *Layia discoidea*, evolutionary divergence of *Holocarpa macradenia* was not accompanied by acquisition of strong internal barriers to gene flow with close relatives; Clausen, Keck, and Hiesey produced a vigorous, partially fertile F₂ generation from crosses between *H. macradenia* and *H. virgata* (Clausen, 1951). Given the great potential for chromosome evolution in *Holocarpa*, the lack of major chromosomal repatterning associated with evolution of the distinctive *H. macradenia* is consistent with the conclusion from studies of *L. discoidea* that genomic reorganization may be less important in rapid evolutionary divergence of peripherally isolated populations than has been widely suggested (see

previous section). In contrast, the potential evolutionary importance of ecological selection in the divergence of hypothesized peripheral isolates in both *Layia* and *Holocarpa* is difficult to ignore; climatic and/or edaphic differences between habitats of paraphyletic “progenitor” taxa and nested “derivative” lineages are extreme. In *Holocarpa*, ecological selection also may have played a significant role in maintaining long-term phenotypic stability among morphologically cryptic, intersterile lineages within *H. heermannii* and *H. virgata*; genetic cohesion by gene flow cannot explain morphological stasis in each of the two taxa.

ADAPTIVE RADIATION AND THE “MADIA PATTERN”

Clausen, Keck, and Hiesey’s biosystematic investigations in Madiinae led to recognition of extensive intersterility between species then treated as members of *Madia* Molina (Fig. 17). Clausen (1951: 134) stated:



Figures 14 and 15. Ecologically separated, partially interfertile members of *Holocarpha* with four pairs of chromosomes. Figure 14 (left). *Holocarpha virgata*. —A. Capitulescence. —B. Involucral bract (abaxial view). —C. Disk floret. —D. Ray fruit (adaxial view). Figure 15 (right). *Holocarpha macradenia*. —A. Habit. —B. Stem segments. —C. Capitulescence. —D. Involucral bract (abaxial view). —E. Disk floret. —F. Ray fruit (adaxial view). —G. Ray fruit (lateral view).

“The species of *Madia* are cytologically and genetically much more isolated from each other than are the *Layias*. . . Most of the species of *Madia* can be linked together through hybrids, but these are sterile, and, moreover, many hybrids have unpaired, nonhomologous chromosomes. There is, therefore, usually only one species to a species complex in *Madia*.” In designating five general categories of fertility patterns in vascular plants, Grant (1971: 101) aptly considered “the *Madia* pattern” exemplary of “annual herbs with . . . related species usually separated by incompatibility barriers and by chromosomal and genic sterility barriers.” As recognized by Clausen (1951) and Grant (1971), sterility barriers in *Madia* and other plant groups exhibiting the “*Madia* pattern” do not necessarily preclude reticulate evolution; Clausen, Keck, and Hiesey (1945) demonstrated that vigorous, largely sterile hybrids in *Madia* had considerable potential to produce fertile, stable, allopolyploid lineages, such as their synthetic “*M. nutrammii*” and the wild species, *M. citrigracilis* D. D. Keck.

Subsequent molecular phylogenetic studies of *Madiinae* and relatives revealed that *Madia*, as treated in all previous senses, was not monophyletic; the smallest clade encompassing all species of *Madia*

sensu Clausen (1951; Fig. 18) also included plants that never had been placed in the genus: two perennials from montane California —*Anisocarpus scabridus* (Eastw.) B. G. Baldwin [= *Raillardiopsis scabrida* (Eastw.) Rydb.] (Fig. 19) and *Carlquistia muirii* (A. Gray) B. G. Baldwin [= *Raillardiopsis muirii* (A. Gray) Rydb.] (Fig. 20)—and the endemic Hawaiian silversword alliance, a monophyletic group comprising 30 woody and semi-woody species in *Argyroxiphium* DC., *Dubautia* Gaudich., and *Wilkesia* A. Gray (Baldwin et al., 1991; Baldwin, 1992, 1996, 2003a; Barrier et al., 1999). The two Californian perennials (*A. scabridus* and *C. muirii*) and the silversword alliance were not shown convincingly to be members of *Madiinae* until publication of Carlquist’s (1959b) anatomical investigations, after Clausen, Keck, and Hiesey concluded their experimental studies of the subtribe. Carlquist (1965, 1974, 1980) also championed the hypothesis that the Hawaiian taxa represent a major example of insular adaptive radiation. The silversword alliance includes trees, shrubs, mat-plants, cushion plants, woody vines, and rosette plants, spans most of the wide spectrum of habitats found in the Hawaiian Islands from dry scrub (< 400 mm rainfall/yr) to rainforests and bogs

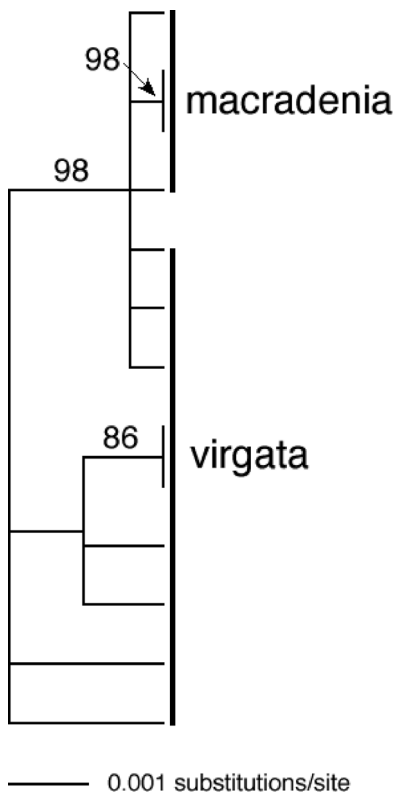


Figure 16. Phylogenetic hypothesis (one of two maximally parsimonious trees) for *Holocarpa macradenia* and *H. virgata* based on analysis of nuclear 18S–26S rDNA external and internal transcribed spacer (ETS and ITS) sequences from representatives of 13 widely-separated populations (Baldwin, unpublished); the clade shown is from a larger tree including representatives of *H. heermannii* and *H. obconica* and outgroup taxa in *Deinandra* [*D. conjugens* (D. D. Keck) B. G. Baldwin and *D. fasciculata* (DC.) Greene]. Branch lengths correspond to relative time since divergence, under maximum-likelihood optimization; rate constancy of ITS evolution across lineages could not be rejected using Felsenstein's (1988) likelihood-ratio test. Numbers along branches are parsimony bootstrap values (only values > 85% are shown).

(> 12,300 mm/yr), and extends along an elevational gradient from near sea level (75 m) to high alpine (3750 m) (Figs. 21–24; Carr, 1985; Carr et al., 1989; Robichaux et al., 1990; Baldwin & Robichaux, 1995; Baldwin, 1997, 2003a, b, c).

Clausen, Keck, and Hiesey were aware of Gray's (1852) early inclusion of the Hawaiian genera *Argyroxiphium* and *Wilkesia* in Madiinae; Keck (1936: 8) conducted a systematic study of *Argyroxiphium* "...with the expectation of treating it in ... Madi(i)nae," and astutely suggested that members of the Hawaiian silversword alliance, as currently recognized, "...would appear to constitute an insular

group unto themselves" (Keck, 1936: 10), although his inclusion of *Wilkesia* in *Argyroxiphium* has not been upheld (Carlquist, 1957; Carr & Kyhos, 1986; Baldwin et al., 1990; Baldwin & Robichaux, 1995; Baldwin, 1997). At the same time, Keck rejected Gray's (1852) placement of *Argyroxiphium* and *Wilkesia* in Madiinae and surmised that the silversword alliance was "...probably without close relatives" (Keck, 1936: 10). Keck (1936: 11) concluded: "By thus divorcing *Argyroxiphium* from the American genera to which it has been thought related, the most persistently proposed connection between the ancient element in the Hawaiian flora and the New World has been shattered."

Molecular phylogenetic data on historical ecology and on timing and rate of diversification of the Hawaiian silversword alliance uphold Carlquist's (1965) hypothesis that the Hawaiian taxa represent recent adaptive radiation from a tarweed ancestor rather than an ancient lineage without close relatives, as suggested by Keck (1936). Based on rDNA ITS trees, Osborn's (1902) original, ecological criterion for adaptive radiation is met by the silversword alliance; major ecological shifts between wet and dry habitats were evidently associated with diversification on each of the four major island groups occupied by the lineage, with the possible exception of the youngest island, Hawai'i (Fig. 25; Baldwin & Robichaux, 1995; see also Robichaux et al., 1990). Simpson's (1944) rapid-diversification criterion for adaptive radiation is also met; inability to reject rate constancy of molecular evolution across clades in the ITS trees and time-calibration of a node outside the Hawaiian lineage allowed estimation of a maximum age for the most recent common ancestor of the silversword alliance at 5.2 ± 0.8 million years and a minimum diversification rate for the group of 0.56 ± 0.17 species per million years (Fig. 26; Baldwin & Sanderson, 1998). The estimated maximum age of the silversword alliance is roughly comparable to the age of the oldest modern high-island, Kaua'i (ca. 5.1 million years; Clague & Dalrymple, 1987) and much younger than the > 10 million-year-old estimated ages of some other prominent examples of adaptive radiation in the Hawaiian Islands, such as Hawaiian drosophilids (Thomas & Hunt, 1991) and Hawaiian lobelioids (Givnish et al., 1996). The minimum diversification rate estimated for the silversword alliance falls within the upper range of estimated rates for various continental radiations of plants and animals and was regarded by Nee (2001: 661) as "remarkably high."

An expanded perspective on *Madia* that encompasses all of the "Madi(a)" lineage (Baldwin, 1996; Fig. 18), i.e., the clade including all of the taxa in

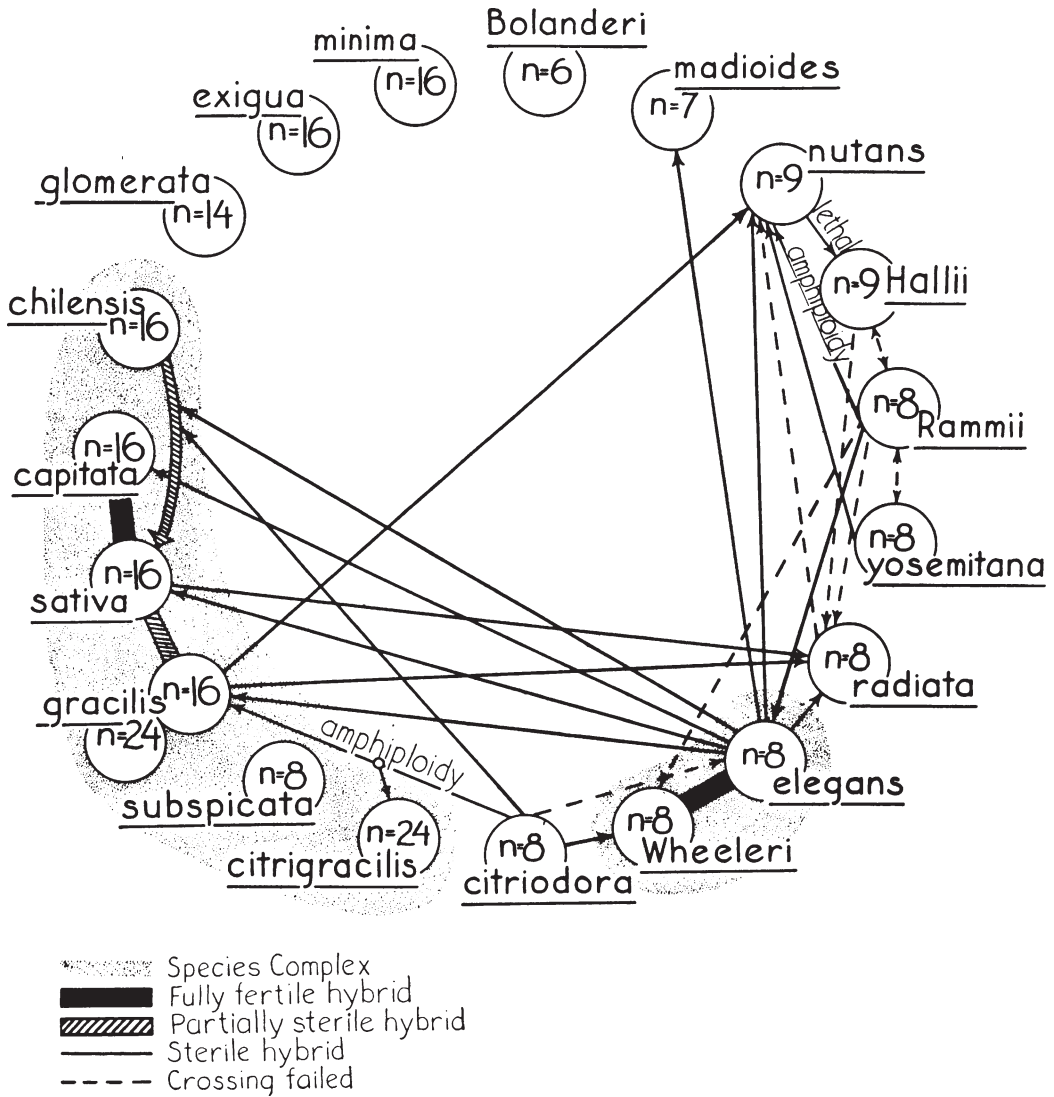


Figure 17. Crossing diagram of *Madia* sensu Clausen (1951). Fully interfertile taxa shown in the diagram are now treated as taxonomically indistinct (*Madia capitata* Nutt. and *M. chilensis* (Nutt.) Reiche are now treated as synonyms of *M. sativa* Molina; *Madia wheeleri* (A. Gray) D. D. Keck is now treated as a synonym of *M. elegans* D. Don ex Lindl.). Some species are now treated in other genera, i.e., *Anisocarpus* Nutt. [*A. madioides* Nutt.], *Harmonia* B. G. Baldwin [*H. hallii* (D. D. Keck) B. G. Baldwin, *H. nutans* (Greene) B. G. Baldwin], *Hemizonella* (A. Gray) A. Gray [*H. minima* (A. Gray) A. Gray], *Jensia* B. G. Baldwin [*J. rammii* (Greene) B. G. Baldwin, *J. yosemitana* (Parry ex A. Gray) B. G. Baldwin], and *Kyhosia* B. G. Baldwin [*K. bolanderi* (A. Gray) B. G. Baldwin]. All taxa shown are annuals except for *Anisocarpus madioides* and *Kyhosia bolanderi*, which are perennial herbs. The “Madia” lineage (Baldwin, 1996) also includes *Anisocarpus scabridus*, *Carlquistia muirii*, and the Hawaiian silversword alliance (30 species in *Argyroxiphium*, *Dubautia*, and *Wilkesia*). Reprinted from *Stages in the Evolution of Plant Species*, by Jens Clausen. Copyright © 1951 by Cornell University. Used by permission of the publisher, Cornell University Press.

Madia sensu Clausen, Keck, and Hiesey (Fig. 17) plus *Anisocarpus scabridus*, *Carlquistia muirii*, and the Hawaiian silversword alliance, reveals strongly contrasting patterns of phenotypic divergence. Life-form evolution and habitat shifts among continental members of the “Madia” lineage (and among conti-

ental tarweeds in general) are dwarfed by adaptive radiation of the Hawaiian silversword alliance; the continental taxa of the group are annual and perennial herbs that occur along a relatively narrow precipitation gradient compared to the wide range of dry, wet, and boggy situations occupied by the semi-woody and

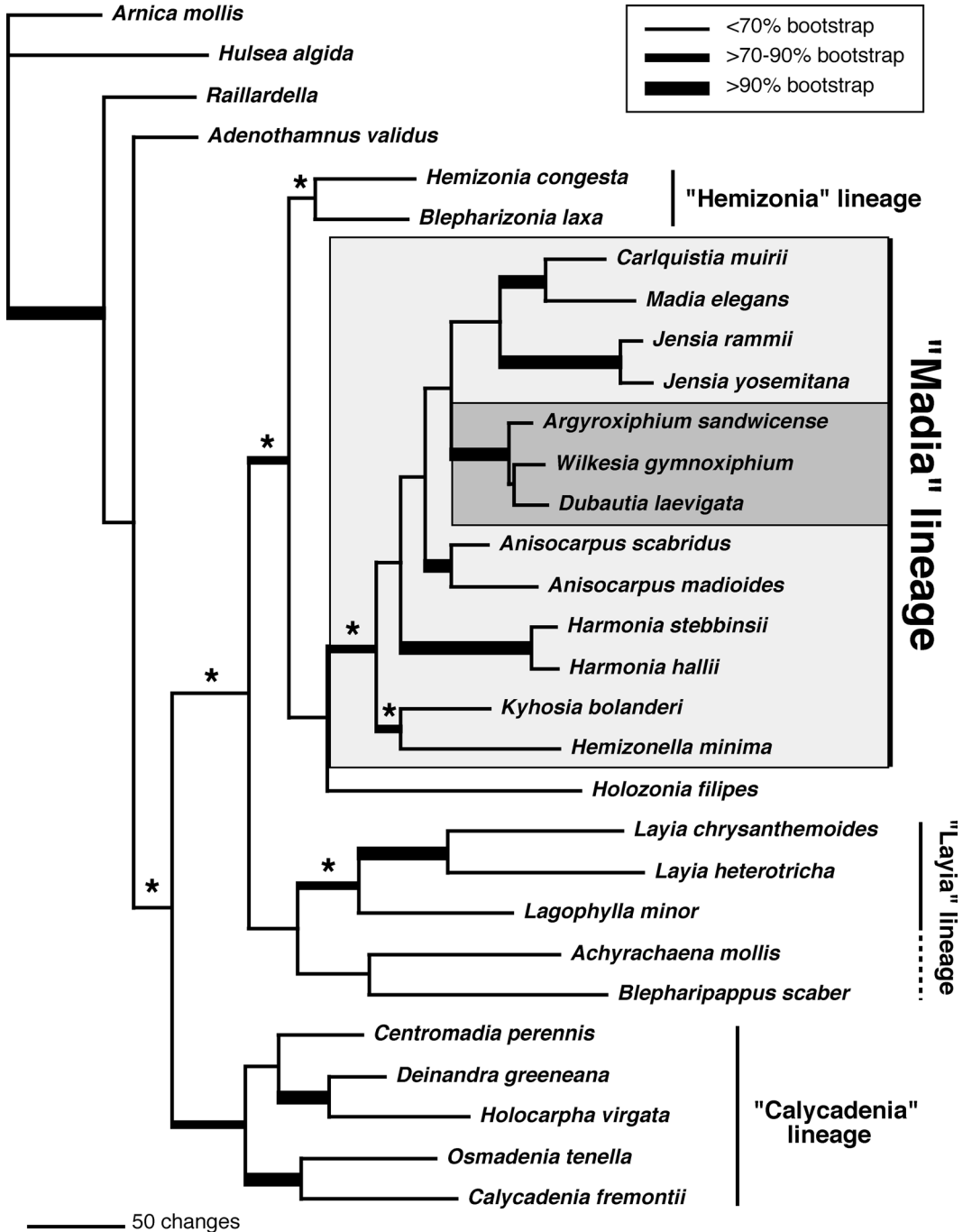
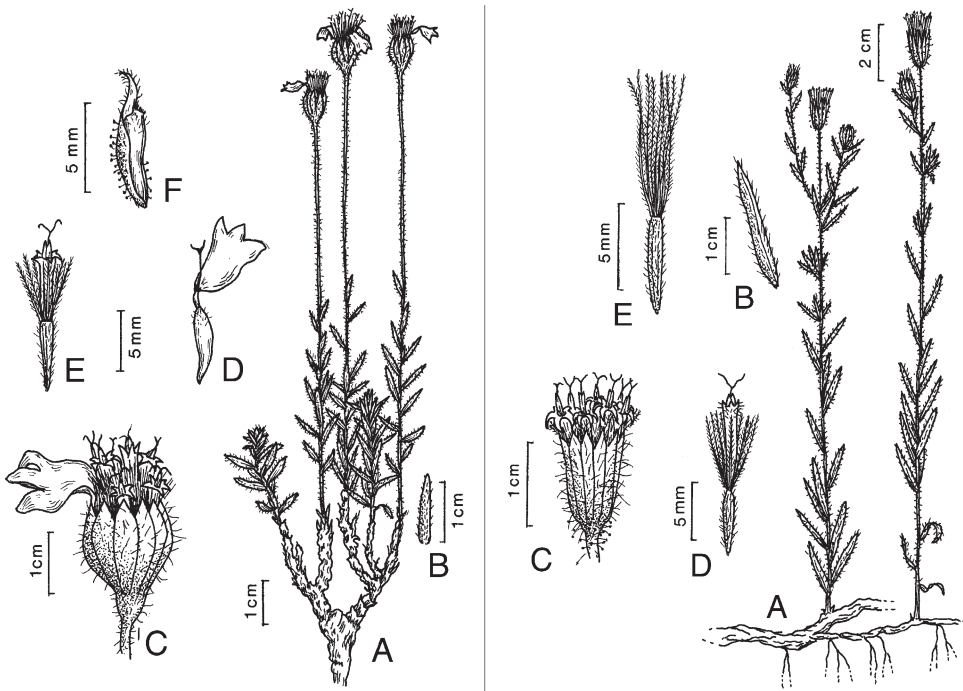


Figure 18. Phylogenetic hypothesis (the most parsimonious tree) for Madiinae based on simultaneous analysis of chloroplast DNA (*trnK* intron) and 18S–26S nuclear ribosomal DNA external and internal transcribed spacer (ETS and ITS) sequences (Baldwin, 2003a, unpublished). The dark box nested within the "Madia" lineage encloses the clade corresponding to the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*). Asterisks (*) indicate that branch support rises to the next level indicated by branch widths with removal of sequences for the three long-branch, monotypic genera: *Achyrachaena* Schauer, *Blepharipappus* Hook., and *Holozonia* Greene. *Raillardella* (A. Gray) Benth. is represented by a *trnK* intron sequence of *R. argentea* (A. Gray) A. Gray and ETS and ITS sequences of *R. pringlei*. Allopolyploidy of the Hawaiian silversword alliance (Barrier et al., 1999) is not resolved by chloroplast DNA or nuclear rDNA sequences. See Appendix 1 for authorship of species names not mentioned in text.

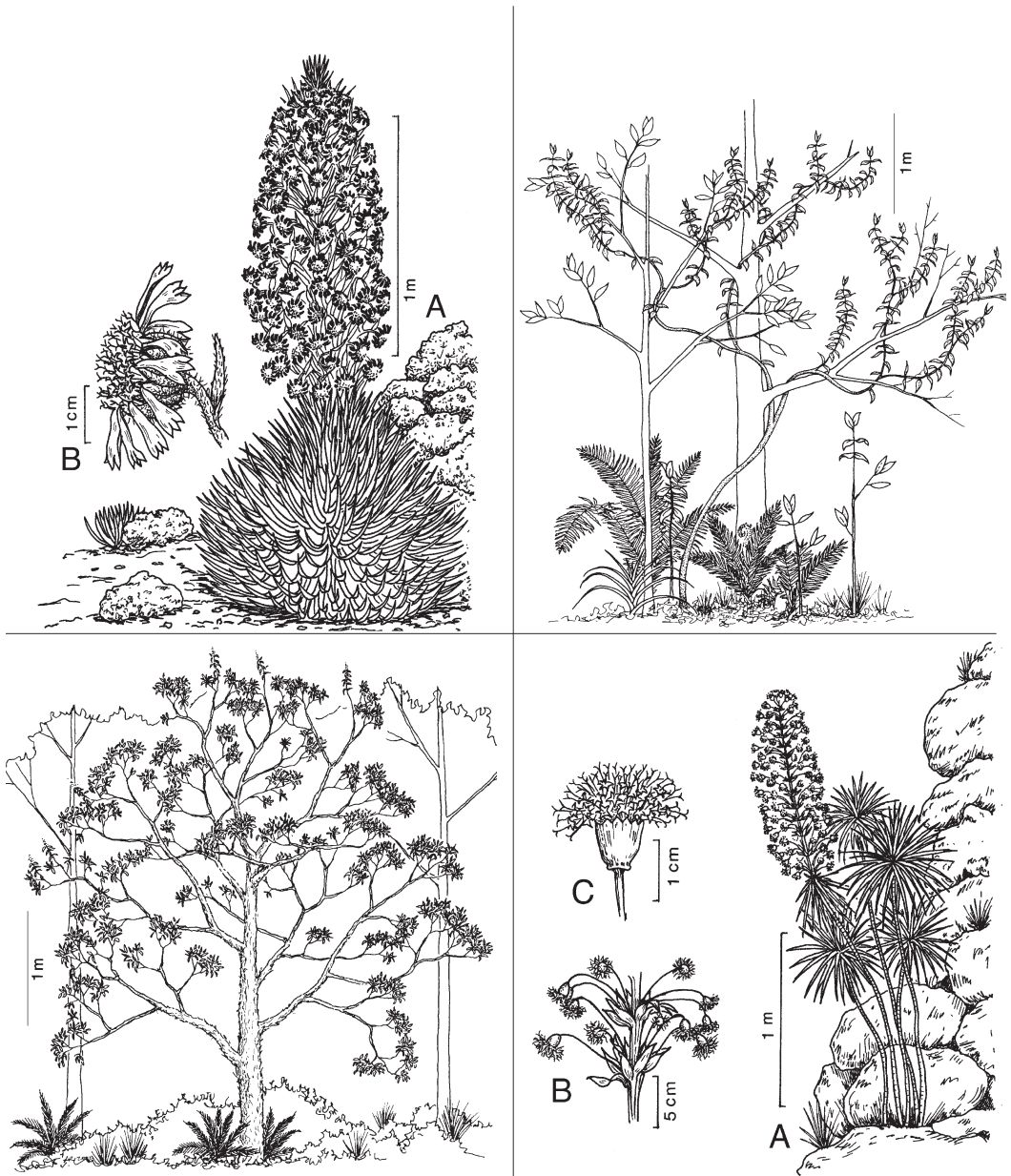


Figures 19 and 20. Californian montane perennials of the “*Madia*” lineage, not included in *Madia* sensu Clausen (1951); although both diploid species were previously treated in *Raillardiopsis* Rydb., the genome of each is evidently more closely related to a different genome in the (allotetraploid) Hawaiian silversword alliance than to the genome in the other diploid (Barrier et al., 1999). Figure 19 (left). *Anisocarpus scabridus*. —A. Habit. —B. Leaf. —C. Head. —D. Ray floret. —E. Disk floret. —F. Ray fruit and half-enveloping involucre bract (obliquely adaxial view). Figure 20 (right). *Carlquistia muirii*. —A. Habit. —B. Leaf. —C. Head. —D. Floret. —E. Fruit with pappus. Both species have been involved in successful crosses with one another and with members of the Hawaiian silversword alliance (Baldwin et al., 1991; Carr et al., 1996; Barrier et al., 1999).

woody Hawaiian species (see Baldwin, 2003a, b, c). Phylogenetic evidence for origin of the silversword alliance after considerable diversification of the “*Madia*” lineage (Figs. 18, 26; see also Barrier et al., 1999) indicates that ecological diversity in the Hawaiian lineage represents a major acceleration of evolutionary change associated with colonization of the Hawaiian Islands. As suggested for diverse oceanic-island lineages in general, adaptive radiation of the silversword alliance probably has been in large part a consequence of ecological opportunity (Simpson, 1953; see Schluter, 2000), with availability of a wide array of empty niches in the Hawaiian Islands and lack of interference with other organisms, possibly aided by intrinsic factors promoting evolutionary change, such as the allopolyploid constitution of the group (Barrier et al., 1999).

Extension of Clausen’s (1951) crossing results to encompass perennial members of the “*Madia*” lineage has indicated strikingly different fertility patterns between the continental and Hawaiian taxa. Crosses

between the continental perennials and between the continental and Hawaiian perennials of the “*Madia*” lineage, not attempted by Clausen, Keck, and Hiesey (see Fig. 17), either have failed or yielded vigorous F_1 hybrids of extremely low pollen stainability (an estimate of fertility), with most stainable grains being abnormally large, tetraporate, and putatively diploid (Kyhos et al., 1990; Baldwin et al., 1991; Carr et al., 1996; Barrier et al., 1999). Observed lack of interfertility between the continental perennials and between the continental and Hawaiian perennials conforms to the results obtained by Clausen, Keck, and Hiesey for the annual members of the lineage (Clausen, 1951) and to the “*Madia* pattern” described by Grant (1971). In contrast, crosses between members of the Hawaiian silversword alliance have yielded vigorous, partially to fully fertile hybrids in all interspecific and intergeneric combinations attempted, despite major morphological and ecological divergence of the taxa (Fig. 27; Carr & Kyhos, 1981, 1986; Carr, 1985, 2003a). Reduced fertility in some Hawaiian hybrid combinations can be attributed



Figures 21–24. Members of the Hawaiian silversword alliance. Figure 21 (upper left). *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat, a monocarpic, thick-leaved rosette plant of dry, alpine, cinder slopes and flats on Haleakala, East Maui. —A. Habit. —B. Head. Figure 22 (upper right). *Dubautia latifolia* (A. Gray) D. D. Keck, a liana (woody climber) of mesic to wet forests on Kauaʻi. Figure 23 (lower left). *Dubautia reticulata* (Sherff) D. D. Keck, a tree or large shrub of wet forests on East Maui. Figure 24 (lower right). *Wilkesia gymnoxiphium* A. Gray, a monocarpic, fibrous-leaved rosette plant of dry slopes and ridges on Kauaʻi. —A. Habit. —B. Segment of capitulescence. —C. Head and distal peduncle.

mostly or solely to one to three whole-arm reciprocal translocations that differentiate genomes of the group (Carr & Kyhos, 1986; Carr, 2003b). Even hybrids of low fertility, i.e., between *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat and *Dubautia menziesii* (A. Gray) D. D. Keck, have been

shown to serve as effective pollen parents in backcrosses, with recovery of full fertility in a subset of B₂ progeny (Carr, 1995, 2003a). Ecological (post-dispersal) selection against hybrids appears to be important in limiting gene flow in the Hawaiian group (Carr, 1995), although such selection has not pre-

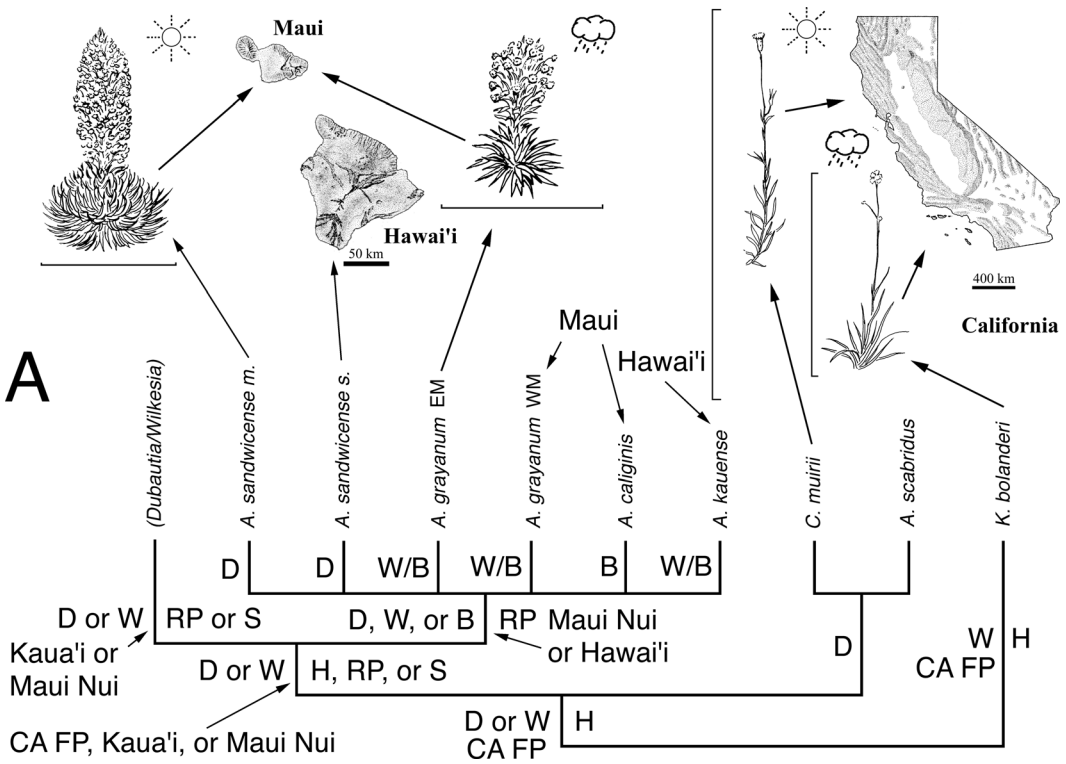


Figure 25 (pp. 84–87). Ecological shifts and major dispersal events during diversification of each of four principal lineages of the Hawaiian silversword alliance, based on the semi-strict consensus of eight maximally parsimonious nuclear rDNA ITS trees (reprinted or adapted from Baldwin, 1997; data from Baldwin & Robichaux, 1995). —A. *Argyroxiphium*, a young-island group (Maui and Hawaii'i), shown in context of “*Dubautia/Wilkesia*” lineage (detailed in Figs. 25B, C, and D) and western North American outgroup taxa—montane, perennial tarweeds of the “*Madia*” lineage (in *Anisocarpus*, *Carlquistia*, and *Kyhosia*). —B. *Wilkesia* and sister group (part of *Dubautia*), restricted to Kaua'i. Habitat abbreviations and symbols: B = bog; D or sun symbol = dry; W = wet; cloud symbol = wet or bog. Habit symbols: H = herb; L = liana (woody climber); M = mat-plant; RP = rosette plant (monocarpic or polycarpic); S = shrub; T = tree. Geographic key: CA FP = California Floristic Province; Maui Nui = prehistoric island uniting Lana'i, Moloka'i, and Maui (and Kaho'olawe, where no members of *Madiinae* are known to occur). Placement of geographic area, habitat, and habit along branches is where ancestral state is unequivocal based on parsimony criterion (Baldwin & Robichaux, 1995). Island occurrences and life-form information for the silversword alliance conform with Carr (1985, 1999). Taxonomic abbreviations: *A. sandwicense*—“m.” = subsp. *macrocephalum*, “s.” = subsp. *sandwicense*; *D. ciliolata* (DC.) D. D. Keck—“c.” = subsp. *ciliolata*, “g.” = subsp. *glutinosa* G. D. Carr; *D. knudsenii* Hillebr.—“f.” = subsp. *filiformis* G. D. Carr, “k.” = subsp. *knudsenii*, “n.” = subsp. *nagatae* (H. St. John) G. D. Carr; *D. laxa* Hook. & Arn.—“h.” = subsp. *hirsuta* (Hillebr.) G. D. Carr, “l.” = subsp. *laxa*; *D. linearis* (Gaudich.) D. D. Keck—“h.” = subsp. *hillebrandii* (H. Mann) G. D. Carr, “l.” = subsp. *linearis*; *D. plantaginea* Gaudich.—“BH” (“Blue Hole”) = subsp. *magnifolia* (Sherff.) G. D. Carr, “h.” = subsp. *humilis* G. D. Carr, “p.” = subsp. *plantaginea*; *D. scabra* (DC.) D. D. Keck—“l.” = subsp. *leiophylla* (A. Gray) G. D. Carr, “s.” = subsp. *scabra*. See Appendix 1 for authorship of species names not mentioned in text.

cluded establishment of hybrids; 38 naturally occurring hybrid combinations between different pairs of species (including intergeneric hybrids) have been documented by Carr (2003a), and evidence for both recent and ancient introgression has been obtained from studies of hybrid zones (Crins et al., 1988; Caraway et al., 2001) and comparison of phylogenetic data from cytogenetic, nuclear rDNA, and chloroplast DNA studies (Baldwin et al., 1990; Baldwin, 1997, 2003c). Hybrid speciation, as well, may explain some conflicts between different lines of phylogenetic data,

e.g., for *D. scabra* (DC.) D. D. Keck (Baldwin et al., 1990; Baldwin, 1997).

The stark contrast between the Hawaiian pattern of interfertility across phenotypically disparate lineages and the pattern of intersterility seen across the less distinctive continental species of the “*Madia*” lineage has evolutionary implications. Lack of strong, intrinsic reproductive barriers between species and genera of the Hawaiian silversword alliance leaves open the potential for homoploid hybrid speciation or introgression involving plants that differ greatly in

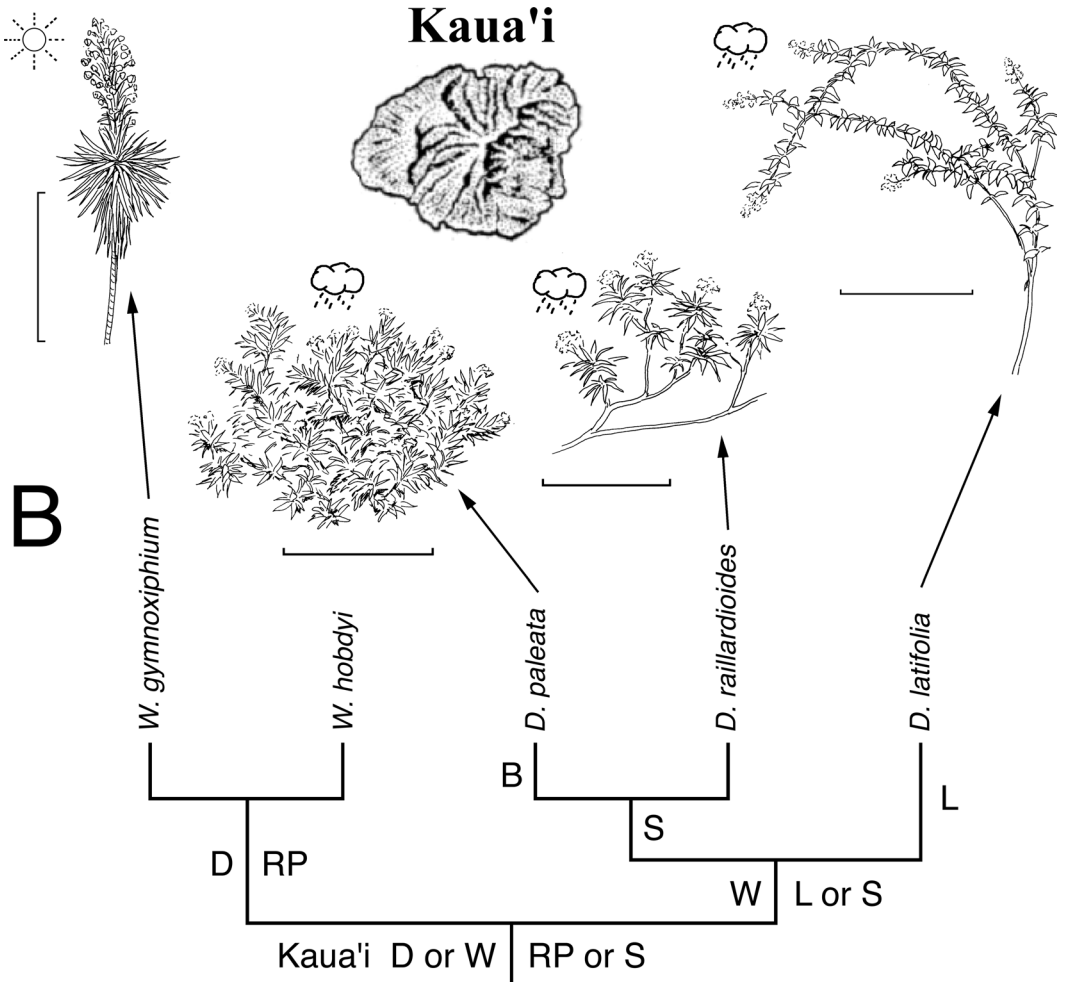


Figure 25. Continued.

life-form or ecological setting, particularly under environmental conditions favorable to recombinant phenotypes (Carr, 1995, 2003a). Intersterility barriers among continental species of the “*Madia*” lineage may limit the evolutionary potential of hybridization to formation of allopolyploids, as demonstrated experimentally by Clausen et al. (1945) for some annual species and as meiotic behavior and diploid pollen formation indicate for hybrids between the continental perennials (Carr et al., 1996; Barrier et al., 1999). Such allopolyploidy has contributed only modestly to diversity in the continental lineages (e.g., *Madia citrigracilis*), but evidently gave rise to the lineage that successfully colonized the Hawaiian Islands and became the silversword alliance (Barrier et al., 1999).

Phylogenetic data from ITS sequences on time since divergence of perennials in the “*Madia*” lineage

(Baldwin & Sanderson, 1998) allows patterns of interfertility to be placed in an understandable perspective (Fig. 26). Lack of interfertility between continental perennials and between continental and Hawaiian perennials may be explained simply by the longer timeframe for evolutionary divergence between those lineages compared to the time since divergence of the Hawaiian lineages from a common ancestor, with gradual breakdown in interfertility through time as a by-product of divergence. Interfertility between members of the silversword alliance is consistent with fertility patterns seen in other (mostly perennial) lineages of Hawaiian angiosperms (see Carr, 1998; Baldwin, 1998) and conforms more closely to the common fertility pattern seen in young woody plant groups in general, i.e., the “*Ceanothus* pattern” (Grant, 1971), than to the “*Madia* pattern,” seen widely in annuals (Grant, 1971). Although the relative

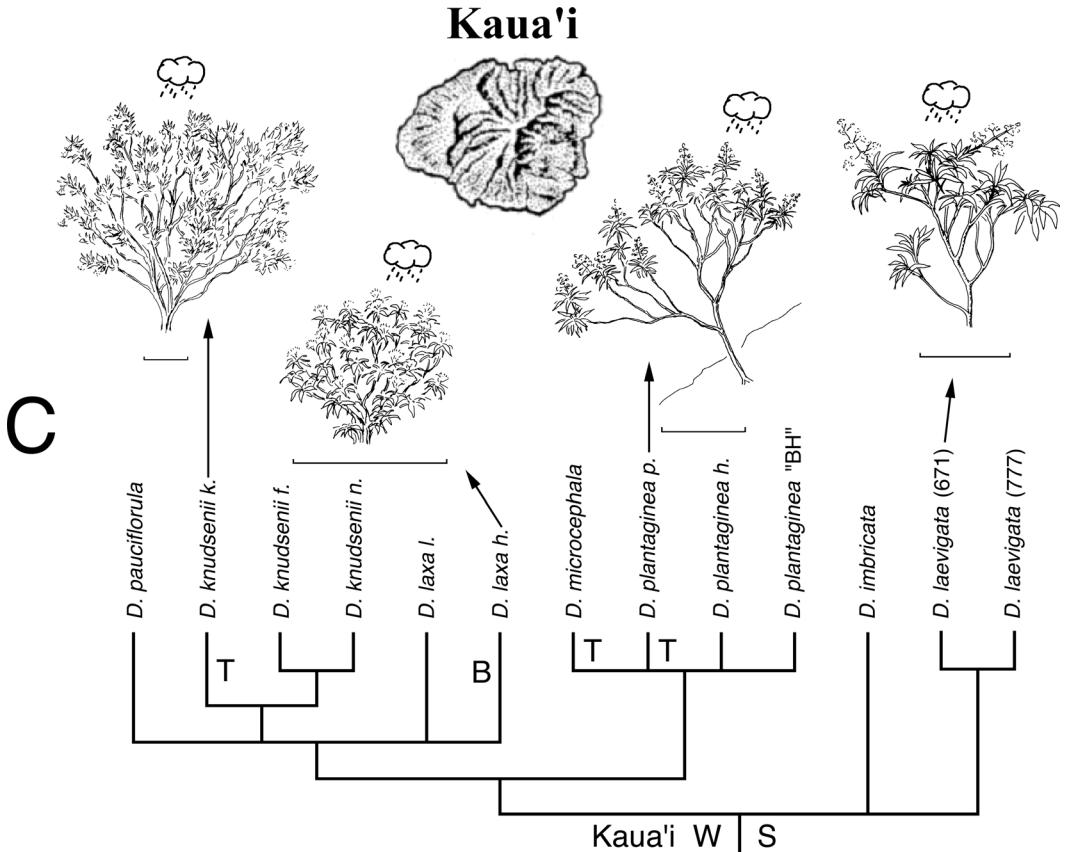


Figure 25. Continued. —C. Members of *Dubautia* with genomic arrangements DG1 and DG3 (Carr & Kyhos, 1986, pers. comm.), native (but not all endemic) to Kaua'i. —D. *Dubautia* sect. *Railliardia*, restricted to one or more young island(s) (not on Kaua'i). For additional details, see p. 84.

timing of divergence of annuals and perennials in the "Madiinae lineage" has not yet been resolved, the generally higher rates of rDNA evolution in the annuals compared to the perennials (Baldwin & Sanderson, 1998) accords with findings for some other angiosperms (e.g., *Sidalcea* A. Gray; Andreasen & Baldwin, 2001) and may reflect more general rates of molecular evolution, which, in turn, could bear on a putatively higher rate of acquisition of post-zygotic reproductive barriers between annuals than between perennials in general. Similar results have been obtained in comparisons between phylogenetic and crossing data for continental annual and insular perennial lineages of the tarweed genus *Deinandra* Greene (Baldwin, unpublished). These findings reinforce Grant's (1971) observations on associations among life history, patterns of interfertility, and the evolutionary potential of hybridization in plants, and illustrate further contrasts in patterns and processes of evolutionary change among closely related lineages of Madiinae.

CONCLUSIONS

Evolutionary investigations of Madiinae in the wake of Clausen, Keck, and Hiesey's pioneering research have led to a greatly expanded circumscription of the subtribe and a more detailed understanding of processes and patterns of diversification in the group. Progress in resolving evolutionary questions in Madiinae through integration of diverse lines of evidence follows in the tradition of Clausen, Keck, and Hiesey and reaffirms the value of systematic data for tackling process-oriented evolutionary questions, as appreciated by the Carnegie team. Clausen, Keck, and Hiesey's evidence for a dynamic evolutionary history of Madiinae, both in relative rates of morphological, ecological, and genetic change and in modes of diversification, has been upheld and extended to finer-scale levels than in the comparisons among genera described by Clausen (1951). Even within individual genera of Madiinae, processes of evolutionary change and the biological properties of

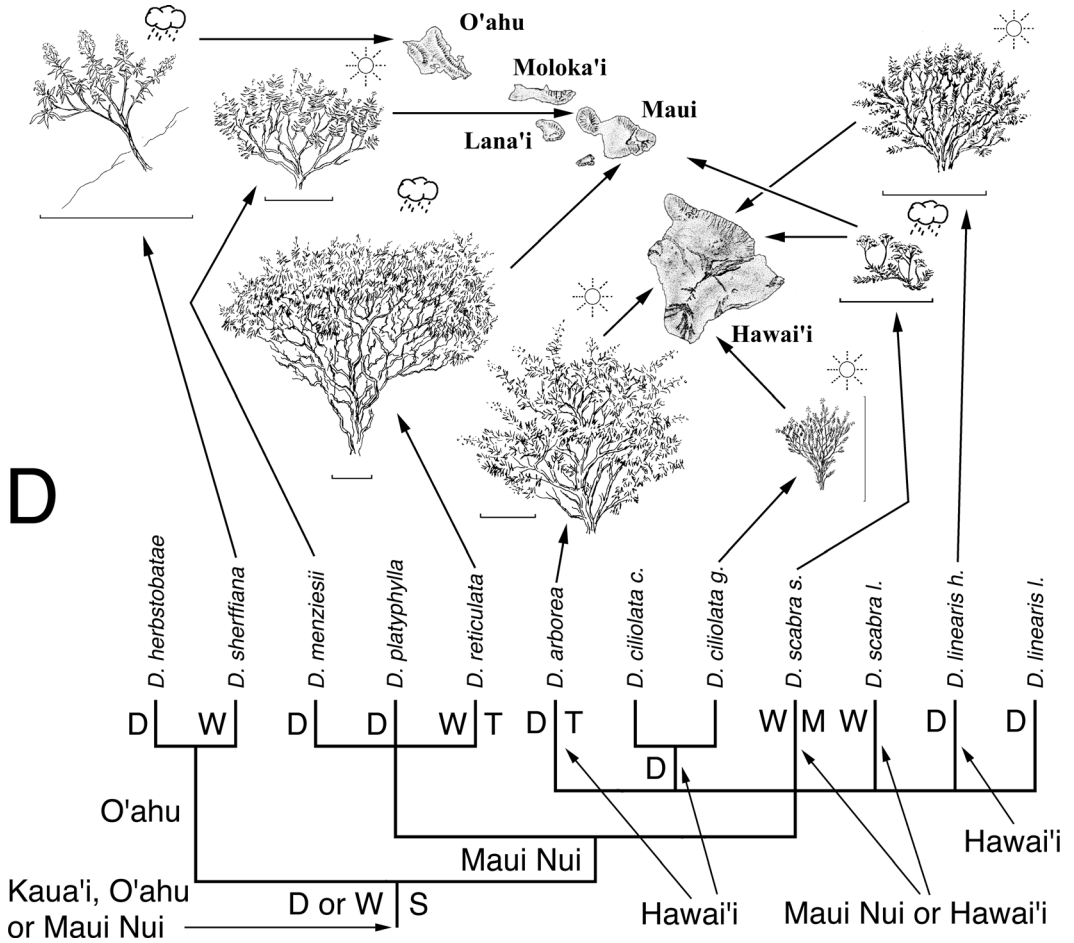


Figure 25. Continued.

lineages may differ greatly. These results underscore the value of phylogenetic data in process-oriented evolutionary studies and the importance of phylogenetic considerations in classification at all levels of evolutionary divergence.

A recurring finding in the re-examination of tarweed evolution using modern systematic approaches has been the discovery of cryptic or semi-cryptic diversity, even in groups that were studied intensively by Clausen, Keck, and Hiesey from an experimental biosystematic perspective (e.g., *Layia*). In part, such diversity appears to reflect ecologically differentiated and evolutionarily divergent—though often interfertile—lineages, as in *L. gaillardoides*. Similar examples have emerged recently from molecular phylogenetic and ecological studies of other plant taxa that were a focus of previous experimental work, such as *Lasthenia* Cass. (Ornduff, 1966; Chan et al., 2002; Rajakaruna et al., 2003). The potential importance of ecologically distinct, cryptic groups

was well appreciated by Clausen (1951: 29–30): “It is now established as a general biological law that species that occupy many kinds of environment are able to do so because they have evolved series of physiologically distinct races, each of which survives within its native zone but is less able to compete in neighboring zones and usually is unable to survive in the extreme ranges of the species. This fitness is primarily physiological; it is determined by genes, and it may or may not be expressed in the external appearance of the plant. Ecological races or ecotypes have therefore generally been overlooked by taxonomists, geneticists, and ecologists, all of whom looked for visible characters that they could classify. Actually, however, the ecological race is a far more important biological entity than the morphological subspecies.” Although infeasible during Clausen’s life, resolving “ecological races” that correspond to natural groups worthy of taxonomic recognition is now possible and desirable, especially in light of the

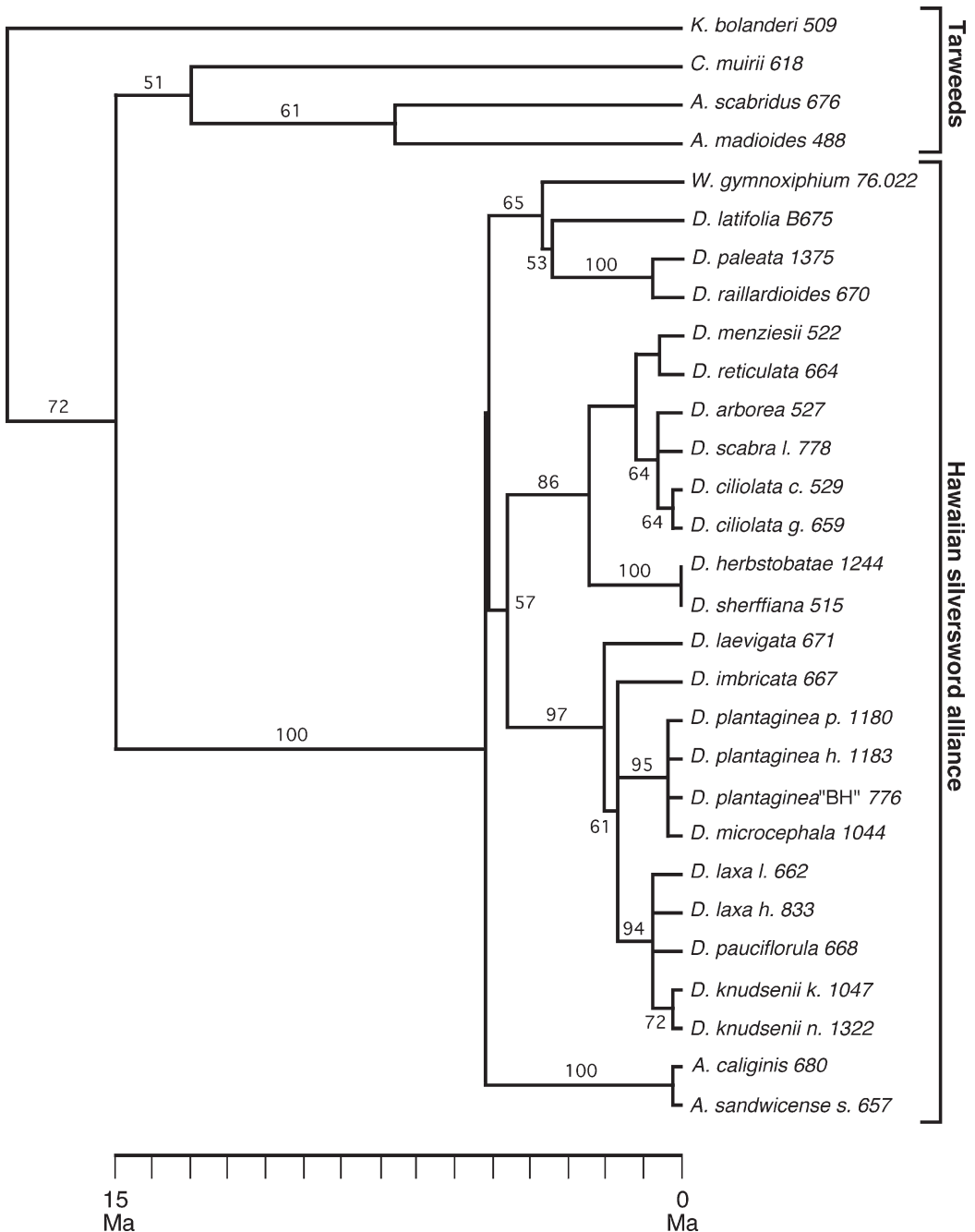


Figure 26. A phylogenetic hypothesis (one of four maximally parsimonious trees) for perennial members of the "Madia" lineage, with time-calibrated branches, based on nuclear rDNA ITS sequences (adapted from Baldwin & Sanderson, 1998). Continental tarweeds (*Anisocarpus*, *Carlquistia* B. G. Baldwin, and *Kyhosia*) and the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) were included in the analysis. The outgroup (*Adenothamnus validus* and *Raillardella pringlei*) is not shown. Rate-constancy of molecular evolution across lineages could not be rejected using Felsenstein's (1988) likelihood-ratio test; branch lengths were optimized to conform to clock-like evolution using maximum-likelihood. External calibration of the node representing the most recent common ancestor of the continental perennials and the Hawaiian taxa was based on the assumption that diversification above that node would not have occurred until after mid-Miocene (15 million years ago), when summer precipitation in western North America began to decline (nearly all continental tarweeds are restricted to areas of summer-dry climate; see Baldwin & Sanderson, 1998). See Figure 25 caption for abbreviations of subspecies in *Dubautia*.

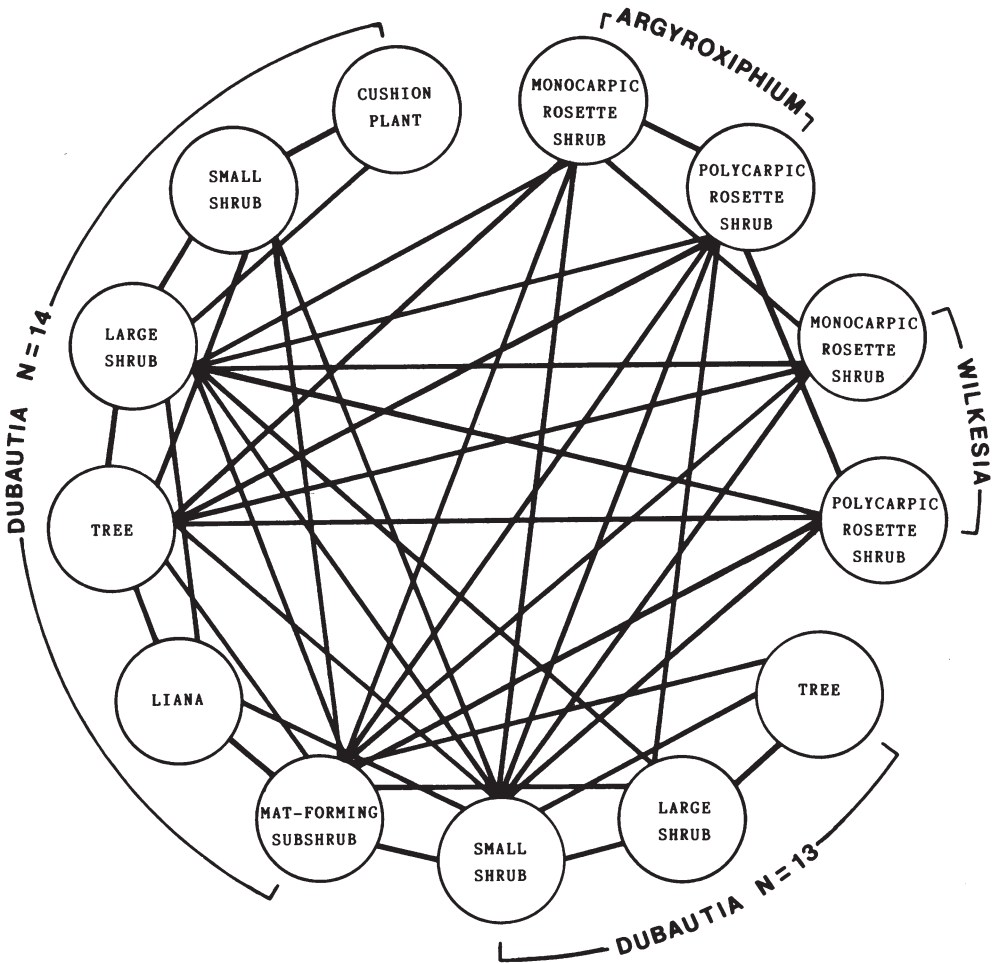


Figure 27. Crossing diagram showing synthetic and natural hybrids between species of different life-form in the Hawaiian silversword alliance based on data of Carr (1985) and Carr and Kyhos (1981, 1986). Crosses in all attempted combinations were successful and yielded hybrids of at least partial fertility. Reprinted from Carr et al. (1989) with permission of the publisher, Oxford University Press.

potential evolutionary importance of such lineages in the face of rapid global change. An important challenge in the coming years for systematists working in well-studied, threatened floras, such as the California flora, will be to resolve ecologically significant, overlooked diversity through application of molecular phylogenetic and experimental approaches, much in the spirit of Clausen, Keck, and Hiesey's classic investigations (see Baldwin, 2000).

The potential of modern plant systematics to contribute to understanding of evolutionary processes and fine-scale diversity is just beginning to be realized, with exciting results (e.g., Rieseberg, 2006 this volume; Sakai et al., 2006 this volume). Spectacular progress by systematists in resolving higher-level plant relationships through application

of molecular phylogenetic methods has created an invaluable framework for integrative systematic studies of young lineages. Recent methodological advances in systematics that allow rigorous estimation of divergence times and diversification rates and the explosive growth in comparative methods have much potential to aid systematists in taking phylogenetic hypotheses beyond the limitations of strictly pattern-based considerations and toward better informed conclusions about how and why evolutionary changes have occurred. The promise of collaborative studies of plant diversification that bring together the combined strengths of systematists, ecologists, and geneticists, so well demonstrated by Clausen, Keck, and Hiesey, has never been greater.

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APPENDIX 1. Authorities for species presented in the figures when otherwise not provided in the text. For a complete listing of accepted names and synonyms for specific and infraspecific taxa in Madiniinae, see Carr et al., 2003.

Achyrachaena mollis Schauer

Argyroxiphium caliginis C. N. Forbes

Argyroxiphium grayanum (Hillebr.) O. Deg.

Argyroxiphium kauense (Rock & M. Neal) O. Deg. & I. Deg.

Blepharipappus scaber Hook.

Blepharizonia laxa Greene

Calycadenia fremontii A. Gray

Centromadia perennis Greene

Deinandra greeneana (Rose) B. G. Baldwin

Dubautia arborea (A. Gray) D. D. Keck

Dubautia herbstobatae G. D. Carr

Dubautia imbricata H. St. John & G. D. Carr

Dubautia laevigata A. Gray

Dubautia microcephala Skottsbo.

Dubautia paleata A. Gray

Dubautia pauciflora H. St. John & G. D. Carr

Dubautia platyphylla (A. Gray) D. D. Keck

Dubautia raillardiioides Hillebr.

Dubautia sherffiana Fosberg

Harmonia stebbinsii (T. W. Nelson & J. P. Nelson) B. G. Baldwin

Hemizonia congesta DC.

Holozonia filipes (Hook. & Arn.) Greene

Lagophylla minor (D. D. Keck) D. D. Keck

Layia heterotricha (DC.) Hook. & Arn.

Madia citriodora Greene

Madia exigua (Sm.) A. Gray

Madia glomerata Hook.

Madia gracilis (Sm.) D. D. Keck & J. C. Clausen ex Applegate

Madia radiata Kellogg

Madia subspicata D. D. Keck

Osmadenia tenella Nutt.

Wilkesia hobbeyi H. St. John