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## STUDIES ON MADINAE: ANATOMY, CYTOLOGY, AND EVOLUTIONARY RELATIONSHIPS

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### INTRODUCTION

The tarweeds (Compositae, tribe Heliantheae, subtribe Madinae) are one of the best-known groups of western plants from the aspects of gross morphology, cytology, and genetics. I have desired to complement this body of information with studies on the anatomy of the subtribe so that a more adequate picture of variation and evolution in this remarkable group could be obtained. The anatomical diversity of the Madinae is, in fact, no less interesting than the variation patterns in cytological, genetical, and morphological characters. The latter features lend themselves well to studies of speciation, whereas the anatomical characters evidence trends in the development of genera or criteria for defining the group as a whole. In a number of instances, species differences are also revealed by anatomical studies. The primary focus of this study is the definition of the subtribe and its genera, and the exposition of phyletic tendencies within the Madinae by combination of anatomical data with that of other disciplines. In order to attain such a picture, the full range of variation in all characters must be obtained. Consequently, detailed information is given below, rather than salient examples of particular trends.

In a series of three papers (Carlquist 1958b, 1959a, 1959b) the nature of glandular trichomes and appendages has been described. The latter two papers also include studies on leaf anatomy in the genera *Calycadenia* and *Holocarpba*. Other contributions deal with leaf anatomy of two genera of Hawaiian Madinae, *Argyroxiphium* and *Wilkesia* (Carlquist, 1957a) and with the vegetative anatomy of Hawaiian Madinae as a whole (Carlquist, 1959c). Wood anatomy of certain Madinae was considered separately in an earlier paper (Carlquist, 1958a). The present paper completes these studies by providing data on vegetative anatomy of the Pacific Coast Madinae, anatomy of involucre and floral histology of the entire subtribe, and chromosome numbers not hitherto reported. The constitution of Madinae as expressed here does not correspond to that of other authors, and is summarized near the end of the paper. The taxonomic treatment of genera and species of California Madinae given by Munz (1959) is accepted here. The taxa of Hawaiian Madinae recognized correspond to the species given by Keck (1936) in *Dubautia* and *Argyroxiphium*, but *Wilkesia* is recognized here as a valid genus. The species of *Raillardella* considered here are those found in Munz (1959), although this genus is not placed in Madinae by that author. Mexican species of Madinae not represented in the United States are not covered in any single floristic treatment. Included in this group are *Adenothamnus validus* (Brandege) Keck, *Hemizonia martirensis* Keck, and the insular species *Hemizonia frutescens* Gray, *H. greeneana* Rose, *H. palmeri* Rose, and *H. streetsii* Gray. *Madia chilensis* Reiche grows in Chile, which is also the native location of *M. sativa* Molina. The report of an endemic tarweed from the Galapagos Islands, *Hemizonia squalida* Hook. f., is an error, as has been shown by Howell

(1935). The type specimen is an individual of *H. corymbosa* (DC.) T.&G. probably from the vicinity of Monterey, California.

### MATERIALS AND METHODS

The basic material for this study consisted of field-collected material, portions of which were preserved in formalin-propiono-alcohol (Johansen, 1940). For some species which could not, for various reasons, be obtained in this manner, herbarium material was used. Such material was expanded in 2.5 per cent aqueous NaOH, washed and stored in 70 per cent ethyl alcohol. Both types of material were embedded in paraffin according to the usual techniques. The staining procedure corresponded to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen, 1940). Materials cleared by means of the sodium hydroxide technique also proved useful for whole mounts and were stained with safranin.

The herbarium specimens which document liquid-preserved material, or from which fragments were taken, are listed below. Herbarium abbreviations are according to Lanjouw and Stafleu (1954). *Achyrachaena mollis* Schauer, *Carlquist* 408 (RSA); *Adenothamnus validus* (Brandegee) Keck, *Brandegee VI-4-1893* (cotype, GH); *Argyroxiphium* spp.: cited in *Carlquist* (1957a) except for flowering material of *A. caligini* Forbes, *Carlquist* 550 (RSA) and *A. sandwichense* DC., *Carlquist* 545 (RSA); *Blepharipappus scaber* Hook., *Keck & Clausen* 3775 (RSA); *Blepharizonia plumosa* (Kell.) Greene, *Carlquist* 418 (RSA), vegetative, *Howell* 8048 (RSA), heads; *Calycadenia* spp.: cited in *Carlquist* (1959b) except: *C. fremontii* Gray, *Hoover* 2244 (UC) and *C. tenella* (Nutt.) T.&G., *Sprague VI-13-1957* (RSA); *Dubautia* (including *Railliardia*) spp.: cited in *Carlquist* (1959c) except: *D. ciliolata* (Gray) Keck, *Carlquist* 613 (RSA), anatomy, *Kruckeberg* 703 (RSA), chromosomes; *Hemizonia clementina* Brandegee, *Abrams & Wiggins* 300 (UC); *H. congesta* DC., *Carlquist* 404 (RSA); *H. corymbosa* (DC.) T.&G. subsp. *macrocephala* (Nutt.) Keck, *Carlquist* 405 (RSA); *H. fasciculata* (DC.) T.&G., *Carlquist* 402 (RSA); *H. fitcbii* Gray, *Carlquist* 417 (RSA); *H. frutescens* Gray, *Brandegee* 1897, *s.n.* (UC); *H. greeneana* Rose, *Carlquist* 475 (RSA); *H. luzulaefolia* DC., *Carlquist* 413 (RSA); *H. minthornii* Jepson, *Carlquist* 407 (RSA); *H. palmeri* Rose, *Carlquist* 470 (RSA); *H. pungens* (H.&A.) T.&G., *Carlquist* 411 (RSA); *H. streetsii* Gray, *Moran* 2950 (UC); *Holocarpha* spp.: cited in *Carlquist* (1959b); *Holozonia filipes* (H.&A.) T.&G., *Wiggins* 8959 (RSA); *Lagophylla glandulosa* Gray, *Wolf* 9073 (RSA); *Lagophylla ramosissima* Nutt., *Carlquist* 415 (RSA); *Layia fremontii* (T.&G.) Gray, *Crum* 1918 (RSA); *L. pentachaeta* Gray subsp. *albida* Keck, *Balls* 18851 (RSA); *L. platyglossa* (F.&M.) Gray, *Campbell* 12991 (RSA); *Madia bolanderi* (Gray) Gray, *Carlquist* 622 (RSA); *M. elegans* D. Don subsp. *densifolia* (Greene) Keck, *Everett* 5204 (RSA); *M. hallii* Keck, *Howell* 18050 (RSA); *M. madioides* (Nutt.) Greene, *Carlquist* 406 (RSA); *M. minima* (Gray) Keck, *Walker* 2036 (RSA); *M. sativa* Mol., *Carlquist* 403 (RSA); *Raillardella argentea* (Gray) Gray, *Gillett* 1155 (MSC); *R. muiirii* Gray, *Smith* 823 (JEPSON); *R. pringlei* Greene, *Feudge* 1868 (RSA); *R. scabrida* Eastw., *Howell* 17194 (RSA); *R. scaposa* (Gray) Gray, *Sprague VII-17-1957* (RSA); *Wilkesia gymnoxiphium* Gray, *Carlquist* 525 (RSA). In addition to these specimens, a number of specimens from the Rancho Santa Ana Botanic Garden Herbarium and the Pomona College Herbarium were studied to determine the presence of particular features. A complete survey of the anatomy of Madinae, species by species, did not seem feasible because the number of species is very large and some close species show no appreciable anatomical differences. *Madia sativa* and *M. elegans*, for example, show no significant anatomical differences. Some selection was necessary, and this was

done on the basis of preliminary studies. Although some closely similar species were intentionally studied, the main focus of the study was an examination of all significant variations in anatomical structure. All the recognized species were studied except in the larger genera *Hemizonia*, *Madia*, *Layia*, and *Lagophylla*. In these genera, every effort was made to detect variation in anatomical structure among species, and the assemblage of species studied in these genera reflects this selection.

### ACKNOWLEDGMENTS

Without the aid of a number of individuals, this investigation would have been severely narrowed in scope. Appreciation is extended to the following for live or preserved plants: Dr. Philip A. Munz, for plants from the Rancho Santa Ana Botanic Garden; Dr. George W. Gillett; Dr. Arthur Kruckeberg; Dr. Thomas R. Pray; and Miss Elizabeth F. Sprague. Acknowledgment is also extended to the curators of the herbaria named above for their generous cooperation in allowing use of materials.

### ANATOMICAL DESCRIPTIONS

#### STEM

The Pacific Coast tarweeds are basically a group of annuals, with a few species which are not truly woody but perennate by means of rosette stems (*Raillardella* spp.; *Madia bolanderi*), a woody "caudex" (*Hemizonia*, section *Fruticosae*; *Raillardella muirii* and *R. scabrida*) or rhizomatous stems (*Holozonia filipes*; *Madia madioides*). *Adenothamnus* may be a shrub, but the only collection does not bear pertinent information. Some of the annuals may produce considerable secondary xylem. The Hawaiian Madinae, by contrast, are either woody perennials (*Dubautia*) or more or less woody rosette plants (*Argyroxiphium*; *Wilkesia*). The stem anatomy is naturally correlated with these differences in habit. The stem anatomy of Hawaiian Madinae has been described elsewhere (Carlquist, 1959c). The present descriptions, therefore, apply to Pacific Coast Madinae. The various types may be considered separately:

#### STEM TYPES.—

1. *Rosette plants*.—The stem of *Madia bolanderi* (fig. 1) is exemplary of this type of construction. A transection of a stem in the rosette region reveals a large amount of parenchyma compared to the volume of the vascular cylinder. One feature of significance is the complete absence of sclerenchyma in pith, cortex, and phloem. This is also true of rosette stems with secondary growth, as shown for *Raillardella scaposa* (fig. 8). Both *Madia bolanderi* and the rosette species of *Raillardella* (*R. argentea*, *R. pringlei*, *R. scaposa*) have two features not found elsewhere in Pacific Coast Madinae: (1) very large secretory canals in pairs beside bundles differentiated as leaf traces; and (2), a clearly defined Casparian strip on the endodermal layer of cells. Smaller secretory canals, and an endodermis lacking a Casparian strip may be found in other Pacific Coast taxa. Comparison of the rosette stems of the Hawaiian genus *Argyroxiphium* (Carlquist, 1959c) with the rosette stems above reveals considerable similarity in regard to parenchyma predominance and large secretory canals. Small bundle-cap fibers and fiber groups on inner margins of bundles, are, however, present in *Argyroxiphium*. A feature of some interest which is common to the rosette stems of both Pacific Coast and Hawaiian Madinae is the presence of carbonized resin deposits in the large air spaces of cortex and pith parenchyma. These are seen in the cortex of *Raillardella scaposa* (fig. 8). The writer (1959c) reported them in the stems of *Argyroxiphium* as well as in *Dubautia*. They also occur in pith, pith rays, and secondary phloem of *Hemizonia*, section *Fruticosae* (fig. 10). In contrast with the rosette stems, inflorescence stems of *Madia bolanderi* and the scapose species of

*Raillardella* have a type of stem construction like those of annuals (section 4, below).

2. *Rhizomatous stems*.—The peculiar rhizomatous stems of *Holozonia filipes* (fig. 7) are relatively thin, but their structural features are not unlike those of *Argyroxiphium* stems. Relatively large secretory canals are present, and relatively small fibrous bundle caps are present in the protophloem regions of the stem. Unlike *Argyroxiphium*, pith rays consist of lignified parenchyma cells.

3. *Large annual stems and fruticose perennial stems*.—These stems are distinguished by a more limited quantity of cortical and pith parenchyma. The fibrous bundle caps are prominent, but do not form a continuous cylinder around the stem. The stem of *Blepharizonia plumosa* shown in fig. 3 is exemplary of this condition. Significantly, the presence of prominent bundle caps which do not form a rigid complete cylinder marks a type of construction which allows for secondary growth. This type may be found in stems of perennials which undergo secondary growth and in the lower stems of annuals in which appreciable secondary growth occurs. Stems which are of this type were observed in the following species: *Adenothamnus validus*, *Hemizonia clementina*, *H. fitcbii* (base), *H. frutescens*, *H. greeneana*, *H. minthornii* (basal stem), *H. palmeri*, *H. pungens* (base), *H. streetsii*, *Holocarpa* spp. (base only), *Madia elegans* subsp. *densifolia* (base) and *M. sativa* (base). Probably the basal regions of many species, including those of category 4 below, would be of this type. The stems of *Dubautia* and *Wilkesia* are of the type just described (Carlquist, 1959c). Certain species of this type have additional features of interest. Secretory canals paired beside leaf traces were observed in *Adenothamnus validus*, *Hemizonia clementina*, *H. fitcbii*, *H. pungens*, and *Madia elegans* subsp. *densifolia*. Secretory canals were reported in *Wilkesia* and most species of *Dubautia* (Carlquist, 1959c). Various degrees of pith and pith ray sclerification are likewise described for *Dubautia*. Relatively thin-walled sclereids occur in pith and pith rays of *Adenothamnus validus*, *Hemizonia greeneana*, *H. palmeri*, *Holocarpa* spp., and probably a number of other taxa of Pacific Coast Madinae.

4. *Small annual stems and inflorescence stems*.—Most of the stems of the Pacific Coast tarweeds, other than regions in and near the basal rosette, could be considered parts of an inflorescence, so that the two divisions in this heading could really be considered the same. The only difference is that in stems of small wiry annuals, such as *Calycadenia tenella*, the closed sclerenchyma cylinder described below extends down to the basal rosette. The chief features of construction of stems in this category are the presence of a sclerenchyma cylinder which is continuous with the bundle caps, pith rays, and pith sclerenchyma (fig. 2). In fact, cells of each of these zones cannot be distinguished from each other. Interestingly, this stem type even occurs in inflorescence axes of rosette plants such as *Madia bolanderi* (fig. 11) and the rosette-species of *Raillardella*. In such species as *Hemizonia clementina* and *H. greeneana*, which do not have a closed cylinder of sclerenchyma in most stem portions, a continuous cylinder of sclerenchyma occurs in peduncles. Instances in which most of the stem was observed to have this sclerenchyma cylinder are as follows: *Achyrachaena mollis*, *Blepharipappus scaber*, *Calycadenia* spp., *Hemizonia congesta*, *H. corymbosa*, *H. fasciculata*, *H. minthornii* (upper stems), *Holocarpa* spp. (viz., *H. virgata*, fig. 2), *Holozonia filipes* (stems other than rhizomatous), *Lagophylla* spp., *Layia*

Fig. 1-6. Fig. 1. *Madia bolanderi*, transection of stem in region of basal rosette.  $\times 60$ . Fig. 2. *Holocarpa virgata*, transection of upper stem.  $\times 180$ . Fig. 3. *Blepharizonia plumosa*, transection of lower stem of young plant.  $\times 205$ . Fig. 4. *Madia bolanderi*, transection of central portion of root.  $\times 300$ . Fig. 5. *Calycadenia multiglandulosa* subsp. *cephalotes*, transection of young upper stem.  $\times 120$ . Fig. 6. *Madia sativa*, transection of outer portion of upper stem.  $\times 150$ .

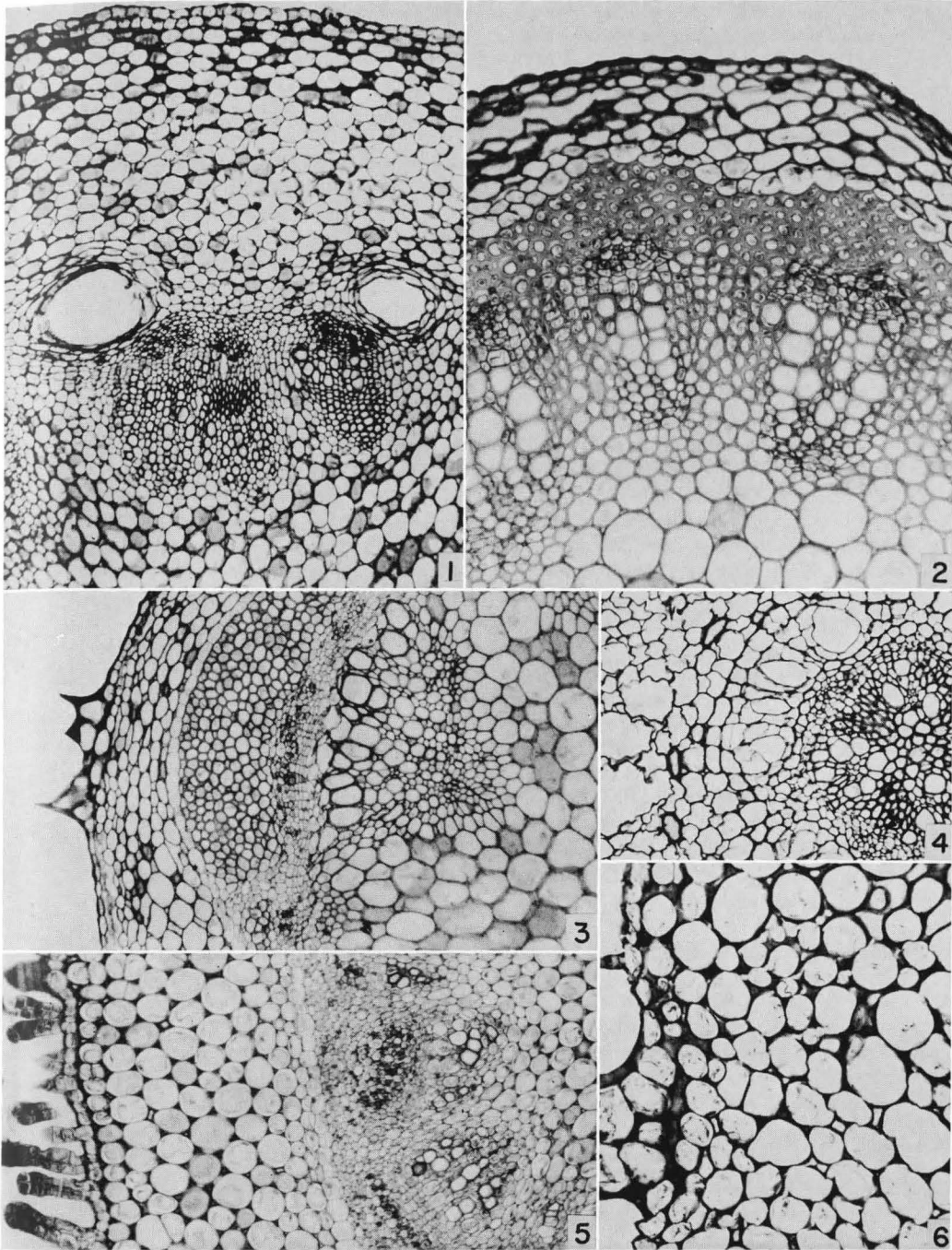


FIG. 1-6

sp., *Madia madioides*, *M. minima*, *Raillardella muirii*, *R. scabrida*. An additional noteworthy feature is exhibited by a few annuals with narrow, wiry stems in which very little secondary growth takes place. In these, as shown for *Calycadenia tenella* (fig. 12), the last-formed portion of the xylem consists of fibers identical with those of the sclerenchyma cylinder. Thus, the phloem strands are isolated within a sheath of thick-walled fibers.

The general stem type discussed above is not confined to tarweeds; the writer has observed it in other wiry annuals, such as *Baeria*. It does, however, appear to be a characteristic feature related to the annual habit, or to those stems of perennials which last only one year or part of one year (e.g., inflorescences of *Madia bolanderi*). The sclerenchyma cylinder appears to be an indurate structure which not only aids in supporting the tall, slender plant body of many annual tarweeds, but which may also have a relation to their resistance to desiccation during the dry months of summer and fall. A typical tarweed, such as *Hemizonia fasciculata*, exhibits, even before flowering, a collapse of cortical tissues, so that only withered papery sheets cover the sclerenchyma cylinder. Thus, the fiber cylinder may be capable of restricting transpiration in the same way that a layer of cork serves in other plants.

Although endodermis in stems of this type does not have a Casparian strip, it is differentiated by means of the somewhat enlarged cells with thin radial walls which often fracture in sectioned material. The endodermis, in stems of this sort, always occurs as a layer just outside the cylinder of fibers, and may be seen in fig. 2, 3 (incomplete fiber cylinder), 5 (outside future fiber zone), 11, and 12. The complete cylinder of fibers, therefore, represents not merely sclerification of bundle caps, or proto-phloem regions, but also ground meristem within the endodermis. Probably the term "cortical fibers" should not apply here on account of the more exterior position characteristic of cortical fibers. Thus, the topography of fibers in these tarweed stems more nearly fulfills the term "pericyclic fibers" than most instances in which fibers are present in dicot stems. The writer, however, agrees with Foster (1949) and Esau (1953) that the concept of pericycle should not apply to dicot stems. Some term other than "pericyclic fibers", then, is needed to describe the mode of occurrence of this sclerenchyma in annual tarweeds. As fig. 5 shows, the zone in which these fibers will be formed is clearly indicated by the smaller diameter of cells in that region. Their origin, however, cannot be described as procambial.

Cortical cells tend to be thin-walled in the annual tarweeds, although a small amount of angular collenchymatic thickening is often present, as shown for *Calycadenia multiglandulosa* subsp. *cephalotes* in fig. 5. A peculiar feature observed in stems of *Madia sativa* (fig. 6), a species in which intercellular pectic accumulations are abundant in leaves, is the occurrence of what may be termed false collenchyma. In this stem, collenchymatic thickenings are very limited, and much of the apparent wall thickness is the result of intercellular depositions of pectic compounds. That this is the case is clearly shown by many intercellular spaces in which deposition of such pectic materials does not completely fill the spaces between cells.

Secretory canals occur in a number of stems in which a complete cylinder of sclerenchyma is present. They were observed in the species of the *Centromadia* section of *Hemizonia*, *H. fitcbii* and *H. pungens*, and in *Layia platyglossa*, *Madia elegans* subsp. *densifolia*, and *Achyrachaena mollis*.

CORK; BARK.—Cork formation is very limited in most stems of annual tarweeds, varying between absence and the modest amount shown for *Madia bolanderi* in fig. 11. In the basal rosette regions of stems, however, considerable cork may be formed (*Calycadenia multiglandulosa* subsp. *cephalotes*, fig. 9). In the old rosette

stems of *Raillardella scaposa* (fig. 8), cork formation likewise is abundant, although no sclerenchyma becomes included in this cork. In addition to the protophloem fiber groups, some of the cortical cells are sclerified in the section of *Calycadenia multiglandulosa* subsp. *cephalotes* shown in fig. 9. True bark, in the Pacific Coast Madinae, is restricted to perennial species of *Hemizonia* in which a basal stem with continued secondary growth is present. In *Hemizonia palmeri* (fig. 10), like *H. greeneana*, *H. minthornii*, *H. clementina*, and other members of the section *Fruticosae*, patches of fibers, alternating with sieve elements and parenchyma cells, are formed in secondary phloem. In rays of the secondary phloem, more nearly isodiametric sclereids may be formed (fig. 10, lower right). Successive periderms are present, and eventually fibers may become involved in these. In fig. 10, left, a band of sclerified phellem cells is shown (dark). Aside from the large amount of periderm activity, bark formation in the Pacific Coast Madinae is thus not unlike that described in *Dubautia* (Carlquist, 1959c).

**SECONDARY XYLEM.**—The wood anatomy of a number of Madinae has been discussed earlier by the writer (1958b). This information may be summarized by saying that although the wood of all Madinae is basically of a generalized helianthoid type, particular specializations attributable to climatic or other factors have resulted in seasonal production of bands. These bands consist of apotracheal parenchyma, as in the less specialized *Dubautias* and *Wilkesia*. Or, as in the more advanced *Dubautias* and *Argyroxiphium*, they may contain vascular tracheids as well. The latter condition was reported by the writer in *Hemizonia minthornii*. Other members of *Hemizonia*, sect. *Fruticosae* do not have precisely this nature. Such bands, in fact, were not present in stems of *Hemizonia palmeri* and *H. greeneana* studied. This might be attributable to the less seasonal maritime climate in which these two Guadalupe Island species exist, but a prominent banded condition is shown by another insular species, *H. clementina*. In this species, bands of thin-walled parenchyma—which may include vessels of ordinary diameter—are evidently an annual production in the xylem at the end of each growing season. Such parenchyma bands are filled with resinous deposits and may possibly also be suberized, although suberization was not specifically tested. *Hemizonia clementina* stands in contrast to the *Hemizonias* named above in that the rays are very wide and composed of thin-walled parenchyma, instead of being relatively restricted in dimensions and composed of lignified cells. The xylem of *H. clementina*, with its relatively narrow fascicular areas which have replacement of thick-walled fibers by thin-walled parenchyma seasonally, is highly distinctive in comparison to other Madinae. Probably the anatomy is related to the fact that *H. clementina* produces a very thick "caudex"-like stem, from which each year slender shoots are produced. An annual production of thin-walled parenchyma is also shown by *Raillardella scaposa* (fig. 8, right), the xylem of which has a banded appearance. A feature of some interest in the woods of annual Madinae is the completion of secondary growth by deposition of a narrow cylinder of vascular tracheids, in contrast with the preceding portions of the xylem in which vascular tracheids are not present. This condition was described by the writer for *Blepharizonia plumosa*. It also occurs in old stems of *Holozonia filipes*.

The writer still holds a conclusion he suggested earlier (1958b), that relatively unmodified woods of Hawaiian Madinae (e.g., *Wilkesia*, *Dubautia raillardioides*) and Pacific Coast Madinae (e.g., *Madia sativa*, *Hemizonia greeneana*) are virtually identical, whereas the many and remarkable specializations in habit and habitat in both groups have been concomitant with alterations in xylem structure. These changes have been, to some extent, similar, so that although the habit of the species of *Argy-*



*roxiphium* is quite different from that of *Hemizonia minthornii*, their banded xylem is quite alike.

Likewise, in respect to primary stem structure, one could easily suppose that the presence of secretory canals and the presence of isolated fibrous bundle caps are relatively unspecialized conditions, and that loss of secretory canals has marked advance in Madinae. Sclerenchyma could then be said to have increased in stems of annual tarweeds, and have been lost in the rosette types, and these changes are correlated with adaptations to particular habitats.

#### ROOT

A root of *Madia bolanderi* is shown in fig. 4. A feature of some interest is the presence of numerous small secretory canals just outside the endodermis. These are a feature found in other Madinae, and were described for *Argyroxiphium* and *Wilkesia* by the writer (1959c) as well as for other Heliantheae (1957b). The number of protoxylem and protophloem poles may vary between two and six, depending on the size of primary roots. Roots of the rosette species of *Raillardella* and of *Madia bolanderi* have a very wide cortex, but differ in no other respect from roots of other Madinae. Thus, roots in this group have features common to many Compositae.

#### NODAL ANATOMY

One significant fact which has emerged from these investigations is that all Madinae possess, in the seedling stage, one or more pairs of opposite leaves. In the later development of the plant, this condition may remain the same, or may be changed to alternate or verticillate. An alternate condition is not infrequently associated with an inflorescence. In *Raillardella*, for example, the basal leaves are opposite, whereas the upper leaves are alternate. The development of the rosette habit has probably been correlated with the development of alternate leaves, however. This is true in *Argyroxiphium* (Carlquist, 1957a) as well as in the rosettes of some annual tarweeds.

The Pacific Coast tarweeds are relatively limited in respect to nodal anatomy. Careful examination of species with wide leaf bases failed to show any in which multilacunar nodes are present. As a generalization, one may say that trilacunar nodes, either alternate or opposite, are present in the lower leaves of all the Pacific Coast Madinae. The writer has already described this in the genera *Calycadenia* and *Holocarpha* (Carlquist, 1959a, 1959b). The smaller upper leaves of the inflorescence may be unilacunar, however. In some cases (e.g., *Calycadenia*, *Layia*), only those reduced bract-like leaves immediately adjacent to the heads were found to be unilacunar. Species in which unilacunar nodes were observed on inflorescence leaves or bracts include *Blepharipappus scaber*, *Blepharizonia plumosa*, *Calycadenia multiglandulosa*, *C. truncata*, *Hemizonia fasciculata*, *H. minthornii*, *Holocarpha* spp. except *H. macradenia*, *Holozonia filipes*, *Lagophylla ramosissima*, *Layia platyglossa*, *Madia exigua*, *M. hallii*, *M. minima*, *M. sativa*, and *Raillardella scabrada*. Undoubtedly a number of species have only trilacunar nodes throughout. Species in which this condition was observed include *Achyrachaena mollis*, *Adenothamnus validus*, and *Raillardella scaposa*. Because there is a possibility that small or depauperate plants may bear small leaves with unilacunar nodes, whereas other individuals may not, precise definition of nodal conditions by species is difficult.

Fig. 7-10. Stem transections, exterior at left. Fig. 7. *Holozonia filipes*, transection of mature rhizomatous stem.  $\times 140$ . Fig. 8. *Raillardella scaposa*, transection of older portion of basal stem.  $\times 90$ . Fig. 9. *Calycadenia multiglandulosa* subsp. *cephalotes*, transection of older stem in transition region.  $\times 95$ . Fig. 10. *Hemizonia palmeri*, transection of bark of older stem.  $\times 55$ .

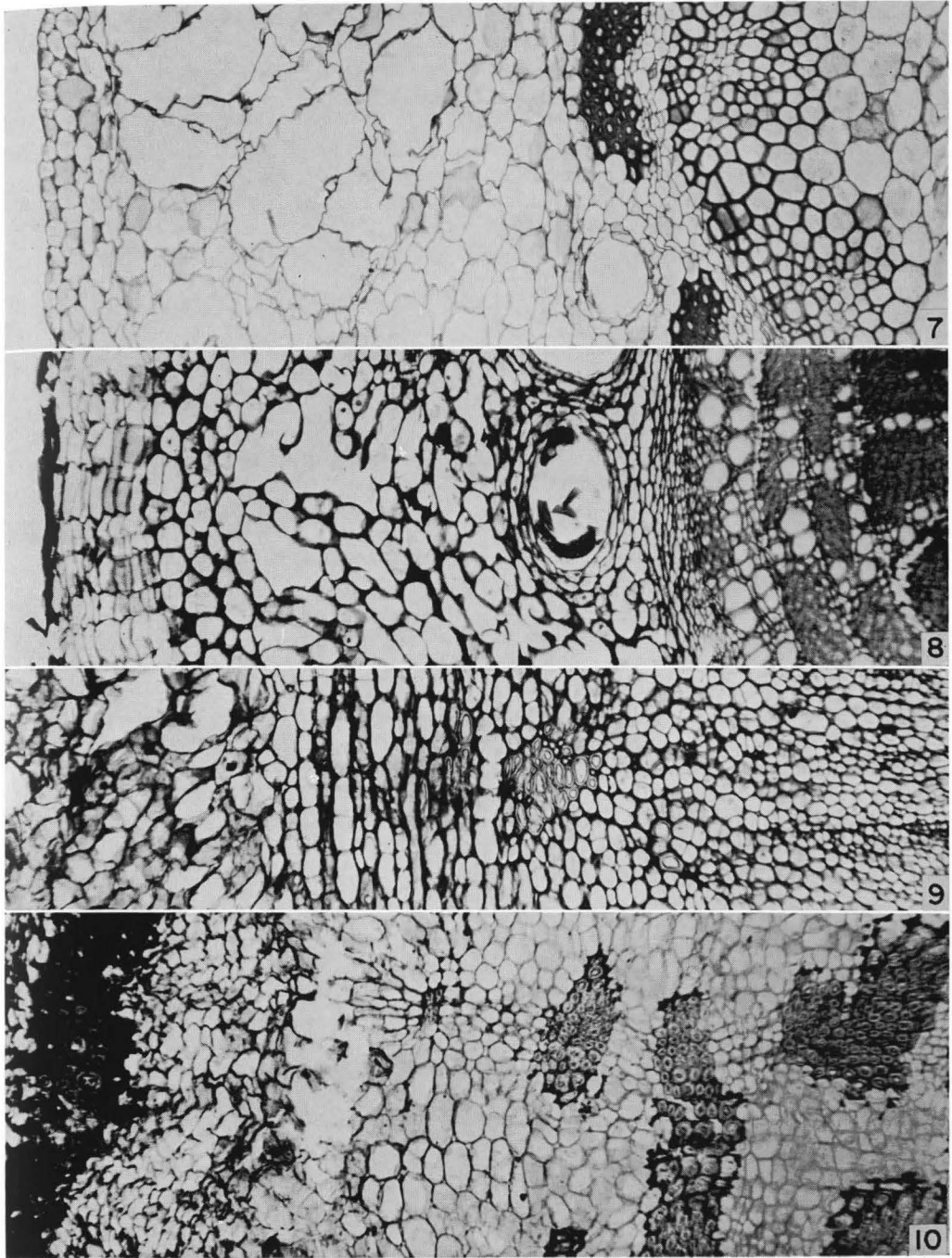


FIG. 7-10

The nodal conditions of *Madinae* are highly varied, and encompass all known basic types except opposite unilacunar nodes. They may be summarized as follows:

*Unilacunar, alternate*: upper leaves of Pacific Coast *Madinae* only, listed above.

*Trilacunar, alternate*: Many Pacific Coast *Madinae*, plus certain species of *Dubautia* (Carlquist, 1959c).

*Trilacunar, opposite*: Seedlings and early leaves of Pacific Coast and Hawaiian *Madinae*, as well as the adult leaves of some species (e.g., *Achyrochaena mollis*, *Calycadenia oppositifolia*, *Madia bolanderi*, *M. madioides*, *M. minima*, *Raillardella muirii* and the rosette species of *Raillardella*). The rhizomatous stems of *Holozonia* bear opposite scale-leaves with nodes of this type. A number of *Dubautia* species have this nodal condition (Carlquist, 1959c).

*Trilacunar, verticillate*: Reported for *Dubautia ternifolia* and *D. waialealae* (Carlquist, 1959c). During field work in the Hawaiian Islands in 1958, the writer discovered occasional plants of *Dubautia menziesii* in which verticils of three leaves each (with trilacunar nodes) occur, so this species may be added. Such nodes have also been reported for *Wilkesia* (Carlquist, 1958), in which many more than three leaves per verticil are present.

*Multilacunar, alternate*: This condition occurs in all the species of *Argyroxiphium* (Carlquist, 1957).

*Multilacunar, opposite*: Reported for four species of *Dubautia* (Carlquist, 1959c).

*Multilacunar, verticillate*: Reported for *Dubautia railliardioides* (Carlquist, 1959c). The possibility of this nodal condition was indicated for *Argyroxiphium grayanum* (Carlquist, 1957a). During field work on Puu Kukui, Maui, in the summer of 1958, the writer discovered that verticillate leaves are not as infrequent as they have been supposed (e.g., Keck, 1936). Nodes with verticils of four to six leaves occur frequently either on younger plants or on older plants which have given rise to new lateral shoots because of flowering or injury. Nodes of these leaves, which may be termed juvenile leaves, have venation like that indicated for *Dubautia railliardioides*, except that more leaves are present per verticil. Therefore, *Argyroxiphium grayanum* is evidently the second instance in dicotyledons in which multilacunar verticillate nodes have been reported.

The foregoing outline indicates that the range of nodal conditions is extraordinarily wide. The basic condition appears to be a trilacunar condition, opposite at least in the seedling stages, often alternate in later-formed leaves. Reduction to a unilacunar condition has occurred in upper leaves of Pacific Coast tarweeds, to a limited extent. The development of trilacunar, verticillate nodes in *Dubautia* and *Wilkesia* probably represents a minor variant on the trilacunar, opposite condition. The development of multilacunar nodes is probably related to the acquisition of a broad, lanceolate leaf shape by the *Dubautias* of the rain forest, as well as by *Argyroxiphium*.

#### LEAF ANATOMY

The writer has described the leaf structure and ontogeny of *Argyroxiphium* and *Wilkesia* (Carlquist, 1957a), the leaf anatomy of *Dubautia* (Carlquist, 1959c), and, in Pacific Coast *Madinae*, leaf anatomy of *Calycadenia* (Carlquist, 1959a) and *Holocarpa* (Carlquist, 1959b). In the present paper, therefore, the leaf anatomy of the remaining genera of Pacific Coast *Madinae* is described and the principles of leaf construction in the group are considered.

Leaves of the Pacific Coast tarweeds show great variety of structure not only between species and genera, but also within a single plant. This latter variable is very great, and occurs in two ways: (1), differences between basal and upper leaves; and

(2), differences between the base and apex of a single leaf. A description of variables in anatomy of leaves within each species would be excessively repetitious. Consequently, an account of these variables for the Pacific Coast tarweeds as a whole is given below, followed by an account of "typical" leaves of the species studied, as seen in a transection taken about halfway along the length of a leaf.

**DIFFERENCES BETWEEN BASAL AND UPPER LEAVES.**—Comparison between basal and upper leaves is illustrated here for *Hemizonia congesta* (fig. 22 and 23 respectively). As a generalization, one may say that although upper leaves are highly varied among the tarweeds, the basal leaves show relatively close resemblance from one genus to another. The differences may be summarized as follows:

1. *Gross Morphology.*—Leaves of the basal rosette, and lower leaves of the lower portions of stems, are longer and wider than upper leaves. They are more often toothed or lobed than upper leaves, which are entire except in *Layia* and *Achyrachaena*. Basal leaves are prominently widened at the base, and although they are apparently always trilacunar, marginal veins branch upwards from the lateral veins in the leaf base, and additional branches toward the margin may occur farther up, as shown for *Argyroxiphium sandwichense* (Carlquist, 1957a). If lower leaves are opposite, they often form a common sheath in which adjacent lateral veins from each leaf pair may or may not be united in their downward course into the stem. Upper leaves do not have sheathing bases, in general, and are either sessile or somewhat petiolate.

2. *Venation.*—Both upper and lower leaves of tarweeds have longitudinally elongate areoles, such as those figured for *Dubautia linearis* (Carlquist, 1959c) or *Calycadenia multiglandulosa* subsp. *cephalotes* (Carlquist, 1958b). Lower leaves have bundles in a single plane (fig. 14, 22) or with only a small arc of bundles recurved toward the lower surface of the leaf (fig. 29). The first-formed leaves of the basal rosette have little or no recurvature of bundles, however. Lower leaves above the basal rosette frequently show some degree of recurvature, as accounts below show. In the majority of the tarweeds, upper leaves, especially those near the capitula, have prominent recurvature of bundles (fig. 23, 25, 28). This process, in highly advanced genera, such as *Blepharizonia* (fig. 27), *Calycadenia* (Carlquist, 1959a) and *Holocarpus* (Carlquist, 1959b) results in meeting of the lower margins beneath the midvein; anatomical union of veins from each margin is achieved, so that a cylindrical or saccate pattern of venation is present in the uppermost leaves of some species in these genera.

3. *Fiber Strands.*—Strands of fibers are present in the margins of a species; they are more prominently represented in basal leaves (compare fig. 22 and 23). In some cases, there is only a slightly more prominent representation of fibers at the phloem pole of several marginal bundles (fig. 24). In other instances, the marginal strand of fibers may be markedly more prominent than fibers at the phloem pole of other bundles in the leaf, and may have a circular outline in transection (fig. 13, 15). A feature of particular interest is that this strand of fibers may not be associated with conducting elements in lower leaves (fig. 20, 22). This condition is reminiscent of the separation of fiber strands from collateral bundles in the leaf of *Argyroxiphium* (Carlquist, 1957a).

4. *Mesophyll.*—The mesophyll of basal leaves is thinner than that of upper leaves, but this fact is chiefly related to the occurrence of isolateral construction on upper leaves, whereas lower leaves are usually bifacial. Bifacial construction may also occur in upper leaves if the species is characteristic of shaded situations (*Madia madioides*, fig. 13), wet habitats (*Madia bolanderi*, fig. 21), or is a vernal annual (*Achyrachaena*

*mollis*, fig. 14). As a generalization, one may say that leaves produced during the summer and fall by tarweeds growing in open, dry situations are isolateral. Palisade is present on the lower surface of upper leaves even if the bundles do not form a complete cylinder around the leaf in recurving toward the lower surface of the leaf (fig. 18, 23). Lower leaves may have only spongy chlorenchyma (fig. 22) or palisade parenchyma with rather large air spaces. Bundle sheaths or bundle-sheath extensions tend to be larger or more frequent on lower leaves than on upper leaves.

5. *Pectic Accumulations*.—One feature of very considerable interest in *Madinae* is the presence of intercellular pectic accumulations in leaves. These deposits are usually absent or very inconspicuous in leaves of the basal rosette (fig. 22), whereas they are very prominently represented, and may fill the intercellular spaces, in the spongy mesophyll of upper leaves (fig. 23, 25, 27). Accumulations may be restricted to the central portion of the leaf (fig. 18, 24). The writer believes that the presence of pectic accumulations may represent an adaptation to the excessively dry, hot conditions under which tarweeds grow and flower in summer and early fall. One could imagine that pectic compounds, which are highly hydrophilic, are a means of retention of moisture. The isolateral, often subterete leaves with condensation of form through recurvature of the margins, coated with resin-like secretions from glandular hairs or densely coated with uniseriate trichomes (*Lagophylla*) and with intercellular spaces filled with pectic compounds would certainly seem to represent a remarkable series of adaptations to these conditions. Basal leaves, especially those of the basal rosette, are formed under relatively mesic vernal conditions, so such adaptations would be unnecessary. The writer was able to bring some experimental evidence to this supposition. A plant of *Madia bolanderi* from Tioga Pass, California, was grown from August, 1957, to August, 1958. This species, which is a perennial of marshy or wet habitats, produces only rosette leaves until it flowers, usually in July or August. The writer was therefore able to collect and fix rosette leaves formed during both winter and summer months. Leaves fixed in March, 1958 (fig. 20) are very thick, with large intercellular spaces in the mesophyll; intercellular accumulations of pectic compounds are so small and scarce as to be nearly imperceptible. Leaves fixed in August of the same year (fig. 21) are thinner, with smaller intercellular spaces which are filled with pectic deposition (gray background in mesophyll). Plants were not grown under water-stress conditions, so that this increase must represent the influence of either increased temperature or increased isolation. This does not rule out the possibility that decrease in available moisture may also play a part in formation of these deposits. The most striking accumulation of pectic compounds was observed in leaves of plants of *Blepharizonia plumosa* (fig. 27) which the writer collected in a very dry, alkaline area of the Inner Coast Ranges near Livermore, California. Pectic accumulations were so great—or so hydrophilic—that the use of a formalin solution during mounting of paraffin sections caused swelling of pectic materials. Sections were distorted in shape by this swelling, and the pectic deposits spread over the slide, rendering most of the sections useless. The writer observed that in all the species of *Madia* studied, pectic deposition was considerable. In *Madia madioides*, however, such deposits were relatively small and restricted to the central portion of the leaf (fig. 13), a fact which may be related to the comparatively cool, mesic, shaded places where this species grows.

Fig. 11-16. Fig. 11. *Madia bolanderi* transection of upper stem.  $\times 115$ . Fig. 12. *Calycadenia tenella*, transection of upper stem.  $\times 150$ . Fig. 13. *Madia madioides*, transection of lower leaf, including margin.  $\times 115$ . Fig. 14. *Achyrochaena mollis*, transection of upper leaf, including margin.  $\times 105$ . Fig. 15. *Raillardella muirii*, transection of leaf, including margin.  $\times 120$ . Fig. 16. *Raillardella scaposa*, transection of leaf of basal rosette.  $\times 130$ .

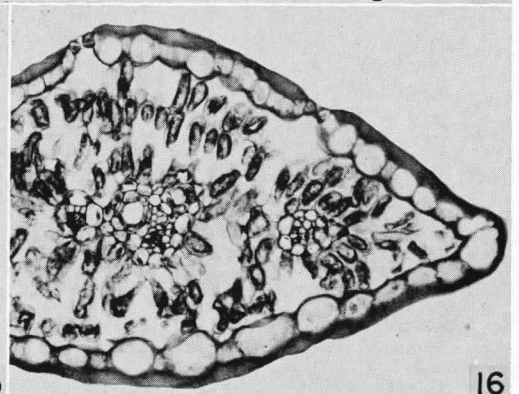
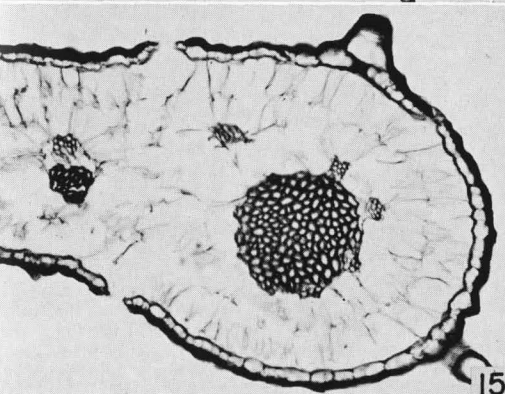
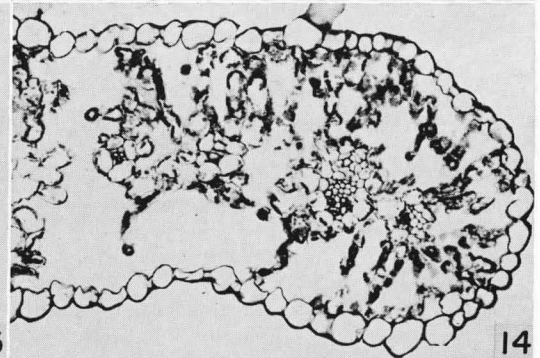
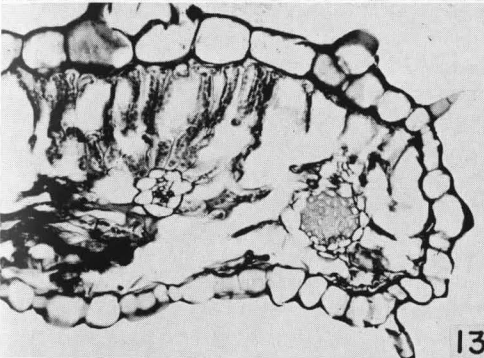
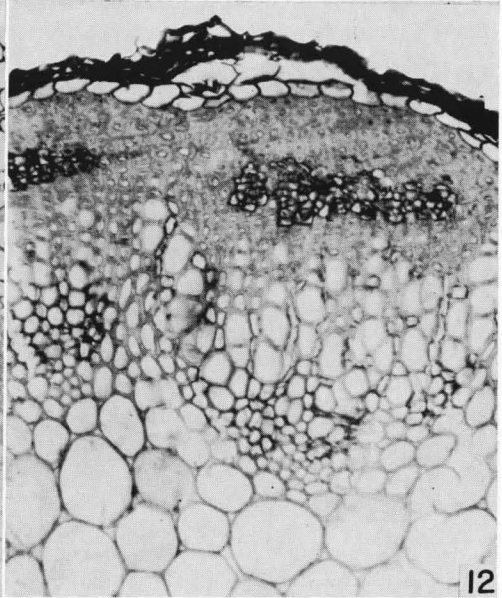
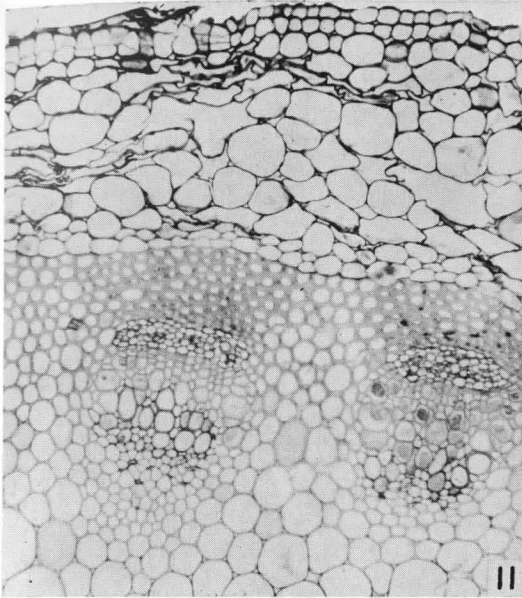


FIG. 11-16

The ability to form intercellular pectic deposits appears to be basic in Madinaeae. This property may be lost or modified by adaptation to particular habitat conditions. For example, in the species of *Dubautia* which grow in cool, shady rain-forest conditions, pectic deposits are lacking altogether. The apparent richness of such compounds in cell walls in the leaf of *Dubautia menziesii*, a species which grows on dry alpine areas near the summit of Haleakala, Maui, was mentioned earlier (Carlquist, 1959c). Leaves of *Dubautia ciliolata*, a species which occupies similar habitats on Kilauea and Hualalei, Hawaii, show small intercellular pectic accumulations at the interstices of mesophyll cells (fig. 65, lower right). A parallel situation seems to occur in *Wilkesia*, a genus which occurs in drier portions of the rain forest of Kauai. Leaves of this plant lack pectic accumulations (Carlquist, 1957). In bracts of the inflorescence—which is formed during the drier summer months—the writer has noticed relatively thick-walled mesophyll cells. The thickness of these walls is probably due to richness in pectic materials. Likewise, thick-walled mesophyll cells are present in the bracts of the heads (fig. 66). The enlarged portion of such a bract (fig. 67) shows that actual intercellular deposition of pectic compounds occurs (center), in addition to the great thickness of many cell walls. Leaves of the remaining genus of Hawaiian Madinaeae, *Argyroxiphium*, show massive accumulations of pectic compounds, although such depositions are absent in leaves of a young seedling (Carlquist, 1957a). This would seem to indicate an adaptation to dry conditions in two species from xeric localities on Haleakala, *A. sandwichense* and *A. virescens*. Two species from exceptionally moist bog habitats on Puu Kukui, Maui, *A. caligini* and *A. grayanum*, also show these accumulations. In view of the relatively clear correlation of pectic accumulation with insolation, temperature, or aridity, or a combination of such factors in the Pacific Coast tarweeds, I suspect that *Argyroxiphium* is primarily adapted to relatively xeric locations, and that entrance into the extreme bog conditions has been secondary.

Ontogenetically, intercellular pectic accumulations are formed at a very early stage in leaf development. One feature which is particularly striking in leaves in which abundant deposits are formed is that air spaces never develop. Rather, intercellular spaces are filled with pectic materials onward from the time of initiation of these spaces. This was clearly observed in young leaf primordia of *Blepharizonia plumosa* and *Hemizonia luzulaefolia* (fig. 26). Where pectic accumulations are less prominent, they appear formed mostly before maturation of the leaf, so that air spaces are developed at an early stage and increase in volume much more greatly than do the pectic deposits. The physiological significance of pectic deposition needs to be explored experimentally.

6. *Trichomes*.—Uniseriate non-glandular trichomes which have a widened base composed of short, thick-walled cells are characteristic of Pacific Coast tarweeds. They tend to occur, however, much more abundantly on leaves of the basal rosette and on lower leaves than on upper leaves. For example, leaves of the basal rosette of *Hemizonia luzulaefolia* are covered with a felt of uniseriate trichomes; upper leaves of the main stem and inflorescence are notable instead for their large, capitate glandular trichomes. For example, the species of *Lagophylla* have an almost lanate covering of uniseriate trichomes on their upper leaves; this condition is present to a

Fig. 17-23. Transsections of leaves, adaxial face at right. Fig. 17-19. *Hemizonia mintbornii*, transsections of upper leaves. Fig. 17. Transsection near base.  $\times 125$ . Fig. 18. Transsection midway along length of leaf.  $\times 110$ . Fig. 19. Transsection near apex of leaf.  $\times 110$ . Fig. 20-21. *Madia bolanderi*, transsections of leaves. Fig. 20. Transsection of leaf fixed in March, 1958.  $\times 110$ . Fig. 21. Transsection of leaf fixed in August, 1958.  $\times 135$ . Fig. 22-23. *Hemizonia congesta*, transsections of leaves. Fig. 22. Transsection of lower leaf.  $\times 125$ . Fig. 23. Transsection of upper leaf.  $\times 60$ .

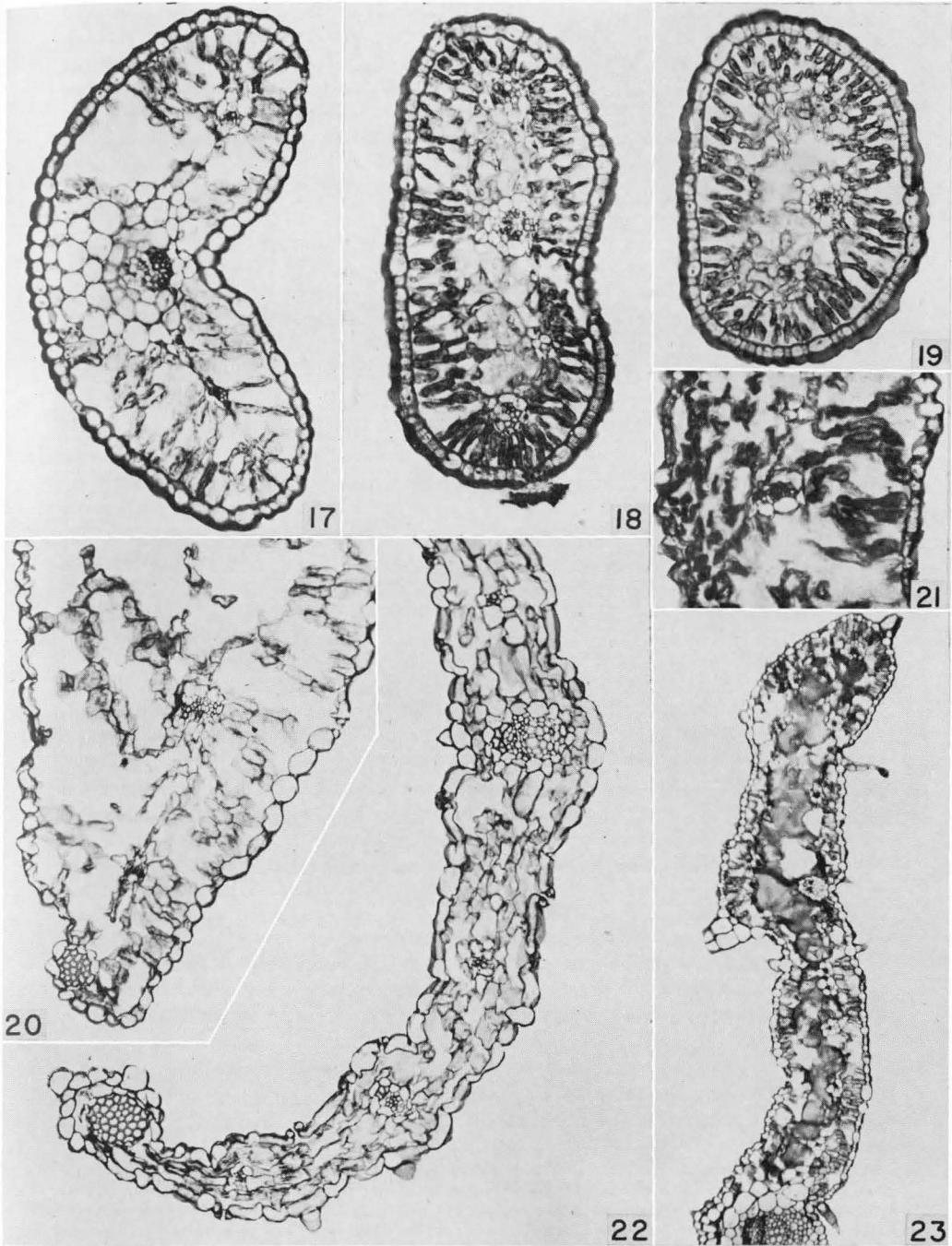


FIG. 17-23



lesser extent on a number of species of *Madia*, such as *M. ballii*. If there is no marked decrease in uniseriate non-glandular trichomes on upper leaves, however, there is usually a marked increase in the presence of glandular trichomes. Only the upper leaves of *Lagophylla*, particularly those near the heads, bear the funnel-shaped glandular trichomes characteristic of that genus. The increasing abundance of glandular trichomes on upper leaves seems to be correlated with the observations above on pectic accumulations. Many species, such as *Hemizonia minthornii*, have short-lived glandular trichomes (Carlquist, 1958b) which soon coat the leaf with a resin-like varnish. This, together with the thick-walled nature of epidermal cells (fig. 18, 27) on upper leaves, and the more nearly subterete shape induced by recurvature of bundles or reduction in number of bundles (fig. 18), and the greater pectic accumulations seems clearly related to desiccation-resistance. In the leaves of *Argyroxiphium caliginii*, *A. sandwichense*, *Lagophylla* spp., and *Raillardella argentea*, the silvery felt of uniseriate trichomes may be an adaptation to habitats of high insolation.

DIFFERENCES FROM BASE TO APEX OF A SINGLE LEAF.—Considerable difference in structure may occur between base and apex of a leaf, both in upper and lower leaves. A comparative series is shown for an upper leaf of *Hemizonia minthornii* (fig. 17-19). The respects in which differences occur are as follows:

1. *Venation*.—In upper leaves, where marginal bundles are most frequently recurved to the lower surface of the leaf, the base of the leaf shows no such recurvature. If a trilacunar node is present, three veins, which lie in a single plane, occur in the leaf base. Branches from lateral veins may increase the number of veins present in the basal portion of a leaf. Recurvature of bundles, if present, takes place above the base. This conformation is shown by a venation drawing of an upper leaf of *Calyca-denia* by the writer (1959a). If little recurvature occurs, such change in orientation of marginal veins occurs near the tip. An example of this is seen in *Hemizonia minthornii* (fig. 19), in which marginal veins may be obscure because the large tracheary elements appear like parenchyma. If marginal strands of fibers are present in a leaf, these usually begin at some point above the base and extend to the tip; they are not ordinarily present in the most basal portion of the leaf.

2. *Mesophyll*.—The most conspicuous difference between the leaf base and distal portions is the relative amount of parenchyma which is composed of more or less isodiametric cells, and which is associated with small intercellular spaces and is not abundantly filled with chloroplasts. Such parenchyma is like that of the bundle sheath, so that in a basal portion of a leaf, a considerable proportion of the mesophyll may be occupied by a bundle sheath or sheath extension. In fact, a section of a leaf base just above the juncture with the stem reveals little or no photosynthetic parenchyma. Comparison of fig. 17 and 18 reveals the reduction in bundle sheath tissue. If intercellular pectic deposits are present in a leaf, they are associated with spongy parenchyma internal to palisade parenchyma, and are not present in the basal portion of a leaf.

3. *Trichomes*.—Some species show a change in indument from base to apex of a single leaf. Among the more striking examples are upper leaves of certain species

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Fig. 24-29. Sections of leaves, adaxial face above. Fig. 24. *Hemizonia greeneana*, transection of upper leaf, including margin.  $\times 85$ . Fig. 25. *Madia sativa*, transection of upper leaf, including margin.  $\times 90$ . Fig. 26. *Hemizonia luzulaefolia*, longitudinal section of leaf primordium, showing appearance of pectic materials in mesophyll.  $\times 240$ . Fig. 27. *Blepharizonia plumosa*, transection of upper leaf, including midvein.  $\times 120$ . Fig. 28. *Lagophylla ramosissima*, transection of upper leaf, including margin.  $\times 105$ . Fig. 29. *Hemizonia pungens*, transection of lower leaf, including margin.  $\times 220$ .

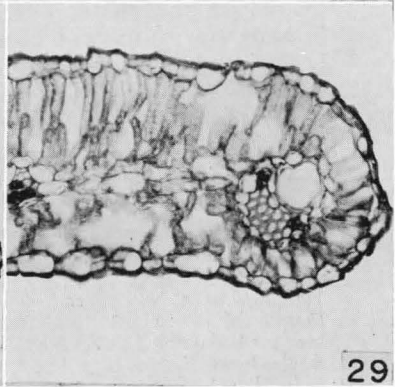
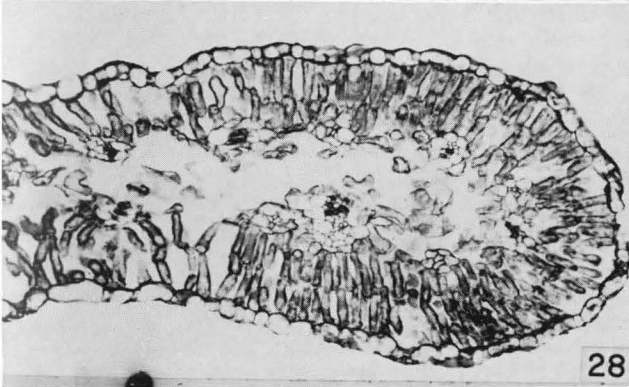
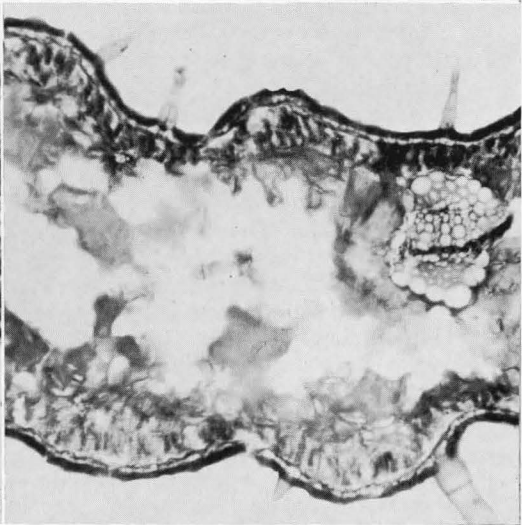
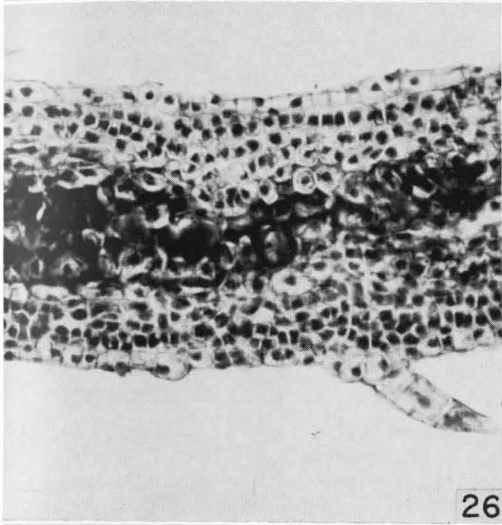
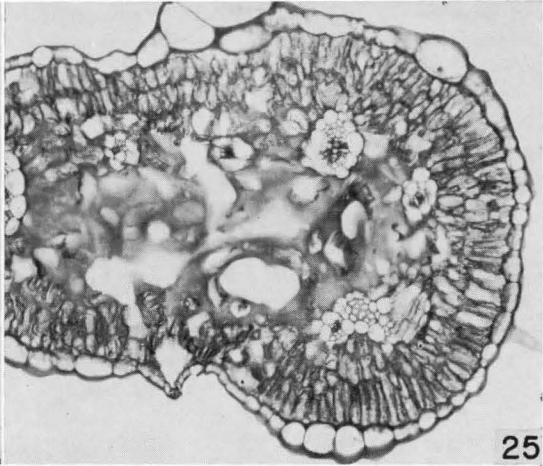
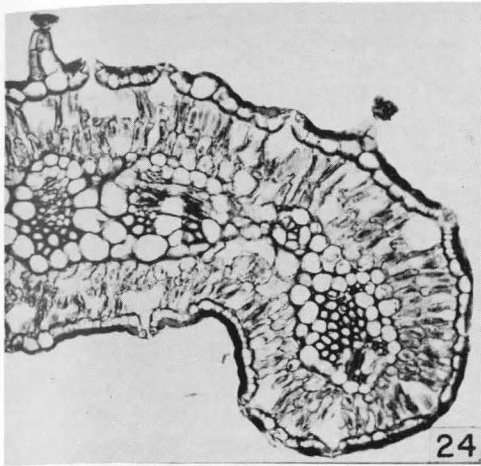


FIG. 24-29

of *Calycadenia*, in which large uniseriate trichomes are present near the base, especially along the margins, and absent in distal portions. Conversely, the characteristic tack-shaped glands occur in distal portions of the leaf, and may be restricted only to the tip. An account of trichome distribution in *Calycadenia* is provided elsewhere by the writer (1959a).

COMPARATIVE DESCRIPTIONS.—Despite the extensive variations outlined above, the genera of Madinae have characteristic features which can, to a certain extent, be shown to be related to the taxonomic system. The bases for the descriptions below are transections of the leaf, taken approximately midway along the length of the leaf. Descriptions of glandular trichomes characteristic of leaves of particular species are omitted here because they have been covered in other papers. The coverage of the genera below is not to be considered an exhaustive treatment in the larger genera, but rather an attempt to discover characteristic features for each taxon.

1. *Achyrachaena*.—Leaves in this monotypic genus (fig. 14) seem clearly related to the growth habit of this vernal annual. The bundles lie in a single plane, with no recurvature around the margins. A conspicuous thin-walled bundle sheath is present on the midvein, and smaller sheaths occur on lateral veins. A small number of fibers may be present at the phloem pole of the midvein and other larger veins, but no fibers are present at the margins. The leaf is bifacial, with lacunate palisade above and spongy tissue below. No pectic accumulations are present. Numerous uniseriate non-glandular trichomes are present.

2. *Adenothamnus*.—Leaves of this perennial monotypic genus are reminiscent of those of the insular *Hemizonias*. A small arc of recurved veins is present at the margins. The midvein has a bundle-sheath extension, and bundle sheaths are present on lateral veins. The sheath of the midveins contains a cylinder of fibers enclosing the bundle; this cylinder extends to the adaxial epidermis. Fiber strands are present on the phloem poles of many of the lateral veins, and the marginal strand of fibers is in contact with phloem poles of several veins. Palisade is present on both surfaces. Only capitate glandular trichomes with biseriate or quadriseriate stalks (Carlquist, 1958b) are present on the epidermis.

3. *Blepharipappus*.—In the single species, there is marked recurvature of bundles to the lower surface. In lower leaves of the main stem, they form a lower series of bundles over the abaxial surface except for the midvein, which has a bundle-sheath extension. In the uppermost leaves, the veins form a complete cylinder, and bundle sheaths are inconspicuous or absent. Fibers are present only in a limited area beside the phloem pole of the midvein of lower leaves. On leaves other than those of the basal rosette, palisade is present on both surfaces, and the central portion of the leaf is occupied by spongy parenchyma which forms a single "pectic channel" (see Carlquist, 1957a, for definition) in the uppermost leaves. In leaves of the main stem where a bundle-sheath extension is present, two such channels are present. Short uniseriate non-glandular trichomes are present on both surfaces.

4. *Blepharizonia*.—Leaves of the only species (fig. 27) show the same patterns in vascular structure as leaves of *Blepharipappus*. Fibers are present on some of the lateral veins of some leaves of the main stem as well as on the midvein. Palisade

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Fig. 30-35. Fig. 30-31. *Hemizonia fitchii*, transection of upper leaf, adaxial face above. Fig. 30. Margin.  $\times 135$ . Fig. 31. Midvein region.  $\times 155$ . Fig. 32-33. *Hemizonia fitchii*, transections of bracts, adaxial face below. Fig. 32. Involucral bract; ray corolla below.  $\times 110$ . Fig. 33. Receptacular bract.  $\times 135$ . Fig. 34-35. *Holocarpba heermannii*, transections of bracts, adaxial face at right. Fig. 34. Receptacular bract.  $\times 160$ . Fig. 35. Involucral bract.  $\times 160$ .

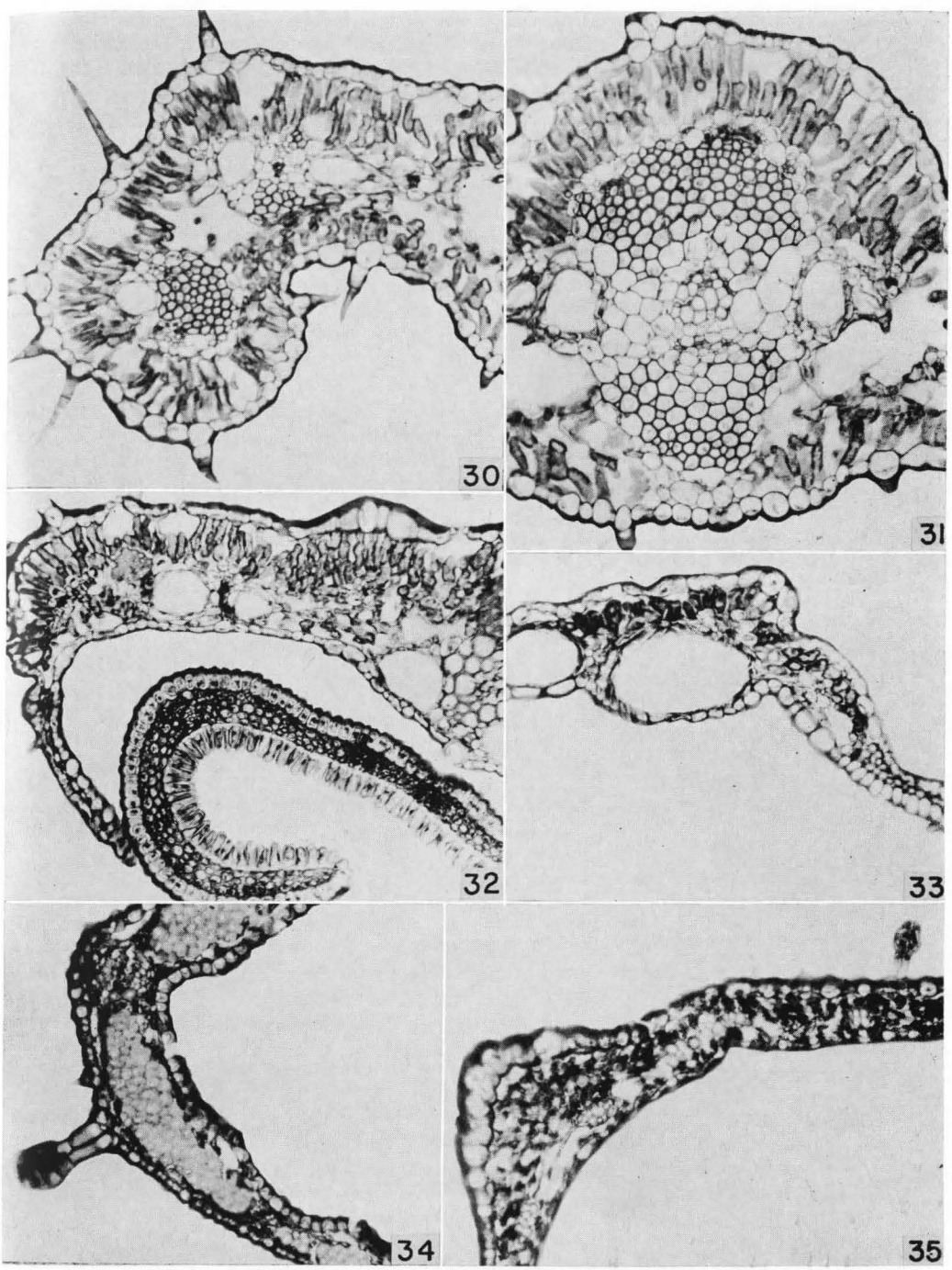


FIG. 30-35

parenchyma, spongy parenchyma, and pectic accumulations are as described for *Blepharipappus*. Uniseriate non-glandular trichomes (fig. 27) are abundant, in addition to the peculiar tack-shaped multiseriate glandular trichomes (Carlquist, 1958b), which are present on all surfaces of the leaf.

5. *Calycadenia*.—The leaf anatomy of the various species is detailed in Carlquist (1959a).

6. *Hemizonia*.—

Section *Fruticosae*. This section contains the perennial species of the genus, all of which are insular except for the rather distinctive species *H. mintbornii*, the leaves of which are illustrated in fig. 17-19. In this species, veins lie in a single plane, except for a small amount of recurvature at the tips of the leaves. Bundle sheaths are present, but less conspicuous on lateral veins. No fibers are present, but sclerified parenchyma cells occur in the bundle-sheath extension of the leaf base (fig. 17). Palisade parenchyma is isolateral; spongy tissue with pectic accumulations forms a pectic channel in the center of the leaf. Capitulate glandular trichomes (described in detail, Carlquist 1958b) occur on all surfaces of the leaf. *Insular species of section Fruticosae: Hemizonia greeneana* (fig. 24) shows a limited recurvature of the leaf margin and its included bundles. A bundle sheath extension, which may include some collenchyma, is present on the midvein, and bundle sheaths occur on lateral veins. The parenchyma of the bundle sheath extends between the veins, occupying the central mesophyll instead of spongy parenchyma. A cylinder of fibers surrounds the midvein, and fiber groups are present at the phloem pole of most veins. The marginal fiber group contacts the phloem poles of several veins. Prominent capitulate glandular trichomes are present on the leaf surfaces. *Hemizonia palmeri* is different from *H. greeneana* in having spongier parenchyma on the lower surface and a rather dense coating of uniseriate trichomes on both surfaces. *Hemizonia frutescens* differs from *H. greeneana* in that fewer lateral veins have fiber strands, and the central portion of the mesophyll does not consist of cells like those of the bundle-sheath parenchyma. Fibers are lacking on all veins in the uppermost leaves of *H. frutescens*, but the marginal fiber strands are present. *Hemizonia clementina* differs from *H. greeneana* in that fiber strands occur only at the margins and as a sheath around the midvein. In addition, the central portion of the mesophyll does not consist of cells like the bundle sheath parenchyma. A pair of secretory canals is present beside the midvein, and canals are present near some lateral veins. *Hemizonia streetsii* is the simplest of the insular *Hemizonias* in that no bundle-sheath extensions are present, bundle sheaths are minimal, secretory canals are absent, and fibers are present only in the margins.

Section *Centromadia*. Preliminary studies showed that except for glandular appendages, little difference occurs between the species of this section with the exception of *H. fitchii*. Leaves of the main stem of *Hemizonia pungens* (fig. 29) are like those of *H. greeneana*. They differ in the presence of secretory canals—paired beside the midvein and usually solitary beside other veins—and in the lack of parenchyma like that of the bundle sheath occupying a central position in the mesophyll. Leaves of all species in this section show one marked difference from other species of *Hemizonia* in that the cylindrical sheath of fibers which surrounds the midvein extends to the apex of the leaf, where, distal to the termination of the vein itself, it forms a sharp spine. Leaves of *H. fitchii* comparable to those described for *H. pungens* show a number of differences. The central portion of the mesophyll consists of highly lacunate spongy tissue (fig. 30, 31) which contains moderate accumulations of pectic materials. A particularly noteworthy feature discovered in this species is the occurrence of an arc of bundles above the midvein (fig. 31). These bundles have the same

orientation as the midvein, and originate as a peripheral portion of the procambium of the midvein. The only comparable occurrence elsewhere in Madinae is the much more extensive upper set of bundles which occurs in leaves of *Argyroxiphium* (Carlquist, 1957a). The occurrence of these bundles in *Hemizonia fitchii* is obviously independent. In addition to the tack-shaped trichomes characteristic of this species (Carlquist, 1958b), uniseriate non-glandular trichomes (fig. 30) are abundant. Pectic accumulations in leaves of *Hemizonia*, section *Centromadia*, are definitely present, although they are not nearly as abundant as in other tarweeds.

Section *Hemizonia*. Two species of this section, *H. congesta* and *H. luzulaefolia*, were studied. In upper leaves of *H. congesta* (fig. 23), there is recurvature of bundles approximately halfway to the midvein. A bundle sheath extension is present on the midvein, and small bundle sheaths occur on other veins. Sclerenchyma is present opposite both phloem and xylem poles of the midvein, but is not present elsewhere in the leaf. A thin layer of palisade parenchyma is present on both surfaces, but a wide zone of loose spongy parenchyma, filled with pectic accumulations, occupies the center of the leaf. Both capitate glandular trichomes with biseriate stalks and uniseriate non-glandular trichomes are present on both surfaces. Upper leaves of *H. luzulaefolia* show even more specialization in vascular structure than do those of *H. congesta*. In structure, they are very much like comparable leaves of *Blepharipappus* or *Blepharizonia*. An arc of recurved bundles extends to the midvein on the lower surface of the leaf, and thus a pectic channel is present on either side of the midvein-sheath extension. No fibers are present. Numerous capitate glandular hairs are present on both surfaces. The anatomy of the upper leaf of *H. luzulaefolia* is not unlike that of the condensed leaf of *H. congesta*.

Section *Deinandra*. Two species of this section, *H. fasciculata* and *H. corymbosa*, were investigated. In structural features, they seem quite similar to other *Hemizonias*. *Hemizonia fasciculata* shows a very limited recurvature of the margin and its bundles. A recurved arc of bundles may be present only at the tip of the leaf. A cylinder of fibers was observed around the midvein near the base of lower leaves of the main stem, and an arc of fibers adjacent to phloem of the midvein of upper leaves, but no other sclerenchyma occurs in the leaves studied. Bundle-sheath extensions are limited to basal portions of leaves of the main stem. Lacunate palisade tissue is present on both surfaces, and prominent accumulations of pectic compounds occur in the central portion of the mesophyll. In *H. corymbosa*, a recurved arc of bundles was observed only in upper leaves. Sclerenchyma was seen only on the midvein, and its distribution around the midvein is like that figured for *H. fitchii* (fig. 31). Neither secretory canals nor marginal fibers were seen in leaves of *H. corymbosa* or *H. fasciculata*, although both species have minimal recurvature of marginal bundles. Investigation of more species in this section would be appropriate to establish if these characters are common to all species of the section.

7. *Holocarppha*.—Leaves of this genus have been described in a separate paper (Carlquist, 1959b).

8. *Holozonia*.—Leaves of the only species, *H. filipes*, are virtually identical to those of *Blepharipappus* or *Blepharizonia* in anatomical respects. The glandular trichomes, however, are distinctive, and more nearly like those of *Lagophylla* (Carlquist, 1958b).

9. *Lagophylla*.—Leaves of only one species, *L. ramosissima*, were investigated. Upper leaves (fig. 28) show recurvature of veins to the lower surface; this recurvature may extend to the midvein on the lower surface. A bundle sheath is present on the midvein; this sheath extends to both surfaces in the base of the leaf, to the upper

surface only in upper portions of the leaf. Bundle sheaths, usually one or two cells in thickness, are present on other veins. No fibers or other sclerenchyma were observed in the leaf. Palisade parenchyma is present on both surfaces, and the central portion of the mesophyll is occupied by open spongy tissue in which moderate accumulations of pectic materials were observed. A pair of secretory canals was observed beside the phloem pole of the midvein. On both surfaces of leaves of all species, a dense covering of elongate uniseriate non-glandular trichomes is present. Upper leaves of all species possess, on both surfaces, tack-shaped glandular trichomes (Carlquist, 1958b) which are like those of *Holozonia*, except that the capitate portion is more obconical and may even show invagination of the glandular layer (*L. congesta*).

10. *Layia*.—Only one species of this genus, *L. platyglossa*, was investigated in detail. Leaves of this species seem related to the vernal annual habit of this plant. The bundles lie in a single plane, and no recurvature could be observed at the margins. A bundle-sheath extension is present on the midvein, an inconspicuous sheath on lateral veins. No sclerenchyma was observed. Palisade parenchyma is present on both surfaces; no spongy parenchyma or pectic accumulations were observed.

11. *Madia*.—Species in this genus representative of various distinct growth forms were investigated. Rosette leaves of *M. bolanderi* (fig. 20, 21) show a small arc of recurved marginal bundles only at the tips. In the leaf shown in fig. 20, a fiber strand not associated with a vein is seen. Sclerenchyma bands occur above and below the midvein. In leaves of the inflorescence axis, no sclerenchyma was observed. Corresponding to the mesic habitat of this species, leaves are bifacial, and pectic accumulations occur rather abundantly in leaves formed toward the end of the growing season. In the other perennial species of this genus, *M. madioides*, no recurvature of marginal bundles was observed (fig. 13), but a strand of fibers independent of the veins occurs at margins of leaves. The midvein has a bundle-sheath extension, the central portion of which is sclerified around the vein. Smaller bundle sheaths, without sclerenchyma, are present on smaller veins. Palisade parenchyma is present on the upper surface of the leaf and spongy tissue below, corresponding to the shady habitats in which this species grows. Prominent pectic accumulations are present in the mesophyll, but these do not occlude the rather large intercellular spaces.

In the annual species *M. elegans*, no recurvature of marginal bundles was observed. A bundle-sheath extension containing a pair of secretory canals is present on the midvein; fiber strands are small in bundle sheaths, except for the marginal vein, which has a large strand of fibers adjacent to the phloem pole. Palisade parenchyma is present on the upper surface of the leaf, spongy chlorenchyma on the lower surface. A zone of less photosynthetic parenchyma rich in pectic accumulations is present in the center of the mesophyll. Leaves of the diminutive annual *M. minima* lack marginal recurvature of bundles. A bundle sheath, extending to the lower surface, is present on the midvein. Fibers are present beside the phloem pole of the midvein and the marginal veins. Palisade parenchyma is present above, and spongy parenchyma on the lower surface of the leaf. Upper leaves of *Madia sativa* (fig. 25) show a small arc of recurved bundles. Fibers are present around the midvein, and by the phloem pole of most other veins. As shown in fig. 25, a small strand of fibers, independent of a vein, may be present in the margin. A bundle-sheath extension, containing colenchymatous cells and a pair of secretory canals, is present on the midvein, and smaller bundle sheaths, some with a secretory canal, are present on lesser veins. Palisade parenchyma occurs on both surfaces, and the central portion of the mesophyll consists of loose spongy non-photosynthetic tissue, the intercellular spaces of which

are largely filled with pectic accumulations. Both capitate glandular trichomes and uniseriate non-glandular trichomes occur on both surfaces of the leaf. A peculiar feature not observed in any other tarweed is the occurrence of fishhook-shaped uniseriate non-glandular trichomes on leaves and stems of *Madia hallii*; these are present in addition to the typical uniseriate non-glandular trichomes.

12. *Raillardella*.—In the fruticose species *R. muirii* (fig. 15), there is recurvature of marginal bundles around a very large marginal fiber strand. Fibers are also present beside both poles of the midvein, and adjacent to phloem of many other veins. A bundle-sheath extension is present on the midvein. Palisade occurs on both surfaces, as do uniseriate non-glandular trichomes. The other fruticose species, *R. scabrida*, shows very marked recurvature of the veins, much of the way to the midvein on the lower surface of the leaf, in upper leaves. A sclerenchyma sheath is present on the midvein, which has a sheath extension, but not on the other veins. Loose palisade occurs on the upper surface, and spongy chlorenchyma on the lower surface. Rosette leaves of the remaining species, *R. pringlei*, *R. scaposa* (fig. 16), and *R. argentea*, have the following characters in common: no marginal recurvature of bundles occurs; a bundle-sheath extension is present on the midvein, which is jacketed at xylem and phloem poles by sclerenchyma; palisade parenchyma is present on both surfaces; and the central mesophyll consists of spongy chlorenchyma. *Raillardella scaposa* is distinctive in the presence of secretory canals, paired beside the midvein and solitary beside other veins (fig. 16). Pectic accumulations were observed to be abundant in the central mesophyll of *R. argentea*, but appeared absent in *R. scaposa* leaves. On account of the method of preparation, the occurrence of such deposits in leaves of *R. muirii* and *R. scabrida* could not be determined. The abundant felt-like covering of uniseriate non-glandular hairs on leaves of *R. argentea* is distinctive, although sparser covering of such trichomes is present in the other species.

LEAF ANATOMY: SUMMARY.—A surprisingly large number of characters—some of which are not characteristic of other Compositae studied—occur in leaves of Madinae. The absence of such characters in such genera as *Achyrrachaena* and *Layia* seems to reflect modifications of a particular life form. Salient features of tarweed leaves are as follows:

1. *Marginal recurvature of veins*.—This peculiarity of upper leaves occurs in all tarweeds, with the exception of the genera *Achyrrachaena* and *Layia*. It was not noticed in Hawaiian Madinae, although the vascular complexity of leaves of *Argyroxiphium* probably represents a parallel phenomenon. The possible ecological significance of this character is discussed above.

2. *Presence of fibers as prominent marginal strands*.—This feature was found in all genera of Madinae except the vernal annuals (*Achyrrachaena* and *Layia*), genera with considerable recurvature of bundles (*Blepharipappus*, *Blepharizonia*, *Holozonia*, *Lagophylla*) and the Hawaiian genera. The occurrence of fiber strands not in contact with veins was observed only in *Madia* and *Hemizonia*. The occurrence of fibers near phloem poles of major veins, or at least the midvein, was found in all genera except *Layia*, and is particularly prominent in *Dubautia* and *Wilkesia*. The occurrence of fiber strands not in contact with veins in leaves of *Argyroxiphium* is reminiscent of the independent strands in *Madia* leaves.

3. *Pectic accumulations*.—This peculiar character has not been reported in leaves of Compositae other than Madinae, and thus forms one of the best characters of the group. It was observed in all the Pacific Coast genera except the vernal annuals *Achyrrachaena* and *Layia*. It occurs in the Hawaiian genera *Argyroxiphium* and *Dubautia*. In *Wilkesia*, such accumulations occur in bracts of the head.



4. *Isolateral leaf construction*.—This character, although not rare in Compositae, occurs in all the tarweeds except *Achyrachaena*. It occurs in the Hawaiian genera with the exception of *Wilkesia*.

5. *Secretory canals*.—These were observed in leaves of *Calycadenia*, *Hemizonia*, *Lagophylla*, *Madia*, and *Raillardella*, as well as in the Hawaiian genera *Argyroxiphium* and *Dubautia*. The most common mode of occurrence is as a pair beside the midvein, and solitary near smaller veins. The occurrence of secretory canals in *Madinae* is not surprising, because they occur in a number of other Heliantheae, but their similar mode of occurrence among the genera, and the seemingly vestigial representation of such canals places them in contrast with those of other subtribes, such as *Coreopsidinae* (Carlquist, 1957b), where they are abundant.

6. *Trichomes*. Capitate glandular trichomes with biseriate stalks, or a modification thereof, occur on leaves in all genera of *Madinae*, although not necessarily in all species. These trichomes, so characteristic of the tarweeds, are more abundantly represented on peduncles or bracts than on leaves. A summary of their occurrence is offered by Carlquist (1958b). Uniseriate non-glandular trichomes, although not at all restricted to *Madinae*, were observed on leaves of all genera except *Adenothamnus* (in which they are present on involucre bracts).

### INFLORESCENCE

The *Madinae* show exceptional variety in inflorescence construction, and no discussion of diversification of the group would be complete without reference to this variety and to the relationship which the various types bear to each other. The accompanying diagram indicates the structural modes which occur in the group. The terminology and definitions suggested by Rickett (1955) have been followed, although the reader will note that the elements involved in these inflorescences (represented by circles on the diagram) are heads, not individual flowers. Information on these types is best summarized by genus, on account of the fact that certain types are confined to particular genera. In some instances, the relative size of a plant can alter the type of inflorescence (e.g., *Madia minima*). Another difficulty involved in categorizing the inflorescences is the occurrence of bract leaves on a branch of the inflorescence (e.g., "B" in the diagram) in addition to the leaf or bract subtending each branch. This problem, mentioned by Rickett (1955), is expressed here by regarding branches with bract-leaves along them as individual inflorescences, rather than simple peduncles. Thus, in *Madia madioides*, the inflorescence is described as "D, F, or G branching of B axes". If the reader does not believe that presence of leaves along such an axis disqualifies it as a peduncle, this can be read as "an inflorescence of types D, F, or G", but the writer felt that expression of this problem was necessary. A further point which requires clarification is that the difference between dichasial and alternate branching in the inflorescences is not necessarily profound, but is merely dependent; in some instances, on whether or not the opposite-leaved condition of vegetative portions of the plant is continued into the inflorescence. For example, *Madia minima* may have both types E and H.

*Achyrachaena*: B

*Adenothamnus*: B

*Blepharipappus*: F

*Blepharizonia*: F

*Calycadenia*: This genus is of interest because of its transition from basipetal to bidirectional inflorescences. The basipetal type G occurs in some (*C. bispida*, *C. pauciflora*, *C. tenella*). In others, a bidirectional raceme (K) or a compound form of it (L) occurs: *C. ciliosa*, *C. mollis*, *C. truncata*, *C. villosa*. On account of the phyllo-

taxy of the inflorescence, *C. oppositifolia* possesses types C, F (but with opposite branches), and a bidirectional panicle, I.

*Hemizonia*: Most of the species in this genus have a compound panicle, H. Others (*H. lutescens*, *H. minihornii*), were found to have the simple panicle, G, in addition. *Hemizonia balliana* apparently has only type G. The inflorescence of *H. greeneana* may be type G, or a series of F branches.

*Holocarpa*: Like most species of *Hemizonia*, the four species of *Holocarpa* have type H or (in smaller plants) G.

*Holozonia*: H

*Lagophylla*: G or H (depauperate plants have D or F).

*Layia*: B, and B, F, or G branching of B axes.

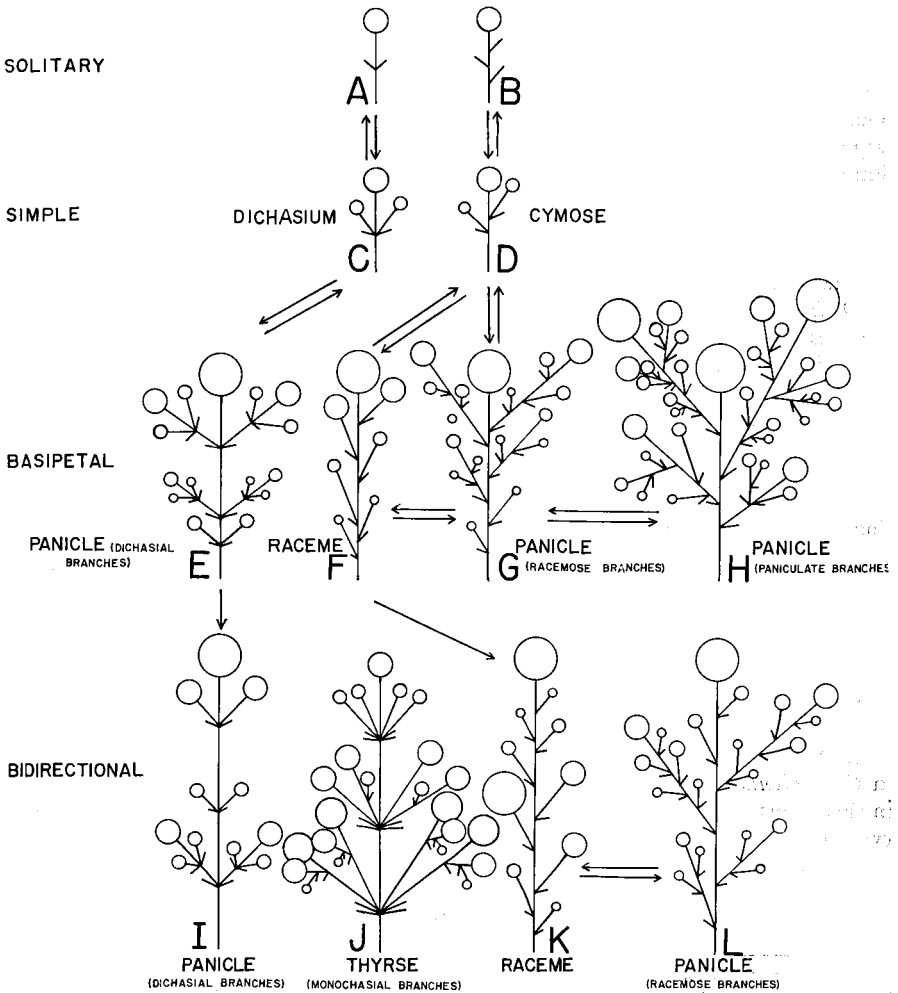


Diagram of inflorescence types in Madinae. Size of circles indicates order of maturation of heads; bract-leaves represented by short lines. Further explanation in text.

*Madia*: Inflorescence types in this genus are all basipetal, but highly varied. Leafy axes occur in some: *M. elegans* has G or H branching of B axes; *M. madioides* has D, F, or G branching of B axes; and *M. capitata* has F or G branching of B axes. Other species lack bract-leaves on the branches, so that, for example, *M. bolanderi* has types D or F, *M. sativa* possesses D, G, or H. *Madia ballii* has inflorescences of type F or G, although peduncles (in F) or lateral axes (in G) branch from nearly the same point, so that a pleiochasium is very nearly achieved. In *Madia minima*, the inflorescence type is E or H, although depauperate plants have type C or even A.

*Raillardella*: Scapose plants have type B; *R. scabrida* has F branching of B axes.

*Argyroxiphium*: The massive inflorescence of *Argyroxiphium* (fig. 36) is a bidirectional raceme (K). Most of the maturation is acropetal, but some heads younger than those in the middle of the axis occur at the base. The inflorescences of the four species always terminate in a head somewhat older than those immediately below. One to several small bracts may occur on peduncles in *A. sandwichense*.

*Dubautia*: Branching in inflorescences of *Dubautia* may be opposite or alternate. Thus, *D. knudsenii* (fig. 41) has a simple dichasium of type C (fig. 41, left), a compound dichasium of type E (fig. 41, right), or rarely a solitary flower, type A. Very large, highly branched panicles like type E but more ramified occur in *D. latifolia*. Simple racemes, type F, occur in some species, such as *D. ciliolata* (fig. 39). In some species with this type, such as *D. menziesii* or *D. platyphylla*, the maturation of the heads in the inflorescence is simultaneous or nearly so. A simple panicle with alternate branching, type G, was observed in *D. paleata*. A panicle with compound branches, alternately arranged, and referable to type H, occurs in most species, such as *D. scabra* or *D. linearis*. In these species, the heads tend to be congested toward the ends of the axes.

*Wilkesia*: *Wilkesia* has an elaborate inflorescence not unlike the raceme of *Argyroxiphium* in gross aspect (fig. 37), but it differs in three respects: (1), development is acropetal, although the heads in the whorl immediately below the terminal head may mature a little later than the terminal head (fig. 38); (2), branching is strictly verticillate; and (3), some of the lateral branches (especially near the base of the inflorescence) are not simple peduncles, but are monochasia with acropetal maturation of the two or three heads. Thus, the inflorescence of *Wilkesia* is a cylindrical panicle, or thyrse, and is represented in a simplified way by type J in the diagram.

DISCUSSION.—The inflorescences of the Pacific Coast Madinae are basically cymose, in that a series of branches develop basipetally below a terminal flower. The branches may be simple or compound, or altogether lacking, in which case a solitary head is present. The difference between opposite and alternate branching patterns, as explained above, is not particularly significant, and alterations from one to the other may occur within a genus or even a species. A feature which does hold particular interest is the change from strictly basipetal development to bidirectional maturation in *Calycadenia*, a change which is associated with the virgate nature of inflorescences in this genus. As the inflorescences of *Dubautia* illustrate, the basipetal maturation of cymose inflorescences is basic in the Hawaiian genera, as it is in the Pacific Coast tarweeds. The species of *Dubautia* in which nearly simultaneous maturation of the numerous simple branches takes place (*D. menziesii*, *D. platyphylla*) suggest how change to the bidirectional type, seen in *Argyroxiphium*, may have taken place. The

Fig. 36-41. Inflorescences of Hawaiian Madinae. Fig. 36. *Argyroxiphium caliginis*. Fig. 37-38. *Wilkesia gymnoxiphium*. Fig. 37. Inflorescence excepting lowermost verticils. Fig. 38. Terminus of inflorescence. Fig. 39. *Dubautia ciliolata*. Fig. 40. *Dubautia scabra*. Fig. 41. *Dubautia knudsenii*.

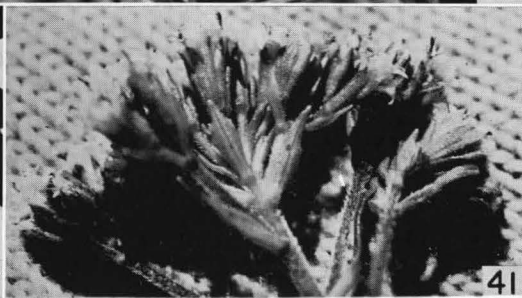
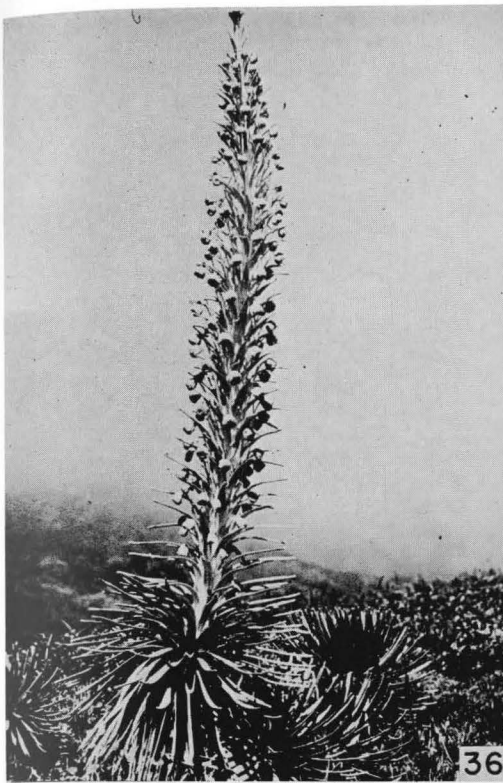


FIG. 36-41

massive, elongate inflorescence of *Argyroxiphium* seems to be related to the considerable acropetal development, just as the virgate inflorescences of *Calycadenia* show an identical bidirectional pattern. The acropetal development both of the inflorescence axis and the lateral branches in *Wilkesia* probably represents the furthest advance in this type of evolution.

#### CAPITULUM

The structure of the capitulum in Madinae is of particular interest, both because it is one of the main characters of the group and because modifications of the basic structure have provided an interesting series of variations which have not been understood in all instances. A description of basic conditions and alterations thereof lends more perspective than a description by genus.

**BASIC CONDITION.**—The least modified involucre of Madinae have a single series of involucral bracts, each of which partly or wholly enfolds a ray flower. There are no involucral bracts which are not associated with ray flowers. Interior to the ray flowers are disk flowers, each of which is axillary to a bract which must be, by definition, a receptacular bract ("receptacular palea" or "receptacular chaff" of various authors). Probably a spiral arrangement of the flowers and their bracts, in which the ray flowers and outermost disk flowers are not arranged into two well-defined circles, is the primitive condition. Such an arrangement is shown by *Hemizonia minthornii* (fig. 54). Other examples of this condition are the three species of *Hemizonia*, section *Centromadia*.

**ARRANGEMENT INTO CONCENTRIC CIRCLES.**—In *Blepharipappus scaber*, *Hemizonia* section *Hemizonia*, *Holocarpha*, and two species of *Layia*, *L. chrysanthemoides* and *L. fremontii*, there are receptacular bracts throughout the head, but unlike the instances mentioned above, the ray flowers and the outermost receptacular bracts have become arranged into two concentric series. The ray flowers are of approximately the same number, and alternate with receptacular bracts of the outer circle. The receptacular bracts in this outer circle are, in the taxa named, more or less connate by their edges. This change has undoubtedly followed closely upon the attainment of a discrete circle of outer receptacular bracts.

**LOSS OF INNER RECEPTACULAR BRACTS.**—Following the development of a discrete outer circle of receptacular bracts, the inner receptacular bracts have been lost. The remaining circle of receptacular bracts are united by their edges, as indicated above, with the exception of *Achyrachaena*, in which they are separate. Ray flowers are alternate with the receptacular bracts, and of the same number, or nearly so. Most of the Pacific Coast tarweeds fall into this category, and examples are furnished by *Calycadenia*, some species of *Hemizonia* (section *Deinandra*, section *Fruticosae* except *H. minthornii* and *H. clementina*), *Holozonia*, *Lagophylla*, *Layia* (except the two species mentioned above), and *Madia*. Special cases under this category include the following:

1. *Argyroxiphium sandwichense* and *A. caligini*.—These species have evidently not formed a discrete circular arrangement of the outer series of receptacular bracts: *A. grayanum* (fig. 52) shows a close approach to this. In *A. sandwichense* (fig. 51)

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Fig. 42-47. Transections of bracts. Fig. 42. *Calycadenia villosa*, receptacular bract, adaxial face below.  $\times 200$ . Fig. 43. *Madia madioides*, involucral bract (above) and adjacent ray achene (below) in transection.  $\times 170$ . Fig. 44-46. *Madia sativa*, involucral bract transections. Fig. 44. Tip of bract, adaxial face at left.  $\times 165$ . Fig. 45. Bract cut at lower level, adaxial face at right; adjacent ray achene lower right.  $\times 140$ . Fig. 46. *Raillardella scaposae*, central portion of receptacular bract, adaxial face below.  $\times 165$ . Fig. 47. *Raillardella muirii*, central portion of receptacular bract, adaxial face below.  $\times 160$ .

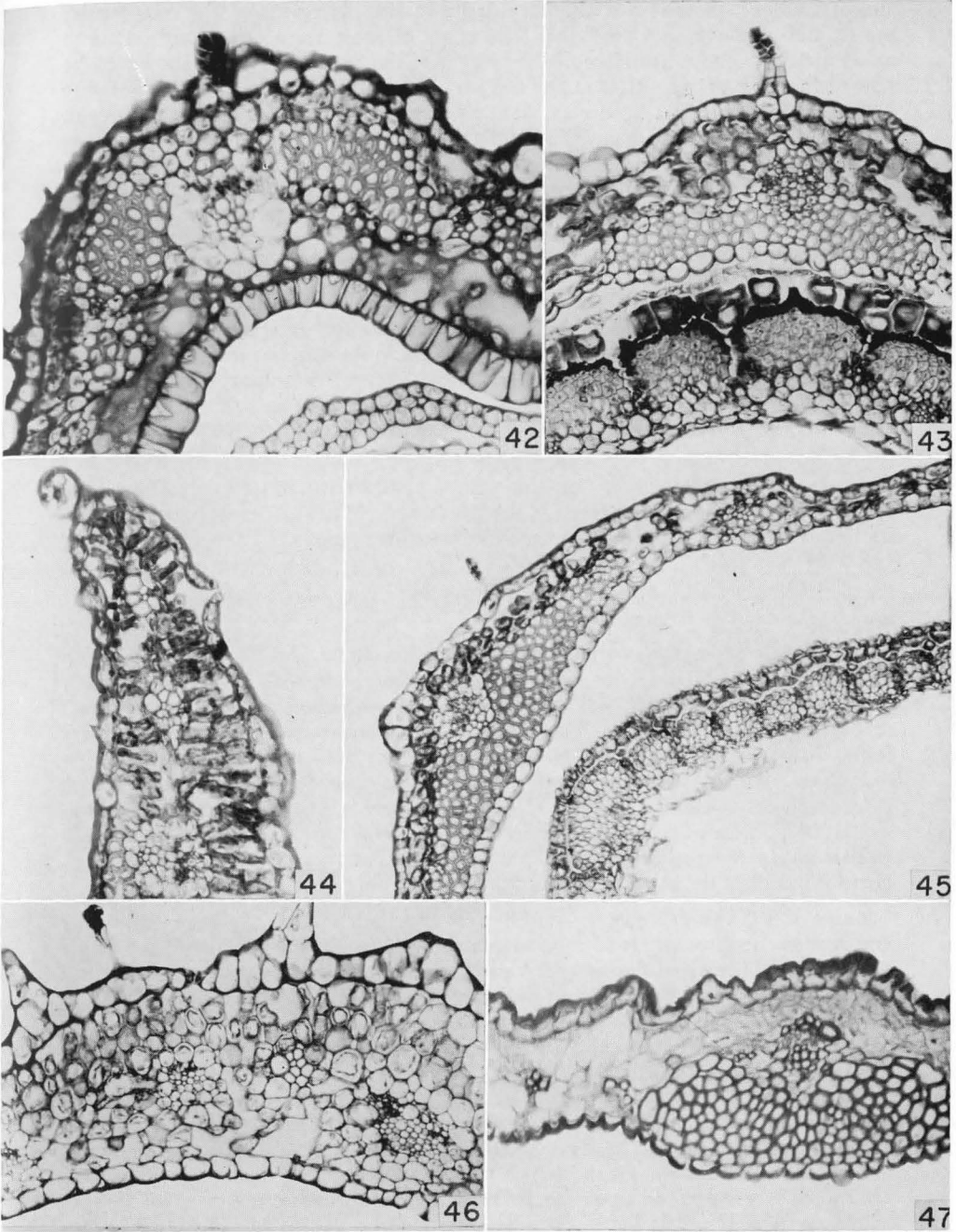


FIG. 42-47

and *A. caligini*, there is a slight irregularity in the placement of the receptacular bracts, and although they are united, the edges of some are not precisely united to adjacent edges, but to a surface of the bract near the edge. This might, however, be related to a sort of gigantism in the heads of this genus, because probably increase in the size of heads has been basic in the formation of the genus *Argyroxiphium*. Of considerable interest, in any case, is the presence of occasional receptacular bracts inside the outer circle of such bracts (fig. 51) in *A. sandwichense* and *A. caligini*. This would seem to be an indication of incomplete loss of such inner bracts.

2. *Hemizonia clementina*.—Specimens of this species show incomplete loss of receptacular bracts, so that one or more series may be present within the outer circle of receptacular bracts.

3. *Hemizonia corymbosa*.—Like the above species, the writer's collection of *H. corymbosa* subsp. *macrocephala* shows one or two series of receptacular bracts inside those of the outer circle, although they are lacking in the central portion of the head. Thus *Hemizonia clementina* and *H. corymbosa* represent transitional conditions. *Hemizonia corymbosa* has an additional exceptional feature in that the number of ray flowers may exceed the number of receptacular bracts of the outer circle. This probably represents a secondary addition of ray flowers.

4. *Blepharizonia plumosa*.—In this genus, involucre bracts are adnate, at least at their bases, to the circle of receptacular bracts (fig. 57). This seems to be a specialization over the general condition described for this category.

5. *Madia minima*.—In this species (fig. 56), the number of disk flowers within the circle of receptacular bracts is reduced to one or two. *Madia exigua* shows nearly the same amount of reduction.

REDUCTION OF RAY FLOWERS.—Following the attainment of the organization described in the above section, with ray flowers alternate with bracts of the outer circle of receptacular bracts, ray flowers (together with the involucre bracts which enfold them) have been lost. There are several instances in which ray flowers are fewer than the receptacular bracts. One instance has been mentioned above, *Argyroxiphium* (fig. 51-52). Other species in which this transitional condition occurs are *Adenothamnus*, *Madia bolanderi*, *Raillardella scabrada* (fig. 58), and those individuals of *Raillardella scaposa* in which one to several ray flowers occur. Some individuals of *R. scaposa* have entirely discoid heads. The number of ray flowers in *R. pringlei* is almost the same as to fewer than the number of receptacular bracts.

ABSENCE OF RAY FLOWERS.—Ray flowers and their bracts have been completely lost, so that the involucre is a "false involucre", because it consists only of the single series of united receptacular bracts. Aside from the genus *Dubautia*, which forms a special case described below, the Hawaiian Madinae evidence this condition only in *Wilkesia* (fig. 53). The use of the term "false involucre" in *Wilkesia* by Degener (1946) and the recognition of this type of construction by Good (1956) show that this fact has been acknowledged, although the use of the non-committal term "bract" by Keck (1936) sidesteps the problem. In the Pacific Coast Madinae, discoidy has been attained in *Raillardella*, which shows the interesting transitional cases mentioned above. Completely discoid heads occur in *R. argentea* (fig. 59), *R. muirii*, and most individuals of *R. scaposa*. Of the genera traditionally accepted as Madinae, *Layia discoidea* (or *L. glandulosa* subsp. *discoidea*) provides an interesting case, for absence of the ray flowers nearly led to taxonomic recognition of this plant as a new genus of Helenieae (Clausen, 1951). Genetic work, however, showed that the discoid habit is separated by a relatively limited number of gene pairs from the radiate condition

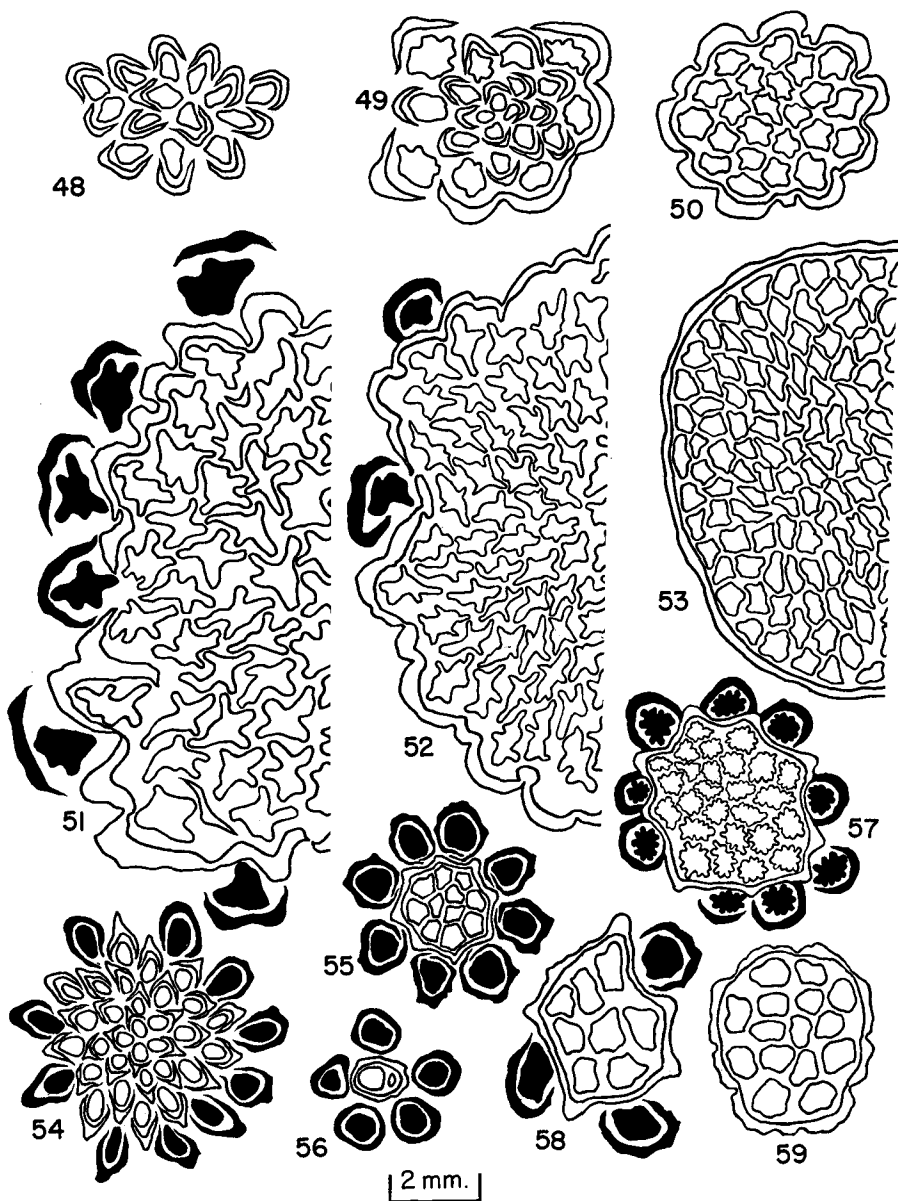


Fig. 48-59. Transsections of capitula of Madinae, in region of achenes. Involucral bracts and ray achenes shown in black, receptacular bracts and disk achenes in outline. Fig. 48. *Dubautia laxa*. Fig. 49. *Dubautia paleata*. Fig. 50. *Dubautia knudsenii*. Fig. 51. *Argyroxiphium sandwichense*. Fig. 52. *Argyroxiphium grayanum*. Fig. 53. *Wilkesia gymnoxiphium*. Fig. 54. *Hemizonia minthornii*. Fig. 55. *Hemizonia greeneana*. Fig. 56. *Madia minima*. Fig. 57. *Blepharizonia plumosa*. Fig. 58. *Raillardella scabrída*. Fig. 59. *Raillardella argentea*.



in *L. glandulosa* (Clausen, 1951). Keck (1936) believes that the discoid head of *Wilkesia* is derived from a type with a paucity of ray flowers, such as *Argyroxiphium grayanum*. One may well ask how discoid species could be identified as belonging to Madinae—a problem which the history of *Layia discoidea* emphasizes. The writer first sensed that *Raillardella* is madinean by the nature of glandular trichomes and by the fact that ray flowers, when present, occur *outside* the circle of united *receptacular* bracts, whereas in true Senecioneae (to which tribe *Raillardella* has hitherto been assigned), the ray flowers occur *inside* the circle of united *involucral* bracts. In completely discoid genera, however, the problem might be more difficult. For example, one might question whether or not such genera as *Palafoxia*, *Chaenactis*, and *Oreochaenactis* should be suspected of having madinean affinities. The reasons why these genera cannot be included in Madinae are given in the concluding section of this paper, and similar considerations apply to other genera which might bear some resemblance to Madinae.

BASIC CONDITION LESS RAY FLOWERS.—The head of *Dubautia laxa* (fig. 48) appeals to the writer as extremely similar to that of *Hemizonia mintbornii* (fig. 54) without the ray flowers and their associated bracts. There is no direct evidence that heads in *Dubautia* (an exclusively discoid genus) are derived from heads bearing ray flowers, but if, as Keck (1936) suspects, *Dubautia*, *Argyroxiphium*, and *Wilkesia* are related, then one would suspect radiate heads in the ancestry of these genera, on account of their presence in *Argyroxiphium*. The report of Sherff (1944) of a putative intergeneric hybrid between *Argyroxiphium* and *Dubautia* is pertinent in this regard. If this is the mode of derivation of the discoid condition in *Dubautia*, then all the bracts of the involucre in this genus are receptacular bracts. Authors dealing with *Dubautia*, however, seem merely to term them "bracts" or "bracts of the involucre" (Sherff, 1935; Degener, 1946). In any case, further evolution in the head of *Dubautia* from the condition illustrated in fig. 48 seems to have been characterized by loss of the central bracts, as is indicated by Sherff (1935) for *D. railliardioides*. He implies this for other species (e.g., *D. laxa*) by giving a slightly lower range in number of bracts than in number of flowers per head. Changes concomitant with the loss of central bracts appear to be the development of a discrete circle of bracts, the loss of all bracts but these, and their union by their edges. *Dubautia paleata* (fig. 49) shows an intermediate stage, whereas *D. knudsenii* (fig. 50) shows the most advanced condition, as do *D. magnifolia* and all the species Sherff (1935) included in *Raillardia*. Thus, evolution in the capitulum of *Dubautia* has paralleled changes in the heads of the Pacific Coast tarweeds, although ray flowers are not involved in the former.

DISCUSSION.—The designation of bracts as involucral and receptacular has seemed desirable to me because it is a way of demonstrating changes in the structure of the capitula of Madinae. Such a distinction depends on suppositions concerning the origin of the capitulum, however, and upon uniform application of terms. I have used the term "involucral bract" for bracts to which ray flowers are axillary. In other Heliantheae in which bracts are present in varying numbers outside of these to which ray flowers are axillary, these would also be termed involucral bracts. Receptacular bracts are those to which disk flowers are axillary. If ray flowers and involucral bracts have been lost, then only receptacular bracts could be said to be present. The reader should note that this only applies to radiate heads, or discoid heads which have been derived from radiate ones. If a primitively discoid condition exists—as I believe is the case in some tribes—such bracts should be termed involucral. This usage seems desirable to me because it has phylogenetic as well as topographic significance. This usage is

at variance with the conclusion reached by Briquet (1917), who has discussed the problem. Briquet regards bracts without axillary flowers as involucre bracts, and bracts in the axils of which flowers (*either* disk or ray) occur as receptacular paleae. I find this usage unacceptable because it obscures phylogenetic lines and would be difficult to apply in some cases. For example, in the helianthoid genus *Lagascea*, several united bracts form a cylinder around the single flower of each head, one of these bracts would have to be a receptacular palea and the remainder involucre bracts, despite their obvious equivalence. More significantly, the cylinder of united bracts in Senecioneae would have to be regarded as equivalent to those of advanced Madinae (e.g., *Raillardella argentea*), contrary to what has apparently been quite a different origin. The only advantage of Briquet's usage is that it is easily applicable in all cases, regardless of origin of the capitular structure. The writer believes that most authors have not intended this usage, and that through a better knowledge of the origin of capitular types, we can differentiate adequately between receptacular and involucre bracts, despite similarities in topography and structure. The writer does believe that there is clear evidence that the capitulum of Pacific Coast Madinae has originated from a type such as is illustrated in fig. 54, and that subsequent changes have followed the steps outlined above. A similar origin is logical for Hawaiian Madinae, although there is no direct evidence that ancestors of *Dubautia* did have ray flowers. The presence of ray flowers in *Argyroxiphium* and their loss in *Wilkesia* are not questioned by any of the authors who have dealt with these genera.

#### ANATOMY OF BRACTS

As in leaves of Madinae, there may be marked variation in structure in the bracts of the involucre in a single species. These variations occur in two respects: (1), involucre bracts may differ from receptacular bracts in anatomy; and (2), structure may change between the base and apex of a single bract, whether involucre or receptacular. Rather than covering these alterations in detail for each species, a summary of these variations will serve as a general indication.

DIFFERENCES BETWEEN INVOLUCRAL AND RECEPTACULAR BRACTS IN A SPECIES.—Receptacular bracts are often much thinner than involucre bracts, especially below the apical portions. This is reflected in the fewer layers of mesophyll cells. Often, such a bract is only one or two layers of cells thick near the margins. Margins of involucre bracts may also be thin, but thin areas near the margins are much more extensive in receptacular bracts. This is shown for *Hemizonia fitchii* (fig. 32-33), in which the mesophyll of margins in receptacular bracts consists of fibers, whereas mesophyll of margins consists of thin-walled parenchyma in the involucre bracts. Receptacular bracts are not always thinner than involucre bracts, as the photographs of a species exceptional in this respect, *Holocarpha beermannii* (fig. 34-35) show. The most prominent way in which receptacular bracts differ from involucre bracts is the greater proportion of sclerenchyma and lower proportion of chlorenchyma in the former as compared to the latter. This is clearly shown by *Holocarpha beermannii* (fig. 34-35). Other species in which this is prominent include *Calycadenia tenella*, *C. truncata*, *C. villosa*, *Hemizonia congesta*, and *H. minthornii*. Sclerenchyma, when present in receptacular bracts, occurs mainly outside of veins and their bundle sheaths, although a small strand of fibers may be present near the phloem pole of veins (fig. 42, 47).

DIFFERENCES BETWEEN BASE AND APEX OF A BRACT.—Basal portions of a bract—particularly a receptacular bract—are much thinner than the apical portions. The thickness of the tip is related to the abundance of chlorenchyma in that region. Con-

comitant with this is the greater presence of sclerenchyma near the base of a bract. This contrast is shown for *Madia sativa* in fig. 44-45. Palisade parenchyma is abundant at the tip in bracts of this species, whereas only a thin layer of spongy parenchyma occurs in lower regions. Another noteworthy feature is the occurrence of more or less prominent hippocrepiform thickenings on cells of the adaxial epidermis of bracts. These thickenings are related to the reflexing of bracts in the fruiting head, and their prominence, with respect to species and genera, seems related to the behavior of bracts in the head in particular taxa. They are always more prominent in the lower portions of the bract, and absent in the apical portions, or nearly so.

COMPARATIVE DESCRIPTIONS.—Differences between genera or species depend chiefly on: (1), the nature of sclerenchyma distribution, and the relative amount present; (2), the presence of pectic materials in intercellular spaces; (3), the relative thickness of parenchyma, and whether it is spongy, palisade, or non-photosynthetic; and (4) the presence or absence of secretory canals.

1. *Achryachaena*.—Involucral bracts consist of thin-walled photosynthetic parenchyma except for prominent fiber strands located adaxial to each vein; fiber strands occur in margins. Receptacular bracts have smaller fiber strands, none of which occur in margins, which are uniseriate.

2. *Adenothamnus*.—Involucral bracts contain thin-walled photosynthetic parenchyma; fiber strands are alternate with the veins. Bundle-cap fibers occur at phloem poles. Secretory canals are paired beside veins. Receptacular bracts have the same structure.

3. *Blepharipappus*.—Involucral bracts have an outer layer of palisade tissue, and inner layers of spongy chlorenchyma with pectic accumulations in intercellular spaces. No fibers are present. Receptacular bracts are identical except that no palisade is present.

4. *Blepharizonia*.—Involucral bracts have a ground tissue composed of isodiametric chlorenchyma cells; fiber strands alternate with the veins. Receptacular bracts are the same.

5. *Calycadenia*.—Involucral bracts in this genus have an outer layer of palisade and an inner layer of spongy parenchyma. Pectic accumulations were observed in intercellular spaces in *C. multiglandulosa* subsp. *cephalotes*, *C. tenella*, and *C. villosa*. Fibers were not observed in involucral bracts of these except for a bundle cap on the midvein of *C. tenella* bracts. The receptacular bract of *C. villosa* (fig. 42) illustrates several characteristic features of receptacular bracts in this genus: prominent strands of fibers occur as a pair beside the midvein, and lesser strands alternate with other veins; a prominent bundle sheath surrounds the midvein, and a few sclerenchymatous elements are adjacent to the phloem pole. Pectic accumulations are abundant near the adaxial surface of the bract, and the hippocrepiform thickenings on the adaxial epidermal cells are exceptionally prominent. The receptacular bracts of *C. multiglandulosa* and *C. tenella* are like those of *C. villosa*, but fiber strands are lacking beside lateral veins in *C. villosa* and are absent in *C. tenella*. Receptacular bracts of *C. trun-*

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Fig. 60-67. Fig. 60. *Argyroxiphium sandwichense*, transection of receptacular bract, adaxial face below.  $\times 160$ . Fig. 61. *Argyroxiphium caligini*, transection of receptacular bract, adaxial face below.  $\times 130$ . Fig. 62. *Dubautia knudsenii*, transection of receptacular bract.  $\times 60$ . Fig. 63. *Dubautia laxa*, transection of receptacular bract, adaxial face at left.  $\times 125$ . Fig. 64-65. *Dubautia ciliolata*. Fig. 64. Transection of receptacular bract, adaxial face below.  $\times 125$ . Fig. 65. Mesophyll from leaf transection, showing accumulation of pectic materials in intercellular spaces at cell interstices (lower right).  $\times 530$ . Fig. 66-67. *Wilkesia gymnoxiphium*, transection of receptacular bract, adaxial face below.  $\times 120$ . Fig. 67. Same, showing accumulation of pectic materials in intercellular space, center.  $\times 310$ .

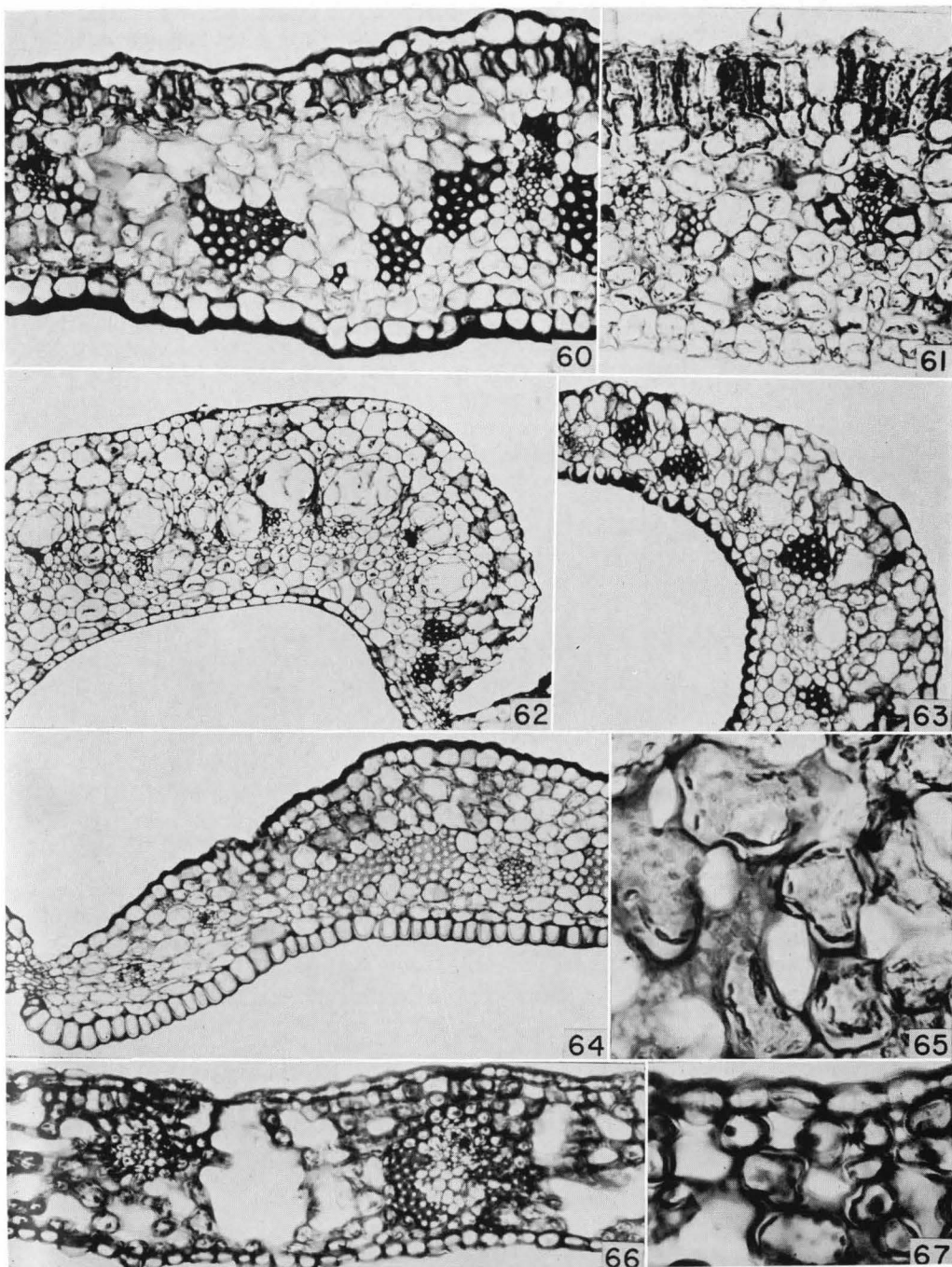


FIG. 60-67

*cata* subsp. *scabrella* are like the involuclral bracts in this taxon, and have a notably thin mesophyll containing very small fiber strands alternate with the bundles. Pectic compounds are very abundant.

6. *Hemizonia*.—Bracts of a member of section *Centromadia*, *H. fitchii*, are shown in fig. 32-33. Involuclral bracts of this species (fig. 32) are notable for their development of both spongy and palisade tissue, the association of prominent fiber strands with the phloem poles of larger veins, the sclerification of bundle sheath cells around the midvein, and the presence of very large secretory canals paired beside the midvein and paired or single beside the lesser veins. In the receptacular bracts of this species (fig. 33), only a relatively spongy and compact chlorenchyma is present; the bract is much thinner, and only one to three veins are present. A pair of very large secretory canals occur in the central portion of the bract, and the margins are very thin, containing a mesophyll of fibers and tapering to a uniseriate wing. Sections of involuclral and receptacular bracts of another species in this section, *H. pungens*, showed similar features, although sclerenchymatous elements are less abundant and pectic accumulations are present. Only one pair of secretory canals per bract was observed in both types of bracts of this species.

In section *Fruticosae*, *H. minthornii* shows differences between involuclral and receptacular bracts. Involuclral bracts have a ground tissue of spongy chlorenchyma abaxially and loose spongy parenchyma adaxially; the only sclerenchyma observed was a bundle cap on midveins. In receptacular bracts, additional sclerenchyma is present in the form of strands of fibers which alternate with the veins, and the parenchyma of the bract has uniformly small intercellular spaces. In *Hemizonia greeneana*, involuclral bracts show an outer layer of chlorenchyma and an inner layer of non-photosynthetic parenchyma. Both of these are composed of more or less isodiametric cells with small intercellular spaces. Fibers are present both adaxially and abaxially to the midvein; in addition, one or more strands of fibers are present between the veins, providing a condition like that shown for another taxon in fig. 60. Receptacular bracts are like the involuclral bracts, differing only in having fewer chloroplasts in the parenchyma and in having each vein completely ensheathed by sclerenchyma. *Hemizonia palmeri* shows virtually the same structure as *H. greeneana* for both involuclral and receptacular bracts.

The two species of *Hemizonia* section *Hemizonia* studied, *H. congesta* and *H. corymbosa*, are alike in their bract structure. Involuclral bracts show an abaxial palisade and an adaxial spongy tissue, the intercellular spaces of which are occluded by pectic compounds. No sclerenchyma was observed. In receptacular bracts, on the contrary, palisade is absent outside the pectic-rich spongy tissue, and several strands of fibers not associated with veins are present in the mesophyll.

In section *Deinandra*, *H. fasciculata* shows several distinctive features. Involuclral bracts show a bundle-sheath extension on the midvein, a thin palisade layer, and a relatively wide band of spongy tissue full of pectic deposits. Sclerenchyma is restricted to two large bands of fibers beside the midvein, much like the condition shown in fig. 64 for *Dubautia ciliolata*. Receptacular bracts are alike, except that palisade is absent and bundle-sheath extensions are present on the pair of lateral veins, as well as on the midvein.

7. *Holocarppha*.—The bracts of all species of *Holocarppha* are much alike; *H. heermannii* (fig. 34-35) may be used as an example. In involuclral bracts (fig. 35), spongy photosynthetic parenchyma with small deposits of pectic materials in intercellular spaces is present. A few fibers are present beside the phloem pole of bundles, and a few such cells may occur as strands alternate with the veins. In receptacular

bracts (fig. 34), spongy parenchyma with pectic deposits is also present. Bundle-cap fibers are apparent, but the fiber strands between veins are massive. The only differences among the species from the description given above is the slightly greater prominence of fiber strands in the involucre bracts of collections of *H. obconica* and *H. virgata* studied.

8. *Holozonia*.—Involucre bracts of the only species contain both spongy and palisade parenchyma. Sclerenchyma is lacking. A pair of secretory canals is present beside the midvein. Receptacular bracts show the same pattern.

9. *Lagophylla*.—The two species which were investigated, *L. glandulosa* and *L. ramosissima*, are similar. Involucre bracts contain spongy chlorenchyma. Sclerenchyma is restricted to the fiber strands which alternate with the vascular bundles. A pair of secretory canals is present beside the midvein. Receptacular bracts prove to have the same structure, except that fiber strands beside the midvein are larger.

10. *Layia*.—Palisade is prominent in the involucre bracts of *L. platyglossa*. As in *Lagophylla*, sclerenchyma is restricted to fiber strands which alternate with the vascular bundles. A pair of small secretory canals was observed beside the midvein. Receptacular bracts also follow this pattern. The above features were also found in bracts of *L. fremontii*.

11. *Madia*.—Bracts in the species of *Madia* investigated are highly diversified. The least specialized condition appears to be present in *M. bolanderi*. Involucre bracts of this species have a ground tissue of spongy chlorenchyma. Sclerenchyma is restricted to extravascular strands; two large strands are paired beside the midvein, and other smaller ones alternate with lateral veins. Receptacular bracts are identical, but thinner. Involucre bracts and receptacular bracts of *Madia elegans* are alike. Both spongy and palisade chlorenchyma are present, and instead of a pair of fiber strands beside the midvein, a single strand is present adaxially to the midvein. Lesser strands alternate with lateral veins. The trend toward union of the pair of fiber strands beside the midvein is present in *Madia sativa*. Involucre bracts of this species (fig. 45) show a massive single strand adaxial to the midvein. Other smaller strands alternate with lateral veins, and sclerified bundle caps are present on lateral veins, as well as thick-walled bundle-sheath cells, in receptacular bracts, which are otherwise like the involucre bracts. Involucre bracts of *Madia madioides* (fig. 43) are like those of *M. sativa*; the single large fiber strand adaxial to the midvein is the only sclerenchyma in the bract. Receptacular bracts are identical, except that a pair of strands is present beside the midvein. The furthest advance in bract structure in the genus appears to be the condition found in *M. minima*. In this species, the single fiber strand in involucre bracts is present adaxial to the midvein; it is very much flattened and extends around about a third of the perimeter of the bracts. One may say that in places, these fibers supplant the epidermis, because the adaxial epidermis beneath the strand is, in fact, mostly composed of such fibers, rather than the epidermal cells with hippocrepiform thickenings one might expect. The united circle of receptacular bracts shows similar zones of fibers, the number of which corresponds to the number of receptacular bracts involved.

12. *Raillardella*.—The resemblance of the receptacular and (where present) involucre bracts in the fruticose species of this genus to those of the advanced *Madia* type is quite striking. The receptacular bracts of *Raillardella muirii* (fig. 47) and *R. scabrada* have the same single band of fibers adaxial to the midvein. Bundle-cap fibers are also present on the midvein. Parenchyma cells are apparently more or less isodiametric. Bracts of the other species, *R. pringlei*, *R. scaposa* (fig. 46), and *R. argentea*, lack the prominent zone of fibers altogether. Between some of the lateral

veins, groups of large cells, which might be identified as fibers in transection occur. Examination of these cells in clearings and macerations shows that few fibers are present in the bracts, but that the wide short cells with lignified walls are actually tracheary elements with typical metaxylem thickenings. Mostly, these groups of cells are not associated with phloem in collateral bundles, but occur as isolated xylem strands. Parenchyma in these species consists of nearly isodiametric chlorenchyma, with large intercellular spaces. A pair of secretory canals was observed beside the midvein in the base of receptacular bracts of *R. argentea*.

13. *Argyroxiphium*.—The involucrel and receptacular bracts in this genus are very similar to each other, and descriptions for one may apply to the other for each species. The bract of *A. sandwichense* shown in fig. 60 has a thick mesophyll divided into two portions. One or two layers of palisade are present on the abaxial surface of the bract. Beneath this are layers of more or less isodiametric parenchyma cells with fairly small intercellular spaces and few chloroplasts. The intercellular spaces are filled with pectic compounds. Epidermal cells are thick-walled on both surfaces, but without hippocrepiform thickenings. Numerous strands of fibers are present between the bundles in the mesophyll. Additional similar fibers are present as bundle caps by the phloem. Some of the fiber groups may be fused into larger aggregations. Bracts of *A. grayanum* and *A. virescens* are like those of *A. sandwichense*. Bracts of *A. virescens* in particular show that the fiber strands are alternate with the veins and not primarily associated with them. This fact is also shown by bracts of *A. caligini* (fig. 61) which are like those of the other species, except that secretory canals are paired beside each of the major veins, and that the fiber strands are somewhat less prominent than those in the other species.

14. *Dubautia*.—The species of *Dubautia* are quite numerous, and bract structure can best be described by considering what appears to be the basic condition and describing presumable specializations of this. A seemingly unspecialized situation occurs in bracts of *D. laxa* (fig. 63). The mesophyll is thick, and consists of rounded parenchyma cells with small intercellular spaces. No appreciable intercellular pectic deposits were noticed. The inner epidermis consists of cells with relatively small hippocrepiform thickenings. Secretory canals occur singly or paired in various positions near the veins. Receptacular bracts of this sort were observed in *D. demissifolia*, *D. lonchophylla*, *D. magnifolia*, *D. menziesii*, *D. platyphylla*, *D. scabra*, *D. sberffiana*, and *D. waialealae*. *Dubautia sberffiana* shows small fiber strands. In *D. latifolia*, strands are very massive, occupying the majority of the mesophyll. In *D. knudsenii* (fig. 62), the mesophyll is very thick, with quite small intercellular spaces. Fiber strands are small, and large secretory canals accompany the numerous veins. Cell walls of the adaxial epidermis lack thickenings. Bracts of *D. ciliolata* (fig. 64), on the other hand, have relatively few veins. Fiber strands tend to be large and organized as a pair beside the midvein. Secretory canals are absent, and the adaxial epidermis has the typical hippocrepiform thickenings. The bracts of *D. scabra* are like those of the scapose species of *Raillardella* in that strands which appear like fibers in transection are composed of tracheary elements (which are not notably wide) not associated with phloem.

15. *Wilkesia*.—The bracts of *Wilkesia* (fig. 66) are even more intimately united with each other than those of the species of *Dubautia* in which bracts are united. It is difficult to delimit each bract, in fact, except by determining the position of the midveins, which are larger than lateral veins. The bracts are rather thin, and have a spongy ground tissue of cells which contain numerous chloroplasts. In the large intercellular spaces, pectic deposits occur (fig. 67), and the thickness of the cell walls

of mesophyll cells suggests richness in pectic materials. Fibers are present around the veins, outside the bundle sheath. The adaxial epidermis does not have hippocrepiform thickenings, and secretory canals are absent.

DISCUSSION.—There appears to be a basic similarity among bracts of *Madinae*. The least specialized condition appears to be a bract with fiber strands alternate with the veins, secretory canals beside the major veins, and, to a certain extent, chlorenchyma and hippocrepiform thickenings on the adaxial epidermis. The presence of discrete fiber strands, apparently a primitive character in *Madinae*, may, of course, be specialized compared with the most primitive *Compositae*, just as the enfolding habit of involucre bracts is basic to *Madinae* but probably represents an advanced condition compared to primitive *Heliantheae*. Within *Madinae*, specializations in the orientation of fibers have taken place. The single large strand in most species of *Madia* and in the fruticose *Raillardellas* seems a derived feature, as do the vein-centered strands in *Achyrrachaena* bracts. Probably a loss of fibers has occurred in *Blepharipappus* and *Holozonia*. The loss of fibers, and development of strands consisting of wide tracheary elements in bracts of the scapose *Raillardellas* certainly seems a specialization also. The basic similarity of the Hawaiian *Madinae* to the Pacific Coast genera in respect to bract structure is quite striking. The basic condition described above is present in both *Argyroxiphium* and *Dubautia*, bracts of which show a surprising similarity. Specializations in bracts of Hawaiian *Madinae* parallel those in the Pacific Coast tarweeds to a remarkable extent. Loss of secretory canals has apparently occurred in both groups. The single pair of fiber strands in bracts of *D. ciliolata* is like *Hemizonia fasciculata* or *Calycadenia villosa*; the vein-centered sclerenchyma of *Wilkesia* bracts is like that in *Achyrrachaena*; and there is a great similarity between bracts of *Dubautia scabra* and those of the scapose *Raillardellas*.

#### FLORAL ANATOMY

VENATION.—The patterns of vasculature in ray flowers of *Compositae* are extremely variable, even within a single species, and offer almost insuperable difficulties in description. Moreover, a number of *Madinae* lack ray flowers, so that disk flowers alone provide the only comprehensive comparisons. Unless otherwise stated, all data below refer to disk flowers.

Disk flowers of most *Madinae* have a simplified venation pattern with five bundles in the achene; this venation is identical to that illustrated for *Syntrichopappus lemmonii* by the writer (1956), and is of a type widespread in *Compositae*. Exceptions to this pattern are as follows:

1. *Raillardella*.—A flower of *R. pringlei* (fig. 68) has five main achene bundles which extend upward into the corolla and style bundles. In addition, one to five lesser bundles, which terminate at the summit of the achene, are present. The venation of the corolla and style is of the typical simplified *Compositae* type, and stamen traces include xylem elements. The ovule trace is dichotomous, and is thus unique among *Madinae*, although this character occurs in certain *Heliantheae* (Carlquist, 1957b). The venation of flowers of *R. scaposa* and *R. argentea* agree with the description of *R. pringlei* above. In *R. scabrida* and *R. muirii*, only one bundle additional to the main five achene bundles could be observed in a few achenes, and the remainder are identical to the simplified pattern mentioned above. One curious feature which all species of *Raillardella* have in common, however, is the presence of a strand of phloem in each pappus bristle (fig. 82). This phloem branches from that of collateral bundles at the summit of the achene, and extends most of the length of bristles.

2. *Holocarpba*.—In the achenes of the four species of this genus, bundles additional to the main five are present, as in the scapose *Raillardellas*; not infrequently



five such lesser bundles are present in the achene. The presence of this character in *Holocarpa* is noteworthy because it is absent in all the species of *Hemizonia* examined.

3. *Blepharizonia*.—Achenes of *Blepharizonia* are ten-ridged, and these ridges correspond to ten bundles of equal prominence. Five of them terminate in the achene summit, and alternate with these are five which continue into corolla and style. The venation is otherwise of the simplified type.

4. *Achyraea*.—Achenes of this genus contain strands of phloem in the achenes in addition to the five collateral bundles. Aside from this, the venation is of the simplified type.

5. *Adenothamnus*.—Pappus bristles in this genus contain phloem strands (fig. 76) and one or two bundles in the achene wall additional to the main five.

6. *Calycadenia*.—All the species of *Calycadenia* were observed to have one small feature which distinguishes them from ordinary corolla venation in Compositae. This is the occurrence of a short projection of vascular tissue beyond the point at which the two veins fuse at a lobe-tip (fig. 70).

7. *Madia bolanderi*.—Corolla lobes of this species usually have various veins in addition to those which outline the lobes (fig. 71, a-c). These patterns tend to suggest the occurrence of some sort of median bundle in the corolla-lobe tip, although the commissural bundles obscure the condition.

8. *Layia*.—In the species examined, strands of phloem were observed in pappus bristles.

9. *Argyroxiphium*.—The flower of *A. grayanum* shown in fig. 69 illustrates two distinctive features: the presence of four achene bundles, and the occurrence of short segments of median bundles in corolla lobes. The median corolla-lobe veins are also present in *A. caligini*, but are lacking in the remaining species. The four species all have achenes with four bundles, but achenes with five bundles are not uncommon in all species. A small phloem strand was observed in the base of a pappus scale only in *A. virescens* (fig. 77).

10. *Dubautia*.—Species of *Dubautia* have the typical venation, with usually five bundles in the achene. Of some interest, however, is the presence of phloem strands in pappus bristles of those species which have longer, subterete bristles. Such strands were observed in *D. ciliolata* (fig. 80, 81), *D. latifolia*, *D. menziesii*, *D. platyphylla*, *D. scabra*, *D. struthiolooides*, and *D. thyrsiflora*. These phloem strands branch from collateral bundles in the achene wall (fig. 80) and run most of the length of the bristle. Phloem strands were not observed in pappus structures of *D. knudsenii* (fig. 79), *D. raillardioides*, *D. magnifolia*, *D. laxa*, *D. paleata*, and *D. waialealae*, despite the fact that pappus bristles or scales are just as thick, and might be expected to be as complex in structure, as those in the species listed above. The species in which phloem was observed are all species formerly included in *Raillardia* (Sherff, 1935), whereas the species in which phloem is absent all belong to section *Dubautia*.

11. *Wilkesia*.—Four bundles may occasionally be seen in achenes of *Wilkesia*, but the venation otherwise offers no exceptional features. Despite the massive structure of pappus scales (fig. 78), no vascular elements are present.

DISCUSSION.—The exceptional features above require explanation. Such explanation is not readily apparent in all instances. The more complicated venation patterns, such as additional achene wall bundles in *Raillardella*, *Holocarpa*, and *Blepharizonia*, might be expected in more primitive genera, but these genera are not particularly primitive even among tarweeds. Number of veins in the achene wall is not

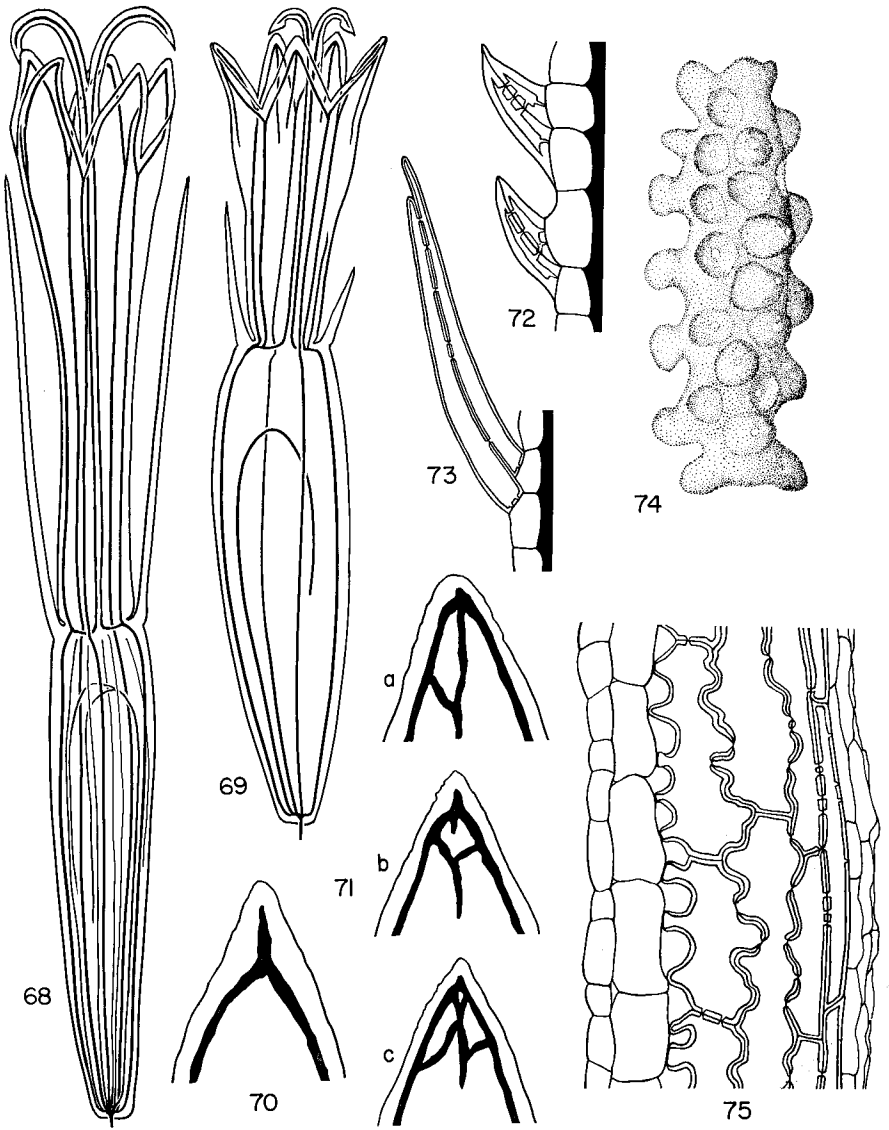


Fig. 68-75. Fig. 68. *Raillardella pringlei*, disk flower, showing venation. All lines except outlines of achene, pappus, corolla, and style represent collateral bundles.  $\times 8$ . Fig. 69. *Argyroxiphium grayanum*, disk flower, same conventions.  $\times 9$ . Fig. 70. *Calycadenia fremontii*, corolla lobe of disk flower, showing venation.  $\times 60$ . Fig. 71. *Madia bolanderi*, corolla lobes from disk flowers, showing (a-c) three variations in venation.  $\times 45$ . Fig. 72. *Achyrochaena mollis*, trichomes from whole mount of achene.  $\times 140$ . Fig. 73. *Dubautia magnifolia*, trichomes from whole mount of achene.  $\times 200$ . Fig. 74. *Hemizonia greeneana*, subhypodermal papillate sclereid from ray achene.  $\times 165$ . Fig. 75. *H. greeneana*, longitudinal section of ray achene wall, epidermis at left, showing papillate sclereids in wall.  $\times 115$ .

correlated with size of achenes: *Argyroxiphium*, in which four bundles predominate in achenes, has the largest achenes in Madinae, whereas the achenes of *Blepharizonia*, which contain ten veins, are relatively small for the tribe. The presence of median bundles in corolla-lobe tips of *Argyroxiphium* may represent a vestige of a primitive condition, as it apparently does in *Lagascea helianthifolia* (Carlquist, 1957b). The same explanation need not, however, apply for *Calycadenia*, in which the terminal vein in corolla-lobe tips is a characteristic of the genus, or in *Madia bolanderi*, in which large corolla size may at least in part be related to the formation of additional veins, although that species does contain a number of characters seemingly primitive in the genus. The occurrence of phloem strands in pappus bristles of both Pacific Coast and Hawaiian Madinae is rather interesting, because this character (except in *Argyroxiphium*, where phloem is minimal) is seemingly related to the presence of long, subterete bristles. Such strands are lacking in paleaceous pappus structures, regardless of dimension, in Madinae. There seems reason to believe that such phloem strands are not necessarily vestiges of a primitive venation pattern. The occurrence of phloem strands in pappus bristles has been reported in certain rather primitive Mutisieae (Carlquist, 1957c), however.

TRICHOMES.—Details of relative presence of trichomes on achenes of Madinae are given by taxonomic works such as Munz and Keck (1959), Sherff (1935), and Keck (1936). The basic trichome type is the so-called "zwillingshaar", a biseriate non-glandular trichome which occurs in many Compositae, and has been figured by a number of authors. As usually illustrated, such a trichome consists of two short basal cells and two long upper cells which terminate at the same level with short divergent points. In Madinae, "zwillingshaare" are usually two-celled, because basal cells are not cut off. In all the genera of Madinae in which trichomes occur on achenes, "zwillingshaare" which have the paired cells coterminous may be found, but not infrequently, as shown in fig. 73, the tips of the two cells do not terminate at the same point. Aside from this, the only major variation in Madinae occurs in *Achyrachaena* (fig. 72), in which the trichomes are very short and wide. Tips of the pair of cells do not diverge.

Uniseriate non-glandular trichomes, two or more cells in length, were observed on corollas in the following taxa: *Achyrachaena mollis*, *Adenothamnus validus*, *Blepharipappus scaber*, *Blepharizonia plumosa*, *Calycadenia* spp. (as mentioned below), *Hemizonia congesta*, *H. corymbosa*, *Holozonia filipes*, *Lagophylla ramosissima*, *Layia pentachaeta* subsp. *albida*, *L. platyglossa*, *Madia bolanderi*, *M. elegans* subsp. *densifolia*, *M. sativa*, and *Raillardella* spp. Among the Hawaiian genera, they occur

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Fig. 76-89. Fig. 76. *Adenothamnus validus*, transection of pappus bristle.  $\times 170$ . Fig. 77. *Argyroxiphium virescens*, transection of pappus scale near base.  $\times 180$ . Fig. 78. *Wilkesia gymnoxiphium*, transection of pappus scale near base.  $\times 125$ . Fig. 79. *Dubautia knudsenii*, transection of pappus scales.  $\times 165$ . Fig. 80. *Dubautia ciliolata*, longitudinal section of achene, showing median section of pappus bristle (left) with phloem strand (dark).  $\times 200$ . Fig. 81. Same, transection.  $\times 180$ . Fig. 82. *Raillardella argentea*, transection of pappus bristles, showing phloem in central portion.  $\times 205$ . Fig. 83. *Dubautia menziesii*, transection of achene, showing a secretory canal (center), and a vascular bundle, to the right of it.  $\times 190$ . Fig. 84. *Argyroxiphium sandwichense*, transection of disk achene, showing a vascular bundle.  $\times 200$ . Fig. 85. *Wilkesia gymnoxiphium*, sclerified trichomes from cleared corolla.  $\times 140$ . Fig. 86. *Calycadenia villosa*, corolla-lobe tip from cleared disk flower, showing sclerified lobe tip (above), multi-seriate glandular trichome with sclerified base (middle) and a similar biseriate trichome (below).  $\times 125$ . Fig. 87. *Hemizonia fitchii*, lobe tip, showing sclereids and trichomes, from longitudinal section of disk flower.  $\times 125$ . Fig. 88. *Achyrachaena mollis*, transection of ray corolla, showing secretory canal interior to vein.  $\times 215$ . Fig. 89. *Dubautia knudsenii*, transection of flower, showing secretory canals in corolla and style.  $\times 145$ .

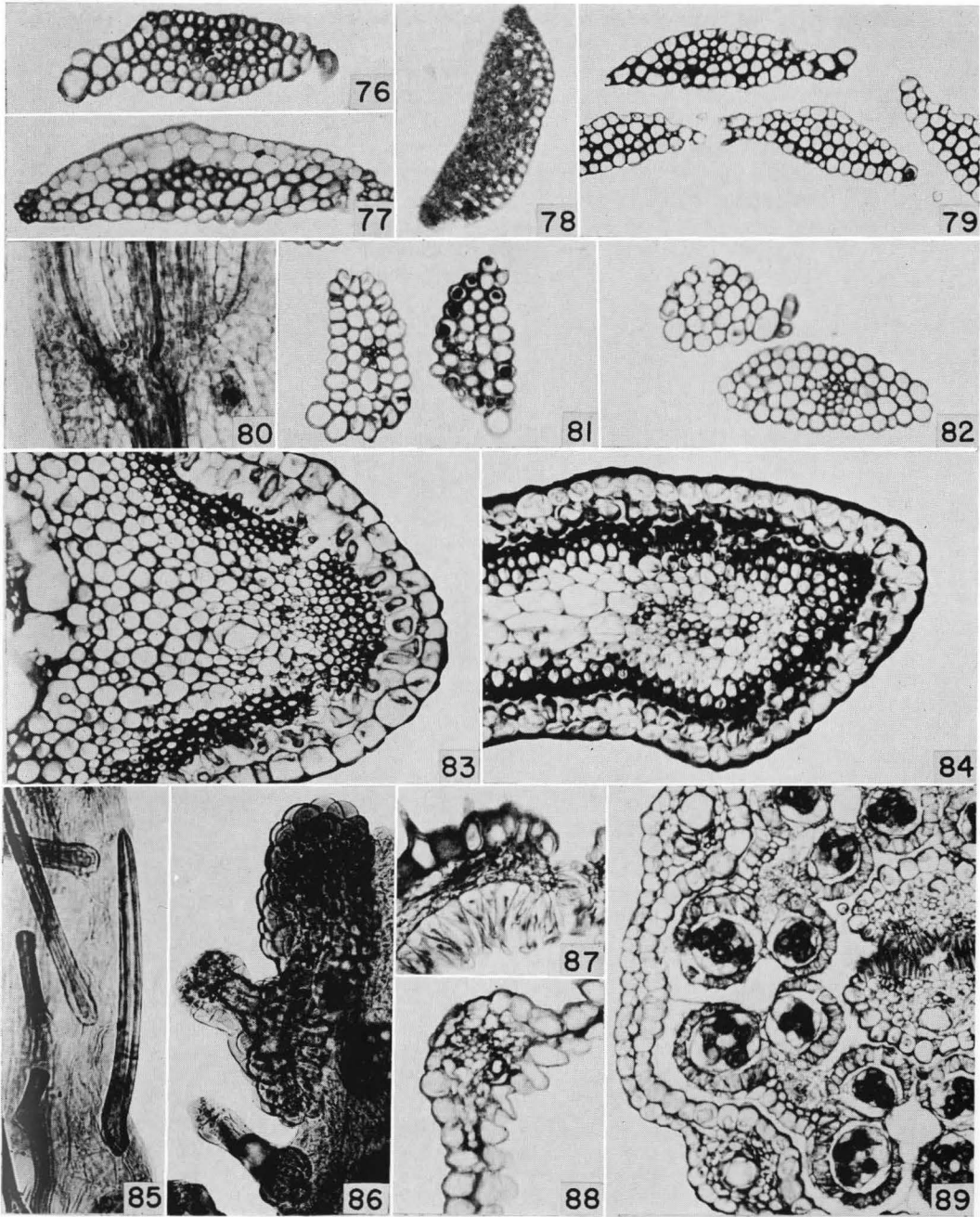


FIG. 76-89

in *Argyroxiphium grayanum* and *A. virescens*, but are lacking in *A. caligini* and *A. sandwichense*; a few were observed on corollas of *Dubautia demissifolia* and *D. paleata*. Such trichomes are doubtless present on corollas of more species than listed above, but these records establish their presence throughout the subtribe. Uniseriate one-celled trichomes occur at the tips of corolla lobes in the *Centromadia* species of *Hemizonia*, as shown in fig. 87. These are characterized by a narrow prolongation of an epidermal cell; a lignified wall is formed inside the thick non-lignified wall characteristic of epidermal cells. The prominent sclerified uniseriate trichomes which occur on corollas of *Wilkesia* (but none of the other genera investigated) are different (fig. 85). They are much more elongate and wider than those of the *Centromadias*, and probably represent reduced, sclerified two-celled uniseriate trichomes (which also occur occasionally on *Wilkesia* corollas). Biseriate glandular trichomes were observed on corollas of *Blepharipappus scaber*, *Blepharizonia plumosa*, *Calycadenia* spp. (see below), and *Holocarpus* spp. Capitate glandular trichomes with biseriate stalks and subdivided heads were observed on corollas of *Hemizonia congesta*, *H. corymbosa*, *H. fasciculata* (where they are sessile), *Madia bolanderi*, *M. elegans* subsp. *densifolia*, *M. minima*, *Raillardella muirii*, *R. scabrifolia*, and, in the Hawaiian genera, *Dubautia knudsenii* (Carlquist, 1958b) and *D. laxa*. Species with capitate glandular trichomes also often have simple biseriate glandular trichomes. The list of species with capitate trichomes could probably be expanded, particularly by species of *Hemizonia* and *Madia*. There are some species, however, in which glandular trichomes seem absent from corollas: *Achyraea mollis*, *Holozonia filipes*, and *Lagophylla ramosissima*. All the species of *Holocarpus* have the short, multiseriate glandular trichomes described by Carlquist (1958b) as being peculiar to this genus. Examination of corollas of *Calycadenia* showed that distribution and types of glandular and non-glandular trichomes is quite varied and warrants more attention than do corolla trichomes in *Hemizonia* and *Madia*, in which both uniseriate non-glandular and capitate glandular trichomes seem rarely absent. One glandular trichome type not observed except in *Calycadenia* is the capitate glandular trichome (with a biseriate or multiseriate, wide stalk) in which the basal and stalk cells are heavily sclerified (fig. 86). Some species also possess marked sclerification of cells at the corolla-lobe tip (fig. 86). So characteristic of species is the distribution of various trichome types that a key to the species can be made:

A. Corolla trichomes present.

B. Glandular trichomes present.

C. Glandular trichomes with sclerified basal and stalk cells; cells at lobe tips sclerified.

D. Uniseriate trichomes present also . . . . . *C. ciliosa*.

DD. Uniseriate trichomes absent.

E. Glandular trichomes without sclerified cells also present.

F. Sclerified glandular trichomes biseriate only . . . . . *C. hispida*.

FF. Sclerified glandular trichomes biseriate to multiseriate . . . . . *C. multiglandulosa*.

EE. No non-sclerified glandular trichomes present . . . . . *C. villosa*.

CC. All glandular trichomes without sclerified cells; uniseriate non-glandular trichomes present; cells at lobe tips not usually sclerified . . . . . *C. tenella*, *C. mollis*, *C. fremontii* (cells of both trichome types thick-walled but not sclerified in *C. fremontii*).

BB. No glandular trichomes present; uniseriate non-glandular trichomes very short, with thick walls.

C. Sclereids present at lobe tips. . . . . *C. truncata*, *C. spicata*.

CC. No sclereids present at lobe tips. . . . . *C. pauciflora*.

AA. Corolla trichomes absent or nearly so. . . . . *C. oppositifolia*.

The presence of both glandular and non-glandular trichomes on corollas, as well as leaves, stems, and involucre is not particularly surprising. The presence of capitate trichomes on flowers of *Madia* and *Hemizonia* seems noteworthy, but the development of distinctive types of glandular trichomes in *Calycadenia* and *Holocarpha* probably represents specialization in these genera, respectively. The similarity of capitate glandular trichomes in *Dubautia* to those of the Pacific Coast Madinae seems significant.

ACHENE WALL.—The achene wall of Madinae, like those of other Heliantheae (Carlquist, 1957b) consists of an epidermis, a hypodermis, and a number of sub-hypodermal sclerenchyma layers, inside of which is the thin-walled parenchyma in which vascular bundles are embedded. The outer surface of the sclerenchyma layer is often coated with massive deposits of resin-like materials which carbonize, giving the achene a black color. In relatively primitive Heliantheae, such as *Fitchia* (Carlquist, 1957b), the sclerenchyma layer is not interrupted. This condition was observed in *Blepharizonia plumosa*. In achenes of *Dubautia* (fig. 83) and *Argyroxiphium* (fig. 84), however, the sclerenchyma band is interrupted in a few places by bands of thin-walled parenchyma. Relatively irregular bands of this sort were observed in *Raillardella*. The most common condition in Madinae is the presence of relatively frequent bands of parenchyma in this layer (fig. 43, 45). This condition, which was reported earlier for *Helianthus* and *Tithonia* (Carlquist, 1957b), was observed in Madinae in *Achyrachaena*, *Adenothamnus*, *Blepharipappus*, *Hemizonia* (disk achenes only), *Holocarpha*, *Madia*, and in the Hawaiian genus *Wilkesia*. In ray achenes of *Hemizonia*, the sclerenchyma layer is very massive and not interrupted by parenchyma bands; the sclerenchyma, in fact, may completely enclose the vascular bundles (*H. greeneana*, *H. congesta*). The presence of the parenchyma bands may be easily detected in gross aspect by a striate appearance of the wall, especially in a preparation which can be viewed by transmitted light. This condition is probably more specialized than the absence of such parenchyma bands.

A feature of particular interest in the achene wall of some Madinae is the presence of what may be termed papillate sclereids (fig. 74). These are relatively thin-walled sclereids, with lignified walls, which have undulate contours. They tend to occur in the outer portion of the sclerenchyma band (fig. 75). A single cell, such as that shown in fig. 74, shows projections and indentations. The center of a projection or indentation may be thin-walled or contain a pit (indicated by small circles in each in fig. 74). Papillate sclerenchyma cells of this nature were observed most abundantly in ray achenes of *Calycadenia*, *Hemizonia*, and *Holocarpha*. In these genera, they are much rarer or absent in the disk achenes. They are definitely not present in the Hawaiian genera, or in *Achyrachaena*, *Blepharizonia*, *Madia*, and *Raillardella*.

There is some variation in Madinae in respect to the hypodermis of the achene wall. A palisade-like hypodermis, with radially elongate cells, was observed in ray achenes of *Hemizonia congesta*. *Blepharizonia plumosa* has such a hypodermis, the cells of which are occasionally thick-walled with prominent pit fields. A hypodermis consisting of two cell layers was observed in upper portions of achenes of *Dubautia menziesii* and *D. struthioloides*, although lower portions (fig. 83) have mostly only a single layer. Approximately three hypodermal layers were observed in ray achenes

of *Calycadenia truncata* subsp. *scabrella*.

Secretory canals, internal to vascular bundles, were observed only in achenes of *Dubautia menziesii* (fig. 83). The veins in the achenes of *Argyroxiphium* (fig. 84) may be large and have distribution of phloem and xylem groups in a pattern other than the typical collateral configuration.

PAPPUS.—The presence or absence of phloem strands in pappus bristles was mentioned above. In both Hawaiian and Pacific Coast genera, the cells of pappus bristles tend to be composed of relatively thin-walled lignified cells, such as those shown in fig. 42 (below), 77, 79, 81, and 82. Thick-walled lignified cells were seen in pappus of *Adenothamnus validus* (fig. 76) and *Wilkesia gymnoxiphium* (fig. 78). The majority of Madinae have elongate trichome-like cells along the margins or surfaces of the bristles or paleae. The presence of these is indicated by such taxonomic treatments as those of Sherff (1935) and Munz (1959), and are detailed for the genus *Layia* by Clausen (1951).

COROLLA-LOBE TIPS.—An interesting feature of some Madinae is the sclerification of cells at the tips of corolla lobes. This was mentioned for *Calycadenia* above, and is illustrated in fig. 86. A sectional view of a lobe tip is shown for *Hemizonia futchii* in fig. 87. Other taxa in which this character was observed include *Holozonia filipes* and *Dubautia magnifolia*.

SECRETORY CANALS.—A feature of some significance is the presence of secretory canals in corollas of Madinae. These occur singly beside vascular bundles in corolla lobes, and either singly or in pairs beside each bundle in the tube. The only Pacific Coast genera which possess such canals are *Achyrochaena* (fig. 88) and *Lagophylla*. They are present in some species of *Dubautia*, such as *D. knudsenii* (fig. 89), *D. laxa*, *D. magnifolia*, and *D. microcephala*, all of which belong to the section *Dubautia*. They are definitely absent in other species, such as those of the section *Raillardia* which were investigated. All other taxa, both Pacific Coast and Hawaiian, lack these secretory canals. There are a few species in which a single secretory canal appears in each stigmatic branch of the style, extending downward into the undivided portion of the style as well. These include *Achyrochaena mollis* among the Pacific Coast tarweeds and *Dubautia knudsenii*, *D. laxa*, *D. microcephala*, and *D. magnifolia* among the Hawaiian Madinae. They were not observed in other species of *Dubautia* examined.

#### POLLEN

The pollen grains of Madinae vary in respect to diameter, spine length, spine number, and details of exine and intine. The varied types of preparation employed in this study prevented accurate comparisons of pollen grain size, which does not, however, appear to be of particular importance above the level of species. The other characters were, however, studied, and extremes in expression of these are shown in fig. 90-96. Entire pollen grains were not drawn because in shape they are all sphaeroidal, and they are all tricolporate. The furrows are of moderate length and extend about two thirds of the distance between the two poles. The germ pore is well defined.

The optical sections shown in fig. 90-96 show that there is a group resemblance among the various taxa, despite extremes. All have spines which are inverted-funnel-

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Fig. 90-96. Exine of pollen grains of Madinae. One-third of an equatorial optical section is shown, with germ pores at right and left. Intine shown in black, exine stippled. Fig. 90. *Argyroxiphium grayanum*. Fig. 91. *Argyroxiphium caliginii*. Fig. 92. *Wilkesia gymnoxiphium*. Fig. 93. *Dubautia knudsenii*. Fig. 94. *Madia sativa*. Fig. 95. *Raillardella scaposa*. Fig. 96. *Blepharipappus scaber*.

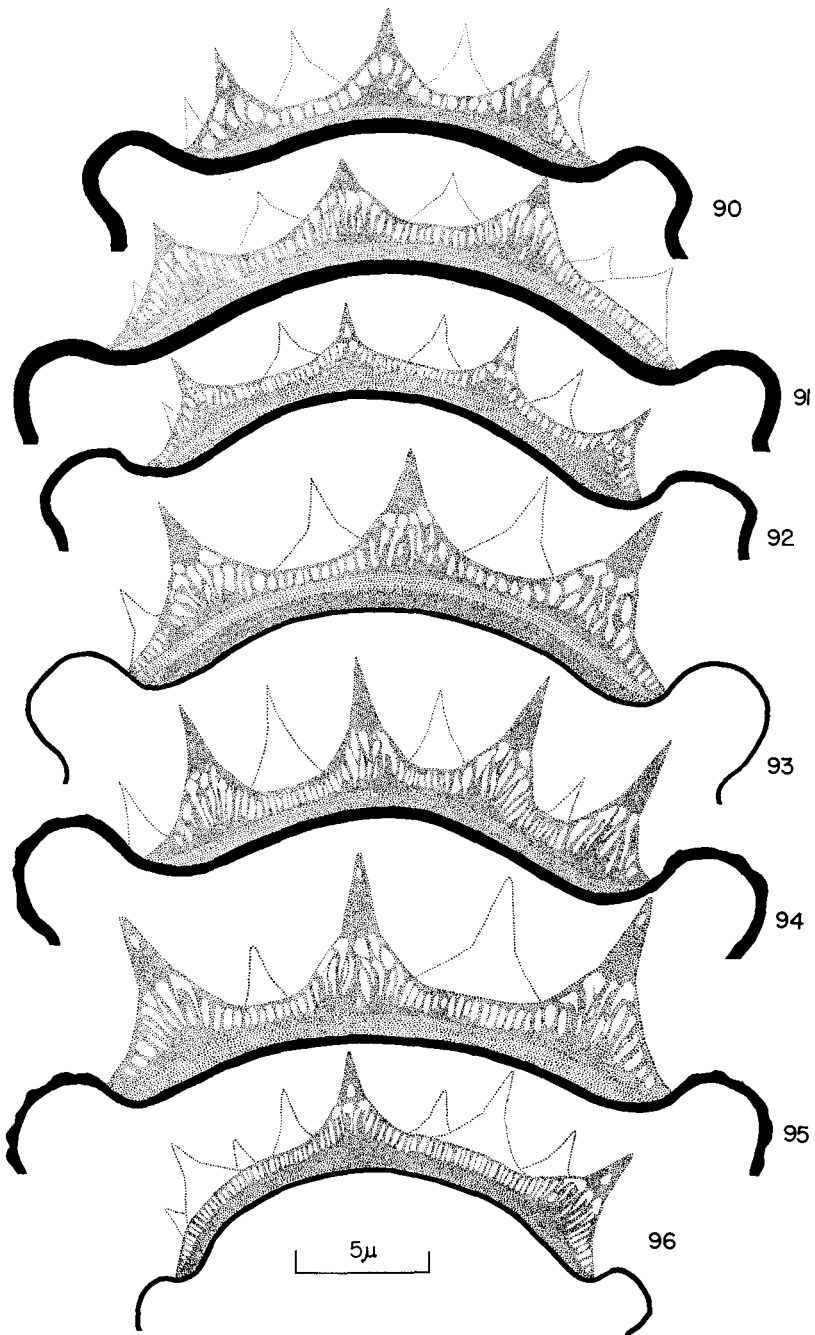


FIG. 90-96



form in shape, with a narrow apical and widened basal portion. The exine is in two layers (ectexine and endexine of Faegri and Iversen, 1950; sexine—or tectum—or nexine of Erdtman, 1952). The exine tends to be lacunate (baculate, in the terminology of Erdtman), and the lacunate layer tends to follow the contours of the grain. These lacunae are present in the spine bases, but do not extend into the apical portion of the spine. In seemingly unspecialized types of exine, such as that shown for *Madia sativa* (fig. 94) and *Dubautia knudsenii* (fig. 93), lacunae in spine bases extend inward nearly to the unsculptured layer. Apparently elimination of the lacunae from the most basal portion of the spine is a specialized character, as in *Wilkesia* (fig. 92). The lacunae at the upper end of the widened portion of the spine are usually notably widened. These expanded portions of adjacent lacunae may be fused. The varied shape of spine-base lacunae is also caused, however, by the fact that they tend to diverge outward, so that a median optical section will show only parts of lacunae in the center of a spine base. Spines may have a single lacuna in the apical portion of the spine (fig. 90, 92, 95, 96). The intine may be quite thick, as in *Argyroxiphium*, or rather thin, as in *Dubautia knudsenii* (fig. 93) and *Blepharipappus* (fig. 96).

In the Pacific Coast Madinae, there is little difference among *Raillardella scaposa* (fig. 95), *Madia sativa* (fig. 94) and *Blepharipappus scaber* (fig. 96), except that these represent a decreasing series in size of spines. *Raillardella* and *Blepharipappus* are rather exceptional, and most of the Pacific Coast Madinae have pollen grains which are indistinguishable from those of *Madia sativa*. Such species include *Achyrachaena mollis*, *Adenothamnus validus*, *Blepharizonia plumosa*, *Calycadenia multiglandulosa*, *Hemizonia congesta*, *H. corymbosa*, *H. fasciculata*, *H. fitchii*, *H. greeneana*, *H. minibornii*, *H. pungens*, *Holocarpa* spp., *Holozonia filipes*, *Lagophylla ramosissima*, *Layia platyglossa*, *Madia bolanderi*, *M. elegans*, and *M. minima*. Interspal exine has a very thin lacunate layer in *Holozonia filipes* and *Madia bolanderi*. A lacuna in the apical portion of the spine was seen in *Blepharizonia plumosa* and in some spines of *Calycadenia multiglandulosa* subsp. *cephalotes* as well as in the spines of *Blepharipappus* (fig. 96). Irregularities in the thickness of the intine covering germ pores was observed in *Madia sativa* (fig. 94) and *Raillardella scaposa*. All the species of *Raillardella* have large spines, but the lacuna in the uppermost portion of the spine was observed only in *R. scaposa* (fig. 95). The intine thickness of most Pacific Coast Madinae is approximately that indicated for *R. scaposa*, and is often only slightly thinner than the unsculptured layer of the exine.

Among Hawaiian Madinae, the pollen grains of *Dubautia* show close similarity to those of *Raillardella* in the large spine size. Sculpturing within the spines is also comparable to the typical pattern of Pacific Coast Madinae. The thickness of intine and exine of *Dubautia* is quite similar to that of the Pacific Coast Madinae, so that it would be extremely difficult to distinguish between the two groups. The pollen grains of *Argyroxiphium* (fig. 90, 91) are distinctive in their larger size, but the spines are shorter and more numerous. This is especially noticeable in *A. sandwichense* (fig. 91), and a species which resembles it closely in pollen grain structure, *A. caligini*. In *A. grayanum*, spines appear to be more acuminate. The lacunae appear larger, and are not appreciably present in the most basal portions of the spines. Pollen grains of *A. grayanum* also show smaller diameter and fewer spines than those of *A. caligini* and *A. sandwichense*. The pollen grains of *Wilkesia* (fig. 92) combine large pollen grain size with small spine size. Like *A. grayanum*, lacunae are absent in the most basal portion of the spine. The apical portion of each spine does contain a prominent lacuna. Pollen grains of *Wilkesia* are possibly the most distinctive in Hawaiian Madinae.

Selling (1945) has provided some useful brief descriptions of the pollen grains of *Dubautia latifolia*, *D. laxa*, *D. menziesii*, *D. microcephala*, *D. molokaiensis*, *D. paleata*, and *D. plantaginea*, as well as *Argyroxiphium grayanum*. No previous description of the pollen grains of Pacific Coast Madinae seems to have been prepared. Comparison of these patterns with those of other Heliantheae, however, reveals that the remainder of Heliantheae may not share all the characters found in madinean pollen grains. Interspinal lacunae were seemingly absent in the exine of other Heliantheae investigated by the writer, although not in *Fitchia*, in which they are small and infrequent (Carlquist, 1957b). Certainly knowledge of detailed exine patterns in more genera and species of Compositae is needed, but the evidence presented above is certainly not opposed to the generic composition of Madinae expressed here. One feature of considerable interest is the thick intine present on grains of most taxa, especially *Argyroxiphium*. In view of the extremely divergent habitats of the species, the thickness of the exine, which does not vary with these habitats, cannot be correlated with physiological conditions.

#### STYLES

The writer has found that descriptions of styles of disk flowers in Compositae are often vague, based on general shape characteristics. Differences among styles in a group of composites depend on presence, placement, and density of particular cell types, and therefore these features should be figured and described in cellular detail.

PACIFIC COAST MADINAE.—Some extreme variations are shown in fig. 97-100. Basically, the stigmatic branches are long and acuminate. Each branch has a pair of well-defined bands of stigmatic hairs which extend from the point of divergence of the branches most of the distance to the apices, although they terminate well short of the apices, often at a level lower than that shown in fig. 99. The outer surface is more or less evenly coated with elongate collecting hairs. The styles of *Raillardella scabrida* (fig. 97) and *Layia platyglossa* (fig. 99) show the two extremes found in most tarweeds in respect to presence of collecting hairs. In *R. scabrida*, the collecting hairs are not present below the cleft, and collecting hairs just above it are shorter than those farther up the style. Species in which styles of this sort were observed include: *Blepharizona plumosa*, *Hemizonia congesta*, *H. corymbosa*, *H. fasciculata*, *H. minthornii* (a few papillate cells below the cleft), *Holocarpha macradenia* (collecting hairs more abundant at the level where stigmatic hairs terminate near the upper end), *Holocarpha virgata*, *Madia bolanderi*, *M. madiooides*, *M. minima*, and *Raillardella muirii*. Species in which collecting hairs were found to be absent from the lower portions of stigmatic branches, like *Layia platyglossa* (fig. 99), include *Calycadenia multiglandulosa* subsp. *cephalotes*, *C. truncata* subsp. *scabrella*, *C. villosa*, *Hemizonia fitchii*, *H. greeneana*, *H. pungens*, *Layia fremontii*, *L. pentachaeta* subsp. *albida*, *Raillardella argentea*, *R. pringlei*, and *R. scaposa*.

Other species of Pacific Coast tarweeds show more or less marked departure from the above types. In *Achyrrachaena mollis*, collecting hairs are absent from the tip of the stigmatic branches, and a few short collecting hairs are present below the point of union between the two branches. *Blepharipappus scaber* (fig. 98) has the most distinctive of tarweed styles in its very short stigmatic branches. The bands of stigmatic hairs extend to the apex of each branch. The outer surfaces of the branches are covered with elongate collecting hairs and short, globular cells. Both of these kinds of cells continue well below the point at which the stigmatic branches join. The styles of *Adenothamnus validus* (fig. 100) are quite distinctive in their large size, but more particularly in the absence of collecting hairs below approximately the level at which the bands of stigmatic hairs terminate. The collecting hairs are particularly prominent at that level.

Another type of variation in style anatomy occurs in relation to the sterility of disk flowers, a feature which has evolved in a number of the Pacific Coast tarweeds. This has resulted in the partial or entire loss of the stigmatic hairs and the diminution in size of the style as a whole. Taxa in this category include *Hemizonia*, section *Centromadia* (inner disk flowers), *Hemizonia*, section *Deinandra* (except some disk flowers in *H. paniculata* and *H. floribunda*), *Holocarpus* (some disk flowers), and four species of *Madia* (*M. citriodora*, *M. elegans*, *M. rammii*, and *M. yosemitana*).

Two other genera, however, *Holozonia* and *Lagophylla*, show no appreciable diminution of style size, although stigmatic hairs are completely lacking in disk flowers. The stigmatic branches are partly united with each other in *Holozonia* and wholly united in *Lagophylla*.

HAWAIIAN MADINAE.—The Hawaiian Madinae have styles which show a group resemblance, and which are separable from those of the Pacific Coast Madinae. Their range in variation is shown in fig. 101-104. The stigmatic branches are not gradually tapered, but have tips which widen and terminate in cuneate or deltoid shape. The bands of stigmatic hairs are paired on each branch, and extend much of the way to the tip, although they terminate some distance short of it. The collecting hairs tend to be aggregated at the level at which the bands of stigmatic hairs terminate. The basic type appears to be that shown for *Argyroxiphium sandwichense* (fig. 102) or *Dubautia sberffiana* (fig. 103). The type shown for *Argyroxiphium sandwichense* also occurs in *A. grayanum* and *A. virescens*. The styles of *Dubautia* are smaller than those of *Argyroxiphium*, corresponding to the smaller flower size, but are very similar in their shape and cellular detail. The only marked departures from this form are as follows. *Argyroxiphium caligini* (fig. 101) has styles in which the branches are markedly truncate. The bands of stigmatic hairs extend to near the tip, and the collecting hairs, which cover the outer surfaces of the stigmatic branch tips, are somewhat shorter than in the preceding species. The stigmatic branches of *Wilkesia* are distinctive in their great length, their acute tips, and their presence of a narrow tapered tip which does not bear collecting hairs. Collecting hairs are very short and blunt.

DISCUSSION.—The type of style characteristic of *Raillardella scabrata* (fig. 97) and other Pacific Coast tarweeds is a relatively unspecialized type. The restriction of stigmatic hairs into a pair of bands, and the lack of collecting hairs below the cleft mark this type as more advanced than less specialized types found in other Heliantheae, such as *Wyethia* (Carlquist, 1957b). The alteration from the *Raillardella scabrata* type to the *Layia platyglossa* type is a small one; the style of *Achyrochaena* likewise represents only a small change from the basic condition. The distinctive type found in *Blepharipappus* seems unspecialized in its collecting hairs, but highly modified in its truncated stigmatic branches. The style of *Adenothamnus* seems to represent a modification toward the conformation basic to the Hawaiian Madinae. The difference between Pacific Coast and Hawaiian Madinae may not be as great as it might seem at first sight. The similarity between styles of *Adenothamnus* and *Dubautia* is extremely close except for the shorter, wider branches in *Dubautia*. Some of the Pacific Coast Madinae, such as *Hemizonia congesta*, have stigmatic branches which approach the shorter, wider shape closely. Within the Hawaiian Madinae, the style of *Wilkesia* shows marked departure from the *Dubautia*-type, a departure correlated with other anomalous features of this genus. The style of *Argyroxiphium caligini* is surprisingly different from those of the other *Argyroxiphium* species, and represents a local variation involving a foreshortening of the stigmatic branches not unlike the situation which has been attained in *Blepharipappus*.

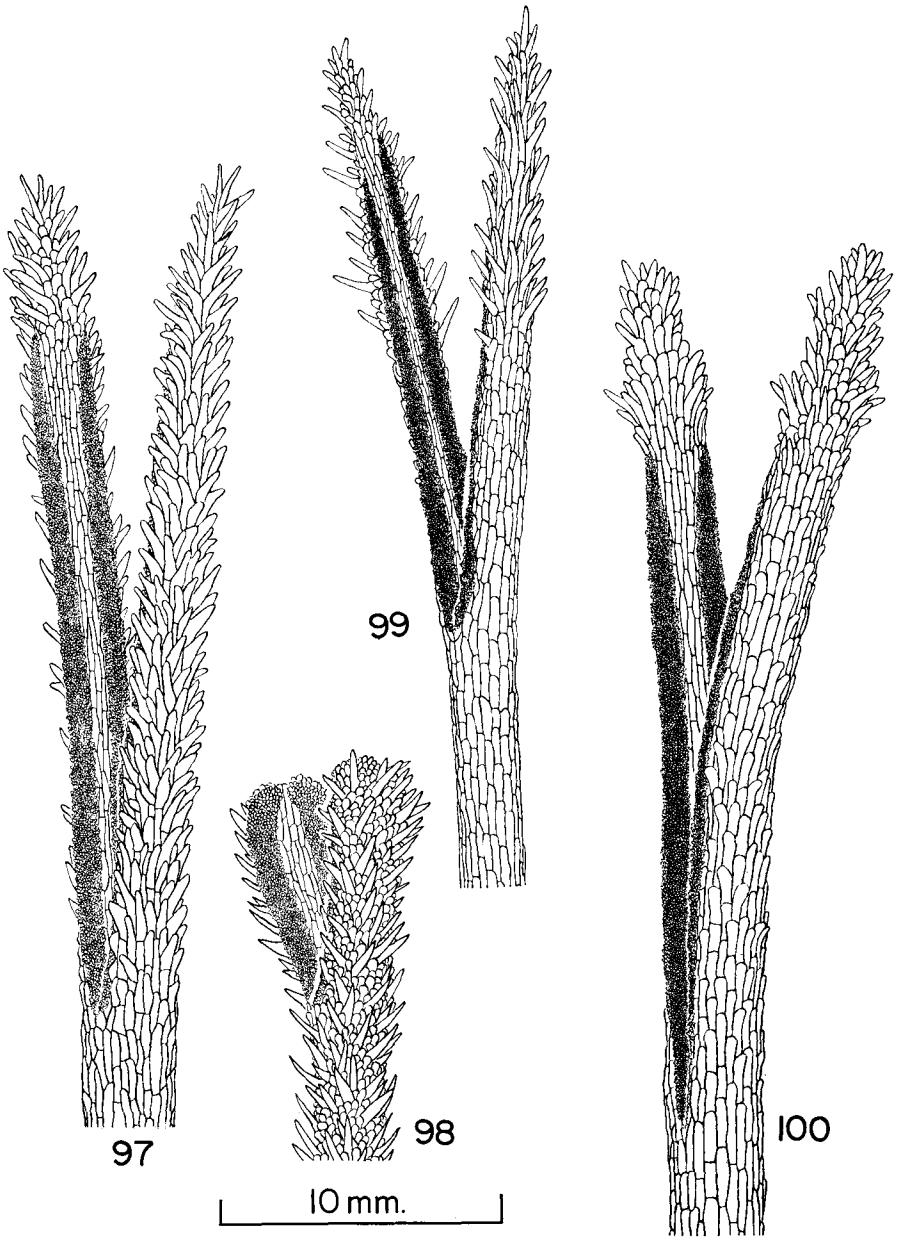


Fig. 97-100. Disk-flower styles of Pacific Coast Madinae, showing stigmatic branches at early anthesis. Fig. 97. *Raillardella scabrida*. Fig. 98. *Blepharipappus scaber*. Fig. 99. *Layia platyglossa*. Fig. 100. *Adenothamnus validus*.

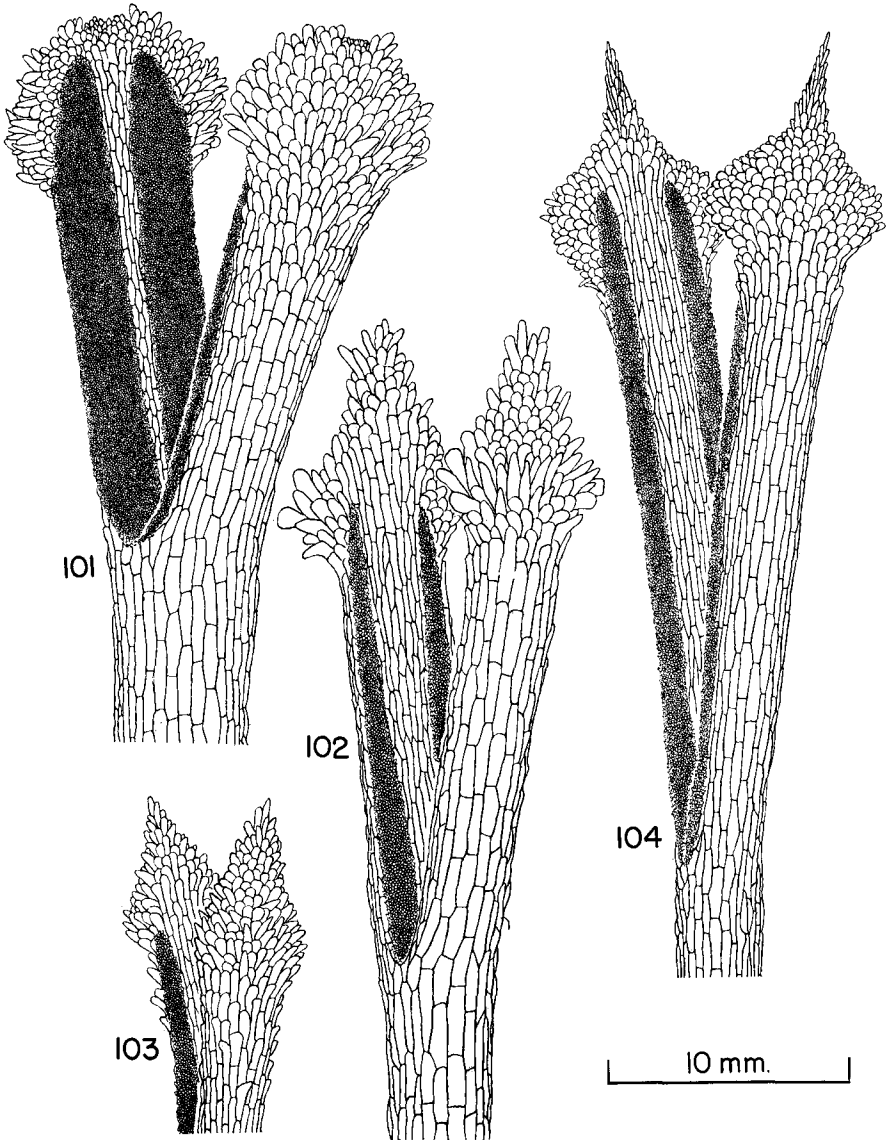


Fig. 101-104. Disk-flower styles of Hawaiian Madinae, showing stigmatic branches at early anthesis. Fig. 101. *Argyroxiphium caliginii*. Fig. 102. *Argyroxiphium sandwichense*. Fig. 103. *Dubautia sberffiana*. Fig. 104. *Wilkesia gymnoxiphium*.

### CHROMOSOME NUMBERS

The chromosome numbers of Pacific Coast Madinae are now well known; listing of these provides a very good comparison among Madinae. The arrangement of species follows that of Munz (1959), with species not present in the California flora

inserted at places which seem appropriate; genera are arranged alphabetically. Chromosome numbers in the Hawaiian Madinae are rather poorly known, and a number are reported here for the first time; listing of these is alphabetical, and follows the listing of the Pacific Coast species.

SPECIES	NUMBER	SOURCE
<i>Achyrachaena mollis</i>	n=8	Johansen, 1933
<i>Blepharipappus scaber</i>	n=8	Clausen et al., 1941
<i>Blephariparizonia plumosa</i>	n=14	Johansen, 1933
subsp. <i>viscida</i>	n=14	Munz, 1959
<i>Calycadenia tenella</i>	n=9	Clausen et al., 1934
<i>C. truncata</i>	n=7	Johansen, 1933
subsp. <i>scabrella</i>	n=7	Munz, 1959
<i>C. mollis</i>	n=7	Johansen, 1933
<i>C. villosa</i>	n=7	Johansen, 1933
<i>C. ciliosa</i>	n=6	Johansen, 1933
<i>C. multiglandulosa</i>		
subsp. <i>bicolor</i>	n=6	Johansen, 1933
subsp. <i>cephalotes</i>	n=6	Clausen et al., 1934
subsp. <i>robusta</i>	n=6	Munz, 1959
<i>C. hispida</i>	n=6	Clausen et al., 1934
subsp. <i>reducta</i>	n=6	Munz, 1959
<i>C. oppositifolia</i>	n=7	Clausen et al., 1934
<i>C. pauciflora</i>	n=5	Johansen, 1933
<i>C. spicata</i>	n=4	Clausen et al., 1934
<i>Hemizonia</i>		
Section <i>Fruticosae</i> :		
<i>H. clementina</i>	n=12	Johansen, 1933
<i>H. greeneana</i>	n=12	Johansen, 1933
<i>H. palmeri</i>	n=12	new record (fig. 113)
<i>H. minthornii</i>	n=12	Clausen et al., 1934
Section <i>Deinandra</i> :		
<i>H. kelloggii</i>	n=9	Johansen, 1933
<i>H. pallida</i>	n=9	Johansen, 1933
<i>H. arida</i>	n=12	Clausen, 1951
<i>H. corymbosa</i>	n=10	Johansen, 1933
subsp. <i>macrocephala</i>	n=10	Munz, 1959
<i>H. balliana</i>	n=10	Clausen et al., 1934
<i>H. mohavensis</i>	n=11	Clausen et al., 1934
<i>H. lobbii</i>	n=11	Johansen, 1933
<i>H. pentactis</i>	n=11	Johansen, 1933
<i>H. ramosissima</i>	n=12	Johansen, 1933
<i>H. fasciculata</i>	n=12	Johansen, 1933
<i>H. paniculata</i>	n=12	Johansen, 1933
subsp. <i>increscens</i>	n=12	Johansen, 1933
<i>H. floribunda</i>	n=13	Johansen, 1933
Section <i>Centromadia</i> :		
<i>H. pungens</i>	n=9	Johansen, 1933
subsp. <i>maritima</i>	n=9	Venkatesh, 1958
subsp. <i>interior</i>	n=9	Venkatesh, 1958
subsp. <i>laevis</i>	n=9	Venkatesh, 1958
<i>H. parryi</i>	n=12	Venkatesh, 1958
subsp. <i>congdoni</i>	n=12	Venkatesh, 1958
subsp. <i>australis</i>	n=11	Venkatesh, 1958
subsp. <i>rudis</i>	n=11	Venkatesh, 1958
<i>H. fitchii</i>	n=13	Venkatesh, 1958
Section <i>Hemizonia</i> :		
<i>H. multicaulis</i>	n=14	Johansen, 1933
subsp. <i>vernalis</i>	n=14	Munz, 1959
<i>H. lutescens</i>	n=14	Clausen et al., 1937
<i>H. tracyi</i>	n=14	Clausen et al., 1937

SPECIES	NUMBER	SOURCE
<i>H. luzulaefolia</i>	n=14	Johansen, 1933
subsp. <i>rudis</i>	n=14	Munz, 1959
<i>H. congesta</i>	n=14	Johansen, 1933
<i>H. calyculata</i>	n=14	Johansen, 1933
<i>H. clevelandii</i>	n=14	Johansen, 1933
<i>Holocarpba macradenia</i>	n=4	Clausen, 1951
<i>H. virgata</i>	n=4, 5	Clausen, 1951
<i>H. obconica</i>	n=4, 6	Clausen, 1951
subsp. <i>autumnalis</i>	n=6	Munz, 1959
<i>H. heermannii</i>	n=6	Clausen, 1951
<i>Holozonia filipes</i>	n=14	Johansen, 1933
<i>Lagophylla minor</i>	n=7	Munz, 1959
<i>L. dichotoma</i>	n=7	Johansen, 1933
<i>L. glandulosa</i>	n=7	Johansen, 1933
subsp. <i>serrata</i>	n=7	Munz, 1959
<i>L. ramosissima</i>	n=7	Johansen, 1933
<i>L. congesta</i>	n=7	Munz, 1959
<i>Layia cbrysanthemoides</i>	n=7	Johansen, 1933
subsp. <i>maritima</i>	n=7	Clausen, 1951
<i>L. fremontii</i>	n=7	Clausen et al., 1934
<i>L. leucopappa</i>	n=7	Clausen et al., 1941
<i>L. munzii</i>	n=7	Clausen et al., 1941
<i>L. jonesii</i>	n=7	Johansen, 1933
<i>L. platyglossa</i>	n=7	Johansen, 1933
subsp. <i>campestris</i>	n=7	Johansen, 1933
<i>L. septentrionalis</i>	n=8	Clausen et al., 1941
<i>L. discoidea</i>	n=8	Clausen et al., 1941
<i>L. glandulosa</i>	n=8	Clausen et al., 1934
subsp. <i>lutea</i>	n=8	Munz, 1959
<i>L. pentachaeta</i>	n=8	Clausen et al., 1934
subsp. <i>albida</i>	n=8	Munz, 1959
<i>L. gaillardoides</i>	n=8	Johansen, 1933
<i>L. hieracioides</i>	n=8	Johansen, 1933
<i>L. paniculata</i>	n=16	Clausen et al., 1941
<i>L. carnosa</i>	n=8	Johansen, 1933
<i>L. heterotricha</i>	n=8	Clausen et al., 1941
<i>Madia bolanderi</i>	n=6	Clausen et al., 1936
<i>M. madioides</i>	n=7	Johansen, 1933
<i>M. nutans</i>	n=9	Clausen, 1951
<i>M. ballii</i>	n=9	Johansen, 1933
<i>M. rammii</i>	n=8	Clausen et al., 1934
<i>M. yosemitana</i>	n=8	Johansen, 1933
<i>M. radiata</i>	n=8	Clausen et al., 1934
<i>M. elegans</i>	n=8	Johansen, 1933
subsp. <i>vernalis</i>	n=8	Munz, 1959
subsp. <i>densifolia</i>	n=8	Munz, 1959
subsp. <i>wheeleri</i>	n=8	Munz, 1959
<i>M. citriodora</i>	n=8	Clausen et al., 1937
<i>M. anomala</i>	n=16	Johansen, 1933
<i>M. subspicata</i>	n=8	Clausen et al., 1945
<i>M. gracilis</i>	n=16, 24	Clausen et al., 1945
<i>M. citrigracilis</i>	n=24	Clausen et al., 1945
<i>M. sativa</i>	n=16	Johansen, 1933
<i>M. capitata</i>	n=16	Johansen, 1933
<i>M. chilensis</i>	n=16	Clausen, 1951
<i>M. glomerata</i>	n=14	Clausen et al., 1934
<i>M. exigua</i>	n=16	Johansen, 1933
<i>M. minima</i>	n=16	Clausen, 1951
<i>Raillardella argentea</i>	n=18	Kyhos, Raven, et al. (unpub.)
<i>R. muirii</i>	2n=16	Kyhos, Raven, et al. (unpub.)
<i>Argyroxiphium caliginii</i>	2n=28	new record (fig. 105)
<i>A. grayanum</i>	2n=26	Scottsberg, 1953

SPECIES	NUMBER	SOURCE
	n=14	new record (fig. 106)
<i>A. sandwichense</i>	n=14	new record (fig. 107)
<i>Dubautia ciliolata</i>	n=14	new record (fig. 108)
<i>D. knudsenii</i>	2n=26	Skottsberg, 1953
<i>D. laxa</i>	n=14	new record (fig. 109)
<i>D. menziesii</i>	n=13	new record (fig. 110)
<i>D. molokaiensis</i>	2n=26	Skottsberg, 1953
<i>D. scabra</i>	n=14	new record (fig. 111)
<i>Wilkesia gymnoxiphium</i>	2n=ca. 24	new record (fig. 112)

The records attributed to Munz (1959) above are previously unpublished counts made during the tarweed studies of Clausen, Keck, and Hiesey. According to Hiesey (personal communication), an unpublished count of *Argyroxiphium sandwichense*,  $2n=28$ , was made by Dr. Clausen. The writer believes that the count  $2n=26$  for *A. grayanum* may be in error because several pollen mother cells in preparations by the writer clearly showed  $n=14$ .

The highly varied numbers in Madinae require interpretation. There are some obvious instances of polyploidy, such as the case of natural amphiploidy described for *Madia citrigracilis* by Clausen, Keck, and Hiesey (1945). Some interesting aneuploid series, such as those of *Holocarppha* and *Hemizonia*, section *Centromadia*, have also occurred. One can only guess in these cases the basic chromosome number on which repatterning has taken place. Venkatesh (1958) has suggested that possibly additional chromosomes have been added to the  $n=9$  genome of *H. parryi* (section *Centromadia*) by hybridization with other Hemizonias. Clausen (1951) has given a detailed account of chromosome repatterning in the genus *Holocarppha*. The basic number in the Hawaiian Madinae appears to be  $n=14$ , which in turn may well be a polyploid number based on  $x=7$ . Such polyploidy would not be unexpected in a group of perennials. The basic number involved in most groups of Pacific Coast Madinae appears to be  $x=7$ , but even if this were true, other numbers must have been basic to the development of certain species groups, such as *Hemizonia*, section *Fruticosae*, or the genus *Holocarppha*. In the Pacific Coast Madinae, polyploidy seems related to the perennial habit in *Holozonia*, as compared to *Lagophylla*, but polyploidy has also developed within groups of annual species also (*Madia*). The basic numbers  $x=8$  or even  $x=9$  might well be possible for Madinae as a whole. The numbers  $n=18$  and  $n=8$  in *Raillardella* are quite interesting, because they compare so closely with the similar range of numbers in the genus *Madia*.

### TAXONOMIC CONCLUSIONS

The data in this study have been assembled primarily with reference to taxonomic and evolutionary concepts. Anatomical characteristics do, in fact, point the way toward a better definition of Madinae as a group, and aid in suggesting relationships and criteria for delimiting genera, and, in some cases, species. Interpretation of anatomical data is not simple, because characters which, on various criteria, may be deemed primitive or advanced are not arranged in neat linear series. There is no reason why a species or genus with mostly specialized characters may not retain a few primitive ones, or vice versa, and the writer believes this has probably occurred in a number of instances. Conclusions are presented below first in terms of genera, then in terms of the group as a whole.

1. *Achyrachaena*.—This monotypic genus is not easily related to any other Madinae, although it clearly belongs in the group. The habit as a vernal annual seems a derived one, and the structure of leaves, bracts, pappus, achene trichomes and the



venation of the achene add to its isolated position in Madinae. The presence of secretory canals in corollas occurs in Pacific Coast Madinae only in this genus and in *Lagophylla*, and this may provide a tenuous bond of relationship. Presumably the placement, by Munz (1959), of *Achyrochaena* near *Lagophylla* reflects some degree of relationship. The infrequency of glandular trichomes seems related to the vernal habit, as suggested below for *Layia*.

2. *Adenothamnus*.—Keck's (1935) transfer of this species from *Madia* to an independent genus is well justified. The fact that the species is known only from the type collection is curious, and additional information, such as wood anatomy and chromosome number, would be useful. Such details as involucre structure, pappus, pollen grains, and gross morphology are reminiscent of *Raillardella scabrida*. The resemblance is certainly closer than to *Madia*. A number of characters mark it as a very distinct genus, however: exclusive presence of capitate trichomes on upper leaves, presence of secretory canals in involucre bracts and leaves, and style morphology.

3. *Blepharipappus*.—The single species offers an array of features which do not closely ally it to any other genus, although it is clearly madinean. The style is curious in that it seems a modification of a rather primitive type; the presence of receptacular bracts throughout the head is best interpreted as a primitive character. The glandular trichomes are of the type basic in Madinae. The leaf anatomy, however, is of the most advanced type in the tarweeds. *Blepharipappus* has certain characteristics reminiscent of *Layia*, *Madia*, or some species of *Hemizonia*, but is certainly a distinctive genus.

4. *Blepharizonia*.—The single species appears to be a specialized end-product of evolution from a generalized *Hemizonia*-like ancestry. It is close to *Calycadenia* in its similar specialization of glandular trichomes, and its leaves, which are among the most advanced in the tarweeds, have a construction like those of *Calycadenia truncata*. Resemblances to *Calycadenia* include the general structure of the involucre, and anatomy of the bracts. *Blepharizonia* differs markedly from *Calycadenia* in other respects: the peculiar achene wall anatomy and achene venation, the union of receptacular with involucre bracts, the shape of leaves, and the chromosome number. These features suggest that *Blepharizonia* and *Calycadenia* have evolved independently from a hemizonioid type.

5. *Calycadenia*.—Anatomical characters amply reinforce the recognition of *Calycadenia* as a genus separate from *Hemizonia*, although its closest affinities appear to be with that genus. The genus could be defined by a combination of anatomical characters: the peculiar glandular trichomes or glands, the leaf shape, the foliar distribution of fibers and pectic compounds, and the type of inflorescence structure. Anatomical diversity within the genus is considerable, however, as corolla trichomes and leaf anatomy indicate, and one could say that repatterning in anatomical features has been exceptional, just as chromosome repatterning has been active in other genera, such as *Holocarpha*. *Calycadenia tenella* is quite distinctive within the genus, as are *C. truncata*, *C. mollis*, and *C. spicata*. There is a measure of alliance among *C. multiglandulosa*, *C. villosa*, *C. hispidula*, and *C. ciliosa*. There is also similarity between *C. oppositifolia* and *C. pauciflora* in respects of leaf structure, anatomy of glandular trichomes, and corolla trichomes, although such features as distribution of glandular trichomes and chromosome number could be used to separate the species.

6. *Hemizonia*.—As Clausen (1951) states, this seems to be a genus in the process of fragmentation. It contains some species with relatively primitive characters, such as presence of secretory canals in leaves and involucre bracts (Section *Centromadia*), a primitive involucre structure (Section *Centromadia*, *H. mintbornii*), and the type of capitate glandular trichomes basic among tarweeds. Section *Deimandra* contains

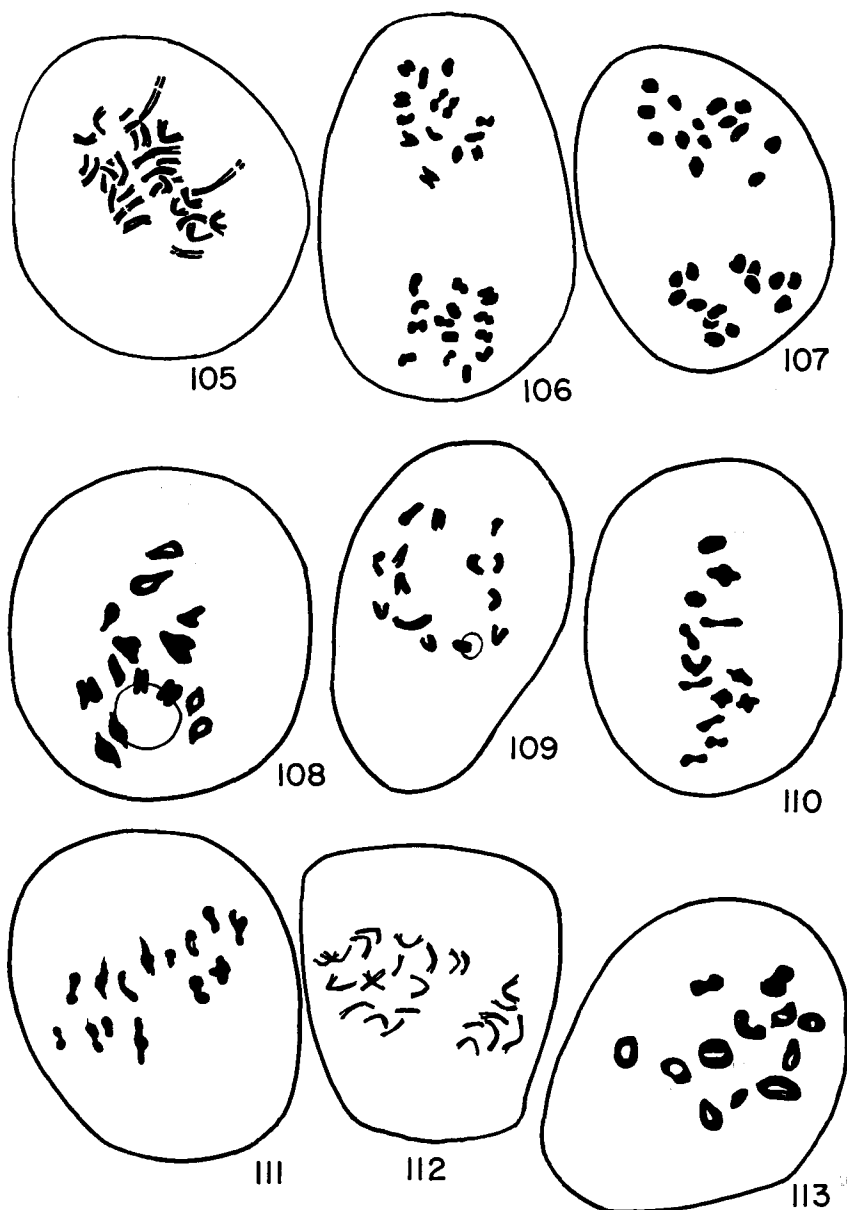


Fig. 105-113. Chromosomes of Madinae. Fig. 105. *Argyroxiphium caligini*, somatic metaphase,  $2n=28$ .  $\times 3200$ . Fig. 106. *Argyroxiphium grayanum*, second meiotic metaphase,  $n=14$ .  $\times 1200$ . Fig. 107. *Argyroxiphium sandwichense*, first meiotic metaphase,  $n=14$ .  $\times 1300$ . Fig. 108. *Dubautia ciliolata*, diakinesis,  $n=14$ .  $\times 1400$ . Fig. 109. *Dubautia laxa*, diakinesis,  $n=14$ .  $\times 2000$ . Fig. 110. *Dubautia menziesii*, first meiotic metaphase,  $n=13$ .  $\times 2100$ . Fig. 111. *Dubautia scabra*, first meiotic metaphase,  $n=14$ .  $\times 5000$ . Fig. 112. *Wilkesia gymnoxiphium*, somatic metaphase,  $2n=\text{ca. } 24$ .  $\times 2900$ . Fig. 113. *Hemizonia palmeri*, diakinesis,  $n=12$ .  $\times 4000$ . As with anatomical materials, collections documenting these counts are listed at the beginning of this paper.

a number of advanced characters, such as sterilization of disk flowers and loss of receptacular bracts. The development of a perennial habit in section *Fruticosae* may represent a secondary acquisition in response to a maritime or insular habitat, but the ability to develop woody species in this section also suggests a relatively unspecialized condition. Woodiness may well have been ancestral in Madinae, despite the annual nature of the tarweeds as a whole. The woody stems of *H. mintbornii*, *H. clementina*, and *H. greeneana* represent three very different anatomical modes. *Hemizonia mintbornii*, *H. clementina*, and the Guadalupe Island species represent three stages in decreasing size of capitula and loss of receptacular bracts. The insular *Hemizonias* are a group which would repay careful and detailed study as examples of insular speciation. The species of Section *Centromadia* form a closely-knit group distinctive in their exceptional representation of secretory canals in leaves and bracts, their capitular structure, and their sclerenchymatous spine-tipped leaves. The writer believes that inclusion of these species in *Hemizonia* is justified, however. Within the section, *H. fitchii* shows advanced glandular trichomes and leaf anatomy; its chromosome number may also be a highly derived one. The species of section *Hemizonia* show relatively unspecialized capitular structure, but advanced types of leaf anatomy (e.g., *H. luzulaefolia*). Although the genus *Hemizonia* seems a plexus containing a number of characters primitive for tarweeds, no species or group of species retains a preponderance of such characters.

7. *Holocarppha*.—The low chromosome numbers and seemingly rapid evolution (Clausen, 1951) which have evidently developed in this genus are certainly paralleled by a high degree of specialization in glandular appendages. The hollow-stalked glands, sessile glands on leaf-tips, and short, multiseriate glandular trichomes on corolla-lobe tips are features present in no other genus of Madinae. The leaves are equal in specialization to the most advanced of Madinae. *Holocarppha* may have had a common ancestry with *Hemizonia*, but advancement has exceeded that in most species of *Hemizonia*. One primitive feature still retained in *Holocarppha* is the presence of receptacular bracts throughout the head: the characters mentioned above, together with bract anatomy and number of achene bundles clearly serve to distinguish *Holocarppha* as a clear-cut genus. Within the genus, there is little choice among the species as to phyletic advancement, but *H. macradenia* seems to represent retention either of more primitive characters, or juvenile characters.

8. *Holozonia*.—The single species, *H. filipes*, is close to the genus *Lagophylla*, and if differences in pappus, achene morphology, perennial habit, and polyploid chromosome number could be overlooked, it could be included in *Lagophylla*. The resemblances include those of leaf structure, tack-shaped trichomes with biseriate stalks, secretory canals in involucre bracts, sterile disk flowers, and more or less united stigmatic branches. The chromosome number is double that in *Lagophylla*. If the two genera are closely related, however, they stand in an isolated position in Madinae, like *Achyrrachaena*.

9. *Lagophylla*.—As indicated above, *Lagophylla* seems closely related to *Holozonia*, but the two genera cannot be derived from a *Hemizonia*-like ancestor as clearly as *Calycadenia*, *Holocarppha*, or even *Blepharizonia* can. The species of *Lagophylla* have evidently followed different patterns of evolution from those which have proceeded within *Holocarppha* or *Calycadenia*, for the chromosome number of all is the same, and anatomical diversification appears to have been slight.

10. *Layia*.—The genus *Layia* is interesting, because it represents conversion to a more vernal habit from what appears to be the basic autumnal-flowering habit of tarweeds. The leaf structure, like that of *Achyrrachaena*, is correlated with this habit.

The absence or infrequency of glandular trichomes may be correlated with the vernal habit, because the secretion of glandular trichomes seems of considerable value to desiccation-resistance in the autumnal-flowering tarweeds. *Layia* may be distinguished from other genera by the vernal habit, the pappus bristles, the usually toothed leaves, and the manner in which involucre bracts enfold achenes. The presence of toothed leaves—which are like those of the basal rosette in other tarweeds—seems to represent a transition directly from juvenile characters to flowering, omitting those stages which are present in the autumnal tarweeds. The resemblance of some species of *Layia* to certain species of *Madia*, such as *M. nutans*, is notable, and some sterile intergeneric hybrids between the two genera have been produced (Clausen, 1951). Within the genus, exploitation of geographical areas appears to have been important in speciation, although some species are widely-distributed and still actively differentiating.

11. *Madia*.—The species of *Madia* show considerable diversity, but the genus is characterized by lack of receptacular bracts other than those of the outer circle, tendencies in anatomy of bracts, the paleaceous pappus, the single strand of fibers near the margin of leaves, and the presence of numerous bract-leaves in the inflorescence. *Madia bolanderi* is exceptional in the genus in a number of characters, such as sub-alpine habitat, rhizomatous rosette stems, corolla lobe venation, paucity of ray flowers, unspecialized structure of bracts, and chromosome number. *Madia madioides* is also distinctive in its perennial habit, but resembles the other species in most respects. *Madia* as now understood is a readily defined genus, and hybridization work (Clausen, 1951) has aided in this definition. The reduction of *Hemizonella minima* to *Madia* is justified both because of the closeness of this taxon to *M. exigua* and because leaf and bract anatomy of *M. minima* are definitely madioid. *Madia* is close to *Layia*, as mentioned above, although a lesser degree of resemblance may be found with some species of *Hemizonia*, section *Deinandra*, and of *Raillardella*.

12. *Raillardella*.—Because this genus has not been previously included in Madinae, the writer feels that reasons for this placement should be given in detail. Earlier, the writer (1958b) demonstrated the identity of glandular hairs between *Raillardella* and *Madia* or *Hemizonia*. The organization of the capitulum, as discussed above, is not senecionean, but (in *R. scabrida*, *R. pringlei*, and *R. scaposa*) identical with that of *Madia bolanderi* or *Adenothamnus validus*. The three species of *Raillardella* named differ in capitulum structure from other species of *Madia* only in lacking the full complement of ray flowers. The loss of ray flowers should certainly not disqualify *Raillardella* from inclusion in Madinae, any more than loss of ray flowers should exclude *Layia discoidea* from the subtribe. Leaves of *Raillardella* show exceptional similarity to those of other Madinae in characters such as: prominent marginal fiber strands (*R. muirii*); recurved marginal veins (*R. muirii*, *R. scabrida*); isolateral palisade (all species); secretory canals in leaves (*R. scaposa*) and bracts (*R. argentea*); and intercellular pectic deposits in leaves (*R. argentea*). The setose pappus bristles containing a central strand of phloem are certainly not foreign to Madinae, for such bristles occur in *Adenothamnus*, *Layia*, and *Dubautia*. Pollen grains are very similar to those of *Madia* or *Adenothamnus*. Styles in the fruticose species are like those of *Madia*, and those figured for the scapose species show close resemblance to those figured for *Layia*, differing only in their somewhat greater size. The fruticose species of *Raillardella* have stem structure identical with that of the annual tarweeds, whereas the stems of the scapose species could not be distinguished in anatomy from those of a tarweed species with similar habit, *Madia bolanderi*. The madioid bract anatomy in the fruticose *Raillardellas* is quite striking. All the characters seem to

point to the fact that *Raillardella* is an alpine or subalpine representative of *Madinae* which has been overlooked as a member of the subtribe simply because of the predominance of low-altitude annual species in the group. The habit of the species of *Raillardella* is precisely what one would expect of an alpine tarweed, and like the lowland tarweeds, the alpine *Raillardellas* grow in dry, exposed situations, such as talus slopes. Like other tarweed genera, *Raillardella* cannot be derived from any living tarweed species, but the resemblances between the genus and *Adenothamnus*, *Layia*, or *Madia* are marked.

13. *Argyroxiphium*.—The peculiar rosette habit of the *Argyroxiphium* species is not like that of other *Madinae*, although perhaps the monocarpic habit of *A. sandwichense* is not really so different from the growth forms of the annual tarweeds, which form a prominent rosette in their earlier stages. The rosette-plant habit, in any case, is one which is prominently represented on oceanic islands, and the causes which have led to this form in *Argyroxiphium* have probably been parallel to the adoption of this form in other Hawaiian genera, such as *Lobelia*, *Brighamia*, *Cyanea*, *Plantago*, and *Bidens*. The massive inflorescences of *Argyroxiphium* are probably related to the rosette habit also. The glandular trichomes of *Argyroxiphium* are identical to those of *Madia*, *Raillardella*, and other Pacific Coast *Madinae*, as well as to those of some species of *Dubautia*. The peculiar leaves of *Argyroxiphium* are unique in their vascular structure, but items of their construction—abundant intercellular pectic accumulations, isolateral palisade, fiber strands—are quite characteristic of *Madinae*. The heads are constructed like those of *Madia bolanderi*. Details of involucre and receptacular bract structure match those of Pacific Coast tarweeds such as *Hemizonia* or *Adenothamnus*. Stigmatic branches of the styles are somewhat different, seemingly more specialized, and possibly adapted to different pollinators. The purplish flower colors in *A. sandwichense*, *A. caligini*, and *A. virescens* are like those which occur in *Madia chilensis* and other species of *Madia*, *Lagophylla*, *Holozonia*, and *Achyrrachaena*. *Argyroxiphium* is probably primarily adapted to dry conditions such as those of higher altitudes of Haleakala Crater. It is interesting to note that *Madia sativa* is naturalized within this crater. Previous to Keck (1936), the relationship between *Argyroxiphium* and *Dubautia* was not suggested. A very pertinent contribution in this regard is that of Sherff (1944), who described an intergeneric hybrid, *Argyrautia degeneri*. This material is deserving of additional study on account of the habitual differences between the two genera, but if Sherff's interpretation of these specimens is correct, there can be little doubt that the relationship between the two genera is close. Within the genus *Argyroxiphium*, anatomical characters provide excellent species characters. These include features of leaf anatomy (Carlquist, 1957a), and distinctions in bract structure, corolla venation, corolla trichomes, pollen, and style anatomy mentioned above.

14. *Dubautia*.—The truly woody habit of this genus is unique in *Madinae*; there are relatively herbaceous species, however. The woody habit is not unexpected considering the insular habitat, for many of the Hawaiian rain forest trees and shrubs are woody representatives of herbaceous groups. The often broad leaves, without specializations in venation, seem to represent an adaptation to rain-forest conditions; thick epidermis, isolateral palisade, and abundance of fibers have been added in the alpine species, which have smaller, thicker leaves. Where glandular trichomes are present, they are identical to those of *Argyroxiphium* and most Pacific Coast *Madinae*. Capitula of more primitive species, such as *D. laxa*, appear to be like heads of a *Hemizonia*, like *H. mintbornii*, without ray flowers. As in *Hemizonia*, organization of the outer bracts into a single circle and loss of the inner bracts have taken place.

Bracts show a remarkable similarity to those of Pacific Coast Madinae as well as to those of *Argyroxiphium*. A further similarity between the two genera is found in style anatomy. There seems little doubt that *Dubautia* is, in fact, related to *Argyroxiphium* and *Wilkesia*. Authors who have dealt with *Dubautia* have disagreed whether or not two genera, *Dubautia* and *Railliardia*, should be recognized, or all the species grouped together. Sherff (1935), in the only modern monograph of the group, recognizes *Railliardia*, a practice which had been followed by previous authors. The following year, Keck (1936) reduced *Railliardia*, without giving sectional distinctions. Authors who have followed Sherff include Skottsberg (1944) and Degener (1946). Sherff (1944) has reiterated his opinion, although no new evidence had really been developed, despite his admission that no single character separates the two genera. Likewise, Degener (1957) has maintained his earlier view. On the other hand, St. John (1950) registers agreement with Keck, and claims a more easily definable genus. St. John recognized the *Railliardia* species as Section *Raillardiaster*, but segregated some *Dubautia* species into a new section, *Mixta*, on account of their combination of some union of bracts (like *Raillardiaster*) with pappus parts like those of section *Dubautia*. In fact, as anatomical preparations show, the species he leaves in Section *Dubautia* do not all have separate bracts, as he claims. The writer has found bracts clearly united histologically in *D. knudsenii* and *D. magnifolia*. Degener's (1957) criticism of St. John's sectional divisions is probably justified, and the most reasonable treatment in the light of present evidence would be the recognition of one genus, *Dubautia*, with two sections containing the species referred by Sherff (1935) to *Dubautia* and *Railliardia* respectively. In rather extensive anatomical studies on these species, I have attempted to find any character by which two genera, with component species corresponding to those of Sherff, could be recognized. There is only one which corresponds to this division: the presence of phloem strands in pappus bristles (although bristles of all species have not been investigated; see above). This character is probably related, as it appears to be in other Madinae, to the presence of long, terete bristles. Such bristles are the only character which might, without exception, differentiate the two genera, but the difference between the two in this respect is not very great. In the remaining morphological and anatomical characters, the writer has found various degrees of differentiation, but no distinctions of generic value. The species of section *Dubautia* include more primitive conditions, in general, and the species treated by Sherff as *Railliardia* have more advanced expressions, but the distribution of such characters among the species renders generic distinctions on this basis impossible. The writer has found that in respect to wood anatomy (Carlquist, 1958a), and other aspects of vegetative anatomy (Carlquist, 1959c), there are distinctive species groups which may be defined on these criteria, but not two genera. If the pappus difference mentioned above were sufficient for generic distinction, then segregation of other species groups in Madinae would be even more justified, such as removal of *Centromadia* Greene from *Hemizonia*, *Raillardiopsis* Rydberg from *Raillardella*, to mention only two. In the writer's opinion, segregation of *Railliardia* is a historical accident, owing to the simultaneous description of two distinctive species which were therefore placed in two genera; continuation of this practice in view of considerable new evidence to the contrary serves no purpose, in the writer's opinion, and Keck's recension is justified.

15. *Wilkesia*.—Following the decision by Degener (1946) that *W. gymnoxiphium* should be considered the only species in this genus, and that the supposed second species should be removed as *Argyroxiphium grayanum*, both *Wilkesia* and *Argyroxiphium* became well-defined units. Keck (1936), however, reduced *W.*

*gymnoxiphium* to *Argyroxiphium*, and stated that "there are no characters of generic value remaining on which to retain two genera". He regarded *A. grayanum* as transitional from the other *Argyroxiphium* species to *Wilkesia*. There are, however, a number of excellent characters which separate *W. gymnoxiphium* from *Argyroxiphium*. These include such leaf characters as presence or absence of pectic accumulations, presence or absence of three series of bundles, gross venation, isolateral versus bifacial construction, and nodal anatomy (Carlquist, 1957a). Likewise, characters of wood anatomy prove significant (Carlquist, 1958a). To these characters, the present study adds the distinctive inflorescence type of *Wilkesia* (with verticillate nodes and monochasial branches), the structure of receptacular bracts, the nature of corolla trichomes and corolla shape, pappus histology, pollen exine, and style morphology and anatomy. These, added to the traditional characters of phyllotaxy and presence or absence of ray flowers, seem unusually decisive in enforcing a generic distinction. Nor can *Wilkesia* be regarded as a derivative from *A. grayanum*. Reduction of the highly complex *Argyroxiphium* leaf to the "normal" type found in *Wilkesia* appealed to the writer (1957a) as highly unlikely. The writer regards *Argyroxiphium*, *Wilkesia*, and *Dubautia* as coordinate genera which show approximately equal relation to each other. In fact, the relation between *Dubautia* and *Argyroxiphium* may be rather close if Sherff's (1944) report of an intergeneric hybrid is valid.

HAWAIIAN VS. PACIFIC COAST MADINAE.—Keck (1936) lists a number of distinctions between these groups. The writer finds that some of these distinctions are, in fact, incorrect, and that the considerable affinity between these two assemblages has never been demonstrated. Considering the characters attributed to "Madinæ" (i.e., Pacific Coast Madinæ) by Keck, the writer finds the following inaccuracies in each of his distinctions:

1. "*Heads heterogamous*".—*Layia discoidea* is an obvious exception, as are the discoid species of *Raillardella*, thus vitiating the contrast with Hawaiian genera, which are both heterogamous and homogamous.

2. "*Ray achenes enclosed by their enfolding bracts*".—If this is true in Pacific Coast Madinæ, as one can say it is, it is equally true in the only pertinent Hawaiian genus, *Argyroxiphium*. Species of this genus have about the same conformation as can be found in species of *Achyrachaena*, *Adenothamnus*, *Hemizonia*, *Madia*, and *Raillardella*.

3. "*Herbs (mostly annuals); a few shrubby species*" and "*Leaves not clustered at ends of stems in perennial species*".—These contrasts of habit are valid, but are precisely what would be expected if a single phylad evolved in (1) the mediterranean climate of a continental area, and (2) the relatively uniform climate of oceanic islands respectively. The tendency of Hawaiian Madinæ to have growth forms of the sort indicated is typical of many insular genera and species, just as the high proportion of annuals in Pacific Coast Madinæ is paralleled by the high proportion of annuals in the California flora as a whole.

4. "*Involucral and receptacular bracts unlike, not adnate, often connate*".—Involucral and receptacular bracts show virtual identity in a number of tarweeds, such as *Achyrachaena*, *Hemizonia minthornii*, and many others. Probably involucral bracts are like receptacular bracts primitively, and differentiation between the two has marked advance in the tarweeds. Receptacular bracts free from each other occur in the two species named and in several species of *Dubautia*. The writer did not observe frequent or prominent union or adnation of involucral to receptacular bracts in *Argyroxiphium* (the only Hawaiian genus to which this could apply), but he did notice

prominent union of involuclral with receptacular bracts in *Blepharizonia*.

5. "Filaments not pustulate-thickened at the base of anthers".—The writer has not been able to find pustulate thickenings at the base of anthers in Hawaiian Madinae, nor do Keck's figures suggest this.

6. "Style-branch appendages not abruptly differing from stigmatic portion, long-attenuate".—This statement is true of Pacific Coast Madinae with the exception of *Adenothamnus*, which has the opposite condition. Also, the stigmatic branches of *Blepharipappus* could certainly not be termed "long-attenuate".

7. "Habitat in western North America".—This statement is quite accurate, but this contrast would be meaningless unless features inherent in the plants themselves suggested that the two groups were unrelated.

Thus, many of the contrasts suggested by Keck do not seem to be valid. Similarities, on the other hand, by which both Pacific Coast and Hawaiian Madinae may be united into a definable group, are given below.

### CHARACTERS AND RELATIONSHIPS OF MADINAE

CHARACTERS.—The following characters are considered to ally all taxa considered above, with the exceptions noted.

1. Capitate trichomes with biseriolate stalks, as well as modifications of these in certain genera (*Calycadenia*, *Holocarpba*, *Holozonia*, *Lagophylla*).

2. More or less abundant intercellular deposits of pectic materials in leaves (and in some cases, bracts) except for vernal annuals (*Achyrachaena*, *Layia*).

3. Opposite leaves with trilacunar nodes, at least in seedling stages.

4. All involuclral bracts with an axillary ray flower; involuclral bracts in a single series (except in *Hemizonia corymbosa*).

5. Each involuclral bract partially or completely enfolding a ray flower. If ray flowers are absent (*Layia discoidea*, *Raillardella* spp., *Wilkesia*, *Dubautia*), the following character holds.

6. A single series of receptacular bracts encloses the disk flowers, or (*Dubautia* spp., *Hemizonia* Section *Centromadia*, *H. mintbornii*), these form part of a continuous spiral series, each bract of which subtends a disk flower. If the single series is present, bracts are united by their edges (except *Achyrachaena*).

7. Involuclral and receptacular bracts contain strands of fibers which are separate from the bundles and alternate with them. Exceptions occur only where the pair of strands are united adaxial to the midvein (*Madia*, *Raillardella*) or all veins (*Achyrachaena*), or where fibers tend to surround the veins (*Wilkesia*), or fibers are lacking (*Blepharipappus*, *Holozonia*, the scapose *Raillardellas*, *Dubautia scabra*). The basic pattern has been subjected to similar alterations in both Hawaiian and Pacific Coast Madinae, so that, for example, *Dubautia ciliolata* bracts are very similar to those of *Calycadenia villosa* or *Hemizonia fasciculata*. Secretory canals are probably primitively present in both geographical groups, and have been lost in some taxa of both.

8. All Madinae seem to show the same basic pattern in pollen-grain exine construction.

In addition to these criteria, there are a number of other features, which may be labeled "tendencies", which are common to a number of species, but to which there are numerous exceptions:

1. Loss of secretory canals. Secretory canals appear to have been primitively present in Heliantheae (Carlquist, 1957b; Cronquist, 1955). If this is true, Madinae repre-



sent an intermediate stage in loss. This loss appears to have occurred first in flowers, then in bracts and finally in leaves. Thus, only a few taxa (*Achyraea*, *Lagophylla*, some species of *Dubautia*) have secretory canals in corollas and styles, whereas a number of taxa have secretory canals only in stems and basal portions of leaves (*Achyraea*, *Adenothamnus*, *Layia platyglossa*, *Madia bolanderi*, *M. sativa*, *Raillardella argentea*, *Wilkesia*, etc.).

2. Marginal fiber strands. These strands, which seem basically a derivation of the fibers associated with phloem of the marginal veins, are prominently represented in a number of genera (particularly Pacific Coast Madinae); the fiber strands may be independent of the bundles, a condition seen in *Argyroxiphium*, *Madia*, and *Hemizonia*.

3. Recurvature of margins, and included bundles, in upper leaves. This is a particularly interesting character of many Pacific Coast Madinae, without any true counterpart among Hawaiian Madinae. The formation of additional series of bundles (*Argyroxiphium*) is a parallel change with the same net result, that of condensation of leaf form; formation of an additional series of bundles was observed in one Pacific Coast tarweed (*Hemizonia fitchii*).

RELATIONSHIPS.—The taxonomic placement of the three Hawaiian genera has been highly varied, as the history given by Keck (1936) illustrates. Likewise, the contents of the Pacific Coast Madinae and the distribution of species among genera in that group have not remained constant, as the synonymy given by Munz (1959) indicates. The writer does not agree with Keck that *Dubautia*, *Argyroxiphium*, and *Wilkesia* should be placed in Heliantheae, subtribe Galinsoginae. Although the writer does not have a detailed knowledge of taxonomy and anatomy of Galinsoginae, examination of these has not suggested the really remarkable similarities which do exist between Hawaiian and Pacific Coast Madinae, and failure to emphasize these similarities by inclusion of the Hawaiian genera in a rather alien subtribe hardly seems justifiable.

The writer considered the possibility that a genus of Helenieae, *Palafoxia*, might have a measure of relationship to Madinae. The glandular hairs (Carlquist, 1958b), despite their complexity, are really quite different from madinean trichomes. The markedly widened bases of these trichomes, and the fact that the division between the two series of cells in trichomes with biseriate stalks occurs in a plane perpendicular to the long axis of the organ which bears it (as opposed to parallel in Madinae) make the resemblance seem a rather superficial one. Leaves do not contain marginal fiber strands or pectic accumulations in *Palafoxia*, and the two series of involucre bracts, the outer without axillary ray flowers, are significant features. In addition, the pappus paleae have a markedly thick midrib which contains vascular bundles which include xylem—a feature which does not occur in Madinae. Similar considerations apply to a genus near *Palafoxia*, *Chaenactis*. Preliminary examinations of various other genera revealed less similarity, and the writer is satisfied that the subtribe can be defined with reasonable discreteness.

Skottsberg (1931) suggested a relationship of the Hawaiian genera to *Robinsonia* of the Juan Fernandez Islands and *Brachionostylum*, of New Guinea. This was accepted by Keck (1936), although it was dismissed by St. John (1950), who claimed that the two genera named belong to Senecioneae and are rather different. The writer has begun a study of the anatomy of *Robinsonia*, *Rhetinodendron*, *Brachionostylum*, *Bedfordia*, and other possibly allied genera, and from observations of this material, he finds the contentions of St. John justifiable. Keck (1936) seems to be persuaded that the American affinities of the Hawaiian genera are dubious because of the pre-

dominantly Indo-malaysian cast of the Hawaiian flora. There are, however, a number of bona fide instances of Hawaiian-American floristic relationships, and the writer does not see, with the evidence now available, how origin other than American could be postulated for the Hawaiian Madinae.

The Madinae, as defined here, form a discrete group despite the remarkable diversity of habitual types. The relationships of the group are certainly with other Heliantheae, as anatomical characters show, but no affinities are notably close. The Madinae, then, represents as well-defined and isolated a group as may be found in the Heliantheae, and is probably more easily delimited than some tribes in Compositae. One may well ask whether such a group is worthy of tribal recognition, such as Jepson (1925) accorded it. The writer regards this designation as possible, but we must have much more information about Heliantheae, Helenieae, and even Senecioneae and Astereae, before a satisfying taxonomic system of higher categories in the family can be achieved, and in Compositae, where superficial resemblances or differences can be misleading, new types of data, such as anatomical, are of particular importance.

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