THE LEAF OF CALYCADENIA AND ITS GLANDULAR APPENDAGES

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ABSTRACT

Carlquist, Sherwin. (Rancho Santa Ana Botanic Garden, Claremont, Calif.) The leaf of Calycadenia and its glandular appendages. Amer. Jour. Bot. 46(2) : 70-80. Illus. 1959.—Large tack-shaped glands are characteristic of the leaves of Calycadenia which are associated with the inflorescence. These glands may be divided into those which are terminal on leaves and those which occur laterally on the surface of the leaf. Lateral glands show stages early in their development which are identical with those of simpler trichomes of Madinae. Terminal glands, which possess more vascularization of the stalk, show a more modified form of development. Vascularization is not derived from protoderm, but from more deeply-seated cells. These cells are included in a zone of elongation which forms the stalk. Vascular bundles may extend to the base of glands which lack vascularization in their stalks. Tack-shaped glands are considered an advanced form of trichome in which internal tissues of the leaf are involved. Within the genus Calycadenia, ontogenetic and comparative studies suggest that the following characters are advanced: reduction to a single terminal gland, "inrolling" of margins to form a cylinder of bundles, concomitant with a central core of fibers or a pectic channel. Systematic distribution of gland occurrence and of types of foliar structure are given.

THE "TACK-SHAPED GLANDS" of Calycadenia (Compositae, tribe Heliantheae, subtribe Madinae) have been recognized by taxonomists as a characteristic of that genus. Such glands occur on leaves of the inflorescence, particularly on those of abbreviated shoots which terminate in heads, and on the outer surface of involucral bracts. These glands are absent on basal leaves; they are lacking on all appendages of Calycadenia tenella. Preliminary studies revealed that tack-shaped glands of Calycadenia are more complicated than those of other Madinae which were described in an earlier paper (Carlquist, 1958). A study of the ontogeny of the glands and a comparison of mature glands within the genus were undertaken basically to demonstrate the relationship between them and the simpler trichomes of other Madinae. Because at least some of the tack-shaped glands of Calycadenia are not simple trichomes, the general term "gland" is used here. On account of the fact that tissues other than epidermal are involved in the mature gland, studies on the ontogeny and mature structure of Calycadenia leaves proved a necessary adjunct to studies on the glands.

MATERIALS AND METHODS.—Leaves of Calycadenia are polymorphic within a single plant. Therefore, basal, intermediate, and upper leaves were studied for each species. The variation within a single plant was most carefully examined in C. multiglandulosa var. cephalotes, in which several leaves in each category from 5 individuals were sectioned. Liquid-preserved collections were utilized for C. multiglandulosa var. cephalotes and C. villosa. For the remaining species, herbarium material proved quite satisfactory for anatomical purposes. Fresh material was preserved in formalin-propionic alcohol (Johansen, 1940). Herbarium material was expanded by treatment with warm 2.5% aqueous NaOH, followed by washing and storage in 70% ethyl alcohol. Both liquid-preserved and herbarium specimen material were embedded in paraffin according to the usual techniques. Sections were stained according to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen, 1940). Leaves of Calycadenia, particularly the upper ones, are mostly subterete. Because of this, 3 types of sections are distinguished here: transverse, sagittal (a median longitudinal section of a leaf radial to the stem axis), and paradermal (a longitudinal section cut parallel to the dorsiventral axis of the leaf). The term "lateral" is used
Fig. 1–8. Ontogeny of terminal glands on upper leaves of *Calycadenia multiglandulosa* var. *cephalotes*. Fig. 1–5, 8 from sagittal sections; fig. 6–7 from paradermal sections. —Fig. 1, One-cell stage. ×480. —Fig. 2, Four-cell stage (two cells in plane of section). ×500. —Fig. 3, 4, Multicellular stage. Fig. 3, ×630; fig. 4, ×485. —Fig. 5, Initiation of glandular layers. ×1140. —Fig. 6, Formation of procambium in stalk region. ×270. —Fig. 7–8, Sections of mature glands. ×180.
here to denote the position of glands along the apparent margins of the leaf, because the true morphological margin, especially in upper leaves, may be recurved and fused with the lower surface of the leaf.

Specimens documenting fresh material or herbarium specimens used are as follows, herbarium abbreviations according to Lanjouw and Staffeu (1954): C. citiosa Greene, Peirson 6449 (RSA); C. hispida Greene, type (POM); C. mollis Gray, Ferris & Bacigalupi 10394 (RSA); C. multiglandulosa DC. var. cephalotes (Greene) Jepson, Balls & Everett 18577 (RSA); C. oppositifolia Greene, Rose 551 (RSA), Mason 4410 (RSA), Grant 796 (POM); C. pauciflora Gray, Ripley & Barney 4690 (RSA); C. spicata Greene, Hall 9852 (POM); C. tenella (Nutt.) T.G., Howell 1074 (RSA); C. truncata DC., McMurphy X-3-1908 (RSA); C. truncata subsp. scabrella (Drew) Keck, Greene 3547 (POM); C. villosa DC., Carlquist 414 (RSA). The taxa recognized here correspond to the classification offered by Munz and Keck (in press). Intraspecific entities not listed were considered similar enough to other members of a species on the basis of preliminary studies so that detailed coverage was regarded as unnecessary. Data on gland distribution were obtained from study of all the Calycadenia specimens in the herbaria noted above. The writer wishes to thank the curators of those herbaria for use of their material. Acknowledgment is due the Rancho Santa Ana Botanic Garden for use of cultivated plants of C. multiglandulosa var. cephalotes. Cultivated plants were necessary for this study because early stages in ontogeny occur on plants which are very difficult to find and identify in the field, and later stages are best obtained from plants from which successive fixations can be made during a season.

ANATOMY OF THE GLANDS.—The tack-shaped glands of Calycadenia multiglandulosa var. cephalotes were utilized because they are intermediate in structure between extremes which occur in the genus, yet they exhibit all critical features present in other species. The glands are goblet-shaped and about 0.5 mm. in length. A single terminal gland (fig. 29) occurs on each upper leaf, and 1–6 glands are present laterally along the edges of the leaf. Additional glands are occasionally present above and below the midvein. The lateral glands (fig. 13) have somewhat narrower stalks than the terminal gland (fig. 7–8). Ontogenetic studies on this species showed that a distinction should be made between terminal glands and those which occur laterally on the leaves. These 2 types are therefore described separately.

The first stage in the ontogeny of a terminal gland is shown in fig. 1, 23. A single protodermal cell at the primordium tip becomes differentiated as an initial by virtue of increase in size. Such an initial is visible on very young primordia, in comparison with initials of simpler trichomes of other Madinae (Carlquist, 1958). The single initial divides in a plane radial to the stem axis. Thus, a biseriate condition is attained. This division is shortly followed by an anticline in each cell; these anticlines are at right angles to the first division. Thus a quadriseriate condition (fig. 2, 24) is basic to the subsequent development of the gland. The 4 cells are soon subdivided by anticlinal, periclinal, and oblique divisions (fig. 3, 4, 25, 26). Such divisions result in a globular multicellular condition (fig. 5, 27). Terminal cells of this structure become differentiated, by virtue of their greater size, as the future secreting cells of the gland. Periclinal divisions (fig. 28) increase the number of layers of secreting cells. The tip of the gland is then widened by numerous anticlines in the terminal layers (fig. 6). Such anticlinal divisions result in the relatively discrete appearance of these layers in the mature gland (fig. 7, 8).

In the development of the stalk of the gland, cell layers other than protoderm participate. The derivation of cell lineages in stages prior to that shown in fig. 6 can be followed by means of cell wall thickness. Cell walls separating protoderm from ground meristem stain more deeply, probably on account of more abundant accumulation of pectic compounds. This can be seen with reasonable clarity in fig. 14 (diagrammed in fig. 28) and more obscurely in fig. 4 (compare with fig. 26). Such a distinction is difficult to make at the stage shown in fig. 6. However, stages prior to this, such as that of fig. 14, illustrate that the central portion of the stalk is derived from ground meristem cells. Figure 6 shows procambium extending into the basal portion of the stalk of the gland. This procambium is derived from longitudinal divisions of ground meristem cells. In the mature gland, there is often a fairly discrete separation between layers derived from protoderm and those which are formed by subsurface meristematic cells. The more nearly isodiametric cells in the terminal portion of a mature gland (fig. 7, 8; seen more clearly in C. truncata, fig. 16) apparently represent protoderm derivatives, whereas the procambiumatous cells of the basal portion of the gland represent ground meristem derivatives (except for the stalk epidermis). Fig. 15 shows, in C. truncata, a line of demarcation which probably separates the 2 cell lineages at a late stage in development. Thus, no procambium in tack-shaped glands appears to be derived from protoderm. The presence of ground-meristem derivatives surrounded, or overarched, by protodermal derivatives cannot be interpreted as an actual intrusion of ground meristem cells. Rather, elongation of the region in which ground meristem cells are present results in the conversion of this portion into a stalk. The ground meristem below this develops into internal tissues of the leaf proper.

The mature terminal gland of C. multiglandulosa var. cephalotes (fig. 7, 8) consists of a broad head supported on a somewhat narrower stalk. The terminal 2 or 3 layers may be distinguished as se-
Fig. 9-14.—Fig. 9-13. Ontogeny of lateral glands on upper leaves of *Calycadenia multiglandulosa* var. *cephalotes*. Fig. 9 from median longitudinal section of shoot apex (primordium in oblique section); fig. 10-13 from sagittal sections of primordia.—Fig. 9. One-cell stage. X430.—Fig. 10. Series of young glands: left and center, biseriate stage; right, quadriseriate stage; basal portion of leaf at left. X430.—Fig. 11. Subdivision of subterminal layers. X510.—Fig. 12. Subdivision of terminal layers which will become secreting cells. X535.—Fig. 13. Mature gland, showing phloem of a vascular bundle which extends into the base of the stalk. X265.—Fig. 14. *Calycadenia truncata*. Sagittal section of leaf primordium adjacent to very young head. X235.
creting cells by means of their resinous contents. The outer cell walls of the surface secreting cells are thin, corresponding to their secretory nature. Epidermal cells adjacent to secreting cells elongate tangentially, so that the epidermis curves around the margin of the head of the gland. These epidermal cells differ from surface secreting cells by their thicker walls, lack of resinous contents, and elongate shape. Within the stalk of the gland, a single vascular bundle is present. This bundle represents the terminal portion of the midvein of the leaf (fig. 29). In structure, the bundle is amphicribral, rather than collateral, when seen in transection.

Comparison between terminal glands of C. multiglandulosa var. cephalotes and those of other species of Calycadenia reveals certain differences. The most massive gland in the genus is that of C. truncata (fig. 14–16), a species which has only terminal glands. The ontogeny of this gland conforms to the pattern described above, except that divisions are more numerous and the resulting gland is larger. The surface layer of secreting cells forms a distinct palisade (fig. 15, 16). Isodiametric subsurface cells, as their staining properties indicate, are also concerned with secretory activities. The vascular tissue of the gland stalk may be directly connected with lateral veins in the leaf as well as with the mid-vein, although a loose fusion of bundles usually takes place in the stalk. Distally, vascular tissue ramifies irregularly to supply the margins, as well as the central portion of the head of the gland. The terminal gland of C. oppositifolia (fig. 17) represents a variation opposite from that of C. truncata in that vascular tissue is absent in the stalk. The midvein of the leaf terminates below the stalk of the gland. Immature stages of this species, like those of lateral glands described below, suggest that the entire gland, except for a few cells included in the base of the stalk, is derived from protodermal initials. Thus the gland as a whole is comparable to that of Blepharizonia plumosa (Carlquist, 1958), although the terminal portion is more nearly like that of Hemizonia fitchii (op. cit.) in its cup-like depression. The terminal gland of C. pauciflora illustrated (fig. 13) is intermediate between those shown for C. multiglandulosa var. cephalotes and that of C. oppositifolia. Vascular tissue does penetrate into the stalk of the terminal gland of C. pauciflora. The particular gland illustrated does not represent the full range of terminal glands in this species, because no vasculature may be present in smaller terminal glands.

In C. multiglandulosa var. cephalotes, lateral glands are present along the sides of the leaf (fig. 29). Like the terminal glands of C. pauciflora and C. oppositifolia, the lateral glands of C. multiglandulosa var. cephalotes are less elaborate. In their ontogeny, these lateral glands more clearly illustrate a trichome-like nature than do the terminal ones. As fig. 9 shows, lateral glands originate from a single cell. This cell is prominently elongate and upwardly appressed prior to subdivision. The first division is anticlinal, parallel to the long axis of the primordium (fig. 10, left and center). Thus, a biseriate condition is initiated. Unlike the ontogeny of the terminal gland, the biseriate condition does not give rise to a quadriseriate condition directly. The next divisions are periclinal which increase the length of the gland primordium (fig. 10, right). When the young gland is approximately 4 cells in length, anticlones occur, beginning with the subterminal layers and extending both to the base and tip of the gland (fig. 10, right). Thus, the quadriseriate condition is attained. This condition is of short duration because further anticlones take place in subterminal layers (fig. 11). Cells of the terminal layer undergo such divisions later (fig. 12). A layer of secreting cells is initiated by such divisions. The remainder of the ontogeny of the gland is featured by repeated divisions, chiefly anticlinal, which widen the stalk but particularly the head. As in the terminal gland, the non-secretory epidermal cells of the head overarch the secretory cells, forming a cup-like shape. During maturation, the gland changes from an upwardly-appressed condition to become perpendicular to the leaf surface. Various degrees of ground meristem involvement occur in the production of a lateral gland. Some ground meristem and procambium derivatives appeared to be present in the stalks of some glands. This is the case with the mature gland shown in fig. 13, where phloem cells are visible in the base of the stalk. In such a gland, the ontogeny is midway between that just described and that of terminal glands of C. multiglandulosa var. cephalotes in that some ground meristem cells become included in the elongating region which forms the stalk. A vascular bundle may extend from a marginal vein (or other vein) of the leaf up to the stalk, or no such vasculature may be present (fig. 29). The ontogenetic stages of lateral glands of C. multiglandulosa var. cephalotes show close similarity to such stages in the tack-shaped trichomes of Blepharizonia plumosa (Carlquist, 1958).

The distribution of tack-shaped glands in Calycadenia may be summarized as follows: (1) Both lateral and terminal glands present on upper leaves; glands present on involucre: C. multiglandulosa and its varieties, some populations C. oppositifolia (e.g., Grant 796), C. villosa. (2) Both lateral and terminal glands present on upper leaves; no glands on involucre: C. hispida, C. mollis, C. pauciflora. (3) Terminal glands on upper leaves; lateral glands lacking or nearly so; glands absent on involucre: C. ciliosa, most populations C. oppositifolia, C. sciicata, C. truncata, C. truncata var. scabrella. (4) Terminal glands lacking on upper leaves; lateral glands present; glands present on involucre: some populations C. oppositifolia (e.g., Mason 4410). (5) No tack-shaped glands present, although capitate trichomes with biseriate stalks present on upper leaves and involucre: C. tenella.
Fig. 15-18. Sections of terminal glands on upper leaves of *Calycadenia*.—Fig. 15-16. *C. truncata*.—Fig. 15. Immature gland from paradermal section. ×190.—Fig. 16. Mature gland, from sagittal section of leaf. ×100.—Fig. 17. Gland from paradermal section of leaf of *C. oppositifolia*. ×285.—Fig. 18. Gland from paradermal section of leaf of *C. pauciflora*. ×190.
In some plants of *C. pauciflora*, glands are almost evenly scattered over the upper leaves, and little distinction can be made between terminal and lateral glands. Small tack-shaped glands which are transitional to capitate trichomes with biseriate stalks were observed in some species. Such transitional glands were always found to have multi-seriate stalks, however. They were observed in involucres of *C. multiglandulosa* var. *cephalotes*, *C. oppositifolia* (Grant 796; Mason 4410), and *C. villosa*, as well as on upper leaves of *C. villosa*.

In addition to terminal and lateral glands, simple biseriate trichomes are developed on leaves of *C. multiglandulosa* var. *cephalotes* (fig. 20). These trichomes are short-lived, and are not present on mature leaves (fig. 21, 22). Earlier stages of lateral glands are not likely to be confused with those of biseriate trichomes, because biseriate trichomes develop much later. Thus, in both fig. 11 and 12, a primordium of a biseriate trichome may be seen in addition to the young lateral gland. In fig. 19, the large leaf primordium has developed a large gland (base seen at extreme left) although no initials of biseriate trichomes are yet evident. Biseriate trichomes are present on all the species of *Calycadenia* examined. The degeneration of biseriate trichomes is related to the formation of a resinous coating over the leaves. Terminal and lateral glands are persistent, however. They bear a resinous droplet which may overflow the edges of the gland and spread onto the leaf. The abundant resinous secretions of upper leaves are probably correlated with the fact that these leaves are functional during the warm and dry months of late summer.

Tack-shaped glands of *Calycadenia* appear to have evolved from simpler multisieriate trichomes. Their complexity, however, is much greater than those of other Madinae (with the possible exception of *Holocarpha*, which will be considered in a later study). No other glandular structures of this complexity have been reported previously in Compositae, although the non-vascularized glands of *Calycadenia* are comparable to the tack-shaped trichomes of *Blepharizoma plumosa*. The series in increasing complexity proposed earlier (Carlquist, 1958) can thus be extended through *Blepharizoma* to *Calycadenia*. Few parallels to *Calycadenia* glands can be found elsewhere among angiosperms. The glabrous structures of *Droseraceae* (Fenner, 1904; Metcalfe and Chalk, 1950) are comparable in that the stalks of such glands contain vascular tissue. Their function is apparently quite different from that of *Calycadenia* glands, however.

**Leaf Anatomy.**—During the year of a *Calycadenia* plant’s existence, various types of leaves are produced. Following germination, a rosette of basal leaves is formed. These leaves are sessile, lanceolate, flat, and 2–4 cm. in length. A prominent line of stiff uniseriate non-glandular trichomes is present along the margins of these leaves, although no tack-shaped glands occur. The margins of these leaves are somewhat to decidedly revolute. The revolute nature of the margin is illustrated in the anatomy (see below) because the true margin of the leaf is evidently joined to the lower surface. With the onset of flowering, a single upright stem is ordinarily produced. In axils of the leaves of this stem, or branches of it, short shoots, terminating in a head, are produced. Leaves on these short shoots, termed “upper leaves” here, represent more or less marked modifications of the basal leaves, and leaves of the upright stem are transitional to them in morphology and anatomy. The upper leaves are commonly shorter (0.5–1 cm.) than basal leaves and subterete in shape. Uniseriate non-glandular trichomes are shorter and less abundant than on lower leaves, or are altogether absent. The subterete shape is probably a reflection of a more complete incurving of the margins than in the basal leaves, as the anatomical data below suggest.

The basal leaves of *C. multiglandulosa* var. *cephalotes* (fig. 22) show isolateral construction. At the margins an arc of bundles which curves toward the lower surface of the leaf may be seen. Basal leaves of *C. truncata* (fig. 32) differ in possessing fibrous bundle sheaths on most of the longitudinally-oriented veins. Spongy parenchyma is present in the form of a pair of marginal pectic channels in basal leaves of *C. truncata*. These differences are not of great importance, however. Leaves of a single plant may vary in respect to presence of fibers in the bundle sheath. The presence of pectic channels, however, does distinguish leaves of *C. truncata* and *C. ciliosa* from basal leaves of other species, which are like those described for *C. multiglandulosa* var. *cephalotes*.

In upper leaves of *C. multiglandulosa* var. *cephalotes* (fig. 21) bundles at the margins form a prominent arc. A small strand of fibers is present in the center of this arc; the fibers are adjacent to the phloem poles of only a few bundles of the arc. As in the basal leaf, palisade is present on the midvein of both upper and lower leaves. A bundle sheath extension is present on both surfaces. A bundle sheath extension is present on the midvein of both upper and lower leaves. In basal leaves, the non-photosynthetic parenchyma of the central mesophyll (fig. 22) is more abundant at the base than at the tip of the leaf. In both upper and lower leaves of *C. multiglandulosa* var. *cephalotes*, a pair of secretary canals adjacent to the midvein was observed (fig. 29). These canals are short-lived, and appear to be crushed in the mature leaf.

Stages in the ontogeny of the leaf demonstrate the nature of the peculiar vascular system. In fig. 19, the youngest two primordia have formed procambium for the midvein. Procambium for the mar-
Fig. 19–22. Transections of leaves of *Calycadenia multiglandulosa* var. *cephalotes*.—Fig. 19. Primordia of upper leaves; edge of apical meristem at right. ×380.—Fig. 20. Half of immature upper leaf. ×250.—Fig. 21. Half of mature upper leaf. ×115.—Fig. 22. Half of section taken toward base of basal leaf. ×90.
ginal veins is differentiated later (fig. 19, left). Although only a single strand of procambium is visible at each margin of the primordium at this stage, at least several marginal bundles appear to originate from this strand. Procambium for the vascular bundle which enters the terminal gland is differentiated at this stage (fig. 6). Fig. 20 shows that the marginal strand of prosenchymatous cells has enlarged. At this stage, it is apparent that only the dark-staining groups of cells at the periphery of this area are procambium which will differentiate into vessels. The central portion of the strand is different, because it gives rise to fibers and parenchyma. At the stage shown in fig. 20, sieve-tube elements and tracheary elements have matured in glandulosa leaves of all the species (fig. 22, 32). Upper leaves gins. A beginning stage is represented by the basal bundles follow the course of the evidently recurved margin of leaf. The procambium of bundles which interconnect the longitudinally-oriented veins is also initiated at this stage. Procambium for the inverted bundles on the lower surface of the leaf and procambium extending from marginal veins to the stalks of lateral glands are formed last. Also visible at this stage are the 2 cell layers which will mature into palisade. Biseriate glandular and uniseriate non-glandular trichomes are mature at this stage; the former degenerate, although the latter persist (fig. 21, 22). They are 1-celled. In addition, as in all species of Calycadenia, some long, several-celled uniseriate non-glandular trichomes are present along the margins of basal leaves and some upper leaves.

Comparison of upper leaves of C. multiglandulosa var. cephalotes with those of other species reveals differences of taxonomic interest. Moreover, they suggest stages in the formation of a tubular construction from a condition in which only a few bundles follow the course of the evidently recurved margins. A beginning stage is represented by the basal leaves of all the species (fig. 22, 32). Upper leaves generally show more prominent recurved arcs of bundles than do basal leaves. However, upper leaves of C. mollis (fig. 33) are much like the basal ones. Upper leaves of C. mollis (fig. 33) seem to illustrate the process clearly, for not only is the margin obviously revolute in gross morphology, but many leaves reveal a recurving in the fiber strand associated with the marginal bundles, so that it has a V-shaped appearance in transsection.

If upper leaves of C. mollis represent the beginning of margin revolution and those of C. multiglandulosa var. cephalotes an intermediate stage, upper leaves of C. truncata (fig. 31) represent the completion of the process. A complete cylinder of bundles is present, and these are interconnected by transversely-oriented bundles.

In respects other than vascularization, upper leaves of Calycadenia vary in respect to: (1) presence and distribution of palisade; (2) presence and distribution of fibers; (3) presence of bundle sheaths and bundle-sheath extensions; and (4) presence and distribution of pectic channels. Fibers may be present as a marginal sheath for the mid-vein and as marginal fiber groups. Marginal fiber groups, if present, are fused at least at the tip of the leaf, although in some species they are fused for most of the length of the leaf (fig. 34). The term "pectic channels," used earlier by the writer (Carlquist, 1957), refers to zones of spongy parenchyma, oriented longitudinally in the leaf, the intercellular spaces of which are partly or wholly occluded by secretions of pectic compounds. The terminal portion of the pectic channel of an upper leaf of C. truncata may be seen in fig. 15, extreme left. The channel is divided by the midvein at this level (compare with transsection, fig. 31).

The species of Calycadenia may be summarized as follows in respect to anatomy of upper leaves: C. cilosa: identical to C. truncata. C. hispida: like C. multiglandulosa var. cephalotes, except that fiber strands are very prominent (touching all bundles except the midvein) and the midvein has a fibrous bundle sheath. C. mollis (fig. 33): fibrous bundle sheath present, in contact with lower epidermis; marginal fiber bundles recurved; remainder of mesophyll is palisade. C. oppositifolia: like C. spicata (fig. 34), but fiber zone dorsiventrally flattened. C. pauciflora: like C. tenella (fig. 30), except that spongy parenchyma is present where fibers are indicated for C. tenella. C. spicata (fig. 34): palisade forming a complete cylinder; bundle sheaths lacking or nearly so; fibers forming a single strand, around which the bundles are disposed, except at the base of the leaf, where it is divided into 2 marginal fiber strands. C. tenella (fig. 30): palisade extending around most of the leaf, except on the abaxial side, where spongy parenchyma is present. Bundle sheaths absent or nearly so. C. truncata (fig. 31): palisade forming a complete cylinder around the leaf, except for the fibrous midvein bundle sheath, which is in contact with the adaxial epidermis; other veins lacking bundle sheaths; vascular bundles forming a complete cylinder around the leaf; a few small fiber strands, not in contact with bundles, present near margins; center of leaf a pectic channel. C. villosa: like C. multiglandulosa var. cephalotes, except that the bundle sheath extends only to the adaxial epidermis.

In their vascular complexity, leaves of Calycadenia are reminiscent of those of another genus of Madinae, Argyroxiphium (Carlquist, 1957). Leaves of Argyroxiphium also possess pectic channels. The formation of three sets of bundles in Argyroxiphium leaves has probably occurred in a manner different from the origin of cylindrical construction in leaves of C. truncata. It is of interest, however, that both genera have undergone changes in foliar vascularization as an accompaniment to the formation of subterete leaves.

The advanced nature of leaf construction in C. truncata is of interest because that species apparently possesses the most elaborate tuck-shaped glands in the genus. These glands are exclusively terminal; loss of lateral glands also seems a special-
Ontogeny of terminal glands on upper leaves of Calycadenia, as seen in sagittal section of primordia; these figures represent drawings of primordia shown photographically: fig. 23 = fig. 1; fig. 24 = fig. 2; fig. 26 = fig. 4; fig. 27 = fig. 5; fig. 28 = fig. 14. The heavy line separates protodermal derivatives from ground meristem derivatives; dotted lines represent probable recent divisions. Fig. 23-28, approx. ×370.—Fig. 29. Reconstruction (from serial paradermal sections) of an upper leaf of C. multiglandulosa var. cephalotes. Broken lines represent veins along lower surface of leaf, unbroken lines veins of upper surface; stippled area = fibers; the two bands of vertical lines represent a pair of secretory canals. ×180.—Fig. 30-34. Diagrams of transections of leaves.—Fig. 30. Upper leaf of C. tenella. ×110.—Fig. 31. Upper leaf of C. truncata. ×11.—Fig. 32. Half of basal leaf of C. truncata var. scabrella. ×50.—Fig. 33. Upper leaf of C. mollis. ×50.—Fig. 34. Upper leaf of C. spicata. ×70. Horizontal lines = palisade; stippled = fibers; crosshatched = pectic channels; xylem of bundles shown in black; spongy tissue left blank in fig. 30.
ized character. Upper leaves of *C. spicata* and *C. oppositifolia* appear specialized in another direction. In these species, a cylindrical arrangement of bundles has been achieved, but the center of the leaf is occupied by a single fiber strand. Correlation between glands and leaf structure in other species is less clear. *Calycadenia multiglandulosa* var. *cephalotes* appears to occupy an intermediate position in the genus, because the glands are less elaborate than those of *C. truncata*, and the leaves do not have a cylindrical construction. The assignment of non-vascularized glands, as in *C. oppositifolia*, to a primitive or advanced position is difficult, however. Vascularized glands must have been derived from non-vascularized trichomes, but non-vascularized glands might in some instances have resulted from reduction of a vascularized condition. The absence of tack-shaped glands in *C. tenella* likewise may be a reduction.

**LITERATURE CITED**


